ORNITHOLOGY Third Edition

FRANK GILL

ORNITHOLOGY

THIRD EDITION

Frank B. Gill

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To my grandfather, Frank Rockingham Downing,
who was the first of many to share with me
his knowledge and love of birds

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Preface

This third edition of *Ornithology* strives to capture the vital features of the biology of birds from a contemporary ornithological perspective. As in the preceding editions, I designed it primarily for undergraduate students, but I have always had in mind, as well, bird enthusiasts young and old, who simply want to know more about birds.

Ornithology invites the participation of persons with great diversity of backgrounds and interests. I hope, therefore, that this book will be useful to similarly diverse readers. To this end, I have tried to share the excitement that birds and some knowledge of them afford me.

This edition, like the earlier ones, avoids theory for theory's sake. It stresses discovery rather than the mathematical models that may guide discovery. To make the book accessible to readers who are not specialists, I define technical terms clearly when they are first used. Additionally, the enhanced, comprehensive index refers the reader to the first use of a term and its definition.

The power of evolution by natural selection is the central theme of this book. The adaptations of birds ranging from morphology and physiology to migration and mating systems are testimony to the pervasive role of Darwinian evolution in action through the millennia. Evolution is responsible for the transformation of birds from dinosaur-like ancestors, for the display traits and mate choices of birds, for their sensitivity to geomagnetism and ultraviolet, and for their advanced intelligence.

Conservation is a strong theme of this edition. Once a sideline of ornithology, conservation science is now a central focus of interest of students and faculties alike. As barometers of environmental quality and ecosystem health, birds engage scientists and the public in the stewardship of landscapes and waterscapes. Most chapters of this book include specific examples of conservation challenges and successes. Chapter 21 provides a broad overview of conservation matters facing birds, with an emphasis on hope rather than despair.

This new edition is overdue, with apologies to colleagues and students who patiently waited too long for an updated text. The advances in ornithology in the last decade have been diverse and substantial. The ornithological literature is a huge and growing enterprise due in part to the major contributions of birds to biological understanding. The task of updating was much greater than I initially thought it would be. Consequently, I revised and updated all chapters with new information

or perspective and completely rewrote some of them. Many more changes will be required to stay currrent.

This third edition of *Ornithology* includes much that will be familiar to those who have used the second edition. It also includes some substantial changes. I have responded gratefully to the constructive suggestions provided by colleagues informally through the years and formally in candid reviews of the second edition solicited by its publisher, W. H. Freeman and Company. With the help of many others, I have also tried to identify exciting prospects for study in the future.

The sequence of chapters in this edition is basically the same as it was in the second edition. This edition, however, contains fewer chapters, 21 rather than 24. The reduction of chapters is due mostly to redeployment of the second-edition contents of Chapter 7 on feeding, Chapter 9 on visual communication, and Chapter 13 on navigation. These topics are now integrated into third-edition Chapters 6 (Physiology), 7 (Senses, Brains, and Intelligence), 10 (Migration and Navigation), and 12 (Mates).

I also reorganized the second-edition chapters on reproduction and development into Avian Life Histories (Part 5) to correspond more strongly to the modern integration of these topics based on life-history theory. First, following the advice of colleagues, I changed the sequence to start this section with Mates (Chapter 12) to establish the core principles of sexual selection. Next, a new chapter, Breeding Systems (Chapter 13), considers the advances in understanding the breeding behaviors of birds, including the roles of extra-pair fertilizations. The next two chapters deal with the fundamentals of avian sexual reproduction to the point of egg laying (Chapter 14) and the incubation of eggs in nests, including the development and hatching of the chick (Chapter 15). Posthatching development plus parental care of chicks follows logically in Chapter 16. Formal life-history theory, including life-table analysis and lifetime reproductive success, the subjects of Chapter 17, then conclude Part 5 and lead to chapters on population dynamics in the final section of the book.

Students and faculty alike responded favorably to the use of boxes to separate particular examples, important technical information, and recent discoveries from the text. This edition continues that innovation to call attention, for example, to the main features of the complete genome sequence of the chicken announced in December 2004 (Box 2–1) and the timely topic of avian flu (Box 18–2).

The substantial appendix on the birds of the world has been repositioned in this edition as a dynamic Web-based resource. "Birds of the World" is available on a free-access companion Web site at www.whfreeman.com/gill3e for both instructor and student. In addition to reviewing the relationships among the families of world birds, the new Web site tracks the rapid-fire advances in our understanding of avian systematics based on DNA sequence analyses, and at the same time includes links to the best visual resources available on the Internet.

The art program features many detailed drawings of birds and their anatomy, some less detailed schematic figures, and some black-and-white photos. Drawings are the dominant feature of the art program. One major addition is the "Closer Look" feature added to various figures throughout the book. This feature is intended to showcase a detail or related concept and to make certain figures less diagrammatic.

Most of us refer to birds by their English names, which seem to change too frequently, to be the same for different species on different continents, or to vary

from list to list. Which English names to use has been an ongoing challenge for many authors.

This edition of *Ornithology* mentions a total of 745 species found throughout the world. It adopts the newly available International English Names recommended by the International Ornithological Congress (IOC) for these species (Gill and Wright 2006). In general, this list adopts names with a history of traditional use. The names, however, conform to a set of rules formulated through a consensus of leading ornithologists worldwide. The rules largely define the use of hyphens, the use of single names, the structure of group names, and so on.

Most of the recommended English names will be familiar and will match those in the second edition. A few, however, differ and await adoption in North America by the American Ornithologists' Union Committee on Systematics and Nomenclature. The following list of the few significant name changes adopted in this book will help readers track and adjust to them.

IOC Recommended Name	Former Name
Great Northern Loon	Common Loon
Black-necked Grebe	Eared Grebe
Common Pheasant	Ring-necked Pheasant
Angel Tern	Common White-Tern
Little Auk	Dovekie
Common Pigeon	Rock Dove or Rock Pigeon
Common Starling	European Starling
Sand Martin	Bank Swallow
Two-barred Crossbill	White-winged Crossbill
Saltmarsh Sparrow	Saltmarsh Sharp-tailed Sparrow

Finally, as in the preceding editions, the English names of bird species are always capitalized to leave no doubt that, for example, a Brown Booby is *Sula leucogaster*, not just a booby that is brown. In accord with Kenneth Parkes (1993), "chicken" or "domestic fowl" refers to domesticated forms of the Red Junglefowl; "turkey" or "domestic turkey," to domesticated forms of *Meleagris gallopavo;* "pigeon" or "homing pigeon," to domesticated forms of *Columba livia;* and "Japanese Quail," to laboratory strains of *Coturnix*, which remain of uncertain taxonomic status.

Possible supplements to this textbook abound in both bookstores and on the Web. *Sibley's Guide to Bird Biology and Behavior* (2001) is an excellent introductory complement to *Ornithology*, complete with a glossary and links to David Sibley's wonderful field guides. The Cornell Lab's *Handbook of Bird Biology* is a major reference work for students to further explore a wide range of topics. Comprehensive accounts of individual species are available in *The Birds of North America, Life Histories for the 21st Century*. Most university libraries subscribe to this encyclopedic work, which also is available on the Web with video and sound (https://bna.birds.cornell.edu/BNA/).

This edition has benefited greatly from comments by many colleagues and students. The next edition will do so also. I sincerely invite creative suggestions, corrections of errors, updates, and reprints containing interesting, new ornithological information. Thank you.

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In addition to the many friends who contributed to the preceding editions of *Ornithology*, acknowledged in those editions, I thank with greatest appreciation those who evaluated the second edition, reviewed draft chapters of this edition, or patiently responded to my queries. Among the many who helped substantially were K. Able, F. Ammer, G. Barrowclough, B. Beason, S. Beissinger, R. O. Bierregaard, C. Blem, K. Bostwick, J. Brawn, W. Buskirk, G. Butcher, C. Caffrey, J. Cecil, R. Crawford, D. Cristol, K. Dial, J. Dosch, S. Doucet, A. Feduccia, J. Fitzpatrick, D. Gill, R. Gill, P. Grant, R. Grant, J. Groth, J. Hagan, J. Hengeveld, S. Hengeveld, F. Hertel, G. Hunt, H. James, E. Jarvis, J. Johnson, S. Kress, D. Lank, S. Lanyon, G. LeBaron, D. Levey, J. Madden, L. Mertz, D. Niven, R. Payne, R. Prum, R. Ricklefs, G. Ritchison, P. Ryan, J. Sauer, S. Senner, F. Sheldon, S. Sillett, B. Slikas, T. Smyth, P. Stettenheim, R. Suthers, R. Telfair, G. Waring, F. Wasserman, J. Wunderle, and R. Zink. Special and enthusiastic thanks go also to Mary Louise Byrd, Jeff Ciprioni, Jerry Correa, Annie Reid, and Patty Zimmerman of W. H. Freeman. They are a great editorial team who greatly improved the book's content, accuracy, and clarity. My wife, Sally Conyne, contributed her editorial and computer expertise. Equally appreciated has been the advice for almost 50 years of my three primary mentors in ornithology—Wesley E. Lanyon, Robert W. Storer, and Harrison B. Tordoff—who continue as trusted consultants and valued friends.

Ornithology: A Short History

In my hand I held the most remarkable of all living things, a creature of astounding abilities that elude our understanding, of extraordinary, even bizarre senses, of stamina and endurance far surpassing anything else in the animal world. Yet my captive measured a mere five inches in length and weighed less than half an ounce, about the weight of a fifty-cent piece. I held that truly awesome enigma, a bird. [Fisher 1979, p. 154]

With no other animal has our relation been so constant, so varied, so enriched by symbol, myth, art, and science, and so contradictory as has our relation with birds. Since earliest records of humankind, birds have served as symbols of peace and war, as subjects of art, as objects for study and for sport. Birds and their eggs range from the most exotic to the commonplace. Their command of our imagination is not surprising, because they are astonishing creatures, most notably for their versatility, their diversity, their flight, and their song.

Birds are conspicuous and found everywhere: Snowy Owls in the Arctic Circle, Black-bellied Sandgrouse in the deserts of the Middle East, the White-winged Diuca Finch at the highest elevations of the Peruvian Andes, and Emperor Penguins hundreds of meters beneath Antarctic seas. Huge eagles and bright parrots course over the rain forests of the world, and bustards, plovers, and larks stride and scurry across the arid plains.

These highly mobile creatures are travelers of the long distance and the short. Some birds, such as the Nicobar Pigeon in Indonesia, move incessantly from island to island, whereas others are master navigators, traveling phenomenal distances. The Sooty Shearwater migrates from islands off Australia to the coasts of California and Oregon, the Arctic Tern from New England to Antarctica, and the Rufous Hummingbird from Alaska to Mexico.

And birds please the eye. Little in nature is more extravagant than the Twelve-wired Bird-of-Paradise, more subtly beautiful than the Evening Grosbeak, more stylish than the Horned Sungem hummingbird, or more improbable than the Javan Frogmouth.

Birds As Cultural and Religious Symbols

All these qualities seem to have provoked wonder and a sense of mystery since the dawn of human existence. Indeed, in almost every early culture, birds were divine messengers and agents. To understand their language was to understand the gods. To interpret the meaning of the flight of birds was to foretell the future. Our words augury and auspice literally mean "bird talk" and "bird view." By the time Greek lyric poetry was flourishing (fifth and fourth centuries B.C.), the words for bird and omen were almost synonymous, and a person seldom undertook an act of consequence without benefit of augury and auspice. This practice still prevails in Southeast Asia and the Western Pacific.

As symbols of ideology and inspiration, birds have figured largely in many religions and in most cultures. The dove was a symbol of motherhood in Mesopotamia and was especially associated with Aphrodite, the Greek goddess of love. For the Phoenicians, Syrians, and Greeks, the dove was the voice of oracles. In Islam, it is said to call the faithful to prayer. In Christianity, it represents the Holy Spirit and is associated with the Virgin Mary. Bearing an olive branch in its bill, the dove continues to be a potent symbol of peace. In contrast, the dove was a messenger of war in early Japanese culture.

The eagle appeared as a symbol in Western civilization as early as 3000 B.C. in the Sumerian city of Lugash. In Greek mythology, the eagle was the messenger of Zeus. At least since Roman times, the symbolic eagle in Europe was the Golden Eagle, and that species also was the war symbol of many North American natives at the time of early English settlement. In 1782, the Bald Eagle became the symbol of the fledgling United States.

Less common than the eagle, but prevalent in myth and legend, is the raven. As Apollo's messenger, the raven reported a nymph's infidelity and, as a consequence, Apollo changed the bird's color from white to black. After 40 days, Noah sent forth both a dove and a raven to discover whether the floodwaters had receded. The faithless raven, according to some accounts, did not return and so earned Noah's curse and, once again, a color change from white to black. The belief in the raven's color change appears in a Greenland Eskimo legend in which the Snowy Owl, long the raven's best friend, poured sooty lamp oil over him in the heat of a disagreement.

In other legends, the raven plays a more favorable role. Native North American folklore described the raven's generosity in sharing its food with men stranded by floodwaters. Norse sailors, like Hindu sailors half a world away, carried ravens, which they released to lead them to land. Two ravens are said to have guided Alexander the Great through a dust storm on his long journey across the Egyptian desert to consult the prophet at the Temple of Ammon.

Diversity of Human Interest in Birds

Not only is our association with birds as old as human society, it is characterized by the diversity of our interest in them. We can do no more here than to consider a few examples of that diversity and, through those examples, come finally to the rich and varied science of ornithology.

The earliest records indicate that eggs have always been part of the human diet. The domesticated chicken, a form of the Red Junglefowl, existed in India before

3000 B.C. and was known in China by 1500 B.C. and in Greece by 700 B.C. Mallard ducks and geese were domesticated in the Far East nearly 1000 years before the time of Christ, and domestication of the turkey in Mexico appears to be very ancient. The Romans developed large-scale breeding and raising of poultry for food, but the practice on that scale disappeared after the fall of the Roman Empire and did not reappear in Europe until the nineteenth century.

The first American poultry exhibition was held in Boston in 1849, and, in 1873, the American Poultry Association (APA) was founded, the oldest association of livestock breeders and growers in the United States. In 1905, the APA published the *American Standard of Perfection*. Now in its latest edition, published in 2001, the book is a wonderfully informative and entertaining illustrated guide to the ideal characteristics of more than 100 domestic fowl, ducks, geese, and turkeys. At present, there are at least 37 different food breeds of chickens and at least 24 ornamental breeds.

The pigeon has had a dual role as a carrier and as a prized food. There were ancient pigeon posts in Babylon, and the bird was used as a carrier in early Egyptian dynasties. The use of carrier pigeons as messengers was commonplace in Roman times and continued into the twentieth century until the invention of the radio and widespread use of the telegraph and telephone.

Falconry is enjoying a modest renaissance. Originating perhaps as long ago as 2000 B.C., the sport flourished in Europe in the Middle Ages, and the Crusaders introduced Islamic techniques that increased and refined European falconry. After a sharp decline in Peregrine Falcons and several small accipiters in Europe and North America in the 1960s, breeding and release programs arose; and now the ancient sport, with its historical tradition of studying and protecting birds of prey, is being revived.

The use of feathers as ornamentation was widespread among North and South American peoples, in Africa, and in the Western Pacific from the earliest known times. The elaborate feather capes of the Hawaiian kings and the feather mosaics of the Mayas and Aztecs were works of art. Among native North Americans, particular uses of feathers as badges of rank and status were common. Feather clothing was also common for protection from weather, much as goose down is widely used today.

Birds have always been influential in the arts. The earliest piece of English secular music of which we know, "Sumer Is Icumen In," is a canon for four voices and the words are those of the thirteenth-century lyric in which the cuckoo welcomes summer with its song. The cuckoo, nightingale, and quail are heard in Beethoven's Sixth Symphony. The eighteenth-century composer Boccherini wrote a string quintet called "The Aviary," perhaps the first complex composition in which a number of birds are imitated. Composers Maurice Ravel and Béla Bartók used bird songs in their works for orchestra, voice, and piano.

Birds as subject and as metaphor are found frequently in opera. Wagner wrote an aria about owls, ravens, jackdaws, and magpies for *Die Meistersinger*. In Puccini's *Madama Butterfly*, a character sings of a robin, and, in *La Bohème*, another sings of swallows. In what is probably the most popular aria in the most popular opera of all time, the "Habanera" in Bizet's *Carmen*, the opening words are "Love is a rebel bird that no one is able to tame."

An interesting confluence of the name of a musician—in this instance, the nickname—and the name of the music brought together one of the most memorable

of American jazz musicians and one of the most memorable tunes: Charlie "Bird" Parker and "Ornithology."

The role of birds in painting and sculpture is impressively large. Birds appeared in paleolithic cave paintings in France and Spain as early as 14,000 B.C. and in neolithic cave paintings in eastern Turkey 8000 years later. In Egyptian tombs at Thebes, very accurate bird paintings appeared before 2000 B.C. In Knossos, on Crete, a well-known Minoan fresco of a partridge and a hoopoe survives from about 1800 B.C. Among the most vibrant and brilliantly colored Roman mosaics are those of birds, from Pompeii.

A remarkable work is an assemblage of bird species in a thirteenth-century illuminated manuscript of the Book of Revelation. Hieronymus Bosch's *Garden of Delights* (about 1500) is filled with birds. Among twentieth-century artists, Matisse and Picasso showed recurring interest in birds, and Brancusi's sleek birds in both chrome and stone are memorable.

Birds are ubiquitous in literature. For its perfect matching of avian and human characteristics, Aristophanes' comedy *The Birds*, has been described as an "ornithomorphic view of man." Birds are prominent enough in Shakespeare's plays and poems to have led the scholar James Harting to write an entire book on the subject, *The Ornithology of Shakespeare*, first published in 1871.

Some lyric poets were excellent ornithologists, notably the seventeenth-century Englishmen Michael Drayton and Andrew Marvell, whose descriptions of birds are very precise. More recently, Shelley's skylark, Keats's nightingale, and Yeats's swan have become the best-known birds in English literature.

Beginning as early as the fifteenth century, books with numerous bird illustrations began to appear. Bird illustrations continued through the centuries, with the Englishmen Mark Catesby and Thomas Bewick (both in the eighteenth century) and the American John James Audubon, whose four-volume work titled *The Birds of America* (1827–1830) is among the most prominent. By the turn of the twentieth century, a great flourishing that continues to this day was underway and served as an impetus to the rise of modern ornithology and field guidebooks.

Among the finest illustrators of the early twentieth century were Bruno Liljefors of Sweden, Archibald Thorburn of England, and Louis Agassiz Fuertes of the United States. Fuertes, with his unerring eye and his faultless sense of the remarkable characteristics of any bird, is believed by some to have made his birds more dazzlingly alive than any other painter. Standing on the shoulders of their predecessors, a host of brilliant and talented bird artists have created works that prevail in beautiful books, in wildlife art shows, and in field guides that just get better and better. Now supplementing the rich modern treasury of twentieth-century bird illustrations are amazing photographs and videos that Liljefors, Thorburn, and Fuertes could never have envisioned.

Early Ornithology

With all the disparate appeal of birds, it is little wonder that some human beings have chosen to study them, a study that has evolved into the modern science of ornithology. Aristotle's fourth-century B.C. *History of Animals* is the first known effort in Western culture to systematically account for what we observe in nature.

and the writing records the first organized scientific research. Birds figure prominently in all of Aristotle's work in natural history. Alexander of Myndos, in the first century A.D., wrote a three-volume work on animals, two of which are about birds. Only fragments survive in quotation. Pliny the Elder (A.D. 23–79) produced an elaborate natural history encyclopedia in 37 volumes, all of which survive. He summarized the work of some 500 ancient authors and offered his own critical point of view. Aelian (A.D. 170–235), a Roman who wrote in Greek, gave much attention to birds in *On the Characteristics of Animals*.

Until the Renaissance, our knowledge of the natural history of birds depended largely on these writers and other Greek and Roman writers. They told us much that was reliable, but they also left us with many wrong notions. The quotations from Alexander's work are based on close and accurate observation, but Aelian was steadfastly uncritical of his sources and perpetuated two remarkably wrong notions about the behavior of cranes: one, that they flew against the wind and swallowed a stone for ballast so as not to be swept off course; the other, that they posted sentinels at night, requiring them to stand on one foot while holding a stone in the other, thereby ensuring that, if the sentinel fell asleep, it would drop the stone and be awakened by the noise.

A major step toward modern ornithology was the growth of field observation in the eighteenth century. In 1789, Gilbert White, an English clergyman, published a natural history of his parish, gathered over 40 years' time. His observations of birds were marvelously precise and beautifully expressed. But he also asked incisive questions about the basic biology of birds, about species, ecological niches, physiology, and migration. Many of his curiosities still pertain to research in ornithology. Contemporary ornithology has benefited from years of careful field observation by devoted amateurs who followed Gilbert White, as well as by professional ornithologists.

Ornithology Today

Our knowledge of birds is more complete than that of most other classes of animals. Owing in part to this wealth of information and in part to their attributes, birds feature prominently in primary biological studies. By the middle of the 1980s, birds provided more textbook examples of biological phenomena than any other class of vertebrates.

Advances in ornithology have been honored with some of the highest awards. The pioneering works of Niko Tinbergen on the evolution of behavior with gulls and of Konrad Lorenz with ducks and geese earned them a Nobel Prize in physiology or medicine. In cell biology and medicine, the discovery of B vitamins and their roles in nutrition came from studies of chickens, which readily reveal dietary deficiency. Albert Szent-Györgyi was awarded a Nobel Prize in physiology or medicine for the elucidation of the Krebs cycle from studies of pigeon breast muscle, as did Payton Rous for studies of avian sarcoma that linked viruses to cancer for the first time.

Broadly speaking, birds have been central to advances in speciation theory and the deciphering of historical relations. The greatest contribution of bird studies has been their role in increasing our knowledge of population and community ecology. Their

contributions to evolutionary ecology and to behavioral ecology follow as a close second. Birds increasingly play central roles in advanced studies of breeding systems, including the dynamics of sexual selection, the roles of kinship and cooperation, and the often subtle strategies employed to maximize lifetime reproductive success.

Birds invite study of the effects of natural stimuli on physiology and behavior because they maintain their natural behavior in captivity and, to some degree, because they are long-lived. The same attributes spur study of the environmental control of reproduction, including the roles of circadian and circannual rhythms. Above all, birds are preeminent subjects for the experimental study of navigation. When trained to fly in a wind tunnel, they enable detailed analysis of the intricacies of powered flight.

Grabbing headlines also are the regular revelations about how birds use their extraordinary senses. We cannot see color differences in the near ultraviolet without special equipment. Birds, on the other hand, use ultraviolet color differences to choose a high-quality mate, to select the best foods, and to congregate with other members of the same species.

Birds have starred in the study of the interplay between inheritance and learning, mediated by the central nervous system. The early development of bird song provides one of the best working models of how a complex, learned motor skill develops. Neurobiologists can track how specific parts of the brain's song system participate in the process of song development. Research on neural pathways that control song and spatial memory in birds led to a major discovery: the fine structure of the adult brain is dynamic, not static. Adult songbirds can form new neurons, replace old ones, and reallocate brain space appropriately to seasonal efforts, whether relocating hidden seeds in the fall or learning new songs in the spring.

Birds have enormous conservation power. Their public appeal motivates millions of people to take time to observe them, to count them, to care about their well-being, and to act on their behalf. Added to their public appeal and economic power is their potential political power. Birds are sensitive barometers of the environment. Recall Rachel Carson's *Silent Spring* (1962), which ignited the modern era of positive environmentalism. Failures of seabird reproduction also heralded the El Niño phenomenon of the Pacific Ocean, which meteorologists now recognize as a driving force of annual climate events. Besides urbanization and modern modes of transportation, mechanized agriculture and forestry have severe effects on bird habitats and populations. Because of their seasonal migrations between the continents, birds more than other animals help us to understand the global nature of these effects.

A few stories of extinction in modern times are well known. Those of the Dodo, Great Auk, and Passenger Pigeon are dramatic. Less well known is an extraordinary story of a battle won by the birds. It took place in Western Australia in 1932 and is known as the Emu War. At the time, it attracted much attention and was covered by the press. It seems that some 20,000 emus threatened wheat fields. Soldiers employing machine guns and artillery spent a month attacking the birds. The emus, in the words of Dominick Serventy of the Australian Wildlife Research Office, "apparently adopted guerilla tactics and split into small units. This made the use of military equipment uneconomic." After the soldiers withdrew, fences were built to separate the emus from the grain.

A satisfactory outcome indeed. Perhaps through basic research and thoughtful practice, birds will continue to charm and fascinate us throughout our own existence.

PART 1

ORIGINS

CHAPTER 1

The Diversity of Birds

It is easy to understand why so many of us are so fond of birds. They are lively; they are lovely; and they are everywhere. [Attenborough 1998, p. 7]

Millions of years ago, a small, bipedal reptile lived among the dinosaurs. From its skin evolved a novel and empowering structure—the feather. Feathered insulation enhanced its ability to control its high body temperature, thereby increasing its activity and endurance. Extensions of feathers on forelimbs and tails led to powerful, graceful flight. Mastery of flight opened a world of ecological opportunities, and a new group of vertebrates—the Class Aves—evolved, and then thrived.

The biggest conservation challenge facing the world is that of maintaining the global fabric of biodiversity. As author David Quammen writes in his *Song of the Dodo* (1996), the global tapestry of life on Earth is in danger of unraveling as key ecological threads are broken. Birds are one of those threads. Birds move in vast numbers across the hemispheres, playing essential roles as consumers of insects, pollinators of flowers, and dispersers of seeds. Birds are pivotal players in ecosystem dynamics and provide essential services to human societies. Birds also serve as barometers of the health of ecosystems, pristine and altered, that serve mankind. Understanding their diversity, their ecology, their history, and their future will serve us well.

This chapter previews the major features of the diversity of birds: their basic form, function, and biology; their major kinds; and their geographical distribution. Chapter 2 examines the evolutionary history of birds from the original fossil bird, *Archaeopteryx lithographica,* and birdlike dinosaurs to modern birds themselves. Chapter 3 briefly considers the reconstruction of evolutionary trees of relationships among birds, now informed by powerful new DNA-comparison techniques.

Basic Characters of Birds

Birds are two-legged (bipedal) vertebrates—the group of animals with backbones that also includes mammals, amphibians, reptiles, and fishes. Despite their diversity of form, birds are a well-defined group of vertebrates. They are distinguished from other (modern) vertebrates by feathers, which are unique modifications of the outer skin. Compared with the scales of reptiles, feathers are filamentous, soft in texture, flexible, lightweight structures (Figure 1–1). No comparable structures exist in other living vertebrates. Dead structures that wear easily and must be replaced

FIGURE 1–1 The courtship display of the King Bird-of-Paradise deploys its full array of elaborate feathers, including racquet-tipped wire tail feathers. [*From Ingram 1907*]

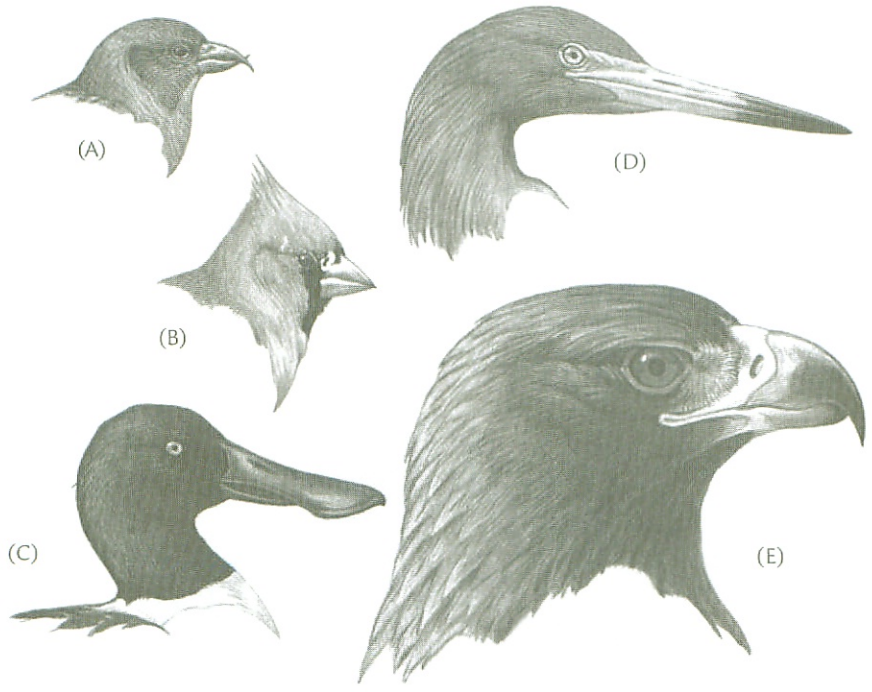

FIGURE 1–2 The bills of birds correspond to their feeding specialties. (A) Red Crossbills extract seeds from pine cones. (B) Northern Cardinals crack large, hard seeds. (C) Northern Shoveler ducks strain food from the mud. (D) Reddish Egrets spear small fish. (E) Golden Eagles tear apart the flesh of their prey.

regularly, feathers are essential for both temperature regulation and flight. They insulate the body and help birds to maintain their high body temperature. Lightweight and strong, the long feathers of the wing generate lift and thrust for flight.

All birds have bills, a distinctive attribute that facilitates instant recognition. The avian bill varies greatly in form and function but is always toothless and covered with a horny sheath (Figure 1–2). The avian bill has no exact parallel among other extant vertebrates; it is approximated only by the snout of the duck-billed platypus, a strange, egg-laying mammal of Australia.

Because birds lack teeth that chew food before swallowing, the avian digestive system is specialized to process unmasticated food. The lack of teeth in birds appears to be a weight-reducing adaptation for flight, because teeth require a heavy jawbone for support. Instead of teeth, birds have a gizzard. The avian gizzard—a functional analogue of mammalian molars—is a large, strong, muscular structure used primarily for grinding and digesting tough food. The gizzards of grain eaters and seed eaters, such as turkeys, pigeons, and finches, are especially large and have powerful layers of striated muscles. Turkey gizzards can pulverize English walnuts, steel needles, and surgical lancets. The internal grinding surfaces of

the gizzard are covered with a rough pleated or folded surface with many grooves and ridges. In some pigeons, it has strong, tooth-shaped projections. The gizzard can also contain large quantities of grit, which grinds food. The gizzards of moas, extinct ostrichlike birds of New Zealand, have been found to contain as much as 2.3 kilograms of grit. The gizzard is not so muscular in birds that eat softer foods such as meat, insects, or fruit; and, in raptors and herons, it may take the form of a large thin-walled sac.

Birds are feathered flying machines (Figure 1–3). Their wings and their ability to fly are familiar attributes but, unlike feathers, are not diagnostic features; bats and flying insects also have wings.

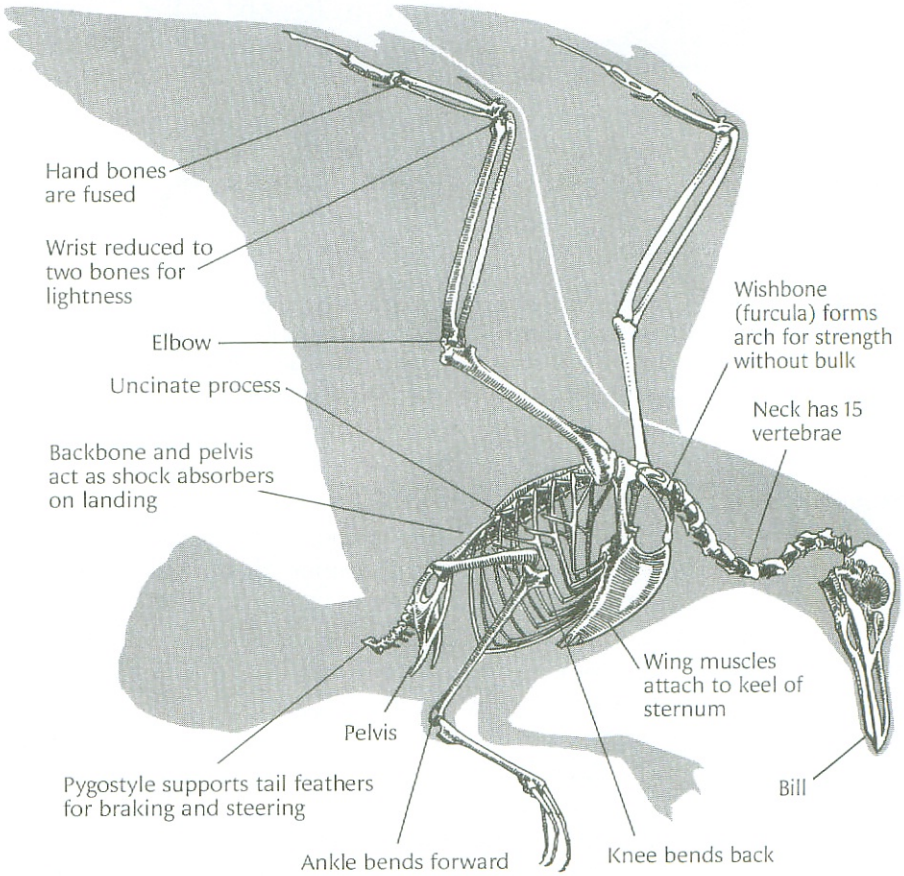

FIGURE 1–3 Adaptations for flight. Supporting the wings of the Herring Gull is a strong but lightweight skeleton. An enlarged, keeled sternum houses and anchors the large breast muscles that empower the wings. The bones of the hand and wrist, which support and maneuver the primary flight feathers, are reduced in number and fused for extra strength. Similarly, the pygostyle, made of fused tail vertebrae, supports and controls the tail feathers, which are used for braking and steering. Strengthening the body skeleton are fusions of the pelvic bones and associated vertebrae, plus horizontal rib projections called uncinate processes. The furcula, or wishbone, compresses and rebounds like a powerful spring in rhythm to the beat of the wings. [*After Pasquier 1983; drawing by Biruta Akerbergs*]

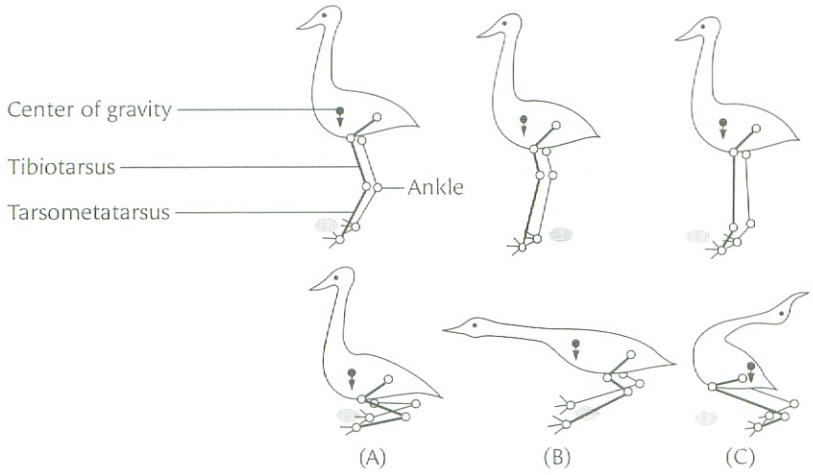

FIGURE 1–4 (A) Leg bones of equal lengths contribute to the balance of long-legged birds. When a bird crouches to incubate its egg, for example, leg bones of different lengths (B and C) would displace the center of gravity. What appears at first glance to be a backward-bending knee joint is really the ankle joint. In birds, the foot bones (three tarsals) are fused both to one another and to the metatarsals, thereby creating a long, strong, single leg element, the tarsometatarsus, which enables birds to walk on their toes rather than on the whole foot. [*After Storer 1971*]

The entire avian body is structured for flight. Bird bones, for example, are typically lightweight structures, being spongy, strutted, and hollow. The skeleton generally is strengthened and reinforced through fusions of the bones of the hands, head, pelvis, and feet. Horizontal, backward-curved projections—called uncinate processes—on the ribs overlap other ribs and so strengthen the walls of the body. The furcula, or wishbone, compresses and rebounds like a powerful spring in rhythm to the beat of the wings. The wing itself is a highly modified forelimb that, with a few remarkable exceptions, is nearly incapable of functions other than flight. Fused hand bones support and maneuver the large and powerful primary flight feathers.

For stable balance on land, a bird's center of gravity is positioned directly over and between its feet, particularly when the bird perches, squats, or rises (Figure 1–4). The equal length of the two main leg bones—the tibiotarsus and tarsometatarsus—of long-legged birds ensures this relation. Foot-propelled diving birds such as loons have sacrificed balance on land for their considerable swimming abilities. For efficient propulsion, they have powerful legs situated at the rear of a streamlined body, which places their center of gravity far forward of their feet when on land.

Arboreal—tree-dwelling—species, which constitute the majority of birds, have feet that tightly grip branches. Among the features of such feet are long tendons that pass around the backside of the ankle joints. When a bird bends its joints to squat, the tendons automatically flex, locking the

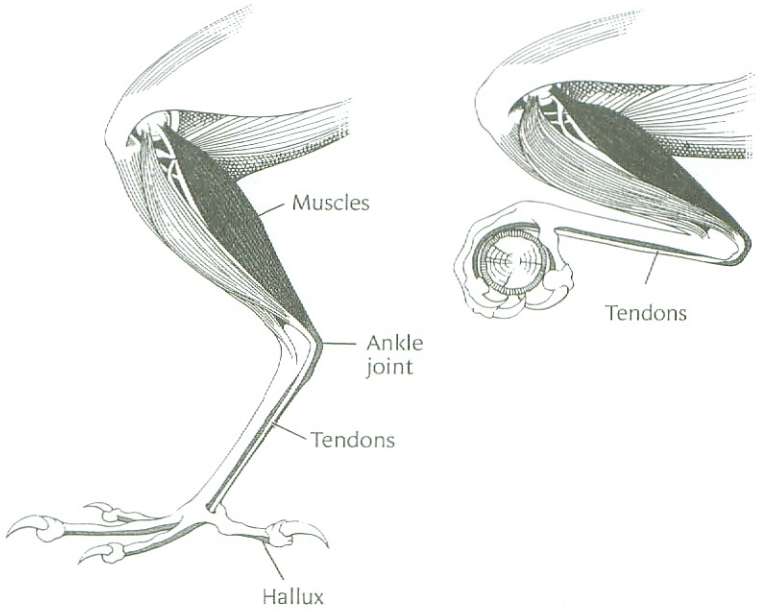

FIGURE 1–5 When a perching bird squats, the leg tendons, which are located on the rear side of the ankle, automatically cause the toes to grip. [*From Wilson 1980, with permission from Scientific American, Inc.*]

toes around the branch (Figure 1–5). When a bird stands, the tension relaxes and the toes open. The foot of the songbirds—Order Passeriformes—is perhaps the most advanced in this respect. A special system of ridges and pads between the tendons that flex the toes and the insides of the toe pads acts as a natural locking mechanism and permits birds to sleep while perching. The large, opposable single rear toe, or hallux, which enhances the ability of a bird to grip a branch, is unusual among vertebrates.

Avian physiology accommodates the extreme metabolic demands of flight and temperature regulation. The red fibers of avian flight muscles have an extraordinary capacity for sustained work and can produce heat by shivering (see Chapter 6). Birds are endothermic; that is, they are warm-blooded and maintain high body temperatures (40°–44°C) over a wide range of ambient temperatures. The circulatory and respiratory systems of birds include a powerful four-chambered heart and efficient lungs, which deliver fuel and remove both waste and heat produced by metabolic activities.

The reproductive systems of birds also are unusual. Birds produce large, richly provisioned external eggs, the most elaborate reproductive cells of any animal. No bird species bears live young like those produced by other classes of vertebrates. Nurturing the growth of the embryos in the eggs and of the young after they hatch requires dedicated

parental care. Most birds form monogamous pair bonds, some for life; but many, it turns out, engage in additional sexual liaisons. As a result, the eggs in one nest may be of mixed paternities and even maternities. Mating systems, spacing behavior, and cooperation afford varied solutions to the challenges of successful reproduction in a highly competitive social world.

Birds have large, well-developed brains, 6 to 11 times as large as those of like-sized reptiles. Bird brains and primate brains exhibit functional lateralization, with left hemispheric dominance associated with learning and innovation in vocal repertoires. Substantial learning by birds guides the mastery of complex motor tasks, social behavior, and vocalizations.

Highly developed neural systems and acute senses in birds mediate feats of communication and navigation. Birds, particularly the songbirds, have the greatest sound-producing capabilities of all vertebrates. The syrinx of birds is a unique sound-producing structure. In contrast with the syrinx, the larynx, the analogous structure in mammals, constrains mammalian vocalizations by its position and structural simplicity. Birds can navigate by using patterns of Earth's magnetism, celestial cues, and perhaps polarized light. Their highly developed color vision reaches into the near-ultraviolet range of the spectrum. Their broad hearing range encompasses infrasounds—sounds below the hearing range of humans.

Adaptive Radiation of Form and Function

Roughly 300 billion birds now inhabit the Earth. The variety of birds is the grand result of millions of years of evolutionary change and adaptation. The current classification of living birds arranges 30 orders, 193 families, 2099 genera, and at least 9700 species (Table 1–1, page 12). Yet this number is only a small fraction of the number of species that have existed since the age of dinosaurs. The earliest birds in the Mesozoic era more than 150 million years ago had feathers and probably could fly after a fashion. Responding to ecological opportunities, subsequent birds diversified in form and function. From the fundamental anatomy of their common ancestor evolved perching songbirds such as robins; nocturnal forest hunters such as owls; aquatic divers such as penguins; oceanic mariners such as albatrosses; shoreline waders such as plovers; and large, flightless ground birds such as the ostrich (Figure 1–6). Birds range in size from only 2 grams (hummingbird) to 100,000 grams (ostrich).

The diversity of birds is due to the evolution of additional varied species adapted to different ecologies and behaviors, a phenomenon called adaptive radiation. Bill sizes and bill shapes change in relation to the types of food eaten. Leg lengths change in relation to habits of perching or

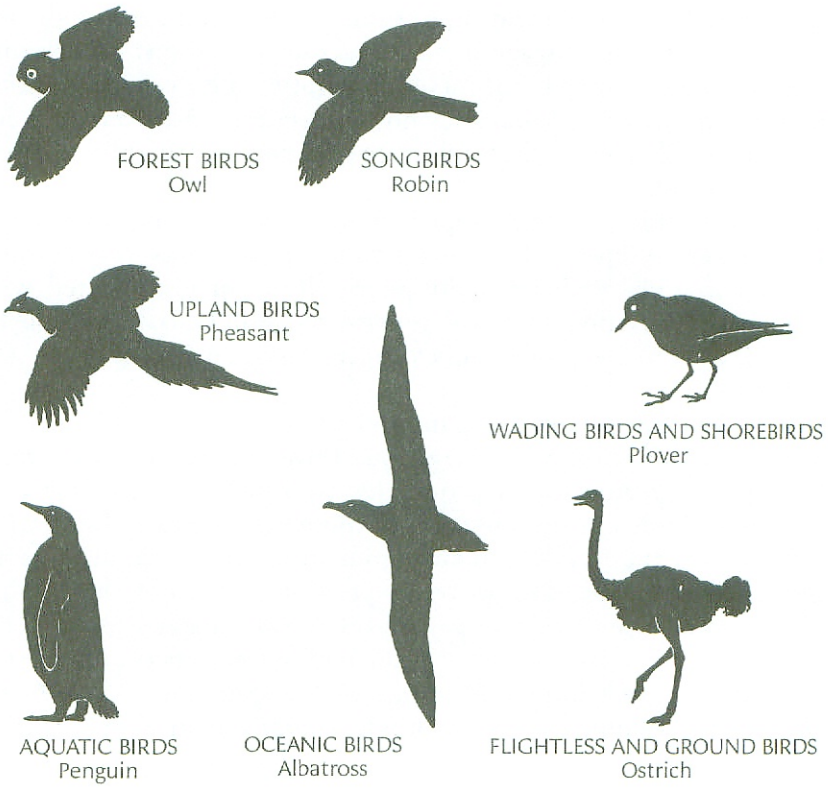

FIGURE 1–6 Birds have evolved along several major lines, each adapted to a particular mode of life. [*From Evolution of Vertebrates by E. H. Colbert. Copyright 1955 John Wiley & Sons, Inc.; reprinted by permission of John Wiley & Sons, Inc.*]

terrestrial locomotion, and wing shapes change in relation to patterns of flight. For example, from a single ancestral species of shorebird evolved aerial pirates such as skuas and plunging divers such as terns, as well as a host of waders, including sandpipers, plovers, turnstones, stilts, jacanas, snipes, woodcocks, curlews, and godwits, each with characteristic leg lengths and bill lengths, shapes, and curvatures. As varied as the habitats that they occupy, shorebirds also include aerial pratincoles, gulls, and skimmers, deep-water divers such as puffins, and the grouselike seedsnipes of South American moorlands. All these related species are members of the Order Charadriiformes (Figure 1–7).

The varied diets of modern birds include buds, fruits, nectar, seeds, invertebrates of all sizes, and vertebrates of many kinds, including carrion.

FIGURE 1–7 Shorebirds, gulls, and allies (Order Charadriiformes): (1) Pheasant-tailed Jacana (Jacanidae); (2) Snowy Sheathbill (Chionidae); (3) Eurasian Woodcock (Scolopacidae); (4) Atlantic Puffin (Alcidae); (5) Blacksmith Lapwing (Charadriidae); (6) Ring-billed Gull (Laridae); (7) Black Skimmer (Rynchopidae).

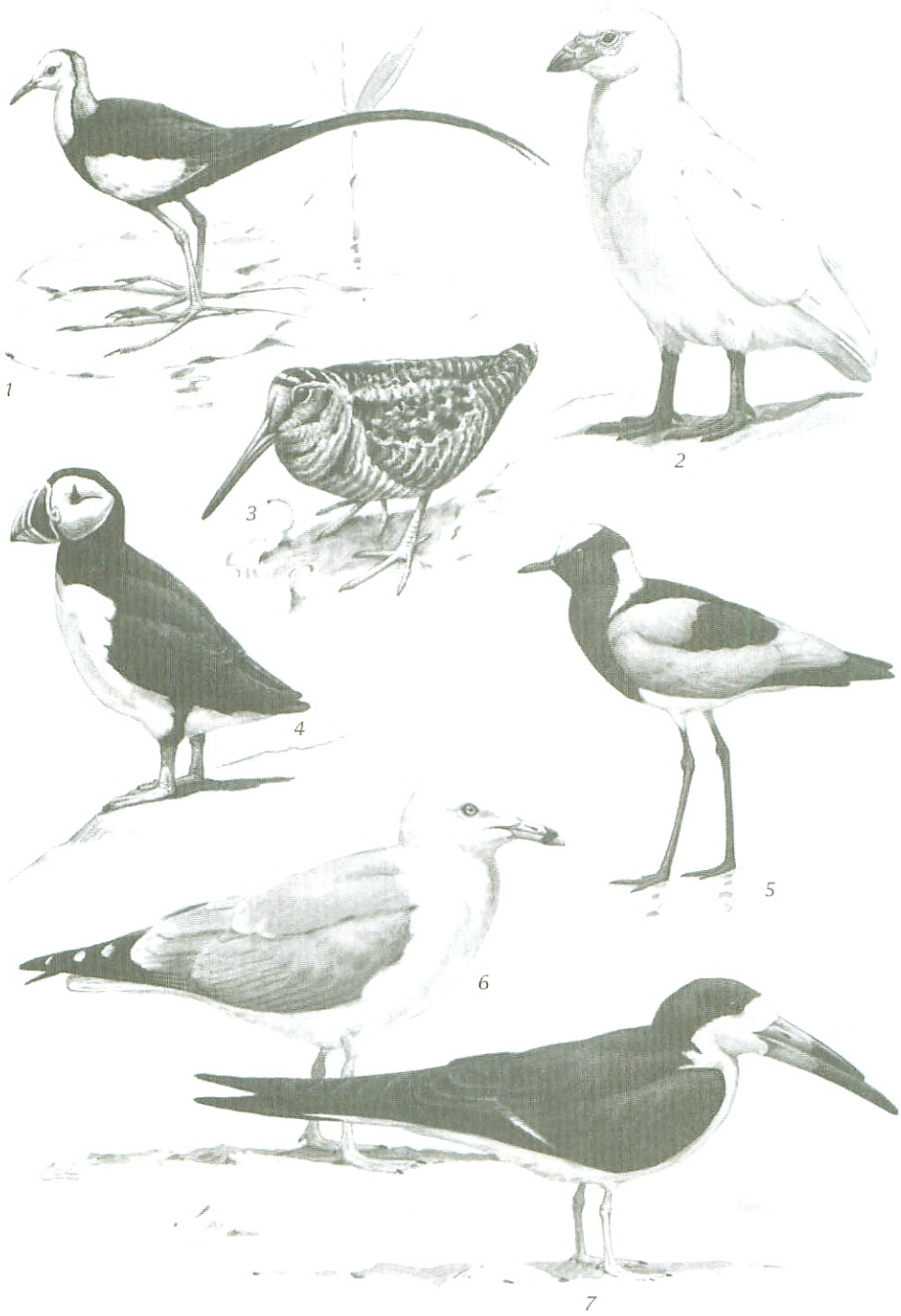
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TABLE 1–1 The orders of the birds of the world

Order	Number of Taxa			Members
	Families	Genera	Species	
Tinamiformes	1	9	47	Tinamous
Rheiformes	1	2	2	Rheas
Struthioniformes	1	1	1	Ostrich
Casuariiformes	2	2	6	Cassowaries, Emu
Dinornithiformes	1	1	3	Kiwis
Galliformes	5	80	290	Gallinaceous birds: grouse, quails, pheasants, chickens, curassows, guans, chachalacas, guineafowl, moundbuilders
Anseriformes	3	52	162	Waterfowl: ducks, geese, swans, screamers
Sphenisciformes	1	6	17	Penguins
Gaviiformes	1	1	5	Loons
Procellariiformes	4	26	112	Tube-nosed seabirds: petrels, shearwaters, albatrosses, storm petrels, diving petrels
Podicipediformes	1	6	22	Grebes
Phoenicopteriformes	1	3	5	Flamingos
Ciconiiformes	3	39	116	Long-legged wading birds: storks, herons, ibises, spoonbills
Pelecaniformes	8	10	65	Water birds with totipalmate feet: cormorants, pelicans, anhingas, boobies, gannets, frigatebirds, tropicbirds, Hammerkop, Shoebill
Falconiformes	3	83	304	Raptors: falcons, caracaras, hawks, eagles, Old World vultures, kites, Osprey, Secretarybird, New World vultures
Gruiformes	11	61	212	Diverse terrestrial and marsh birds: rails, coots, sungrebes, cranes, Sunbittern, Kagu, Limpkin, seriemas, bustards, buttonquails, trumpeters, roatelos
Charadriiformes	17	88	367	Shorebirds and their relatives: sandpipers, plovers, phalaropes, stilts, jacanas, painted-snipes, pratincoles, gulls and terns, seedsnipes, sheathbills, skimmers, skuas, auks, sandgrouse
Columbiformes	1	42	308	Pigeons, doves
Psittaciformes	1	85	364	Parrots, macaws, lories, cockatoos
Opisthocomiformes	1	1	1	Hoatzin
Musophagiformes	1	6	23	Turacos, plaintain-eaters
Cuculiformes	1	35	138	Cuckoos
Strigiformes	2	29	180	Owls, barn owls
Caprimulgiformes	5	22	118	Nightjars, potoos, frogmouths, Oilbird, owlet-nightjars
Apodiformes	3	124	429	Swifts, crested swifts, hummingbirds
Coliiformes	1	2	6	Mousebirds
Trogoniformes	1	6	39	Trogons, quetzals
Coraciiformes	11	51	209	Kingfishers and allies: todies, motmots, bee-eaters, rollers, Cuckoo Roller, hoopoes, wood hoopoes, hornbills
Piciformes	5	8	398	Woodpeckers and allies: wrynecks, piculets, barbets, toucans, honeyguides, jacamars, puffbirds
Passeriformes	96	1218	5753	Perching birds, songbirds, passerines
Totals	193	2099	9702	

Family classification and totals from Dickinson 2003.

Fruits, seeds, and insects nourish the majority of birds, especially the passerine land birds, whose adaptive radiation was coupled to those of flowering plants and their associated insects. Few birds are specialized herbivores; apparently, mammals have usurped most of the terrestrial grazing and browsing niches. In the absence of mammals in New Zealand, numerous species of flightless, herbivorous moas evolved. The long, complex digestive tracts required for green leaves and the weight of slowly digesting plant matter also may limit the flying abilities of avian herbivores or favor flightlessness, as in ostriches.

Corresponding to a diversity of diets is a diversity of bills (see Figure 1–2). A bird's bill is its key adaptation for feeding. The size, shape, and strength of the bill prescribe the potential diet. The land carnivores—eagles, hawks, falcons, and owls—have strong, hooked beaks with which they tear flesh and sinew. Other bill types tear meat, spear fish, crack seeds, probe crevices, or strain microscopic food from the mud. The broad, flat bill of a duck is suitable for straining mud, whereas the chisel-like bill of a woodpecker is suitable for digging into trees to reach insects. Marine predators, such as penguins and cormorants, have bills with curved projections that direct fish toward the esophagus. The varied lengths and curvatures of shorebird bills determine which prey they can reach by probing into the mud (Figure 1–8). Nectar feeders, such as hummingbirds, probe their long, thin bills into floral nectar chambers and draw up nectar through tubed tongue tips. Their bill forms tend to match the lengths and curvatures of preferred flowers, which, in turn, depend on the birds

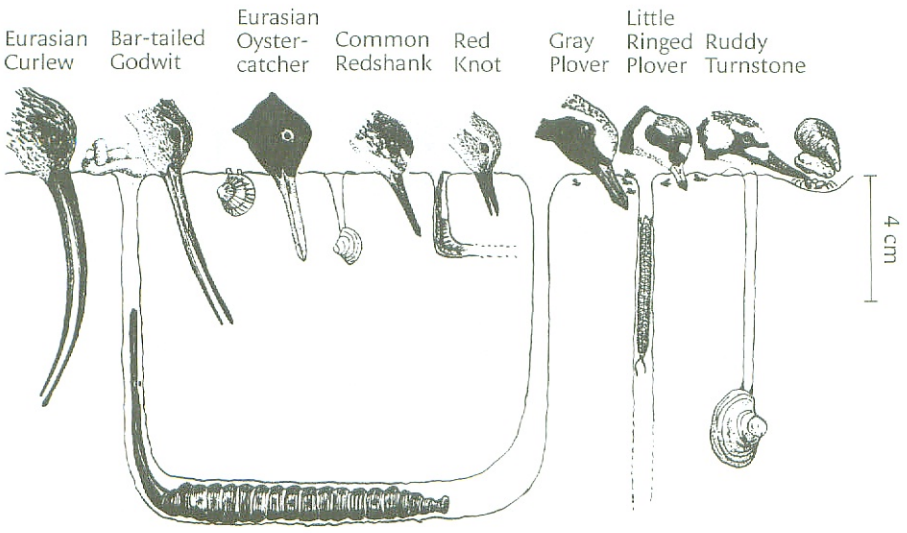


FIGURE 1–8 Varied bill lengths enable shorebirds to probe to various depths in the mud and sand for food. Plovers feed on small invertebrates, mainly by surface pecking with their short bills. Common Redshanks and other species of waders with moderate bill lengths probe the top 4 centimeters of the substratum, which contain many worms, bivalves, and crustacea. Only the long-billed birds such as curlews and godwits can reach deep-burrowing prey such as lugworms. [*After Goss-Custard 1975*]

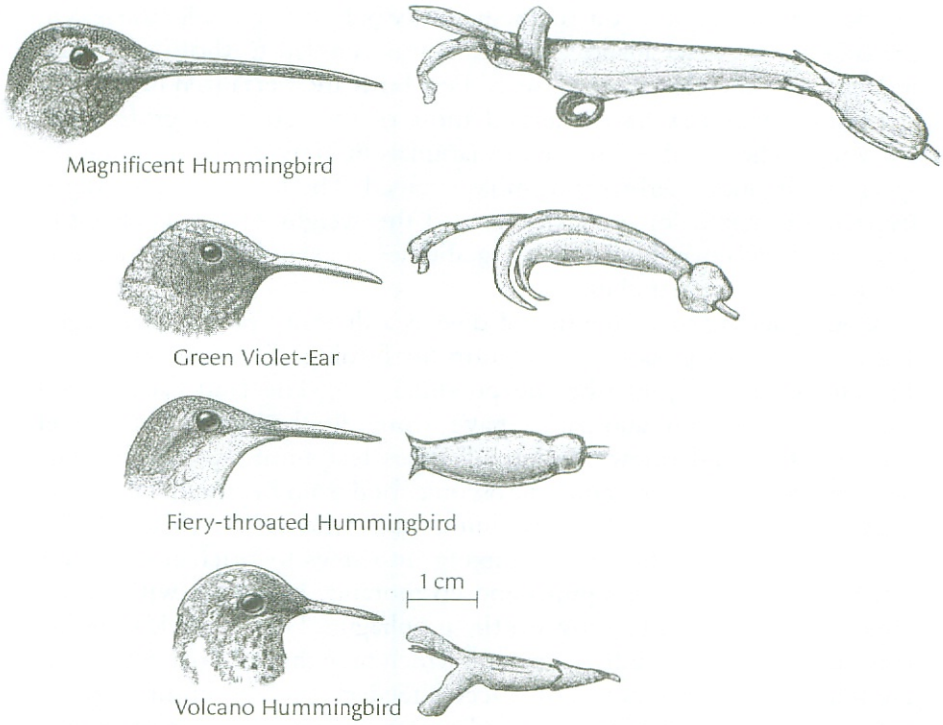


FIGURE 1–9 The lengths and curvatures of hummingbird bills match those of their preferred flowers. [*After Wolf et al. 1976*]

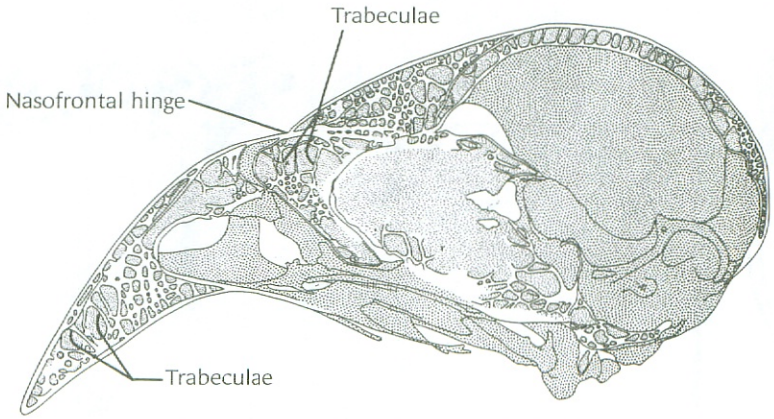


FIGURE 1–10 The form of their large bills enables finches such as the Northern Cardinal to bite hard seeds without straining the nasofrontal hinge (located between bill and skull) with excessive shear forces. Shown here is a cross section of a cardinal skull, revealing the bony struts (trabeculae) in the upper jaw and forehead. The deeper, nontrabecular areas of the upper jaw are shown in fine stippling; other nontrabecular bone is shown in heavier stippling. Lower jaw is not shown. [*From Bock 1966*]

for pollination (Figure 1–9). Even slight differences in bill dimensions influence the rate at which food can be consumed.

The bone configurations that constitute the bill, jaws, and palatal region are an engineer's delight. The avian bill is not rigid; birds can flex or bend the upper half of the bill, an ability called cranial kinesis (see Zusi 1984). The upper mandible, or maxilla, is a flattened, hollow, bony cone reinforced internally by a complex system of bony struts called trabeculae (Figure 1–10). These struts make the bill much stronger than a hollow bill but add little weight. Covering both jaws is a horny sheath, or rhamphotheca, which may have sharp cutting edges (as in boobies), numerous toothlike serrations (as in mergansers), or well-developed notches (as in falcons and toucans). Woodcocks can open just the tip of their bills to grasp earthworms deep in the mud.

The variety of bill forms that can evolve in the process of adaptive radiation is seen in the Hawaiian honeycreepers, which apparently evolved from a flock of small finches that strayed out over the Pacific Ocean from Asia or North America millions of years ago. The finches made landfall on one of the Hawaiian Islands, then flourished and spread throughout the archipelago. Isolated populations changed in genetic composition and appearance, at first imperceptibly and then conspicuously. Subtle changes in bill shapes and bill sizes led to a proliferation of bill types and their related feeding behaviors: from heavy grosbeak-like bills for cracking large legume seeds to long sicklelike bills for sipping nectar from flowers or probing bark crevices for insects (Figure 1–11).

Different modes of locomotion further expand the ecological opportunities of birds. Shorebirds, as already mentioned, include aerial, wading, and diving species. Birds soar through the sky, scurry and stride across the land, hop agilely from branch to branch, hitch up tree trunks, and swim powerfully to great depths in the sea. The combination of forelimbs adapted for flight and hindlimbs for bipedal locomotion gives birds a tremendous range of ecological options.

There are specialized flying birds, as well as specialized swimmers, runners, waders, climbers, and perchers. Wing shapes and modes of flight range from the long, narrow wings of the albatross, adapted for soaring over the oceans, to the short, round wings of wrens, adapted for agile fluttering through dense vegetation. At another extreme are the adaptations of wing-propelled diving birds, such as penguins, which use their flipperlike wings to move underwater (Figure 1–12).

Like the structures of bills and wings, the anatomy of feet and legs corresponds to different life styles (Figure 1–13, page 18). At one extreme are the long, powerful legs of wading and cursorial, or running, birds such as storks and ostriches. At the other extreme are the tiny feet and short legs of aerial specialists such as swifts. The long toes of herons and jacanas spread the bird's weight over a large surface area and facilitate walking on soft surfaces. Sandgrouse scurry on soft desert sands, and ptarmigan can walk on snow by virtue of snowshoe-like adaptations of their feet. Lobes

(Text continues on page 18.)

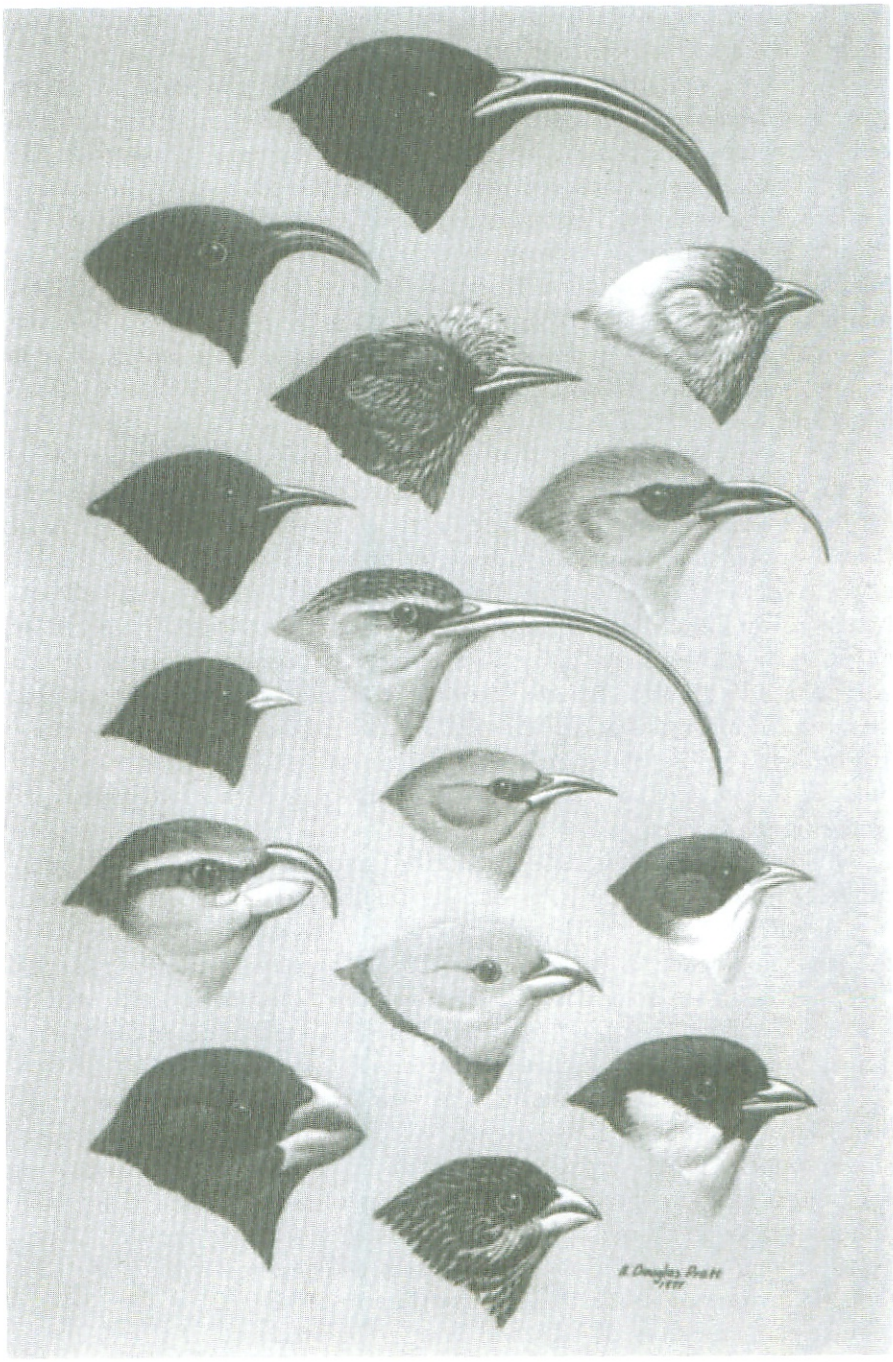


FIGURE 1–11 A classic example of adaptive radiation: Hawaiian honeycreepers have evolved bills that range from thin warblerlike bills to long sicklelike bills to heavy grosbeak-like bills. [*From Raikow 1976; drawing by H. Douglas Pratt*]

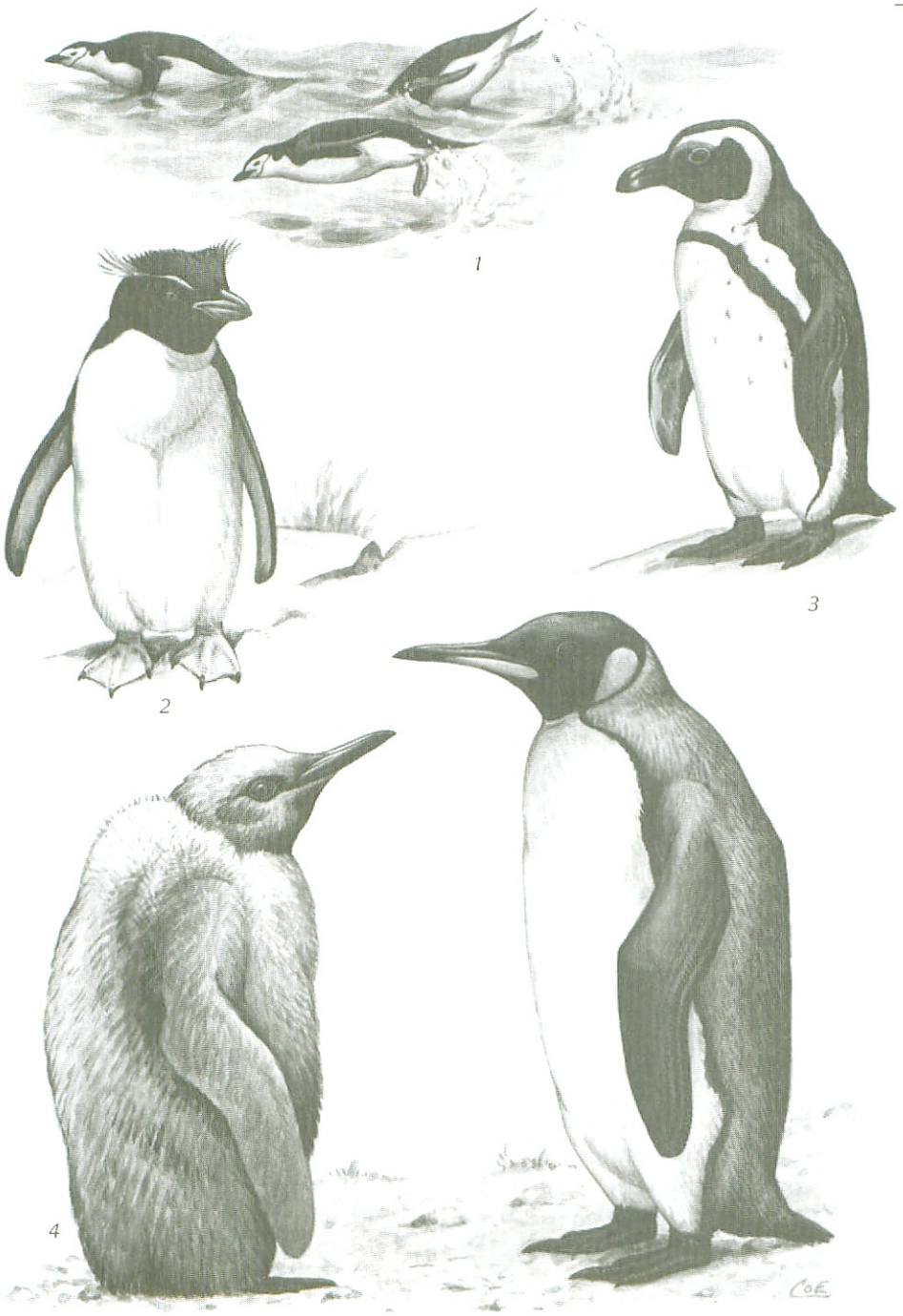


FIGURE 1–12 Penguins: (1) Chinstrap Penguin; (2) Rockhopper Penguin; (3) Jackass Penguin; (4) King Penguin, juvenile (*left*), adult (*right*).

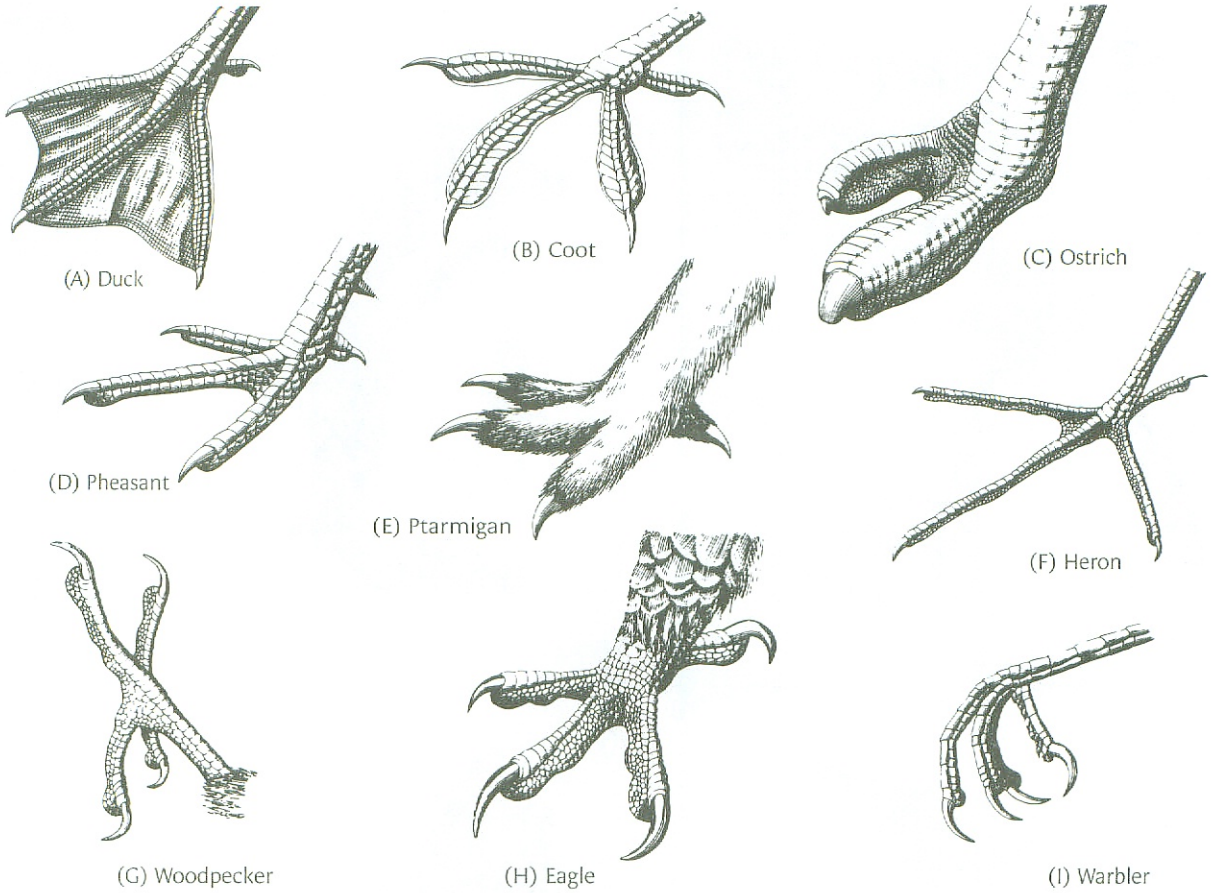


FIGURE 1–13 The feet of birds reveal their ecological habits. Water birds have (A) webbed or (B) lobed toes for swimming; terrestrial birds have toes specialized for (C) running, (D) scratching in dirt, (E) walking on snow, or (F) wading. Other land birds have feet designed for (G) climbing, (H) holding prey, or (I) perching. [*From Wilson 1980, with permission from Scientific American, Inc.*]

on the toes of coots and webbing between the toes of ducks aid swimming. Climbing birds such as woodpeckers have large, sharply curved claws; nuthatches climb downward by gripping a tree's bark with a large claw on the hind toe.

Life Histories

In addition to their form and function, birds have diversified in all aspects of their seasonal and social biology. Reproductive rate, adult life span, and age at maturity, differ more than tenfold among species (Ricklefs 2000a). Albatrosses are long-lived and lay only one egg at a time. Small songbirds, instead, tend to have short life spans and to raise many young together. Some species lay large eggs for their body size; other species lay small and lightly provisioned eggs. Newly hatched young may be help-

less or agile. Parental care may be minimal or prolonged. Such attributes of life history contribute to an individual bird's lifetime reproductive success. They are as subject to evolutionary molding by the environment and by population dynamics as are the shapes of bills and wings.

Natural Selection and Convergence

We accept that the close fit between form and function portrayed so vividly by the diversity of birds and their life-history traits is due to evolutionary adaptation through natural selection. As set forth by Charles Darwin in 1859 and confirmed subsequently through experiment and independent observation, natural selection is simply the predictable predominance of individual organisms with advantageous traits. Healthy individuals leave more offspring than do sickly individuals. Camouflaged chicks are more likely to escape predation and to reproduce themselves than are boldly colored chicks. To be favored by natural selection, however, traits need not be dramatically better. Subtle or slight advantages in egg quality, camouflage, or agility increase in prevalence in a local population. Adaptation by natural selection is a process without plan or purpose, a process that gradually transforms the appearances and abilities of organisms.

A large finch bill can be so advantageous in times of food shortage that the average bill size in a population increases from one year to the next (Boag and Grant 1981). In 1976 and 1977, a severe drought gripped Daphne Island in the Galápagos archipelago. Plants failed to produce new crops of seeds, and seed densities dropped sharply, especially the densities of small seeds. Many finches starved. In regard to the Medium Ground Finch, individual birds with large, deep bills survived in greater numbers than did those with small bills because the large-billed birds could crack the remaining larger, harder seeds. The result was a dramatic increase in average bill size over only one year's time, due to natural selection (Figure 1–14). This intense natural selection was later reversed by the improved survival of small-billed birds during wet years, when small seeds were again plentiful.

The power of natural selection is perhaps best demonstrated through convergence—the independent evolution of similar adaptations in unrelated organisms. Adaptation to similar ecological roles causes unrelated species of birds to become superficially similar (i.e., to converge) in details of appearance and behavior. For example, the meadowlarks of North American grasslands and the unrelated longclaws of the African grasslands are classic cases of convergence in color pattern. Both have streaked brown backs, bright yellow underparts with a black V on the neck, and white outer tail feathers. The meadowlark is related to the blackbirds (Icteridae), the longclaws to pipits and wagtails (Motacillidae). Another classic case of convergence is that of the northern ocean auks and the southern ocean penguins. From different aerial ancestors, species of compact

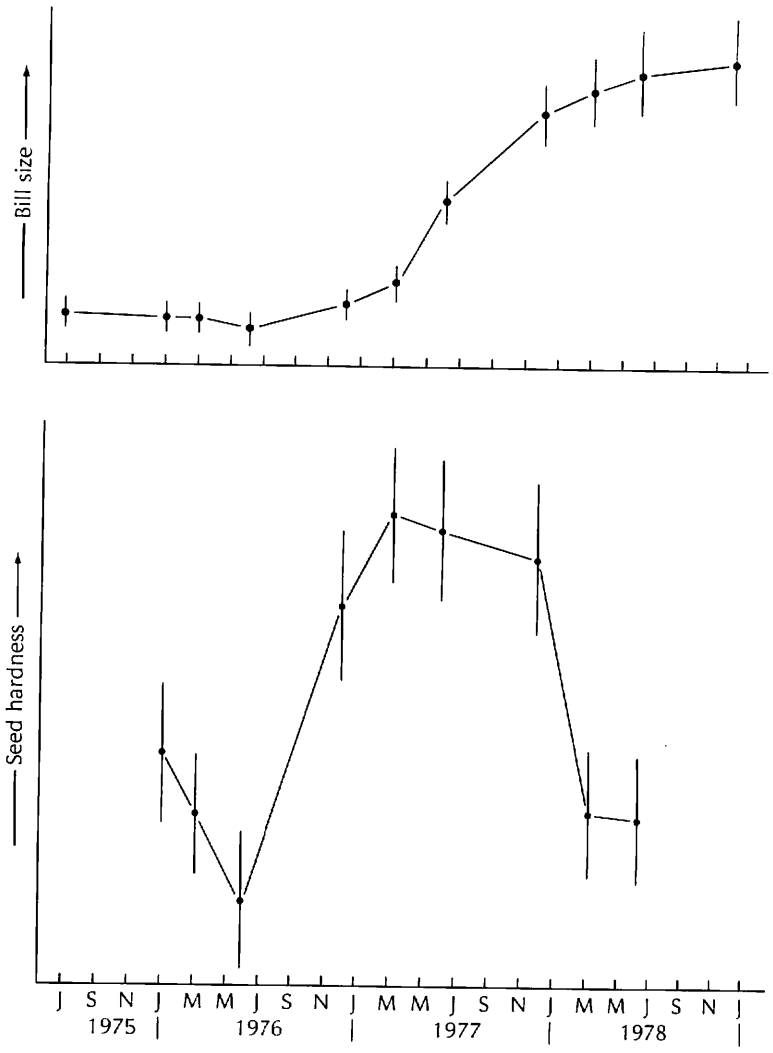


FIGURE 1–14 Increase in bill size (*top*) in the Medium Ground Finch during a period of drought that resulted in intense natural selection. Failure of the usual seed crop on Daphne Island favored individual birds with large bills able to crack the more abundant, large, hard seeds (*bottom*). Abbreviations, starting at left on *x*-axis: J, June; S, September; N, November; J, January; M, March; M, May. [*After Boag and Grant 1981*]

black-and-white seabirds have evolved in both ocean regions, including flightless forms that use their wings to propel themselves underwater to capture marine crustaceans and fish (Figure 1–15).

Biogeography

Biogeography is the study of the geographical distributions of plants and animals. For more than a century, biogeographers have divided Earth into six major faunal regions corresponding roughly to the major continental

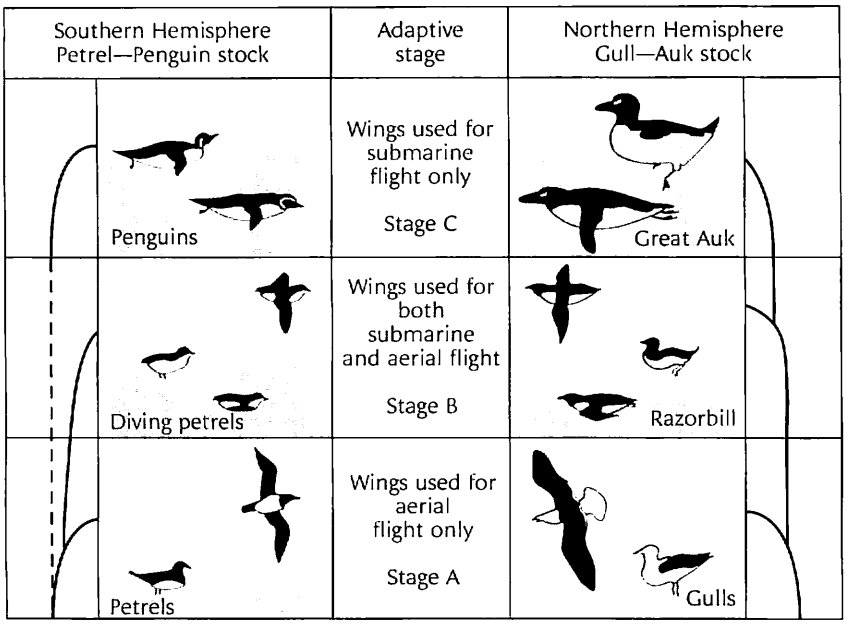


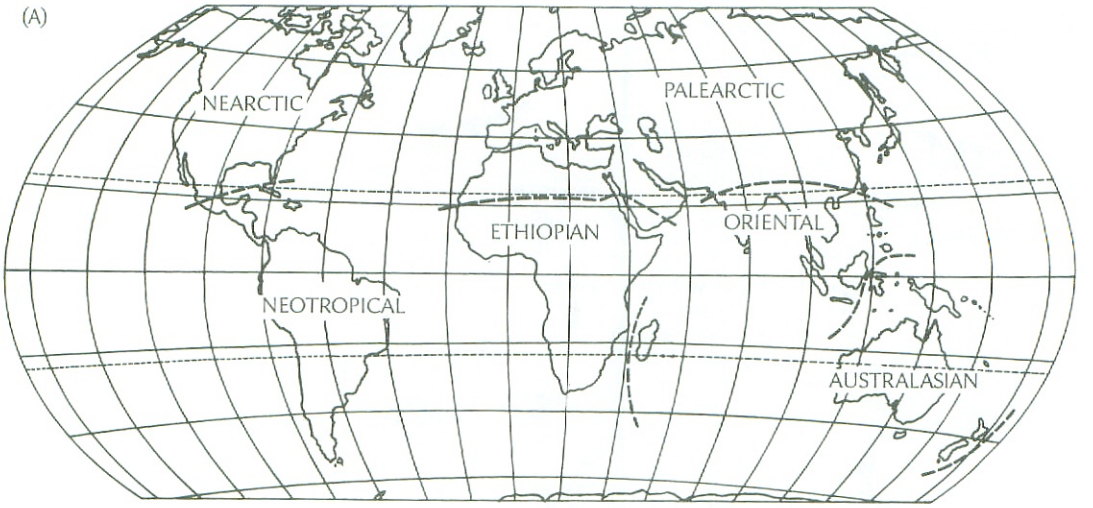
FIGURE 1–15 Convergent evolution of wing-propelled divers. Adaptive stages in the parallel evolution of two stocks of wing-propelled diving birds, the petrels to penguins and the gulls to auks, respectively. [*From Storer 1960*]

areas (Figure 1–16). Each faunal region has its characteristic birds: so-called endemic taxa or species, which are found nowhere else, and other birds that represent major adaptive radiations of more widespread taxa. Waxwings and loons are restricted to North America and Eurasia, the Nearctic and Palearctic regions, respectively. The birds that are endemic to Africa, or the Ethiopian region, include ostriches, mousebirds, and turacos. Australia and New Guinea, the Australasian region, have emus, honeyeaters, and birds-of-paradise. South America, the Neotropical region, has toucans, tinamous, and trumpeters.

Most avifaunas—regional assemblages of bird species—are mixtures of species of varied ages and origins. Some species trace back more than 60 million years to the rearrangement of the continents from the early landmass called Gondwanaland. Other species arose in recent colonizations of new islands or continents. The history of bird distributions can be viewed as a series of waves of adaptive radiations, moving north, south, east, and west from their ancestral origins. New groups of birds replaced older ones and in turn produced complex mosaics of ancient, recent, and new colonists from different regions. The birds of North America include old and new colonists from Asia and South America, remnants of ancient avifaunas, plus diverse species groups that evolved only on that continent—for example, the colorful wood warblers.

Early avian colonists on each continent or major group of islands diversify locally in response to the ecological opportunities available to them. The diversity of finches on the Galápagos Islands and of honeycreepers

(A)


NEARCTIC
PALEARCTIC
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ORIENTAL
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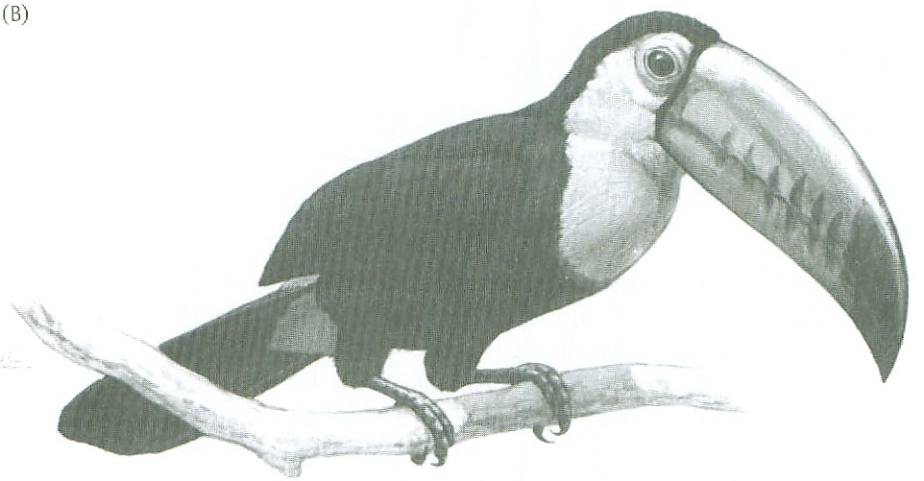
AUSTRALASIAN

(B)



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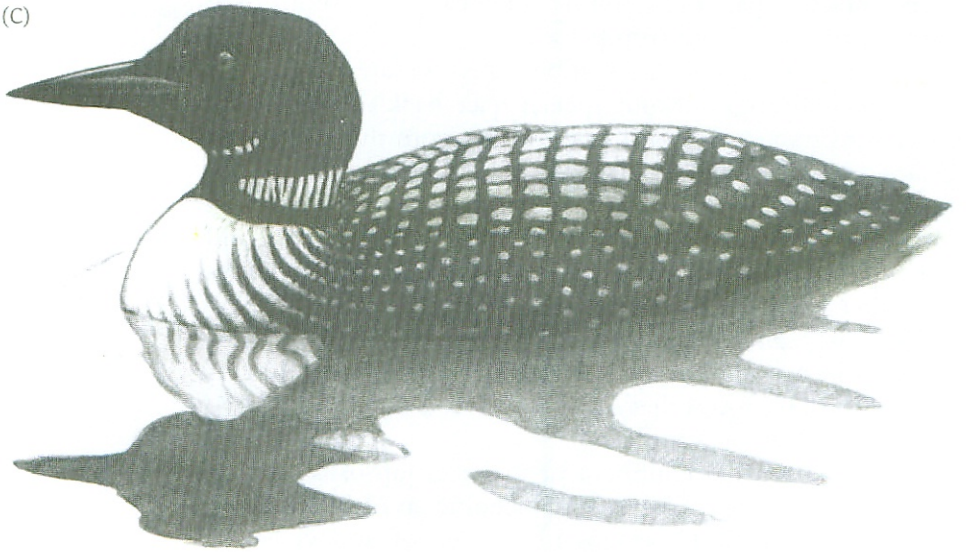


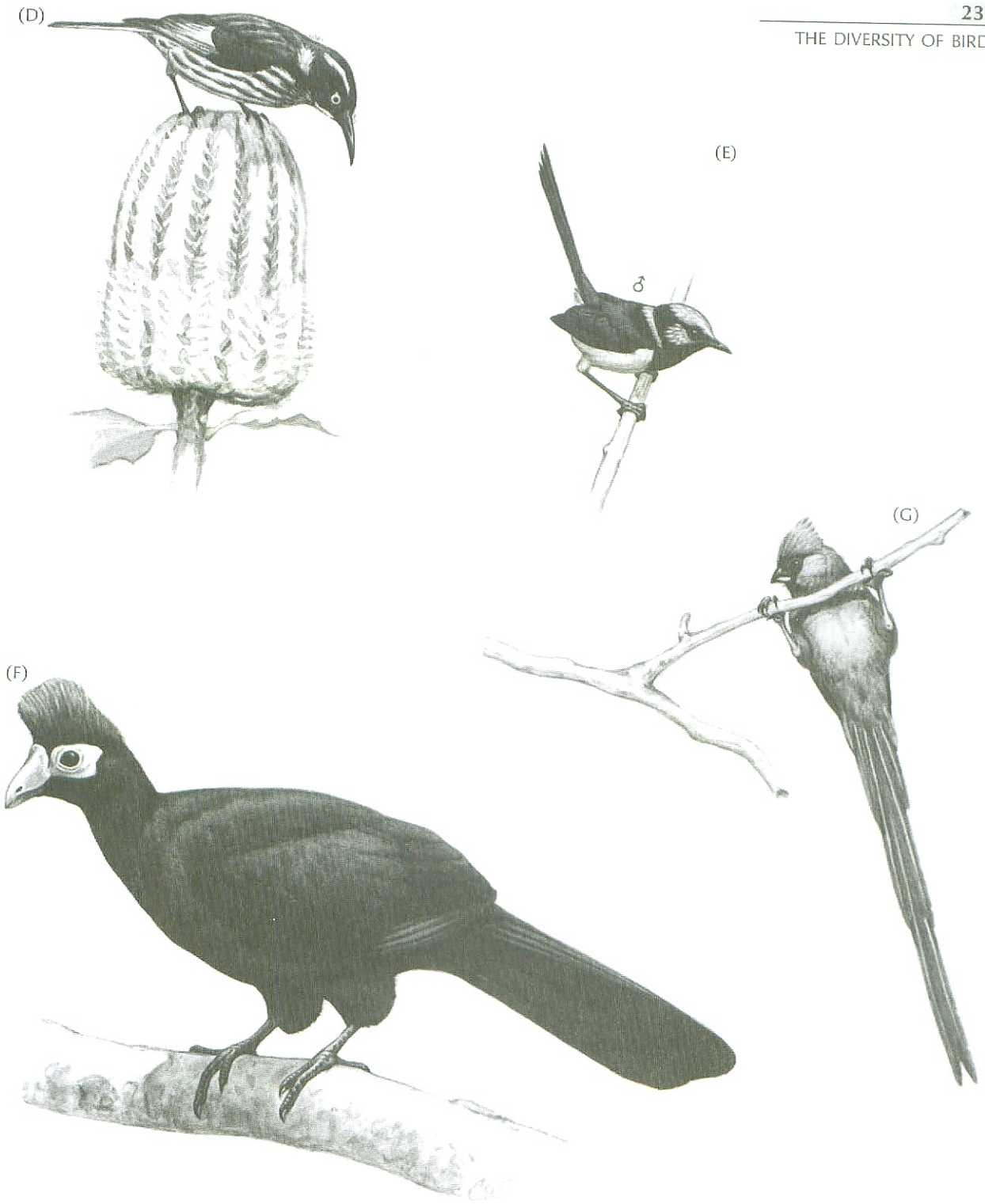


FIGURE 1–16 The six major faunal regions (A) and some of their bird specialties: (B) toucans (Neotropical region); (C) loons (Nearctic and Palearctic regions); (D) honeyeaters and (E) fairywrens (Australasian region); (F) turacos and (G) mousebirds (Ethiopian region).

on the Hawaiian Islands inspired the evolutionary theories of Charles Darwin. Just as dramatic is the diversity of the tyrant flycatchers of South America, which radiated to include new species that look and function like shrikes, wheatears, tits, warblers, pipits, or thrushes from other parts of the world. Australian land birds, related genetically most closely to one another, matched so well the external attributes of shrikes, flycatchers, and small insect-eating warblers that, until 1990, they were misclassified with superficially similar species native to Europe and Asia.

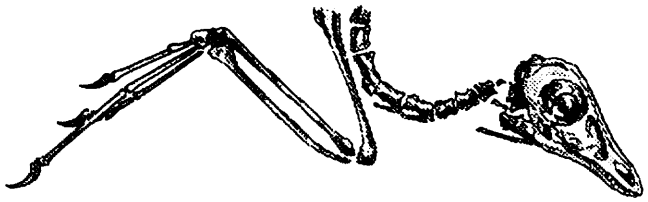
Summary

Characterized as vertebrates with feathers, birds have distinctive bills, maintain high body temperatures, produce large external eggs, and have elaborate parental behavior and extraordinary vocal abilities. The anatomy and physiology of most birds are adapted for flight.

The diversity of birds is due to millions of years of divergence and adaptation by natural selection. The process of adaptive radiation is well illustrated by the members of the Order Charadriiformes, which include terrestrial waders, aerial plungers, and wing-propelled divers. The adaptive radiation of Hawaiian honeycreepers illustrates the way in which bill forms can evolve in relation to feeding habits. In addition to their physical features, birds have diverse life-history traits, mating systems, and reproductive strategies.

The birds of the world constitute geographical assemblages of species; these large groups are called avifaunas. The six major avifaunas are the Nearctic (North America), Neotropical (Central and South America), Palearctic (Europe and Asia), Ethiopian (Africa south of the Sahara), Oriental (Southeast Asia), and Australasian (Australia and New Guinea). Each region has its characteristic birds.

CHAPTER 2



History

The study of the origin and early evolution of birds has never produced as much excitement and public attention as in the past decade. [Zhou 2004, p. 455]

Avian history starts more than 150 million years ago with the transformation of reptilian ancestors into feathered birds with limited flying abilities. Birds then diversified in form and function first in the Mesozoic and then again as modern taxa in the Tertiary. The evolution and adaptive radiation of birds paralleled the independent evolution and rise of placental mammals to their own modern prominence. Increases in atmospheric oxygen over this same period of Earth history, with rapid increases in the early Jurassic and the Eocene, potentially favored the success of these two principal groups of highly active land vertebrates with aerobic metabolism (Falkowski et al. 2005).

The details of the transformation of reptiles into birds, including the role of dinosaurs, have long been the focus of intense debates. A wealth of well-preserved new fossils of both early birds and dinosaurs, mostly from northeastern China, provide a new and expanded scenario of the initial stages of the evolution of birds.

Major episodes of extinction punctuated the long history of life on Earth. The Class Aves participated in several of them, starting in the late Cretaceous. In another episode at the beginning of the Pleistocene epoch about 3 million years ago, climatic changes caused the extinction of at least 25 percent of the existing bird species. Recurrent climatic changes continued to alter habitats and, in turn, the distributions and viabilities of bird populations. In the past century, humans have become the primary force changing and threatening the natural world, including global climates. Birds now face a major new episode of species extinctions.

This chapter first examines the reptilian features of birds and then *Archaeopteryx lithographica*, the earliest known bird. The array of new fossil dinosaurs and of the diverse bird species that followed *Archaeopteryx* is

a source of additional insights into the evolution of feathers and avian flight. This chapter also reviews the main stages of the diversification of modern birds in the Mesozoic era in association with the breakup of Gondwanaland, the ancient southern continental landmass. The stage is then set for Chapter 3, which examines how ornithologists reconstruct evolutionary relationships among species and classify birds according to these relationships.

Birds As Reptiles

Birds evolved from reptiles (Figure 2–1). Thomas H. Huxley, the great evolutionary biologist of the nineteenth century, asserted that birds were "merely glorified reptiles" and accordingly classified them together in the taxonomic category Sauropsida (Huxley 1867). Indeed, birds and modern reptiles have many characters in common (Figure 2–2). The skulls of both articulate with the first neck vertebra by means of a single ball-and-socket device—the occipital condyle; mammals, which evolved from a different line of reptiles, have two of them. Birds and modern reptiles have a simple middle ear with only one ear bone—the stapes; mammals

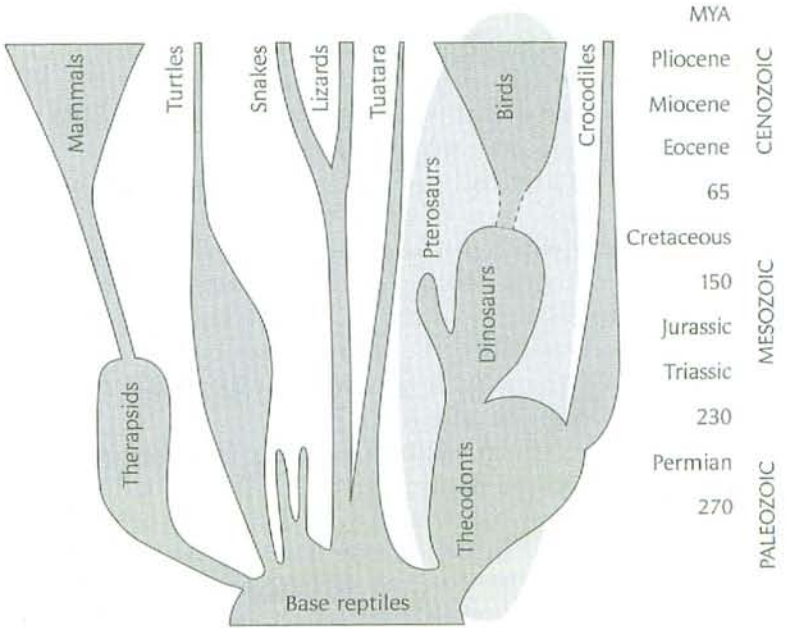


FIGURE 2–1 A simplified family tree of the vertebrates. Birds, dinosaurs, pterosaurs, and crocodiles evolved from one group of reptiles, the thecodonts; mammals evolved from another, the therapsids. Other groups of early reptiles gave rise to turtles, snakes and lizards, and the iguana-like tuatara now found only on little islands near New Zealand. (The dashed lines indicate that detailed lineage between birds and dinosaurs is uncertain.)

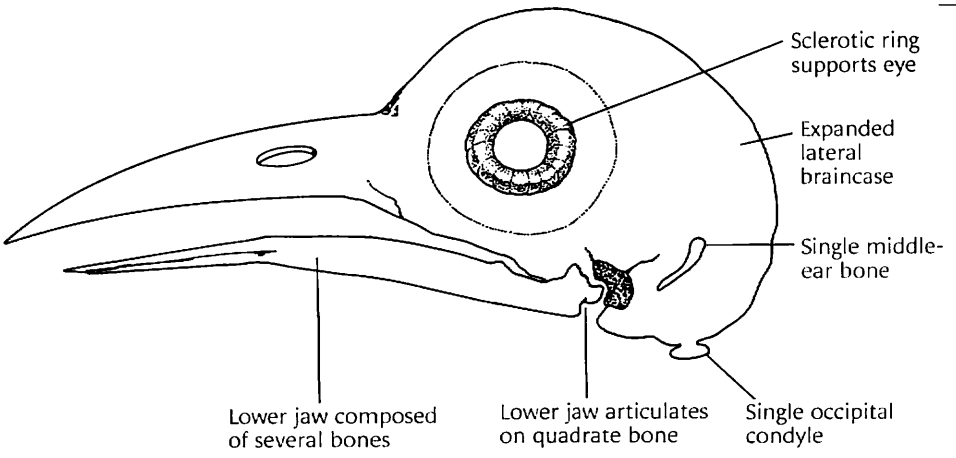


FIGURE 2–2 Some reptilian features of the avian skull.

have three middle-ear bones. The lower jaws, or mandibles, of both birds and modern reptiles are composed of five or six bones on each side: mammals have only one mandibular bone. The ankles of both birds and modern reptiles are sited in the tarsal bones (see Figures 1-2 and 1-3), not between the long lower leg bones, or tibia, and tarsi as in mammals. The scales on the legs of birds are similar in structure to the body scales of modern reptiles.

Both birds and modern reptiles lay a yolked, polar egg in which the embryo develops by shallow divisions of the cytoplasm on the surface of the egg. In birds and in some reptiles, females have two different sex chromosomes, Z and W, and are referred to as the heterogametic sex (see Chapter 14); males are the heterogametic sex among mammals (with X and Y chromosomes). Both birds and reptiles have nucleated red blood cells, whereas the red blood cells of mammals lack nuclei.

Archaeopteryx: The Original Link Between Birds and Reptiles

The similarities between birds and reptiles leave no doubt of their evolutionary relationship to each other. Yet we are not content with that. We want to know which reptiles gave rise to birds and how the transformation proceeded. For this knowledge, we must turn to the fossil record. There, an extinct creature, *Archaeopteryx lithographica*, first signaled the origin of birds from reptiles.

Fine-grained limestone deposits in central Europe contain a record of creatures that occupied that region during the age of dinosaurs—in the late Jurassic period, from 155 million to 135 million years ago (Table 2–1). At that time, central Europe was tropical, sporting palmlike plants. Great warm seas and lagoons covered parts of the European continent. The coastal lagoons attracted pterodactyls, or flying reptiles, some as small as

TABLE 2–1 Geologic time scale

Era	Period	Epoch	Million Years Before Present
Cenozoic (age of birds and mammals)	Quaternary	Recent	0.01
		Pleistocene	1.5–3.5
	Tertiary	Pliocene	7
		Miocene	26
		Oligocene	36–38
		Eocene	53–54
		Paleocene	65
Mesozoic (age of reptiles)	Cretaceous	Late	100
		Early	135
	Jurassic	Late	155
		Middle	170
		Early	180–190
	Triassic		230

From Feduccia 1980.

sparrows and others as large as eagles, which flew on batlike wings made of stretched skin. Sometimes they perished in the lagoons, where gentle fossilization in the fine calcareous sediments preserved their features in exquisite anatomical detail. Also preserved in the same lagoons were the remains of the feathered reptile now called *Archaeopteryx*.

The first evidence of the origin of birds was an impression of just a single feather found in a Bavarian quarry, from which Jurassic limestone was mined for lithographic slabs. The impression was brought to the attention of German naturalist Hermann von Meyer of Munich in 1861. A complete skeleton of a small reptilelike animal with feathers also was found and brought to von Meyer's attention just a few months later. He named the fossil creature *Archaeopteryx* (*archaios*, "ancient"; *pteryx*, "wing") *lithographica*. The discovery of a second complete specimen of *Archaeopteryx* in another quarry near Eichstätt, Bavaria, followed in 1877 (Figure 2–3). It is fully articulated, revealing details of the wing bones, flight feathers, and the pairs of feathers attached to each vertebra of its long tail. These feathers are indistinguishable from modern feathers.

FIGURE 2–3 This fully articulated skeleton of *Archaeopteryx lithographica* was found in 1877 near Eichstätt, Bavaria. [*Courtesy of J. Ostrom*]

Now known from seven specimens and that first feather, *Archaeopteryx* was a crow-sized, bipedal "reptile" with a blunt snout and many small, reptilian teeth. It bore feathers on both wings and tail and probably also over most of its body, like modern birds. It possessed, however, numerous reptilian features. Like the modern guans (Cracidae), it may have been a strong-running, terrestrial "bird" that could leap into trees, jump among large branches, and make short flights between trees. Paleontologists agree that *Archaeopteryx* was capable of gliding and weak flapping but not of long, sustained flights. Indications of *Archaeopteryx*'s flight capability include its large furcula, which probably anchored strong pectoralis muscles, and the acute angle of its scapula, which supported dorsal elevator muscles that helped to lift the wings, as they do in modern flying birds.

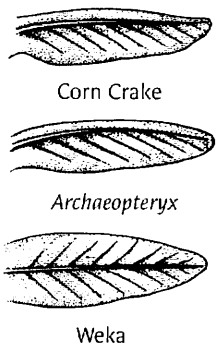


FIGURE 2–4 The vanes of the primaries of *Archaeopteryx* were asymmetrical like those of modern flying birds such as the Corn Crake, a kind of rail; they were not symmetrical like those of flightless birds such as the Weka, a flightless rail of New Zealand. The asymmetry has an aerodynamic function and presumably evolved in relation to flight in this primitive bird. Similar asymmetries are reported for a well-feathered dinosaur named *Microraptor*. [*After Feduccia and Tordoff 1979*]

Additionally, the vanes of *Archaeopteryx*'s primary wing feathers were asymmetrical, a character common to nearly all flying birds and most pronounced in strong fliers (Feduccia and Tordoff 1979). In flightless birds, these vanes are symmetrical (Figure 2–4).

Archaeopteryx was intermediate between reptiles and birds not only in skeletal features (Figure 2–5), but also in its brain and inner ear (Alonso et al. 2004). The brain was three times larger and more advanced than that of similarly sized reptiles, though still smaller than the brains of mod-

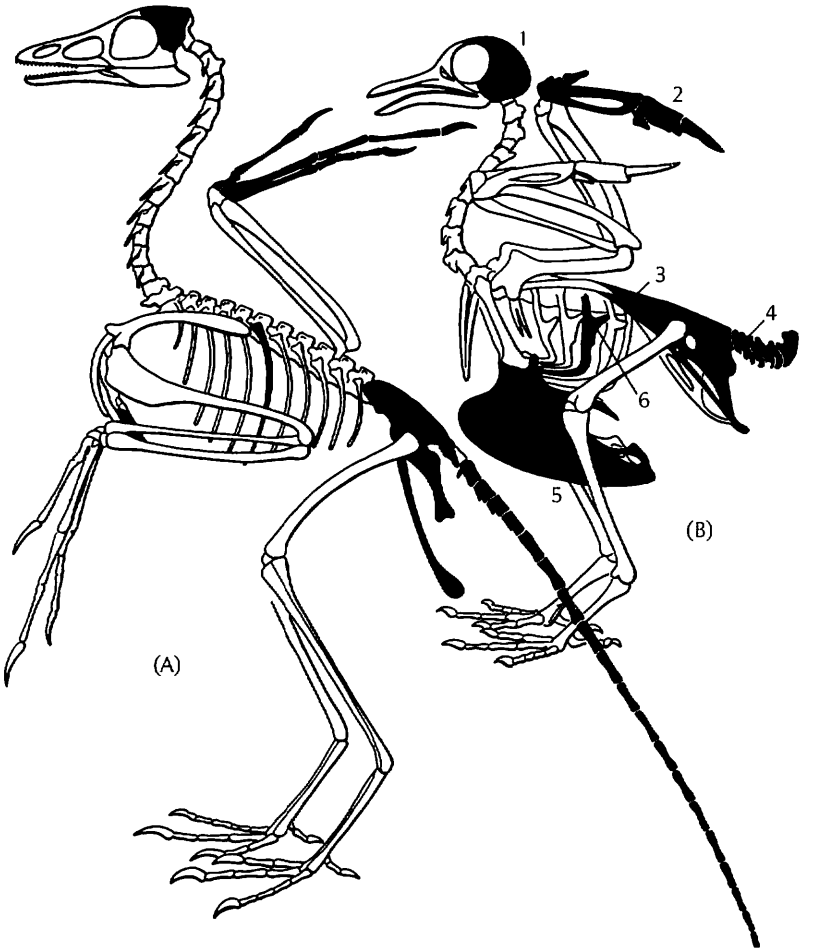


FIGURE 2–5 Skeletal features of (A) the reptilelike *Archaeopteryx* and (B) a modern bird, the domestic pigeon. In modern birds, (1) the braincase is expanded and the head bones are fused; (2) the separate hand bones of reptiles are fused into fewer rigid elements; (3) the separate pelvic bones of reptiles are fused into a single, sturdy structure; (4) the many tail vertebrae of *Archaeopteryx* are reduced in number and partly fused into a pygostyle; (5) the tiny cartilaginous sternum of *Archaeopteryx* has expanded to a large keeled bony structure for the attachment of flight muscles; and (6) the typical reptile rib cage is strengthened with horizontal uncinate processes. [*From Evolution of Vertebrates by E. H. Colbert. Copyright 1955 John Wiley & Sons, Inc.; reprinted by permission of John Wiley & Sons, Inc.*]

ern birds. The brain included enlarged visual centers. Expanded inner-ear structures would have enhanced hearing and spatial orientation. These features suggest that *Archaeopteryx* had evolved the initial neural systems required for flight.

The discovery of *Archaeopteryx* linked the evolution of birds directly to reptiles. It was a timely discovery of an animal that was intermediate between two higher taxonomic categories, a transition from ancestral to descendant stocks. Darwin's prediction of intermediate evolutionary links in *On the Origin of Species by Means of Natural Selection* (1859), published only two years before the discovery of the first two *Archaeopteryx* fossils, seemed to have been fulfilled.

The intermediate morphology of *Archaeopteryx* quickly moved into the center of the debate between opponents and supporters of evolution by natural selection. Creationists, defending their views of the separate and unchanging appearances of birds and reptiles, insisted that Darwinists were misinterpreting the apparent intermediacy of *Archaeopteryx*. On the other side of the debate, Thomas H. Huxley, Darwin's most eloquent champion, was convinced of the link between birds and birdlike reptiles and soon converted leading American paleontologists. Charles Marsh of Yale University was one of these converts. He wrote:

> The classes of Birds and Reptiles, as now living, are separated by a gulf so profound that a few years since it was cited by the opponents of evolution as the most important break in the animal series, and one which that doctrine could not bridge over. Since then, as Huxley has clearly shown, this gap has been virtually filled by the discovery of bird-like Reptiles and reptilian Birds. *Compsognathus* and *Archaeopteryx* of the Old World . . . are the stepping stones by which the evolutionist of to-day leads the doubting brother across the shallow remnant of the gulf, once thought impassable. [Marsh 1877, p. 352; Feduccia 1980, p. 15]

Archaeopteryx contributed to the acceptance of Darwin's theory of evolution as well as to our initial understanding of the origin of birds. Despite a series of challenges, *Archaeopteryx* remains firmly positioned as the oldest and most primitive known bird and the outstanding link to reptilian ancestors, as originally proposed.

Birds As Dinosaurs

There is little doubt that birds evolved from a line of Mesozoic reptiles. Which line and when, however, continue to be matters of intense debate (Prum 2002; Feduccia 2002). One possibility is that birds evolved early, before true dinosaurs, and from a stem group of reptiles called

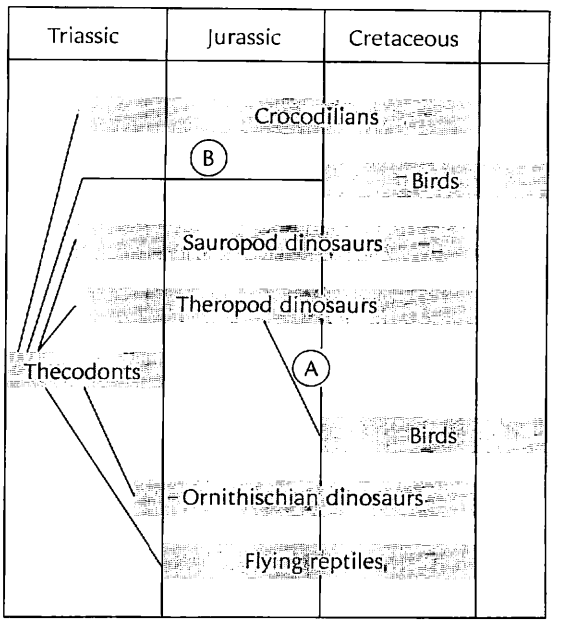


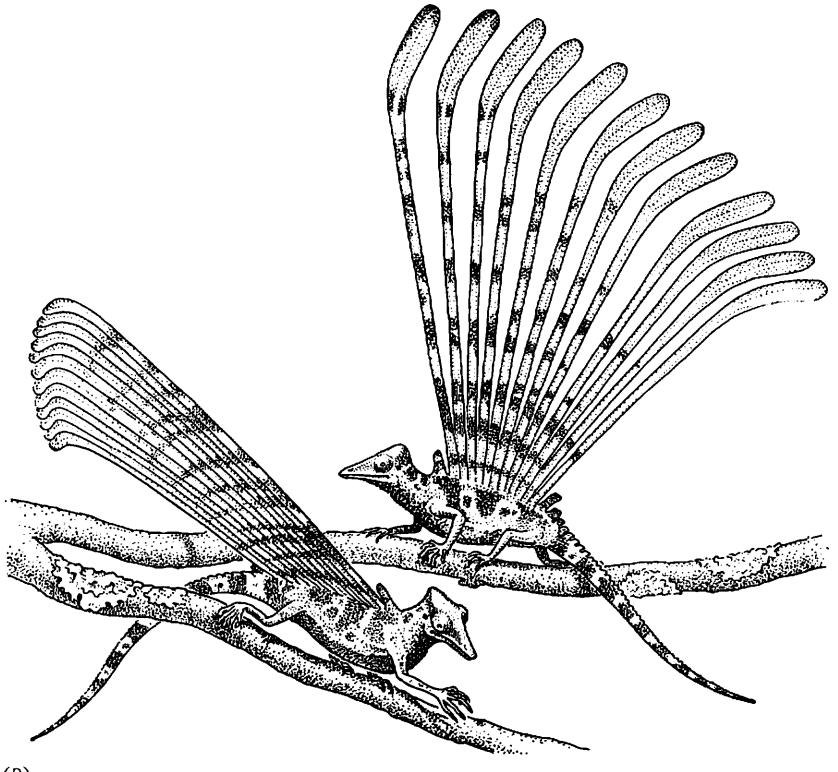
FIGURE 2–6 Historical debate about the evolution of birds. (A) Some experts believe that birds evolved from small theropod dinosaurs. (B) Other experts believe that birds evolved directly from the thecodont ancestors of dinosaurs and crocodiles. New fossils found in the past decade have swayed this debate in favor of the theropod dinosaur ancestors. [*After Ostrom 1975*]

thecodonts. The other possibility is that birds evolved later from small theropod dinosaurs (Figure 2–6).

The thecodont hypothesis of the origin of birds looks to a large group of primitive reptiles that prevailed in the early years of the Mesozoic era. Among them were the lightly built thecodonts, a diverse group of reptiles that gave rise to dinosaurs of different sorts, some of which were arboreal; to flying reptiles called pterosaurs; and to crocodiles. Some thecodonts even had elongated scales that seemed like the natural precursors of feathers (Figure 2–7).

The hypothesis that birds evolved from small theropod dinosaurs goes back to the discovery of fossil *Archaeopteryx*. Thomas H. Huxley (1868) was particularly impressed by the similarities between *Archaeopteryx* and *Compsognathus*, a small dinosaur preserved in the same Jurassic limestone deposits (see Figure 2–7). Although we usually think first of the large, spectacular species, dinosaurs varied greatly in size and habits. They evolved from thecodont ancestors in the Jurassic period and were dominant animals of the Cretaceous period from 136 million to 65 million years ago. One group, the theropod dinosaurs, included not only large carnivores such as *Tyrannosaurus rex* but also many small ones close in size to modern iguanas—agile, lightly built, bipedal, little dinosaurs with many small, sharp teeth. They probably chased small vertebrates and large insects. Some may even have been warm-blooded. The raptorlike "dromaeosaurs" have many characters in common with the earliest birds.

(A)



(B)

FIGURE 2–7 Two possible relatives of birds. (A) *Compsognathus* was a small theropod dinosaur that was preserved in the same limestone deposits as *Archaeopteryx*. (B) *Longisquama* was a lightly built, arboreal thecodont reptile with elongated scales. [*(A) From Heilmann 1927; (B) from Bakker 1975, with permission from Scientific American, Inc.*]

These small dinosaurs include *Velociraptor*, which figured prominently in Michael Crichton's book *Jurassic Park*.

The weight of the evidence has caused the pendulum of the debate to swing powerfully toward early terrestrial theropod dinosaurs as the immediate ancestors of birds (Pandian and Chiappe 1998; Prum 2002). In this proposed scenario, dromaeosaurs such as *Deionychus*, are the closest relatives of birds. Some, such as *Protarchaeopteryx* and *Caudipteryx*, even had feathers (Figure 2–8). Indeed, all of the specific features once thought

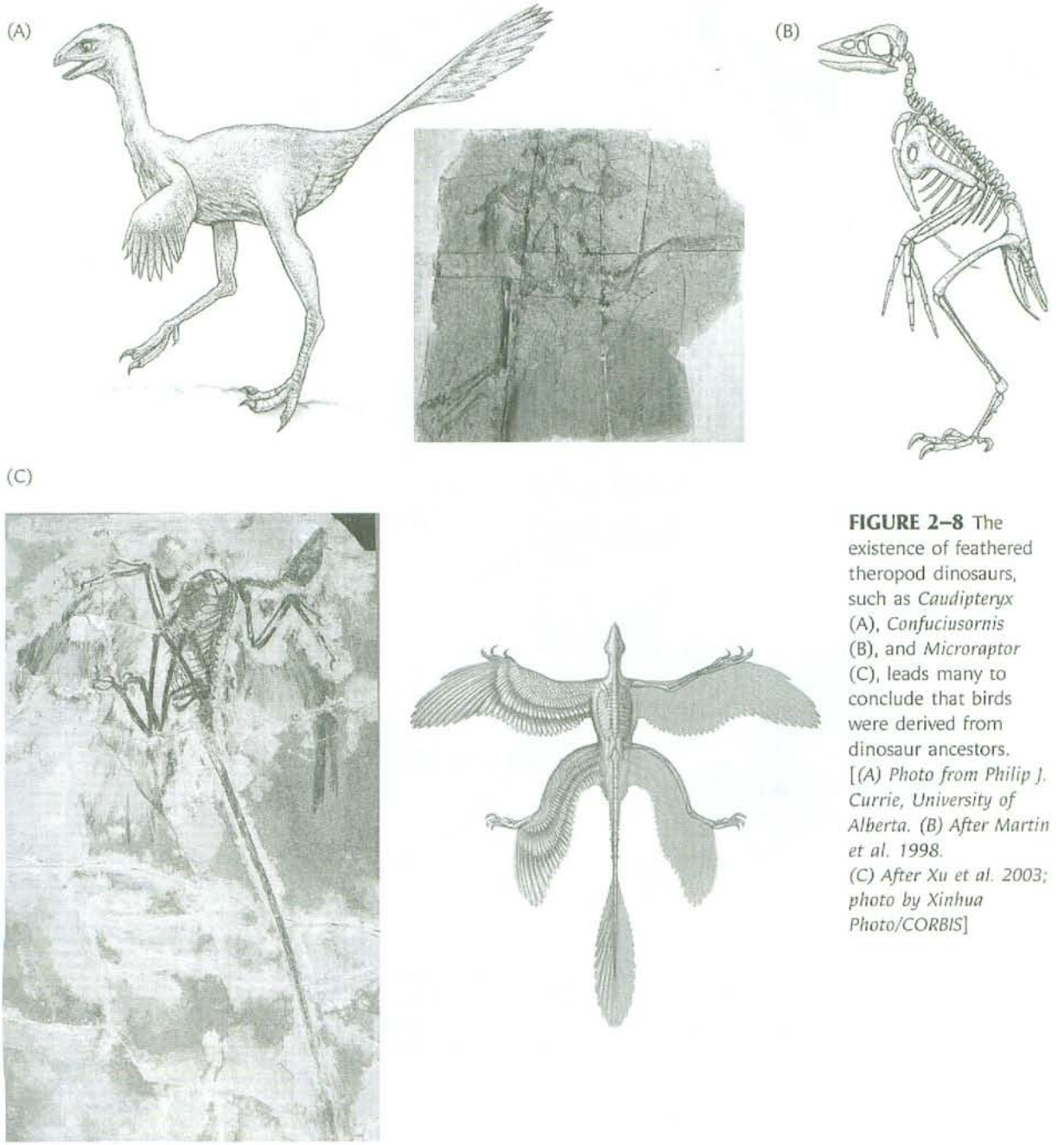


FIGURE 2–8 The existence of feathered theropod dinosaurs, such as *Caudipteryx* (A), *Confuciusornis* (B), and *Microraptor* (C), leads many to conclude that birds were derived from dinosaur ancestors. [*(A) Photo from Philip J. Currie, University of Alberta. (B) After Martin et al. 1998. (C) After Xu et al. 2003; photo by Xinhua Photo/CORBIS*]

to define the Class Aves as unique—feathers, furcula, pygostyle, bill, and even flow-through ventilation of the lung (O'Connor and Claessens 2005; see also Chapter 6)—were present in dinosaurs of the Cretaceous period. These traits of some dinosaurs and the advanced birdlike features of *Archaeopteryx* enabled the improved flying abilities and arboreal life styles of the next stage of avian evolution.

Major issues remain, however. Alan Feduccia and his colleagues disagree with many interpretations. So the debate continues (Feduccia 2002; Feduccia et al. 2005; Zhou 2004). One interpretation, yet to be accepted, is that the dromaeosaurs were an early adaptive radiation of birds comprising all stages of flight and flightlessness, including degenerate feather structures.

A different part of the debate concerns the evolution of the avian hand versus the dinosaur hand. The typical vertebrate hand bears five fingers, or digits, numbered sequentially I, II, III, IV, V. Like the majority of vertebrates with three fingers, including pre-dinosaur thecodonts, the fingers on the bird hand are numbers II, III, IV due to the symmetrical reduction or loss of numbers I and V (Feduccia and Nowicki 2002; Figure 2–9). Dinosaurs (the Dinosauria), in contrast, had only three fingers—

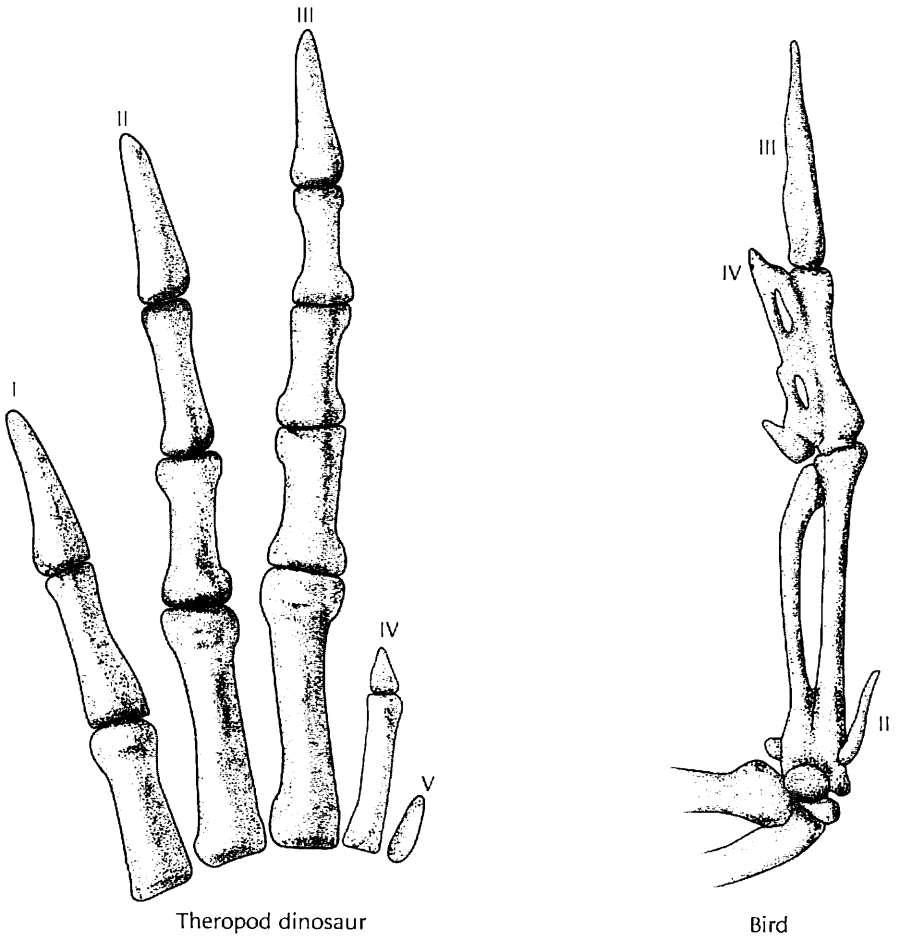


FIGURE 2–9 The hand of a basal theropod dinosaur *(Herrerasauris)* illustrates the reduction of digits IV and V. This condition led to the unique three-fingered hand (I, II, III) of later theropod dinosaurs. Birds lost digits I and V to a different three-fingered hand (II, III, IV). *[From Feduccia and Nowicki 2002]*

digits I, II, III—owing to the reduction or loss of digits IV and V. Thus the central question is whether birds branched off before the dinosaurs evolved their I-II-III hand structure or whether birds somehow changed the unique hand structure of dinosaur ancestors to a more typical (of vertebrates) three-fingered arrangement. Tracking the activity of genes responsible for digit development suggests that bird digit II is really digit I that has shifted its position, siding with the theropod camp (Vargas and Fallon 2004). Feduccia and colleagues (2005; see also Galis et al. 2005) disagree with the interpretation of how gene expression controls the embryology of these digits. They stand by their view that digit II is digit II and that the three-fingered avian hand has the primitive, pre-theropod composition of digits II, III, IV.

What's next? We can expect to see a sharpening of the questions to be resolved and better resolution of the evolutionary transitions from reptiles to the earliest birds in the Jurassic period. Certainly the best is yet to come, because scholarly interest, public attention, and real evidence—both fossil and developmental—are at an all-time high and growing (Box 2–1). In time, resolution of the specific ancestry of birds will inform our interpretation of a whole range of adaptations of birds, from morphology to social behavior (Prum 2002).

BOX 2–1

THE AVIAN GENOME: ONE BILLION DNA BASE PAIRS STRONG

The sequence of the chicken genome—specifically that of the Red Junglefowl, *Gallus gallus*—was published in December 2004 with initial comparisons with those of other organisms (International Chicken Genome Sequencing Consortium 2004; Schmutz and Grimwood 2004). This signature event in ornithology enables a novel perspective concerning what is a bird, and sets the stage for a new era of a broad range of research: from commercial egg production to evolutionary ecology. The chicken genome is only the fourth vertebrate genome to be sequenced.

The first avian genome:

- Is one-third the size of the mammalian genome due to reduced repeat content, pseudogenes, and segmental duplications
- Includes an estimated 20,000 to 23,000 genes
- Includes 38 pairs of large (macro-) and tiny (micro-) chromosomes; the latter are distinguished by high levels of guanosine–cytosine (GC) base pairs compared with adenine–thymine (AT) base pairs
- Includes long blocks of conserved sequences (70 megabases total) that align well with human genome sequences and are likely to be functional in both species despite 310 million years of evolutionary divergence
- Has undergone a novel mode of evolution for some noncoding RNA genes
- Differs from the mammalian genome in the expansion and contraction of multigene families
- Is more amenable than the mammalian genome to classification of its content, owing to reduced pseudogene content

Early Evolution of Birds

Separate from the debate about whether birds are dinosaurs is the recently exposed substantial fossil history of Mesozoic birds. Following the appearance of *Archaeopteryx* in the Jurassic period, birds evolved the definitive features of modern birds and diversified during the Cretaceous period (Figure 2–10). A wealth of new fossil birds from Spain, China, and Patagonia now bridge the once troublesome gap in the fossil record that separated *Archaeopteryx* from modern birds. Basal birds from the early Cretaceous, including *Confuciusornis* and *Jeholornis*, were intermediate between *Archaeopteryx* and more advanced forms. *Confuciusornis* has a horny beak quite like that of modern birds. *Jeholornis* has a long tail like that of *Archaeopteryx* and forelimbs with advanced flight capabilities. Beyond these important links were two major lineages that diversified during the Cretaceous: the Enantiornithes and the Ornithurae. These substantial first avian radiations included all stages of flight and flightlessness.

The Enantiornithes dominated the first phase of early avian evolution (Chiappe 1995; Figure 2–11). Dozens of flight-capable species of diverse ecological forms ranged worldwide. They were as small as sparrows and as large as vultures. They laid their eggs on the ground and underwent annual growth cycles recorded as treelike growth rings in cross sections of their limb bones. Many were arboreal.

Sinornis santensis was a signature species of this radiation. Discovered in China in 1987, this amazing fossil from the early Cretaceous period, 140 million years ago (Sereno and Chenggang 1992), was a toothed, sparrow-sized bird with many features of theropod dinosaurs and *Archaeopteryx*. *Sinornis* also exhibited features intermediate between *Archaeopteryx* and modern perching birds. Advances over *Archaeopteryx* include strengthening and modifications of the hand, forearm, and pectoral girdle for flight functions; the ability to raise the wings high over the body as well as to fold them; a large pygostyle for the support of a tail fan, which improves steering and braking in flight; and a perching foot with an opposable rear

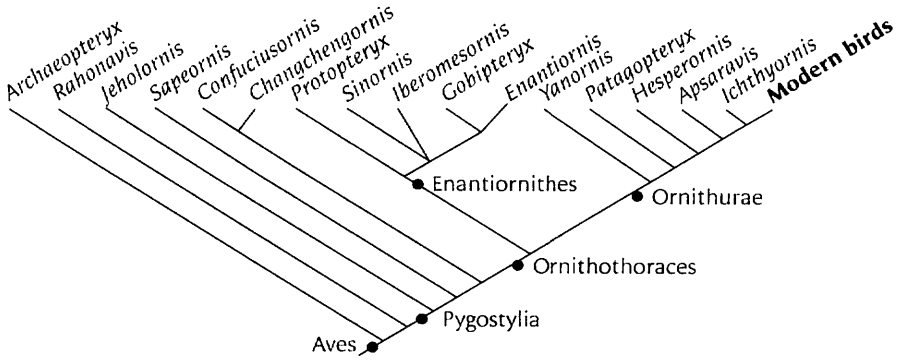


FIGURE 2–10 Relationships among early groups of birds that followed *Archaeopteryx* in the fossil record of the Mesozoic era. [*From Zhou 2004*]

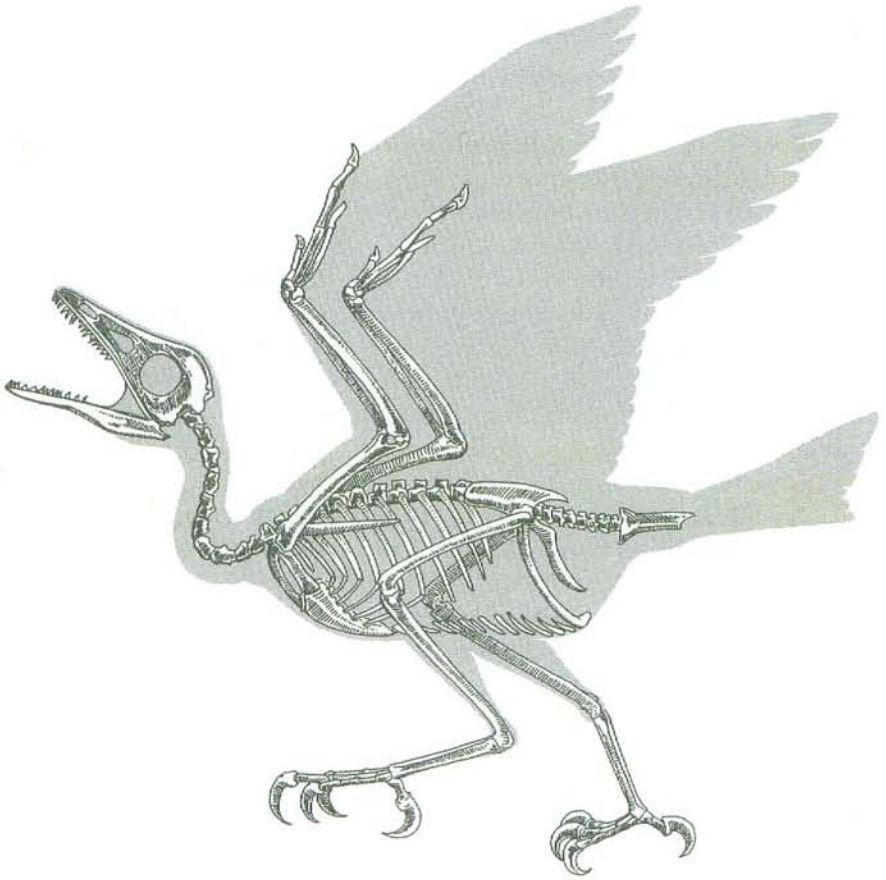


FIGURE 2–11 Enantiornithine birds thrived during the Mesozoic but then disappeared. They diversified into a wide range of water birds and arboreal, perching birds that could fly well. The sparrow-sized species *Sinornis santensis* was a signature species of this now extinct radiation of early birds. It was intermediate between *Archaeopteryx* and modern birds. [*After Sereno and Chenggang 1992*]

toe, the hallux. These features suggest that avian flight and perching abilities evolved in small-bodied birds that followed *Archaeopteryx*.

None of the Enantiornithes survived into the Tertiary. They disappeared along with dinosaurs in the mass extinction that marked the end of the Mesozoic era.

The other lineage, the toothed Ornithurae, ultimately gave rise to modern birds. Like the Enantiornithes, the toothed Ornithurae included small, finch-sized, arboreal species in the early Cretaceous. Later members had advanced wing structure and flight ability and a fully developed perching foot. By the late Cretaceous, ornithurine birds exhibited a wide range of sizes and life styles that mirrored those of modern wading birds, diving birds, perching birds, and even secondarily flightless (having evolved from "flighted" birds) terrestrial forms. Among the best known forms are toothed seabirds—*Hesperornis*, *Ichthyornis*, and their relatives in the extinct Order Hesperornithiformes. They inhabited the Cretaceous seas that cov-

ered the central parts of North America and Eurasia. Some resembled modern loons. They ranged in size from that of a small chicken to that of a large penguin. The largest was *Hesperornis regalis*, from 1 to 2 meters in length. All 13 known species of divers were flightless, with large, powerful, lobed feet. Flying above the same shallow seas were at least six species of toothed, ternlike birds *(Ichthyornis)*.

Most of the Ornithurae disappeared along with dinosaurs in the mass extinction that marked the end of the Mesozoic era. Among the few survivors, however, were the ancestors of modern birds. These ancestors included birds related certainly to modern chickens, waterfowl, and ratites, and perhaps also to shorebirds and tube-nosed seabirds (Clarke et al. 2005).

Evolution of Feathers

At first, the well-developed feathers of *Archaeopteryx* separated it from small dinosaurs of similar form and so started the quest for the ancestor of birds. It turns out, however, that feathers and featherlike structures are not unique to birds, including *Archaeopteryx*. Theropod dinosaurs had them also. The new awareness started with the discovery of the first "feathered dinosaur," the chicken-sized *Sinosauropteryx* with filamentous downlike feathers, and then the turkey-sized *Caudipteryx* with a well-preserved fan of vaned feathers on its tail and forelimbs. Fossil feathers have now been found on more than a dozen theropod dinosaurs and dromaeosaurs not closely related to *Archaeopteryx*.

Ancient feathers included downlike filamentous structures, or "dino-fuzz," and well-vaned, essentially modern feather structures. The relation of dino-fuzz to real feathers remains controversial: arguments range from their being unrelated structures to being precursors of feathers to being simplified feathers of flightless birds (Prum and Brush 2002; Lingham-Soliar 2003; Feduccia et al. 2005).

Less controversial are the well-preserved vaned feathers. A little dinosaur named *Microraptor gui* had front and hind wings that sported outer feathers with asymmetrical vanes, just as in the wings of modern flying birds (Xu et al. 2003; see also Figure 2–8). Feathers clearly evolved in modern form in theropod dinosaurs and then diversified in form and function.

We long presumed that feathers evolved from scales of some kind, centering the debate on what advantages promoted the evolution of feathers from scales. More likely, feathers evolved not as modified scales but as a novel epidermal structure (Prum and Brush 2002; see also Chapter 4). The first feathers, even if they were frayed scales, likely aided temperature regulation as insulation or heat shields, a hypothesis long favored by reptile experts (Regal 1975).

Contrary to many early speculations, feathers did not evolve initially in concert with the evolution of flight. Rather, avian flight followed the initial evolution of vaned feathers. Early forays by gliding and weak flapping flight fostered additional changes in feather form and function on the wings and tail.

Evolution of Flight

How did avian flight evolve, and just how well could *Archaeopteryx* fly? What caused the forelimbs of reptilian ancestors to evolve into protowings in the first place? Two basic theories are in contest: an arboreal theory and a cursorial, or running, theory.

The arboreal theory proposes that the evolution of flight started with gliding and parachuting from elevated perches. Most drawings of *Archaeopteryx* depict an arboreal reptile clambering around trees, grasping branches with clawed fingers. Extensions of the bones of the forelimb enhanced by elongated (flight) feathers enabled the ancestor of *Archaeopteryx* to parachute and glide between trees. This arboreal theory has been favored for many years (Bock 1965; Feduccia 1980; Figure 2–12). A variety of dinosaurs, and even pre-dinosaur thecodonts, were arboreal, and some flew.

The cursorial theory proposes that elongated forelimbs heightened leaping ability in a small, bipedal theropod dinosaur that ran and jumped to catch prey. The cursorial theory is a working corollary of the accept-

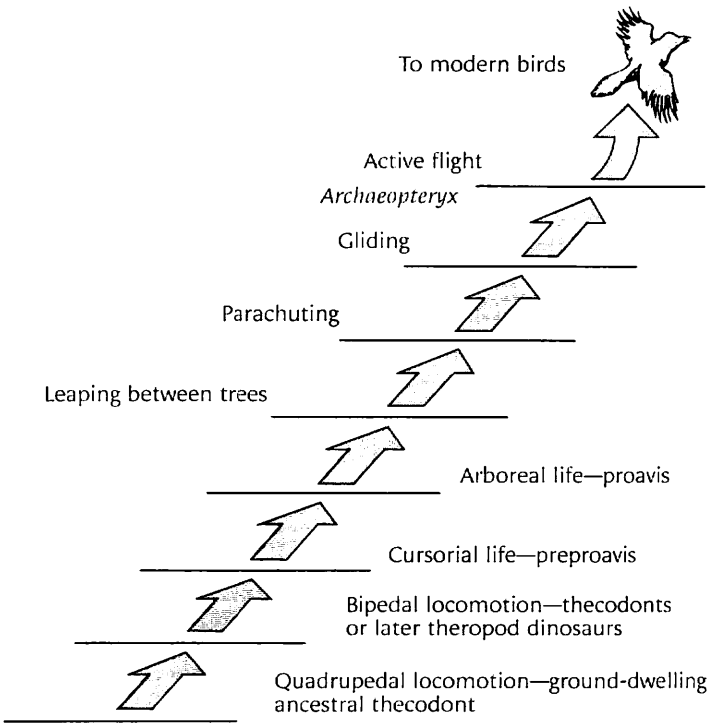


FIGURE 2–12 The long-standing arboreal theory of the evolution of avian flight suggests that, after evolving bipedal locomotion, the reptilian ancestors of birds became arboreal and leaped between trees. Active flight evolved from earlier stages of parachuting and gliding flight that enhanced the leaping abilities of the ancestors of *Archaeopteryx*. [*After Feduccia 1980, adapted from Bock 1965*]

ance of the theropod origin of birds (Pandian and Chiappe 1998; Prum 2002). Extensions of the forelimbs helped to control and extend leaps (Caple et al. 1983, 1984). Elongation of three extensions of the body—two wings and a tail—would not enable flight at first but would help to control the body's position. Faster running, higher jumping, greater reach, and enhanced maneuverability would be the result. The flight capabilities of modern birds would thus be a logical extension of the first small jumps by little dinosaurs.

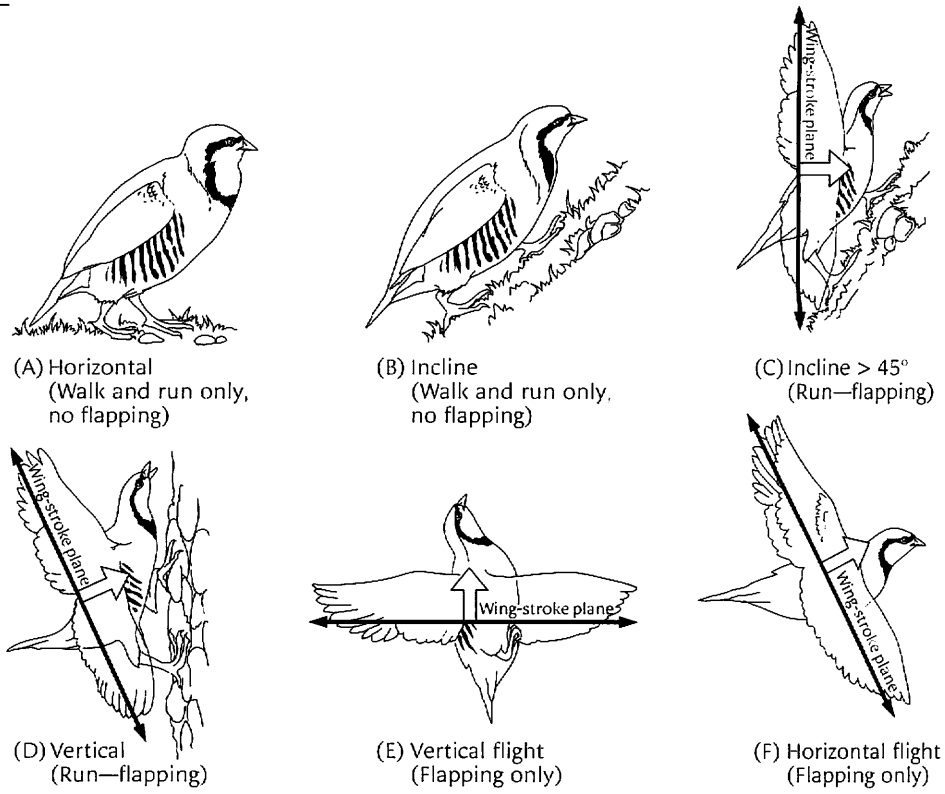
The arboreal versus cursorial theories are not clear alternatives. They likely pose a false dichotomy because the activities of the avian ancestors, as well as those of *Archaeopteryx* itself, mixed these behaviors. The most important step was the evolution of a wing stroke that could produce the main components of powered flight: lift and thrust. A powered wing stroke required transformation of the wrist and shoulder from the skeletal wing-precursors of theropod or other ancestors (Ostrom 1997). What were the behavioral steps that fostered the needed transformation?

Ken Dial (2003a) provided a logical answer. He suggested that flapping their feathered forelimbs helped early birds climb steep inclines, including tree trunks. Chickens and their relatives routinely improve foot traction and climbing ability through wing-assisted incline running (Figure 2–13). Incipient wings could have served avian ancestors in the same way. Continued improvement of such aerodynamic assistance favored changes in wrist and shoulder structure that led to the powered stroke of the avian wing. Protowings, increased arboreal habits, and gliding with feeble flapping—as proposed for the life style of *Archaeopteryx*—would be the next logical evolutionary steps.

The evolution of the bastard wing, or alula, provided the finale. This key to avian flight, a set of small extensible feathers on the wrist that help to prevent stalling at slow airspeeds (see page 119), was found on a 115-million-year-old toothed and goldfinch-sized fossil ornithurine bird, *Eoalulavis hoyasi*, discovered in Spain (Sanz et al. 1996). All the elements for modern avian flight were available and in place. The subsequent evolution of modern, powered flight overhauled both the aerodynamic structures of the body and the physiology that provided energy. These changes opened the door for the diversification of modern birds.

Modern Birds

The Tertiary period that followed the Mesozoic era unleashed the diversity of modern birds as we know them. It also produced some huge, carnivorous, semimodern birds that temporarily occupied some of the niches left vacant by bipedal dinosaurs. Two-meter-tall diatrymas with powerful legs, clawed toes, massive horse-sized skulls, and tearing, eaglelike beaks must have terrorized many lesser creatures before becoming extinct in the



(A) Horizontal (Walk and run only, no flapping)
(B) Incline (Walk and run only, no flapping)
(C) Incline > 45° (Run—flapping)
(D) Vertical (Run—flapping)
(E) Vertical flight (Flapping only)
(F) Horizontal flight (Flapping only)

FIGURE 2–13 Overview of wing positions of a Chukar partridge during wing-assisted incline running, and the proposed transitions to powered flight. (A and B) Birds running over level substrates or shallow inclines do not use their wings to assist running. However, even partial wing development provides assistance to birds climbing inclines greater than 45 degrees. (C and D) A part of the wingbeat cycle (as much as 30 percent) directs aerodynamic forces toward the inclined surface, not skyward, which improves traction. (D through F) Mastery of vertical inclines attains use of wings in ways required for flight. [*From Dial 2003a*]

Eocene epoch (Figure 2–14). In the Eocene, long-legged vulturelike birds *(Neocathartes)* lived in Wyoming beside shorebirds with ducklike heads *(Presbyornis)*. From the Oligocene epoch to the Pliocene epoch, 12 known species of phorusrhacids—predatory birds from 2 to 3 meters tall, with powerful, rapacious bills—ranged throughout South America and north to Florida.

As recently as the last ice age, huge vulturelike teratorns dominated the skies. One teratorn with a 4-meter wingspan was abundant in southern California. Another, known from caves in Nevada, had a wingspan of 5 to 6 meters, and yet another, recently discovered in Argentina, had an 8-meter wingspan. They were the size of small airplanes! These enormous birds symbolize some of the extremes of past avian achievements.

Two waves of explosive evolution of modern birds, however, were the main features of Tertiary ornithology (Feduccia 2003; Figure 2–15). The first wave, starting 65 million years ago, spawned nonpasserine birds

(Text continues on page 45.)

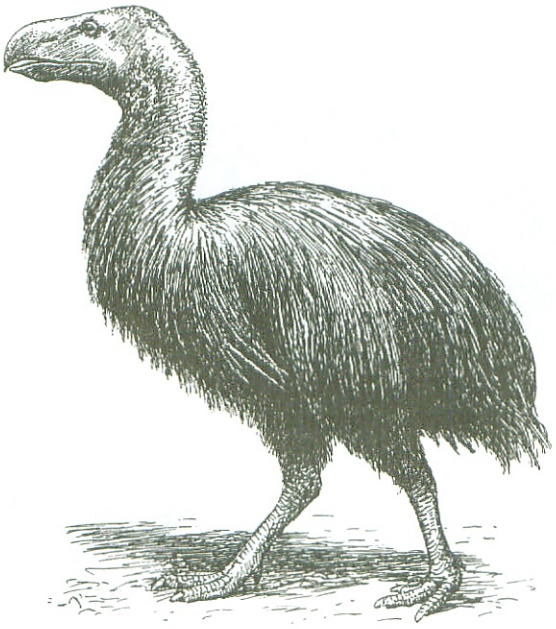


FIGURE 2–14 Large flightless birds, including diatrymas, flourished during the Tertiary period. [*From Heilmann 1927*]

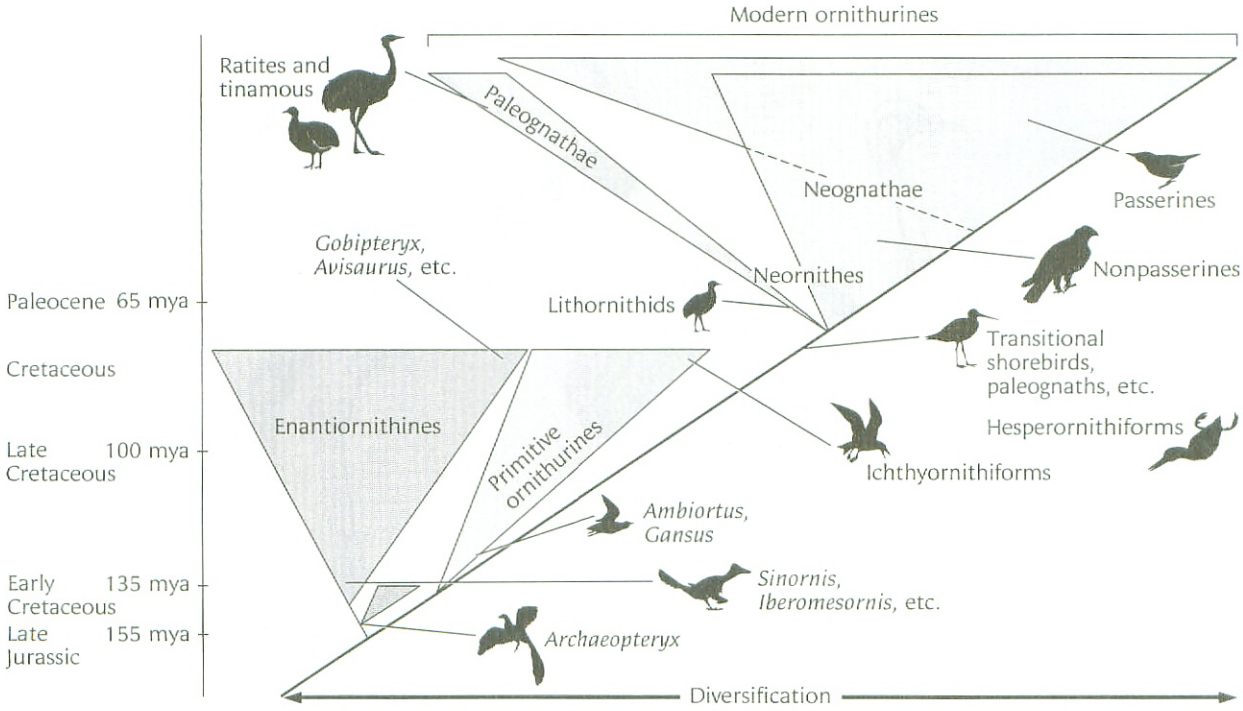


FIGURE 2–15 Model of the evolution of modern birds. Two major radiations, the Enantiornithes and the primitive ornithurines, dominated the Cretaceous period after *Archaeopteryx* but did not survive into the Tertiary. Three major radiations during the Tertiary gave rise to the major groups of modern birds: ratites and tinamous; nonpasserines; and passerines. [*From Feduccia 2003*]

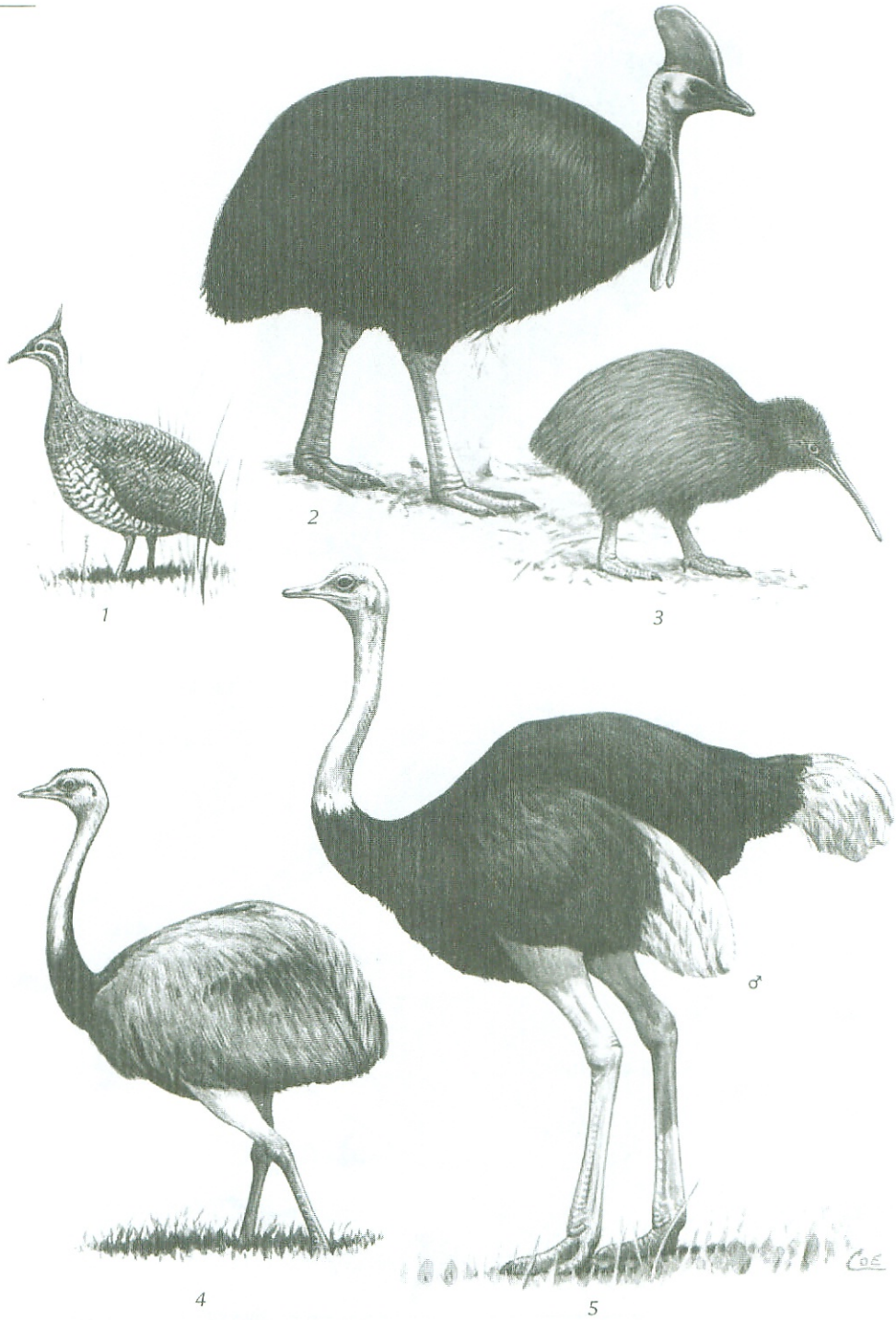


FIGURE 2–16 The large flightless birds of the world, called ratites, and the related tinamous evolved early in the Tertiary period. (1) Elegant Crested Tinamou; (2) Southern Cassowary; (3) Northern Brown Kiwi; (4) Rhea; (5) Common Ostrich.

FIGURE 2–17 Woodpeckers and their allies were a preeminent group of nonpasserine land birds in the Tertiary: (1) Great Spotted Woodpecker; (2) Greater Honeyguide; (3) Double-toothed Barbet; (4) White-chinned Jacamar; (5) White-eared Puffbird.

of most of the orders of birds present today, including ratites (Figure 2–16). Specialized water birds, such as loons, auks, gulls, ducks, cranes, and petrels, invaded aquatic niches during the Eocene epoch, from 54 million to 36 million years ago. Primitive woodpeckers and their relatives also appeared during the early Eocene and became the predominant perching birds during the Miocene epoch (Figure 2–17). Hummingbirds, too, go back to the same epochs of Earth history. Fossils from the early Oligocene of southern Germany reveal that hummingbirds, now restricted to the

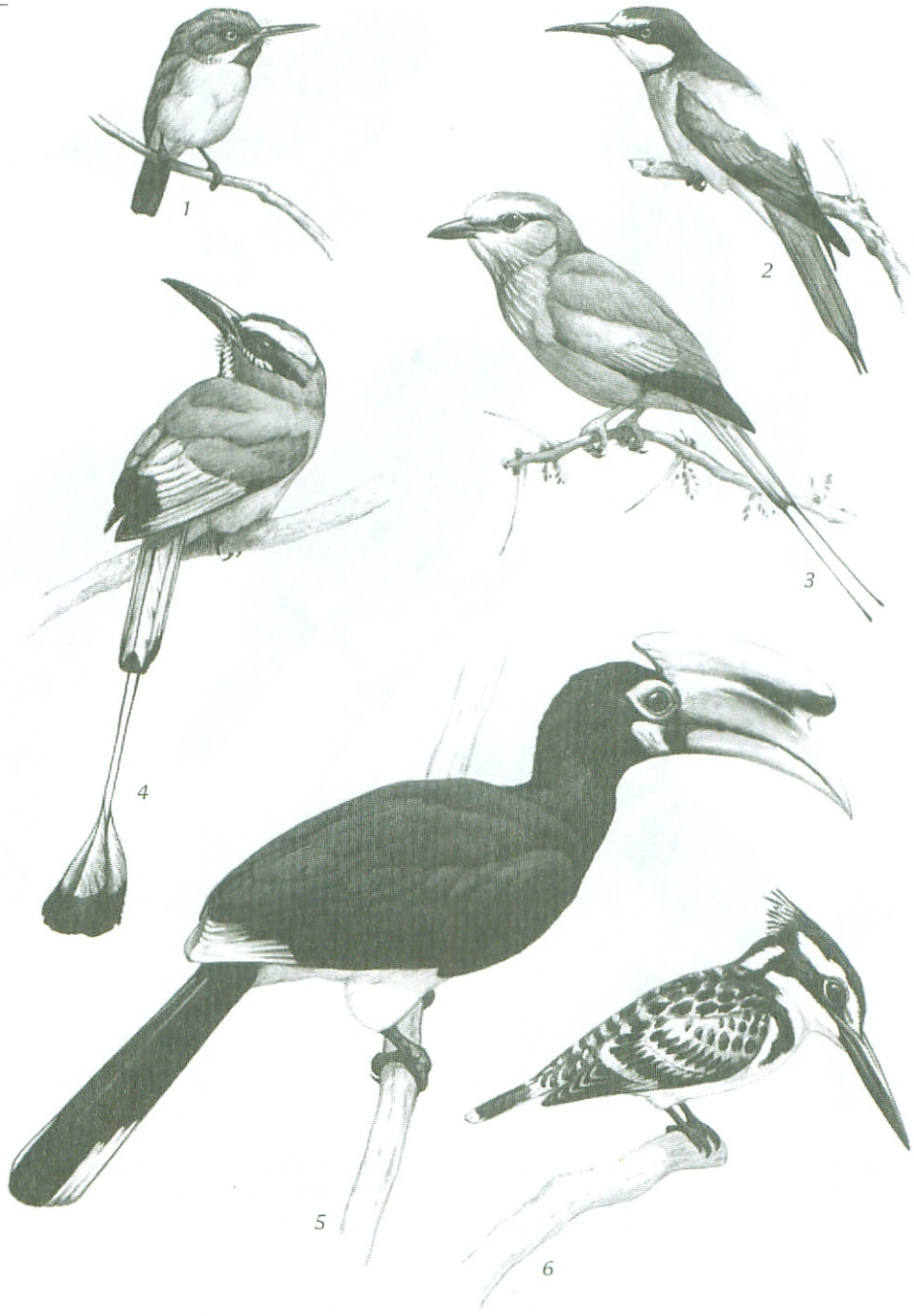


FIGURE 2–18 Rollers, kingfishers, and their allies (Order Coraciiformes) were a dominant group of modern nonpasserine land birds early in the Tertiary period. Modern species include: (1) Puerto Rican Tody; (2) European Bee-eater; (3) Lilac-breasted Roller; (4) Turquoise-browed Motmot; (5) Oriental Pied Hornbill; (6) Pied Kingfisher.

Western Hemisphere, once inhabited the Old World, too (Mayr 2004). Relatives of rollers, kingfishers, and hornbills diversified in the Oligocene epoch (Figure 2–18). By the end of the Tertiary, from 10 million to 5 million years ago, birds had diversified into a broad range of forms that included many modern genera.

The radiation of passerine birds, or songbirds, produced the second wave of new bird taxa in the Tertiary (Barker et al. 2004). The rapid evolution of flowering plants and insects in the Miocene opened new niches for insect-eating, fruit-eating, and nectar-feeding birds; this diversity of ecological opportunities resulted in an explosive radiation of songbirds (Regal 1977). Now they constitute more than half of all existing bird species: more than 5700 by the most conservative estimates. Defining passerine birds are many unique attributes—small size, sperm structure, vocal abilities, perching foot, and high metabolism—but which attributes, if any, were key adaptations that catalyzed their success is still an open question (Raikow and Bledsoe 2000).

The early diversification of birds, both passerine and nonpasserine, took place on a very different Earth; neither the arrangement of the continental landmasses nor their climates resembled those of today. Through much of the Tertiary period, the world's climates were warm from pole to pole; there was no striking polar gradient from frigid to hot as there is today.

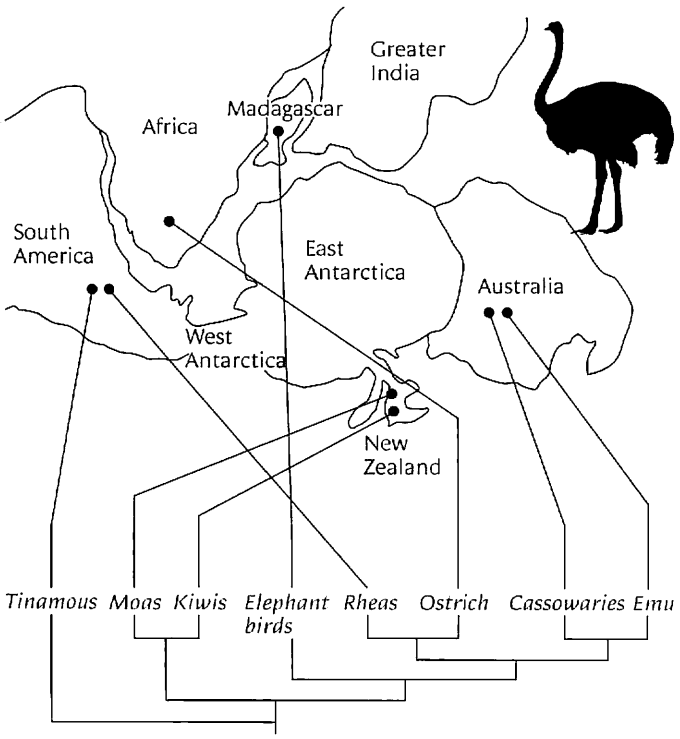


FIGURE 2–19 Ratites and tinamous are distributed throughout the ice-free continents of the Southern Hemisphere that once composed Gondwanaland. [*After Cracraft 2002*]

For example, during the late Eocene and early Oligocene epochs (see Table 2–1 for the geologic time scale), subtropical to tropical climates with abundant precipitation and no frost prevailed in the far north of both North America and Eurasia. The floras of Great Britain and of western Europe in the early Eocene resembled those of the modern rain forests of Southeast Asia. Tropical birds—trogons, parrots, hornbills, barbets, broadbills, and mousebirds—once lived in central Europe. Alligators and large tortoises lived on Ellesmere Island above the Arctic Circle.

The arrangements of continents and their connections also changed over the period of avian evolution. The modern continents have been moving apart since the late Jurassic and Cretaceous periods. Much of the major reorganization during the Mesozoic era of the single great landmass known as Pangaea, with Laurasia in the north and Gondwanaland in the south, preceded the evolution of modern bird taxa. Nevertheless, we now believe that Gondwanaland and its southern continent offspring—South America, Africa, Madagascar, and Australia—played a major role in the evolution and distribution of modern birds (Figure 2–19). Ancient species, including the oldest parrots (Kea, Kaka) and the oldest songbirds (New Zealand wrens), persist as relicts in New Zealand.

The mobility of birds, augmented by changing global climates and connections of land or sea, fostered fusions of isolated avifaunas. The Gondwanaland association of Southern Hemisphere continents fostered the exchange of taxa among Africa, South America, and Australia. Ancestral fowl—moundbuilders in Australia, guans in South America, and guineafowl in Africa—appear to have originated in the main parts of Gondwanaland. Radiations of pheasants, partridge, and grouse in North America came after the northward expansion of ancestral groups into Laurasia and the separation of Laurasia into North America and Eurasia in the Eocene. The birds of South America now include ancient elements from Gondwanaland plus more recent arrivals from North America. Representatives of the ancient Gondwanaland avifaunas are also sprinkled among the modern bird communities of Africa, Madagascar, and southern Asia. The diversity of modern birds is due to the rich 65-million-year history of evolution, expansions, and contractions of new taxa.

Summary

Birds evolved from small, bipedal reptiles more than 150 million years ago in the Mesozoic era. Birds and reptiles have many anatomical features in common—features that distinguish them from mammals, including a single occipital condyle on the back of the skull, a single middle-ear bone, and nucleated red blood cells.

Archaeopteryx lithographica, one of the most important fossils of all time, was a crow-sized, toothed, bipedal reptile with two essential avian features: feathers and a furcula (wishbone). It could clamber around trees and could fly. Known from seven specimens preserved in fine limestone deposited in the late Jurassic period in Bavaria, it represents an evolution-

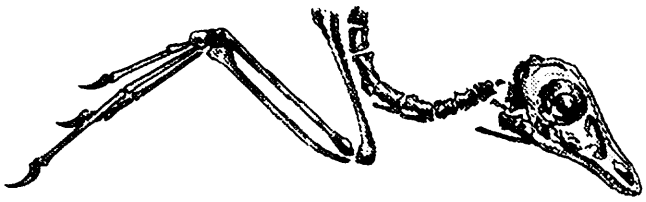
ary link between birds and reptiles. Because of its timely discovery, *Archaeopteryx* fostered acceptance of Darwin's theory of evolution. Exactly which group of reptiles gave rise to birds has been the topic of strong debates. New fossils from China point to small theropod dinosaurs, some of which had feathers, as the ancestors of birds.

Feathers evolved in theropod dinosaurs most likely as a form of insulation and possibly heat protection. Extensions of feathered forelimbs of terrestrial dinosaurs aided running and jumping and then climbing and gliding. The powered wing stroke, combined with the evolution of the alula for controlled slow-speed flight, completed the evolution of avian flight. One fossil species found in China in 1987, *Sinornis santensis*, retained many primitive features but also had advanced features of modern avian flight and perching abilities. Another fossil bird, 115-million-year-old *Eoalulavis*, had a well-developed alula that enabled controlled flight and landing.

Once established, birds diversified in both form and function. Two major radiations of ancient birds, the Ornithurae and the Enantiornithes, prospered in the Cretaceous but then disappeared. The modern orders of birds diverged from one another near the beginning of the Tertiary period, 60 million years ago, followed by the radiation of water birds in the Eocene epoch and land birds in the Miocene epoch.

Avifaunas are the grand result of millions of years of evolution, adaptive radiation, dispersal, and extinction of avian taxa with varied ecological roles. Throughout the history of avian evolution, neither the world's climates nor the arrangement of the continents were as we know them today. Gondwanaland and the southern continents that it produced were a central stage in the early evolution of modern birds. Now many birds occupy only remnants of their original distributions.

CHAPTER 3



Systematics

The ancients looked for a natural order (kosmos) which would explain the bewildering diversity of phenomena.

[Mayr 1969, p. 1]

Comparative biological sciences such as ornithology help us to understand the evolution of diversity. Closely related species have immediate common ancestors, which, in turn, had earlier common ancestors. The tree of genealogical relationships among species—their phylogeny—provides a foundation for taxonomic classification and a framework for understanding the evolution of behavior, ecology, and morphology.

The challenge of reconstructing the history of life belongs to a field of scholarly endeavor called systematics. Systematists are scientists who evaluate evolutionary relationships among organisms through comparisons of fossils, preserved specimens, behavior, and, increasingly, the genetic code of life itself, DNA.

This chapter presents an overview of avian systematics. First is a summary of the nature of species, the fundamental units of biological classification. Then follow the relation between phylogeny and formal classification and the attributes of birds that provide clues to evolutionary history. The chapter concludes with an introduction to some of the primary methodologies of systematics, including cladistics—the study of evolutionary branching sequences—and biochemical genetics—the study of changes in an organism's DNA. Comparisons of DNA sequences now enable unprecedented reconstructions of the evolution of modern birds.

Species and Speciation

The diversity of life is a result of three evolutionary processes: phyletic evolution, the gradual change of a single lineage; speciation, the splitting of one phyletic lineage into two or more; and extinction, the termination

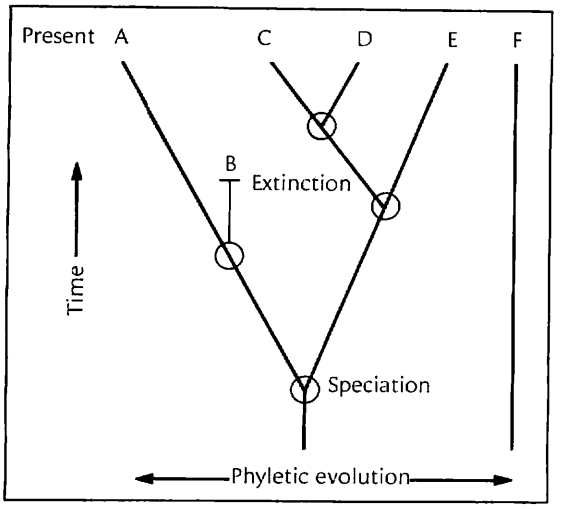


FIGURE 3–1 Diversification of evolutionary lineages includes speciation (circled nodes), the splitting of lineages; extinction, the loss of lineages; and phyletic evolution, the gradual change of a lineage with time. Clusters of similar, related taxa, such as C, D, and E (present in modern times), result from these changes. Taxon A stands alone because its Taxon B went extinct. Taxon F is not related to the other taxa, which had a recent common ancestor.

of a lineage (Figure 3–1). If we had a complete record of life on Earth, we could accurately reconstruct the historical patterns of speciation and phyletic evolution. Extinctions, however, fragment the historical record; they erase the connections between related lineages.

Species are the fundamental units of biological classification. Bird species have characteristic sizes, shapes, songs, and colors, as well as ecological niches and geographical ranges. Different species may interact ecologically, but they do not freely exchange genes or novel genetic-based adaptations. By a definition called the biological species concept, "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1970, p. 12). The criteria in the definition of biological species are the reproductive compatibility of individual organisms and the potential for the blending of differences between two populations.

The evolutionary legacy of the earliest birds includes roughly 100,000 species, of which only 1 in 10 is now with us. Behind this legacy lies the process of speciation—the multiplication of species through the division of one species into two or more as a result of the genetic divergence of isolated populations. Geographical separation of populations reduces the exchange of genes, thereby allowing independent divergence and enabling speciation. Most species of birds evolve as geographical isolates, although other kinds of reproductive isolation may sometimes play a role.

Bird populations become geographically isolated in two principal ways. First, pioneering individual birds may colonize an oceanic island, for ex-

ample, and thus are separated from their main population on the mainland or on other islands. Classic examples of divergence and speciation come from remote islands such as the Galápagos and Hawaiian archipelagos. The birds on the Channel Islands off the coast of southern California also are distinct, as are the kingfishers on small satellite islands off the coast of New Guinea. On the mainland, islands of special habitats, such as desert oases or subalpine mountain forests, may set a similar stage for divergence and speciation of the populations that occupy them.

Fragmentation of habitats that were once continuous is the second way in which bird populations may become isolated. Some ornithologists believe that the dry, cold climates of the Pleistocene epoch, for example, shrank the great Amazonian rain forests into much smaller fragments surrounded by grasslands. Restricted to these forest refuges, toucans, manakins, and flycatchers were among the many kinds of birds that underwent isolation and speciation (Figure 3–2).

Remnant populations are one of the consequences of historical changes. Ostriches, now restricted to Africa, once roamed throughout Asia. Hummingbirds, now restricted to North and South America, once hovered in what is now Germany. Tiny colorful relatives of kingfishers, called todies (see Figure 2–18-1), are currently found only on the Greater Antilles of the West Indies, but they once also lived in Wyoming and France (Olson 1985). Similarly, the endangered Florida Scrub Jay is now separated from the Western Scrub Jay by more than 3000 kilometers (Figure 3–3). Widely separated areas may consequently share peculiar taxa. The African River Martin inhabits the Congo River basin, whereas the closely related White-eyed River Martin inhabits only Thailand; no related species are found between these locations.

Although the general patterns of geographical speciation in birds are well known, the details of the process of speciation are not. Slow adaptive divergence of fragments of large populations and rapid genetic reorganization in small populations appear to be the primary modes of speciation. Still to be resolved are the roles of ecological and social adaptations, as well as the timing and nature of the related genetic changes. Concerns about the practical application of the biological species concept also prompt some ornithologists to question its working merits and to recommend new approaches to the study of speciation and geographical variation in birds (McKitrick and Zink 1988; Cracraft 1989). Chapter 19 considers both the process of speciation and the current debates about the species concept.

Scientific Names

A logical system of scientific names for each species is an essential prerequisite for the study of the biology of birds because nonscientific names of birds tend to vary with locale. The American Goldfinch, for example, is also locally called the yellow-bird, thistle-bird, wild canary, and beet-bird

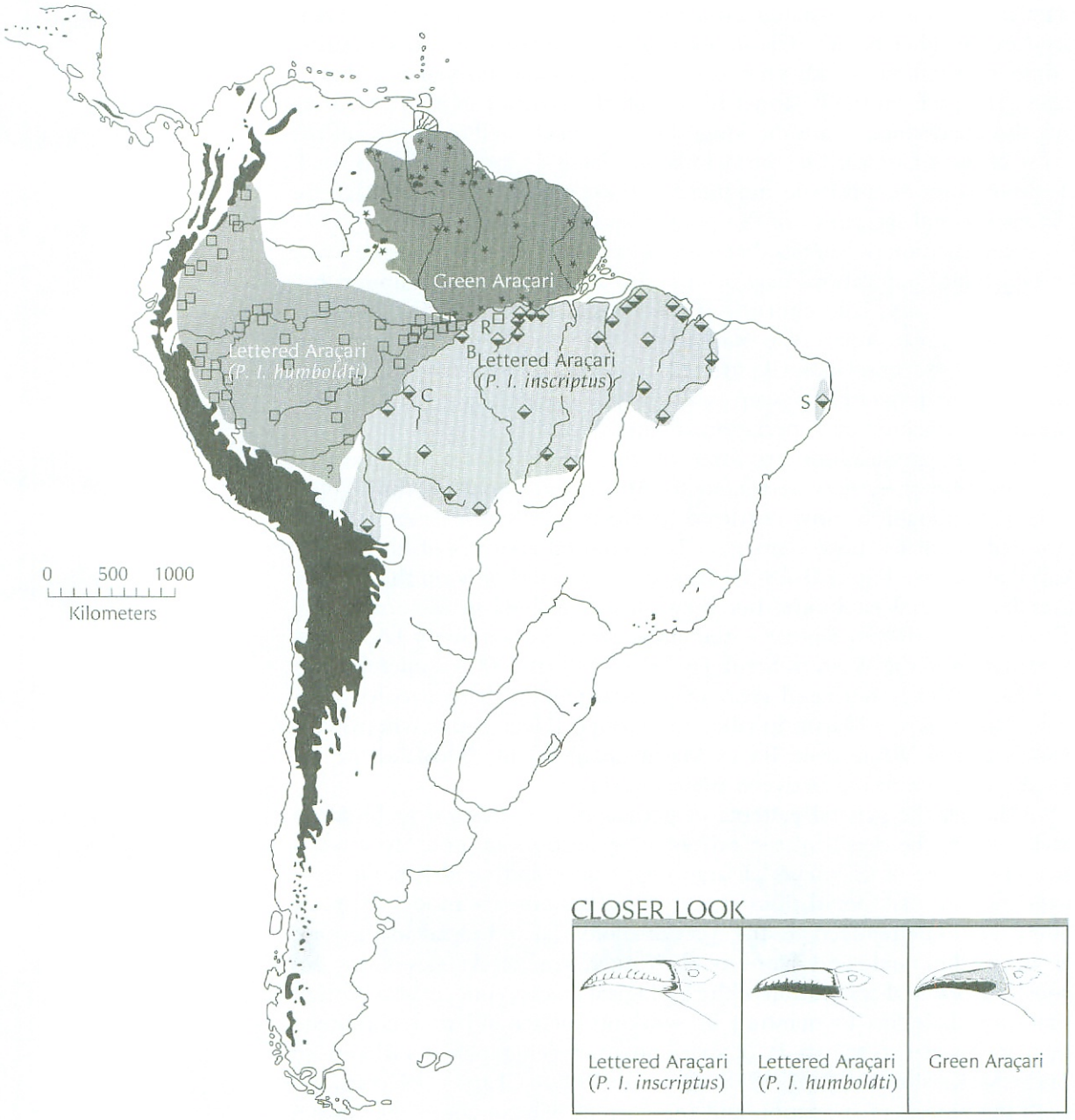


FIGURE 3–2 The ranges in Amazonia of three small toucans (the Green Araçari and two subspecies of the Lettered Araçari) reflect past isolation in refuges of wet forest habitats. [*After Haffer 1974. © Nuttall Ornithological Club*]

(Figure 3–4). Each human culture employs its local bird names, fostering the need for standardized names that allow ornithologists throughout the world to communicate efficiently and exactly.

The science of naming and classifying organisms, including birds, according to standardized rules is called taxonomy, and the scientists who do

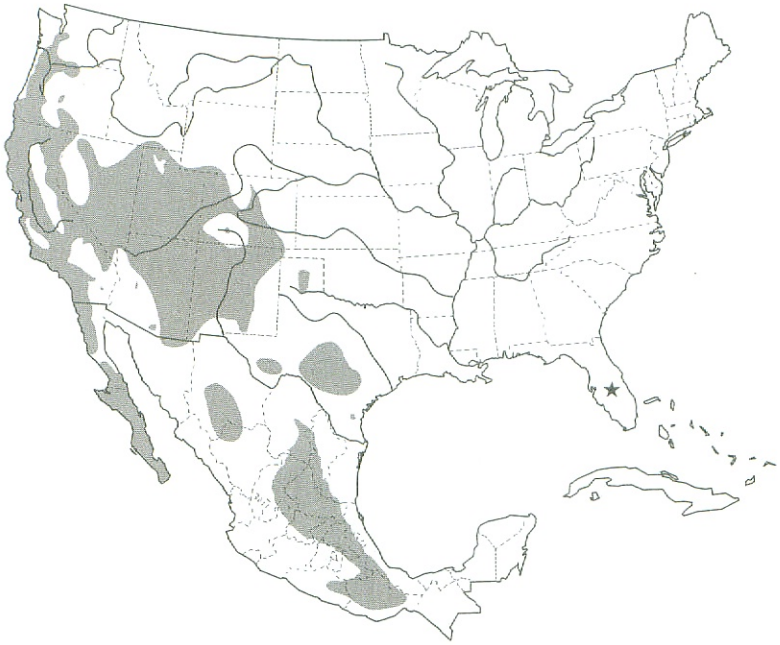


FIGURE 3–3 Distributions of the Florida Scrub Jay (star), now restricted to central Florida, and of the related Western Scrub Jay (shading) in the western United States and Mexico. Past climate and habitat changes fragmented the continuous distributions of this species, isolating the Florida Scrub Jay as a relict and endangered species. [*After Curry et al. 2002*]

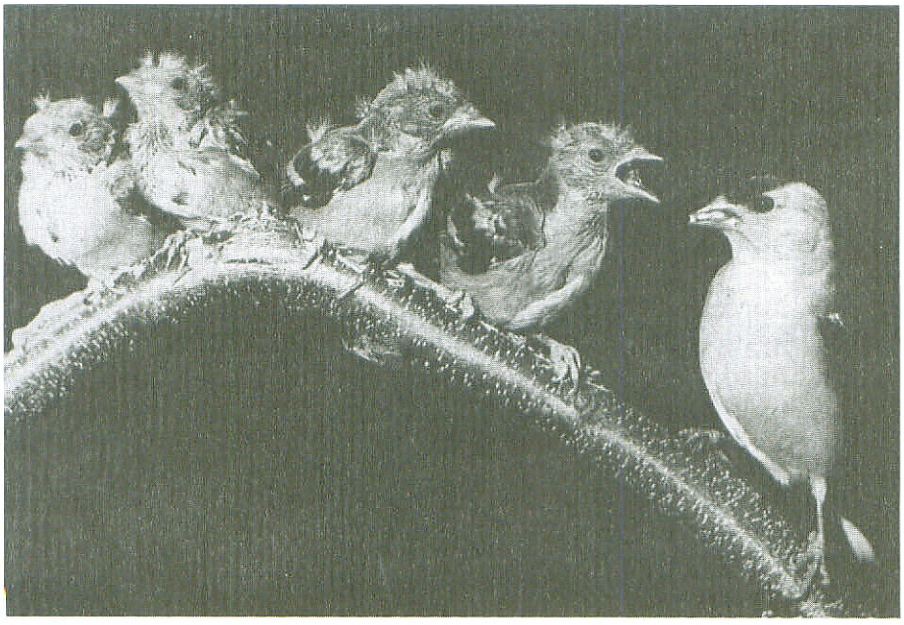


FIGURE 3–4 The American Goldfinch has many local names, such as wild canary, yellow-bird, thistle-bird, and beet-bird. [*Courtesy of A. Cruickshank/VIREO*]

this work are taxonomists. A taxon (pl. taxa) is any group of animals that is recognized in a classification. The Class Aves is a taxon that includes all species of birds.

The rules of taxonomy are based on the system of nomenclature developed from 1735 to 1758 by Carolus Linnaeus, a Swedish botanist. Linnaeus assigned two latinized names to each species: the first denotes the genus—a group of similar species; the second denotes the species. Thus, the American Goldfinch is known formally as *Carduelis tristis*, which is a taxon that includes all populations of that species. This particular combination of names is unique; no other bird species—indeed, no other animal species—may have this same pair of names. Before the work of Linnaeus, names were not standardized in length but consisted instead of a string of descriptive Latin words. The Great Black-backed Gull, for example, was once *Larus maximus ex alba et nigro feu caeruleo nigricante varius* (Willoughby and Ray 1676). Now it is simply *Larus marinus*.

In addition to their Latin scientific names, birds have English names, as well as names in other languages. The American Ornithologists' Union establishes and regularly revises a list of valid names, both English and scientific, for all bird species in North America. The International Ornithological Congress prepares lists of recommended standardized names in English, French, and Spanish (e.g., Gill and Wright 2006).

If we examine an assortment of birds, we can see the possibility of constructing a hierarchy, or ranking, of differences. A cursory survey of North American birds will distinguish woodpeckers from owls. Less obvious are the differences between the Downy Woodpecker, the Red-bellied Woodpecker, and the Northern Flicker or the differences between the Great Horned Owl, the Barred Owl, and the Eastern Screech Owl. Recognition of the subtle differences between the Downy Woodpecker and the Hairy Woodpecker (Figure 3–5) or between the Eastern Screech Owl and the Whiskered Screech Owl requires even more expertise.

Related taxa—those having a common evolutionary history or genealogy, as do the species of woodpeckers or owls or as do birds as a whole—constitute a lineage. Ornithologists classify the diverse species of modern birds into 30 different major lineages, or orders. Owls and woodpeckers

TABLE 3–1 Classification of three species of woodpeckers

Taxon	Downy Woodpecker	Hairy Woodpecker	Northern Flicker
Class	Aves	Aves	Aves
Order	Piciformes	Piciformes	Piciformes
Family	Picidae	Picidae	Picidae
Genus	*Picoides*	*Picoides*	*Colaptes*
Species	*pubescens*	*villosus*	*auratus*

Note: Full scientific names include the genus as well as the species and so, strictly speaking, the scientific name of the Downy Woodpecker, for example, is *Picoides pubescens*.

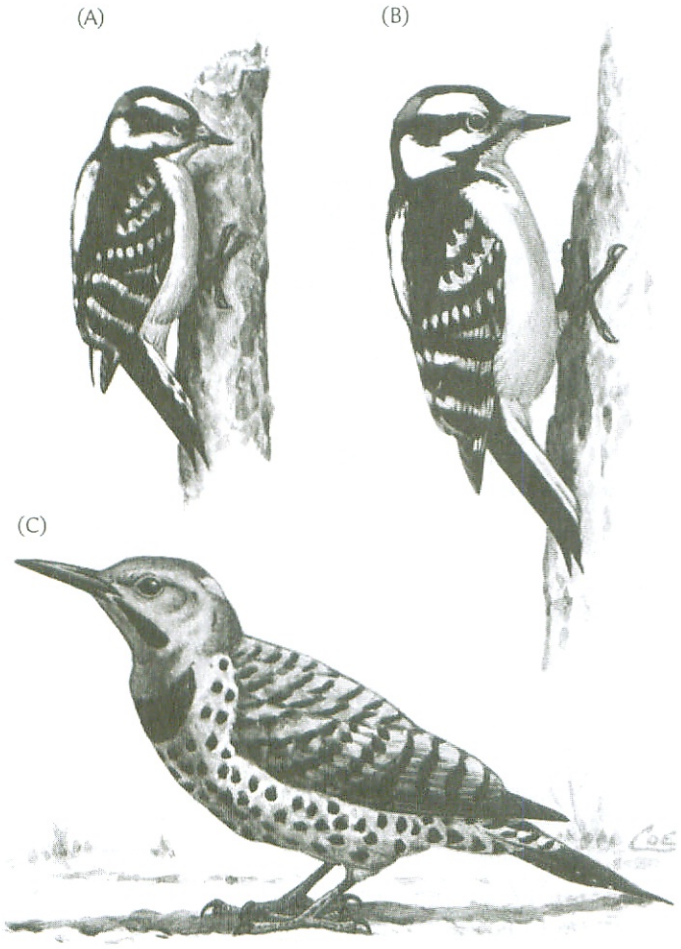


FIGURE 3–5 Three species of woodpeckers: (A) Downy Woodpecker; (B) Hairy Woodpecker; (C) Northern Flicker. The Downy Woodpecker and the Hairy Woodpecker are more closely related to each other than either is to the Northern Flicker.

are in different orders, Strigiformes and Piciformes, respectively. Note that the name of each order ends in "-formes." In turn, each of the 30 orders comprises a hierarchical set of families and genera. All woodpeckers are classified in the same order and in the same family, the Picidae. Each bird family name ends in "-idae." The very similar, closely related Downy Woodpecker and Hairy Woodpecker are classified in the genus *Picoides,* but the less closely related Northern Flicker is classified in the genus *Colaptes,* along with other species of flickers (Table 3–1).

Classification and Phylogeny

The process of naming and classifying birds is an ancient and continuing one. *Ornithologiae,* by Francis Willoughby and John Ray, published in

1676, was the first formal classification of birds. This "cornerstone of modern systematic ornithology" (Zimmer 1926) arranged all birds then known into a logical, hierarchical classification. Nearly a century later, Linnaeus used this elementary classification as the model for subsequent classifications. These early efforts, however, classified birds according to superficial adaptations to aquatic versus terrestrial habitats, for example, rather than according to evolutionary relationship.

Charles Darwin's theory of evolution by natural selection transformed the philosophical basis of systematics into one based on common ancestries. In his classic work *On the Origin of Species by Means of Natural Selection* (1859), Darwin reflected on the hierarchy of similarity due to evolutionary relationships:

> I believe that the arrangement of the groups within each class, in due subordination and relation to each other, must be strictly genealogical in order to be natural; but that the amount of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders. [Darwin 1859, p. 420]

Prevailing classifications of birds attempt to portray the evolutionary relationships of the various lineages as proposed by Darwin. Theoretically, each taxon is monophyletic; that is, it contains sets of birds, called clades, related by evolutionary descent from a common ancestor. A hierarchical organization of taxa indicates the relative closeness or distance of the evolutionary relationships among those taxa.

Taxonomic Characters

Reconstruction of the evolutionary history of birds requires the analysis of specific traits, called characters, that are shared as a result of common ancestry. Conservative characters—those that do not easily change in the course of ecological adaptation—are of the greatest value because they retain clues to ancestors. A constant challenge to accurate reconstruction is the possibility of convergence between unrelated species, which is prevalent in both external appearance and specific attributes (see page 19).

Darwin's champion, Thomas H. Huxley, helped to lay the foundations of modern systematics in birds with his study of the arrangement of the bones of the avian bony palate, the skeletal partition between the nasal cavities and the mouth (Huxley 1867; Figure 3–6). Succeeding generations of ornithologists added new characters to the taxonomic tool kit. Some of the most important ones were the form of the nostrils, the structure of the leg muscles and tendons of the feet, the arrangement of toes, and the morphology of the vocal apparatus. Behavior, vocalizations, and

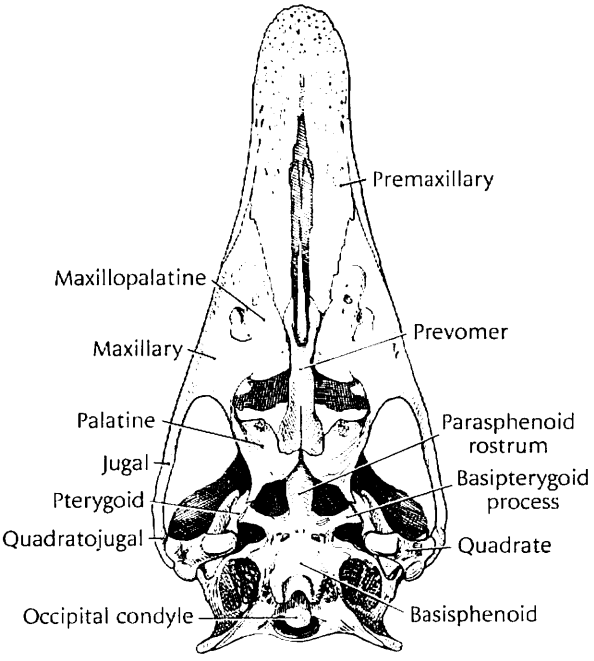


FIGURE 3–6 Bony palate of the Rhea, showing the complex arrangement of bones that represent the unique paleognathous palate of ratite birds. Other orders of birds have different arrangements of the elements of the bony palate. [*From Fundamentals of Ornithology, 2nd ed., by J. Van Tyne and A. J. Berger. Copyright 1976 John Wiley & Sons, Inc.; reprinted by permission of John Wiley & Sons, Inc.*]

proteins yielded clues to evolutionary relationships among some birds. So did plumage patterns of downy young (Figure 3–7).

Unique characters define related groups of species—that is, those with a common ancestor. Songbirds, the members of the Order Passeriformes, for example, have several unique characters. They have a preen gland with a unique nipple structure (see Figure 4–13) and unique sperm (see Figure 14–9). They also have a specialized perching foot with a large hallux (rear-directed toe), uniquely arranged deep tendons, and simplified foot muscles that facilitate perching at the expense of more delicate toe movements (Raikow 1982). These features indicate that members of the Order Passeriformes evolved from a common ancestor; that is, they are monophyletic.

Generally, the more complex the character, the less likely it is that anatomical details will be precisely the same, owing to convergence among unrelated species. The details of foot structure reveal how unrelated birds evolved similar, but not identical, arrangements of the four toes (Bock and Miller 1959). Although most perching birds have anisodactyl feet, with three forward toes and one rear toe (Figure 3–8, page 61), at least eight groups—including most woodpeckers and their allies, most parrots, cuckoos, owls, the Osprey, turacos, and some swifts—have zygodactyl feet, with two forward and two rear toes. Different orientations of the working surfaces (condyles) of cuckoo toe bones versus woodpecker toe

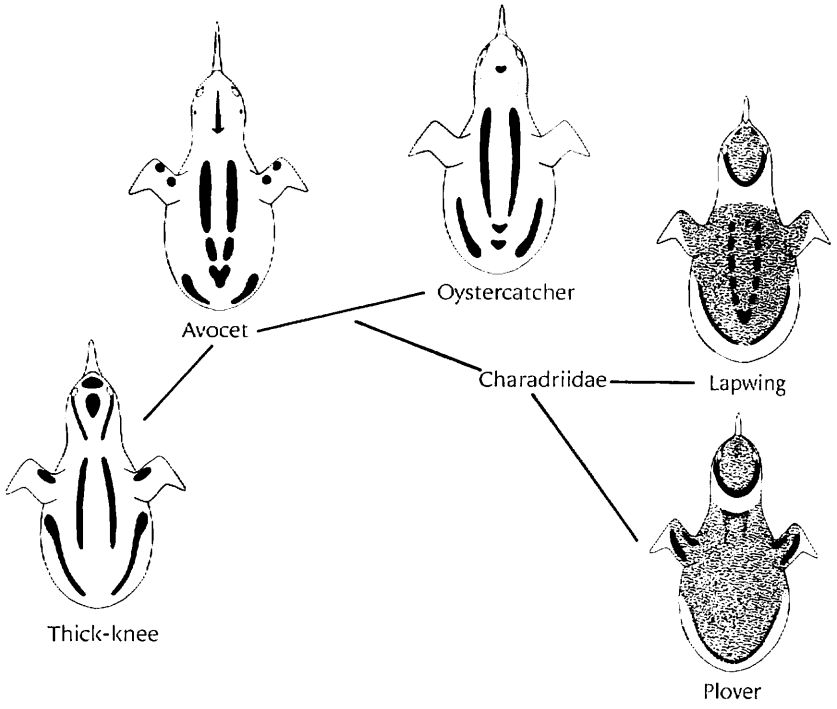


FIGURE 3–7 Plumage-color patterns of downy young shorebirds provide clues to their evolutionary relationships (represented by branching lines). [*After Jehl 1968*]

bones, for example, indicate that these unrelated birds have evolved the zygodactyl foot arrangement in different ways.

Still other toe configurations are possible. The trogons appear to have the zygodactyl toe arrangement, but the trogon's second toe, not its fourth, is directed backward, forming what is called the heterodactyl toe arrangement. The syndactyl foot, with two or three toes fused basally, characterizes the Order Coraciiformes; and the pamprodactyl foot, with all four toes directed forward, characterizes the mousebirds (Order Coliiformes) and some swifts (Order Apodiformes).

Despite the advances in grouping birds on the basis of characters such as foot structure, progress in systematics started to stall in the first half of the twentieth century. Cases of convergence loomed large, and ornithologists failed to discover new anatomical clues that would clarify the prevailing arrangements of the higher categories of birds. Erwin Stresemann, among the greatest German ornithologists, said:

> But as far as the problem of the relationship of the orders of birds is concerned, so many distinguished investigators have labored in this field in vain, that little hope is left for spectacular breakthroughs. . . . Science ends where comparative morphology, comparative physiology, comparative ethology have failed us after neary [sic] 200 years of efforts. The rest is silence. [Stresemann 1959, p. 277]

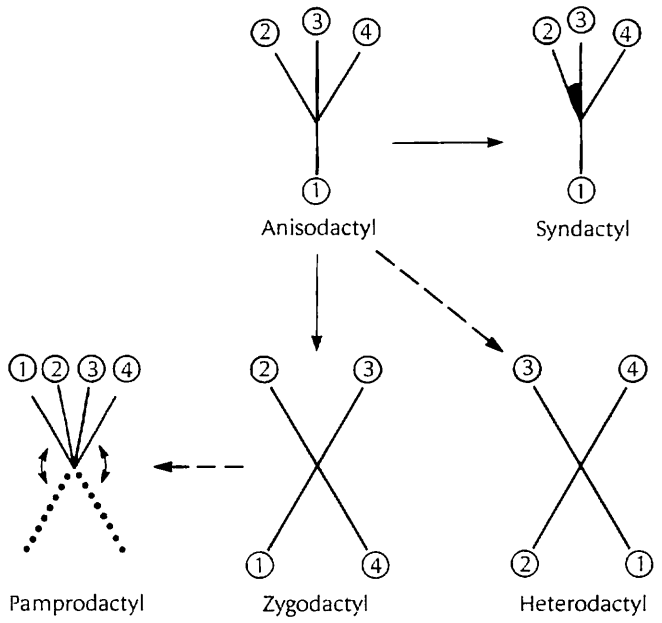


FIGURE 3–8 Toe arrangements of perching birds. Alternatives to the prevalent (anisodactyl) arrangement of three toes in front and the hallux (the first digit) pointing to the rear have evolved several times (solid arrows). The syndactyl foot, in which the bases of toes 2 and 3 are fused, characterizes the Coraciiformes. The zygodactyl arrangement, with two forward-pointing toes and two rear-pointing toes, has been achieved in different ways nine times in the evolution of birds. In trogons, toe 2, not toe 4, is rear directed (heterodactyl). In the pamprodactyl foot, the positions of toes 1 and 4 are not fixed; all four toes may point to the front. Dashed arrows indicate uncertain derivations.

Two major revolutions overcame such despair by infusing new vigor into the analysis of evolutionary relationships among birds. Cladistic character analysis launched one revolution, and new biochemical technologies drove the other. Major advances then followed the adoption of formal methods for tracking historical changes among lineages through comparisons of DNA sequences themselves.

Cladistics

Cladistic analysis—the study of evolutionary branching sequences—enables ornithologists to separate primitive characters from common derived characters and to sort them rigorously across taxa.

Phylogenetic studies require homologous characters, which can be traced to the same feature in the immediate common ancestor of both organisms (Bock 1973, p. 386) and which exist in both their original and their changed states. For example, the flipperlike wings of penguins evolved from the wings of their petrel ancestors. In this case, the wings of petrels represent the ancestral—or primitive—character state, whereas

the flipperlike wings of penguins represent the advanced—or derived—character state.

If two species have a character state in common, we can hypothesize that they have a common ancestor with the same character state. The flipperlike wings common to all penguin species correspond to their common ancestry. Simple hypothetical branching sequences, or cladograms, then portray the distribution of characters of extant species and their hypothetical ancestors. We assume that the cladogram with the fewest evolutionary changes—the most parsimonious one—is the most likely or most plausible phylogeny. Consider three hypothetical bird species that have different feet, crests, and bills (Figure 3–9). In this case, cladogram II, which assumes a common ancestor for A and B that looked like B, is most plausible.

A pioneering example of relationships based on primitive and derived character states is that proposed by Alan Feduccia (1977) in his study of

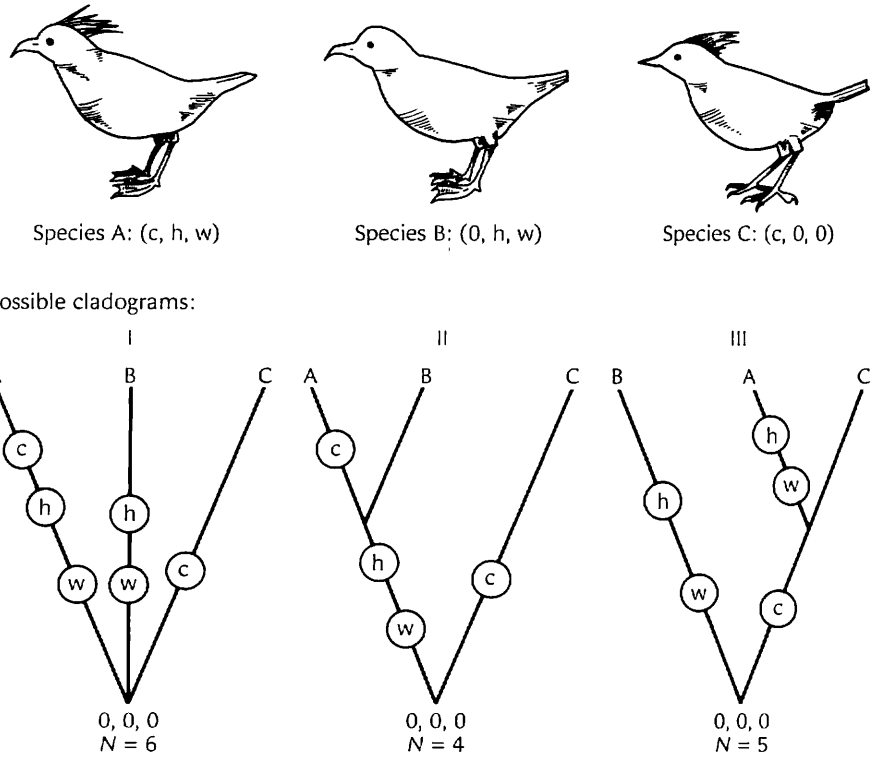


FIGURE 3–9 Possible cladograms for three hypothetical bird species, A, B, and C, that have different combinations of three derived characters: c, crest; h, hooked bill; and w, webbed feet. Primitive character states (no crest, an unhooked bill, or unwebbed feet) are denoted by 0. The changes from primitive (0) to derived character states (c, h, or w) are indicated for the evolution of each lineage (species A, B, or C) from the common ancestor (0, 0, 0). The center cladogram ($N = 4$) is the most parsimonious, requiring fewest total changes to account for the distribution of derived characters among the three species; it also has the advantage that it postulates no convergence between species A and species B.

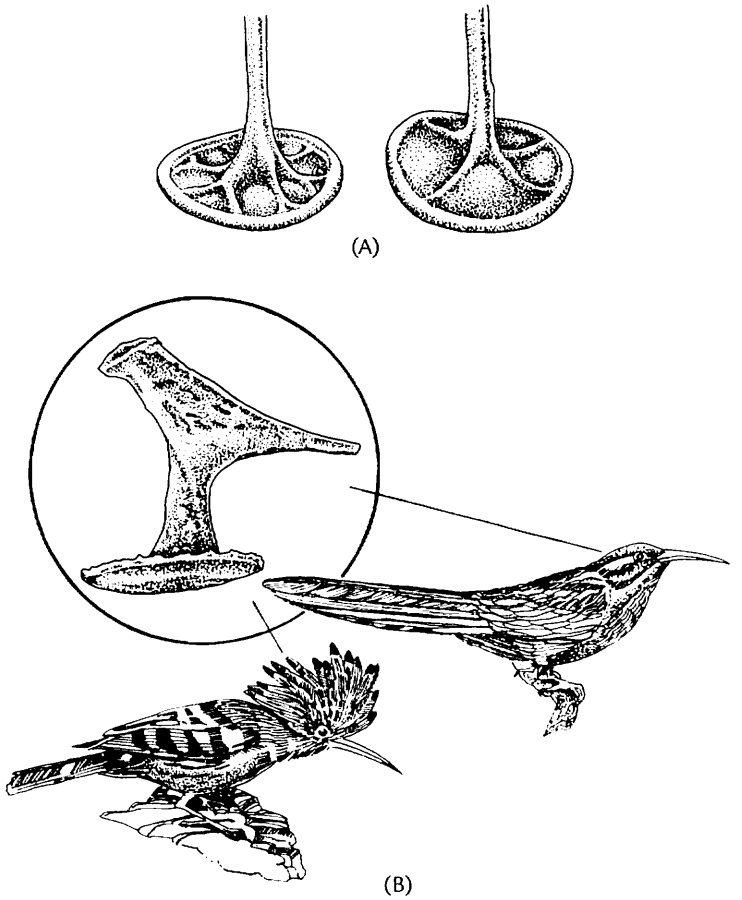


FIGURE 3–10 Primitive (A) and derived (B) anvil forms of the middle-ear bone, the stapes. Both hoopoes (*left*) and wood hoopoes (*right*) have the derived character, which supports the hypothesis of their close evolutionary relationship. [*After Feduccia 1977*]

the stapes (middle-ear bone) of perching birds. The wood hoopoes (Family Phoeniculidae) and hoopoes (Family Upupidae) have a unique derived character state, an anvil-shaped stapes, in common, which supports the traditional hypothesis that the two families are closely related (Figure 3–10). The other birds in the Order Coraciiformes—the kingfishers and their allies—have the primitive, column-shaped stapes.

Biochemical Systematics

With the use of new technologies, direct comparisons of DNA nucleotide sequences of species launched the second revolution in the analysis of evolutionary relationships among birds. Rapidly increasing knowledge of DNA structure enables testing of earlier hypotheses based on morphological characters. In general, biochemical studies tend to corroborate previous morphological evidence of relationships. Sometimes, however, biochemical analyses challenge traditional views, reveal overlooked cases of convergence, and suggest unsuspected relationships among taxa.

BOX 3–1

DNA–DNA HYBRIDIZATION COMPARES TOTAL GENETIC DIVERGENCE

DNA–DNA hybridization estimates the amount of genetic change that has taken place in the entire genome since the time at which two groups diverged from their most recent common ancestor. The estimates of genetic change between species are then used to cluster pairs of species that are most similar. To build a phylogeny, the estimates of genetic change are converted into standardized "distances" that form the basis of a hierarchical branching diagram, or evolutionary tree.

DNA is composed of four primary units called nucleotides. Each of the four different nucleotides has a unique base—adenine (A), cytosine (C), thymine (T), or guanine (G). The linear sequence of the nucleotides forms the genetic basis of life. Hydrogen bonds between certain pairs of bases—guanine and cytosine, adenine and thymine—hold the double-stranded DNA molecule together. However, these bonds can be broken by high temperatures.

Fragments of double-stranded avian DNA from two species form double-stranded hybrid

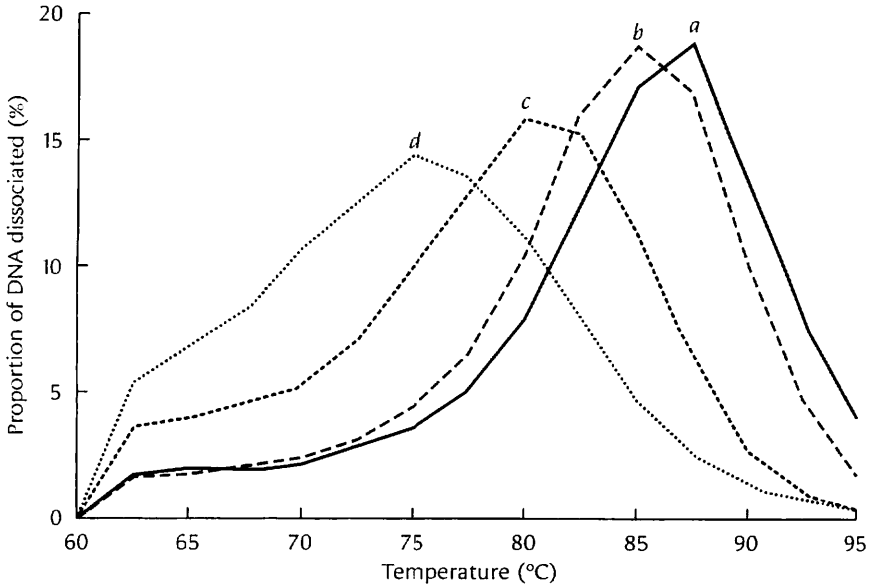


FIGURE 1 Results of a DNA–DNA hybridization experiment. Curves *a* through *d* are examples of heron DNA thermal-dissociation profiles, which show the proportion of the DNA that dissociates at each temperature. Curve *a* is the melting profile of the control, the homoduplex, in which Great Blue Heron DNA is hybridized with itself. It separates at a higher temperature than do the other hybrid DNAs because the best possible match obtains when DNA is hybridized with itself. The other three profiles of hybrid DNAs of different species—heteroduplexes—demonstrate decreasing similarities between Great Blue Heron DNA and the DNAs of the Great Egret (curve *b*), the American Bittern (curve *c*), and the Glossy Ibis (curve *d*).

The difference in the modal, or peak, melting temperatures (ΔT_{mode}) between the homoduplex profile and the heteroduplex profiles is used to estimate the genetic distance. Here, the distance between the Great Blue Heron and the Great Egret is 86.5°C − 85.0°C = 1.5. The genetic distance between the Great Blue Heron and the American Bittern or the Glossy Ibis is 5.5 or 10.5, respectively. [*After Sheldon 1987a, 1987b*]

complexes when the fragments are heated and separated into single strands and then allowed to reassociate under special laboratory conditions. The hybridized DNA complexes of two samples from a single species are stable and separate only at high temperatures, but hybrid DNA complexes of distantly related species, such as a penguin and a warbler, have few sequences in common and readily dissociate, even at low temperatures. Genomic similarity—that is, the number of bases in a specific nucleotide sequence that two species have in common—is revealed by the degree of thermal stability of the DNA–DNA hybrid molecule. Each 1 percent increase in the match between the paired sequences of a hybrid complex requires a 1°C increase in temperature to separate them (see Figure 1).

Fred Sheldon's (1987a, 1987b) DNA–DNA hybridization experiments serve to illustrate this approach to biochemical systematics (see Figures 1 and 2). The experiments demonstrated that the Great Blue Heron is genetically more similar to the Great Egret than to the American Bittern and more similar to both these species than to the Glossy Ibis. The results of these studies also revealed different rates of genetic change among different lineages of herons.

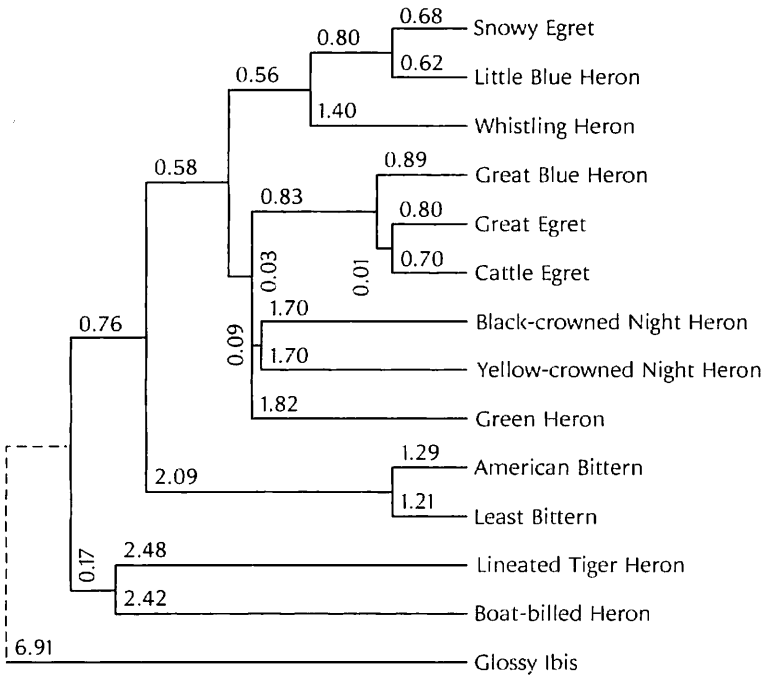


FIGURE 2 Branching diagram, or evolutionary tree, of heron relationships based on DNA–DNA hybridization experiments conducted by Fred Sheldon and colleagues (1987a, 1987b). Species are clustered according to their similarity, which is defined by the hierarchy of branch lengths.

The genetic distance between the Great Blue Heron and the Great Egret measured by ΔT_{mode} in Figure 1 is approximately the same as the branching distance in this tree, which is the sum of three intervening branch lengths (0.89 + 0.01 + 0.80 = 1.7). Notice that most branch tips on the tree line up with each other, because their DNAs diverged at approximately the same rate over time. The American Bittern and the Least Bittern, however, exhibit relatively long total branch lengths, because their DNA diverged (accumulated base-pair mutations) faster. Conversely, the DNAs of the Lineated Tiger Heron and the Boat-billed Heron changed more slowly than the other species in this study. [*After Sheldon 1987a, 1987b*]

The use of biochemical characters in ornithology started in earnest with the analysis of egg white proteins by Charles Sibley (1970). His inaugural studies of egg-white proteins were soon superseded by comparisons of enzymes called allozymes, which in turn yielded to comparisons of DNA sequences themselves. Sibley and his colleague Jon Ahlquist (1990) assembled thousands of samples of DNA from birds throughout the world, representing species from all but three families, in an unprecedented effort to revise the entire Class Aves by a singular molecular technique, called DNA–DNA hybridization (Box 3–1, pages 64–65). Their bold new phylogeny and classification of the birds of the world revitalized avian systematics and challenged many traditions. Some of the challenges have proved to be correct; some have not.

Among the revelations now supported by additional data were previously unappreciated major continental radiations. Many Australian songbirds, for example, had been previously classified with similar Asian and European forms. DNA comparisons showed that diverse Australian songbirds are related to one another and that similarities in morphology and behavior to species elsewhere were examples of convergence. The adaptive radiation of Australian songbirds, so revealed, parallels the extraordinary diversity of marsupial mammals and eucalyptus plants on that continent.

Each year, comparisons of the DNA genomes of birds increase in power and efficiency. Especially fruitful have been comparisons of the nucleotide sequences of a small circular DNA molecule (mitochondrial DNA, or mtDNA) found in the mitochondria of the cytoplasm. Scott Lanyon and John Hall's (1994) sequence analysis of 888 nucleotides of the mtDNA gene cytochrome *b* confirmed one of the interesting results of Sibley and Ahlquist's early DNA–DNA hybridization experiments regarding the relationships of barbets. Barbets are brightly colored, tropical, fruit-eating relatives of the woodpeckers. The results of both biochemical studies indicated independently that the New World barbets were more closely related to the toucans of Central and South America than they were to barbets of the Old World (Figure 3–11). All barbets had been formerly considered most closely related to one another. Instead, the big-billed toucans diverged radically from New World barbets after the barbets had arrived in the tropics.

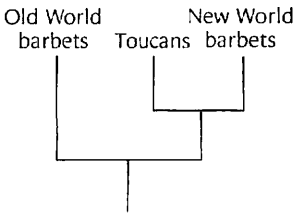


FIGURE 3–11 Evolutionary relationships among Old World barbets, toucans, and New World barbets based on a parsimony analysis of sequence data for the cytochrome *b* gene of the mitochondrial DNA. Despite their different morphologies, the toucans and New World barbets are sister taxa. The Old World barbets and the New World barbets are similar by virtue of having older ancestral traits in common.

Construction of a full phylogeny of modern birds, at least at the level of genera, is imminent, as one chapter of the ambitious Tree of Life project (Cracraft and Donoghue 2004). Automated gene sequencing and a growing selection of genes that evolve at different rates now allow the comprehensive construction of avian phylogenies. The proportion and pattern of large numbers of nucleotide substitutions define genealogical relationships among different clades of birds. Faster-evolving genes such as those encoded by mitochondrial DNA help to resolve relationships among closely related species. Slower-evolving nuclear genes help to resolve more distant or ancient relationships.

For example, Lisa Mertz and her colleagues at the American Museum

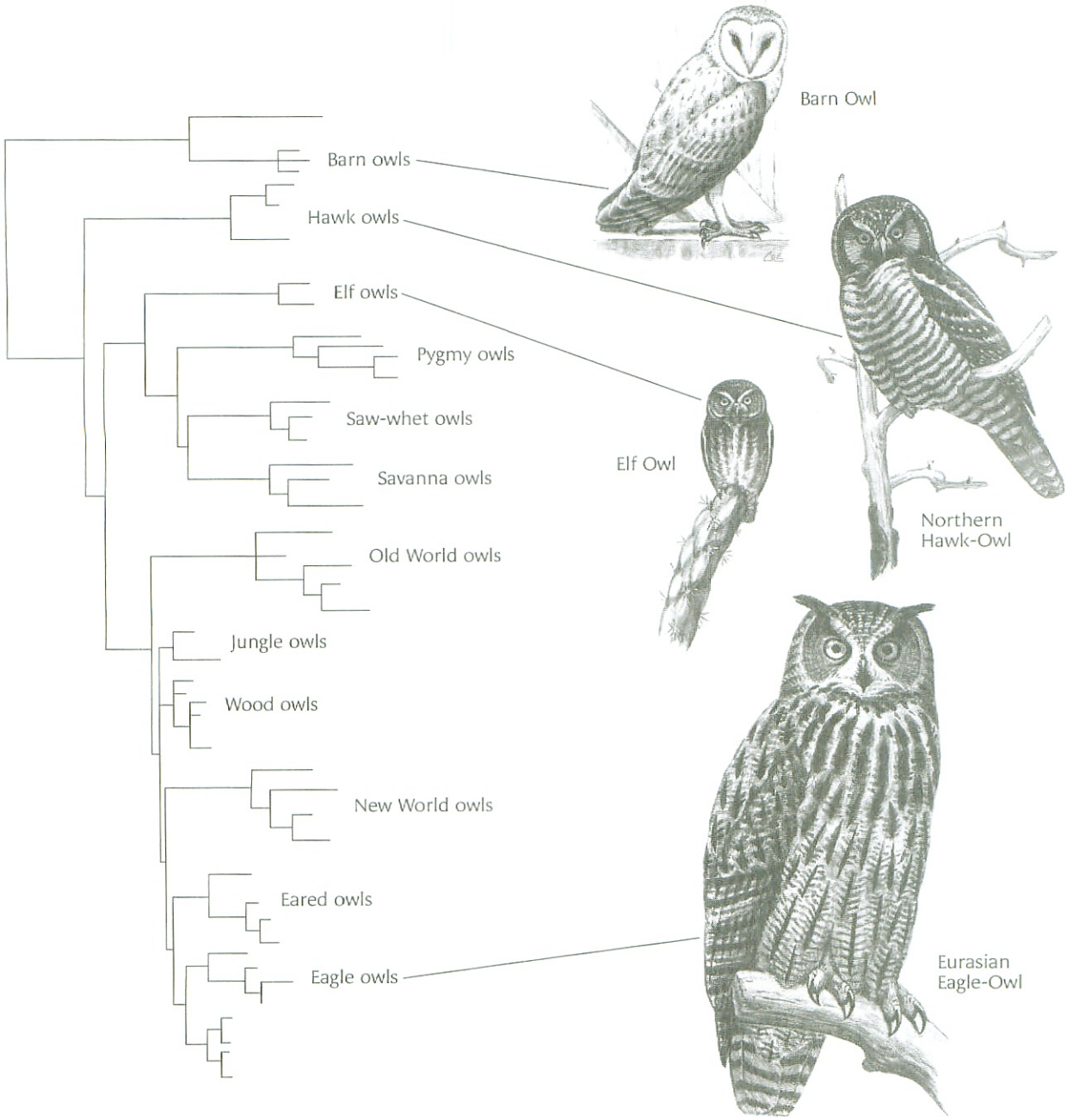


FIGURE 3–12 Phylogeny of the owls of the world (Strigiformes) based on the nuclear *RAG-1* exon. Twelve major clades sequence from the oldest groups (barn owls, hawk owls) through the small owls (elf owls, pygmy owls, saw-whet owls) to a large cosmopolitan clade that includes New World screech owls and the big wood owls, eared owls, and eagle owls. [*Courtesy of L. Mertz and colleagues at the American Museum of Natural History*]

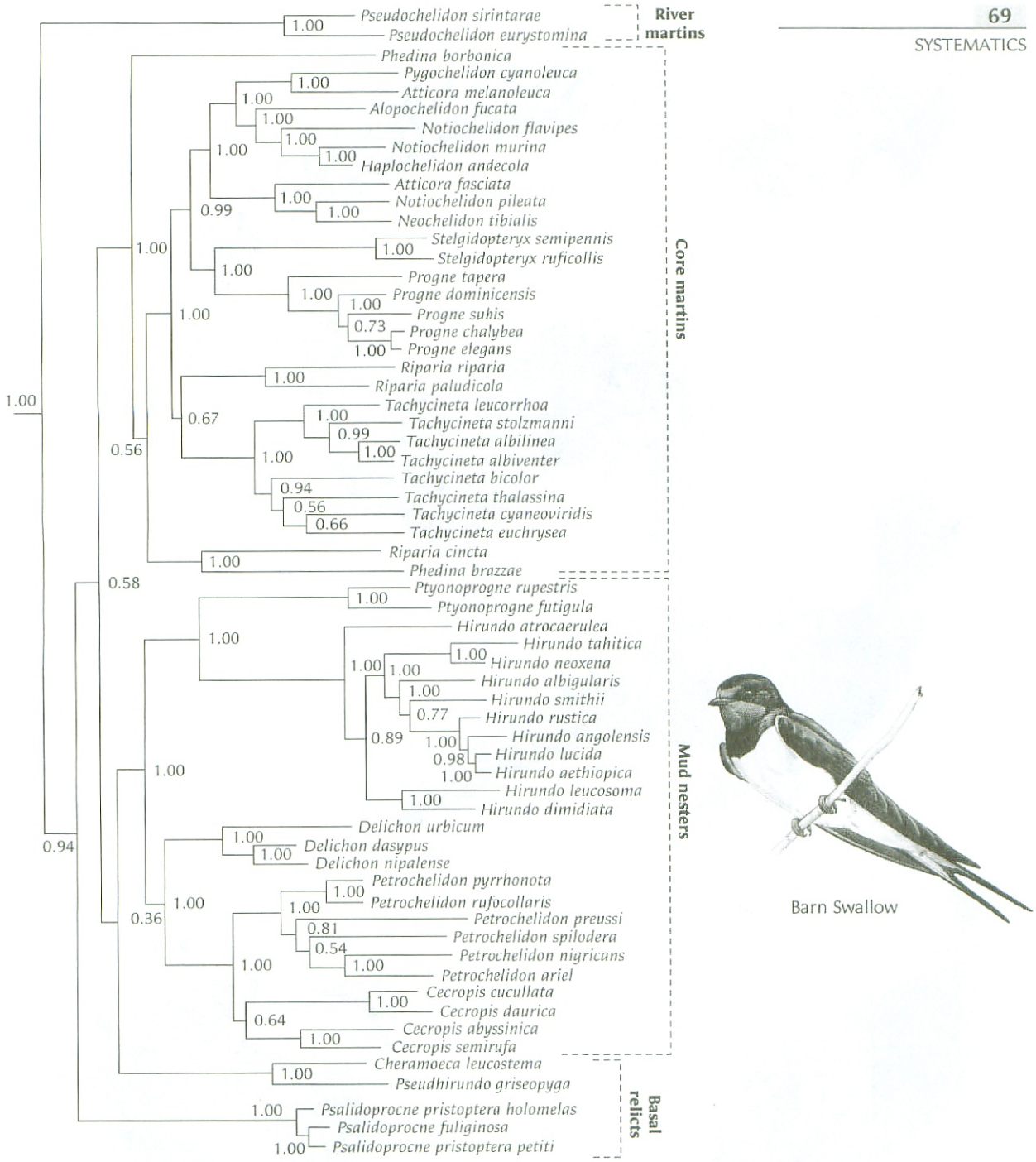
of Natural History deciphered the relationships among the genera of owls (Order Strigiformes) by using the powerful nuclear *RAG-1* gene (exon) (Figure 3–12).

Among the results:

- The barn owls (Tytonidae) and typical owls (Strigidae) are each monophyletic and have a common ancestor.
- The Strigidae comprise three major clades of owls: (1) all members of the Australasian hawk owls (genus *Ninox*); (2) other small owls worldwide including saw-whet owls *(Aegolius)*, little owls *(Athene)*, and pygmy-owls *(Glaucidium)*; and (3) a large assemblage of other owls including the big eagle owls *(Bubo)*, eared owls *(Asio)*, and New World screech owls *(Megascops)*.
- The Snowy Owl is related to the Great Horned Owl and eagle owls in the genus *Bubo*.
- The Long-whiskered Owlet, a tiny, extremely rare species of the cloud forests of Peru, is the sister species of the desert-living Elf Owl.

Construction of phylogenies based on biochemical or morphological characters or on both is the first step toward understanding the evolution of birds. The next step is to map other information onto a phylogeny to explore evolutionary trends in behavior, ecology, and biogeography (Sheldon and Whittingham 1997). The analysis of nest construction by swallows is one such effort. Fred Sheldon and his colleagues (2005) examined the relationships among most of the species of swallows (Family Hirundinidae) of the world by using a variety of techniques, including DNA–DNA hybridization, two mitochondrial genes, and a nuclear gene (Figure 3–13). Such packages of genes that evolve at different rates allow the construction of phylogenies for whole families of birds with resolution of both recent and older branching sequences.

Nest construction is extremely diverse among species of swallows. Some species burrow into hillsides, others adopt tree cavities, and still others build mud nests on cliffs. The use of pure mud to construct hanging nests is unique among all birds. The original DNA–DNA hybridization studies by Winkler and Sheldon (1993) revealed that nest-construction habits reflect the evolutionary history of species. The swallows divided cleanly into mud nesters [e.g., barn swallows *(Hirundo)* and cliff swallows *(Petrochelidon)*]; cavity adopters [e.g., martins *(Progne)* and tree swallows *(Tachycineta)*]; and excavators [e.g., sand martins *(Riparia)*]. Analyses of the majority of swallow species representing all genera with the use of the full toolkit of both mitochondrial and nuclear genes reaffirmed the basic split between mud-nesting species of swallows and the cavity adopters, or core martins. Mud nesting evolved only once in the evolutionary history of swallows and then diversified, principally in Africa where a dry climatic history favored this mode of nesting. The obligate cavity-adoption behavior of the core martins appears to be tied to their evolution in the rich forest habitats of the New World. Three genera *(Pseudhirundo, Cheramoeca,* and *Psalidoprocne)* of excavators proved to be old basal lineages of swallows now restricted to Africa and Australia. The two living species of river martins, one from Congo and the other from Thailand (see page 53), represent the most ancient lineage of all.



Barn Swallow

FIGURE 3–13 Phylogeny of the four primary clades of 61 species of swallows (Hirundinidae) based on comparisons of a nuclear gene *(ND2)* and a mitochondrial gene (for cytochrome *b*). The two disjunct species of river martins *(Pseudochelidon)* of Thailand and Congo, respectively, are the ancient outgroup lineage of the family. Then follow two basal and relictual genera: the Gray-rumped Swallow *(Pseudhirundo)* of Australia and the saw-wing swallows *(Psalidoprocne)* of Africa, which have no known relatives. The rest of the swallow species divide cleanly into the mud nesters, such as the Barn Swallow *(Hirundo)* and allies, and the core martins *(Progne, Tachycineta, Riparia)* and allies. [*From Sheldon et al. 2005*]

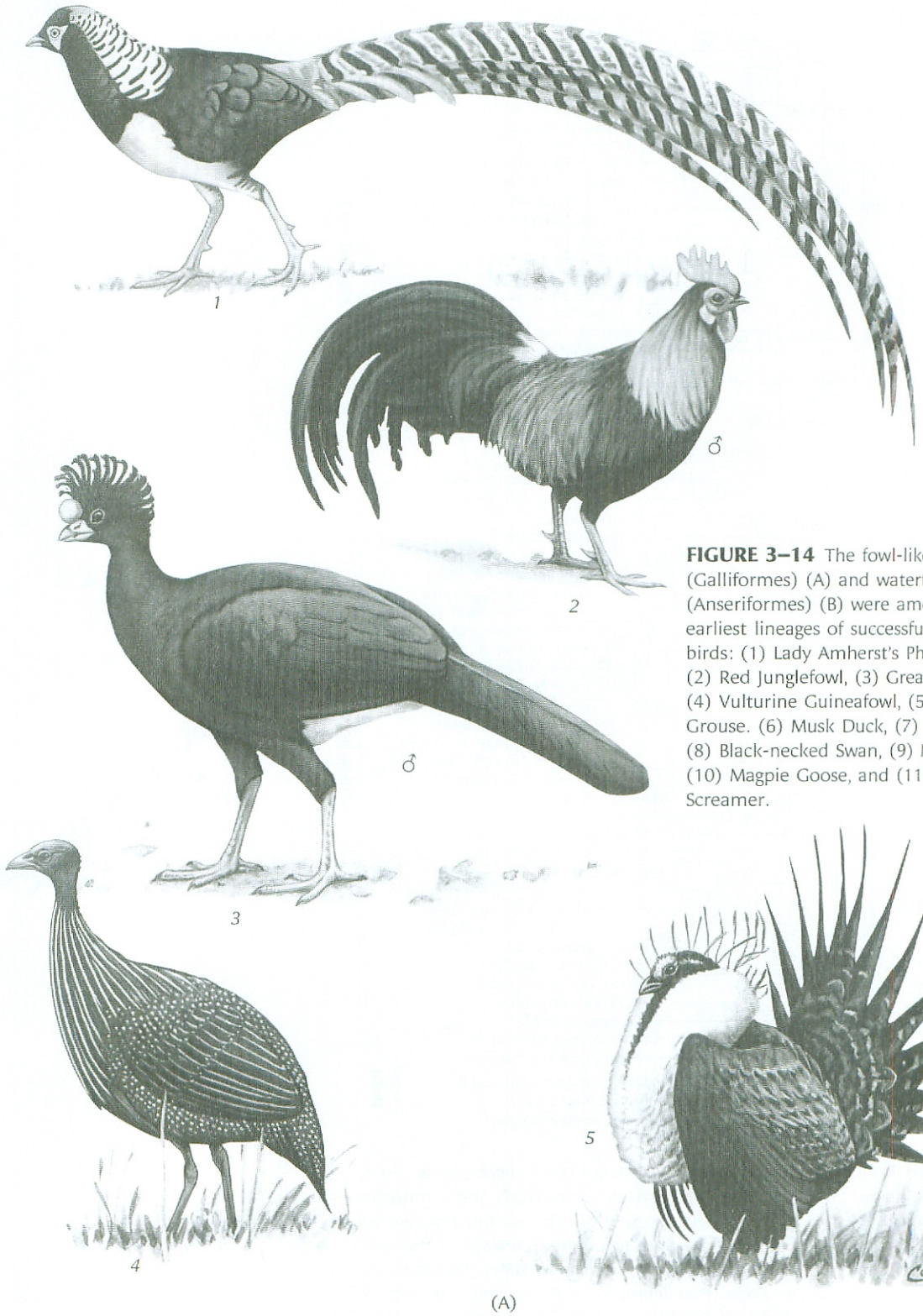
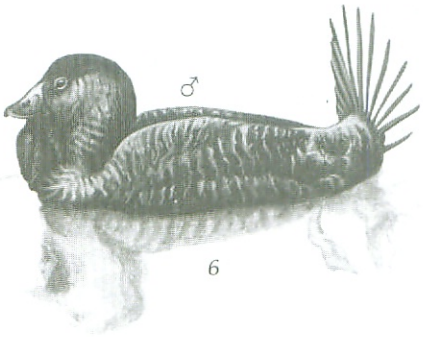


FIGURE 3–14 The fowl-like birds (Galliformes) (A) and waterfowl (Anseriformes) (B) were among the earliest lineages of successful modern birds: (1) Lady Amherst's Pheasant, (2) Red Junglefowl, (3) Great Currasow, (4) Vulturine Guineafowl, (5) Sage Grouse. (6) Musk Duck, (7) Smew, (8) Black-necked Swan, (9) Mallard, (10) Magpie Goose, and (11) Horned Screamer.



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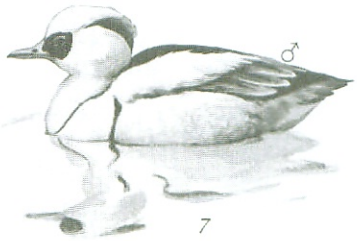

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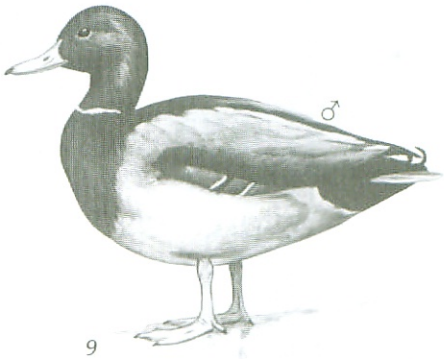

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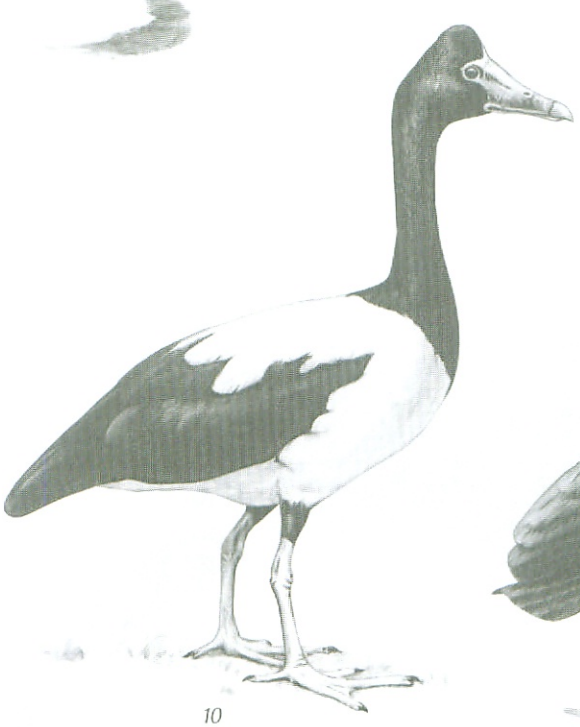

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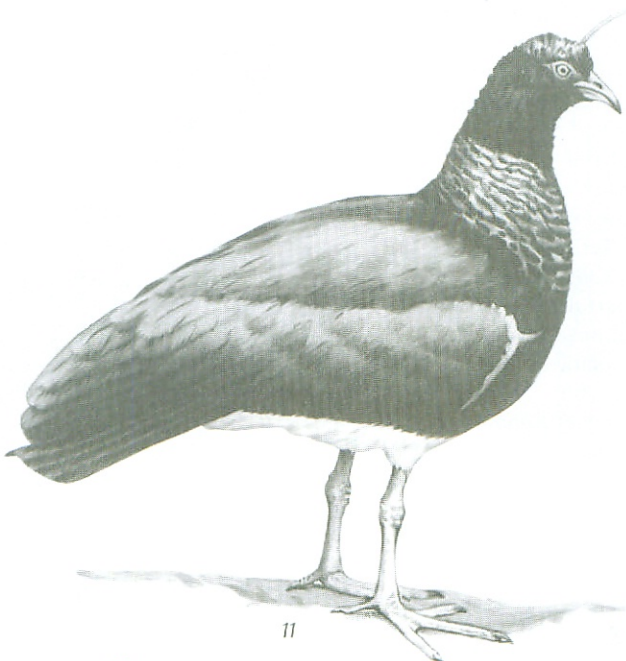

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(B)

The use of mitochondrial genes allowed these researchers to finely resolve the relationships among species in each major group of more recently evolved species. For example, the mud nesters divide cleanly into mud-cup nesters (barn swallows and crag martins), enclosed-mud nesters (cliff swallows and red-rumped swallows), and modified-mud-cup nesters (house martins).

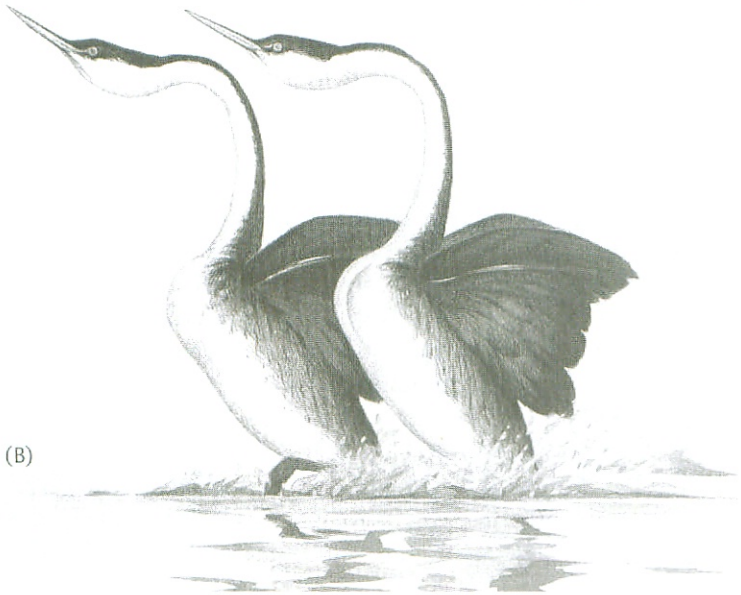
The concordance between phylogenetic relationships and nest-building behavior overturns the historical view that the nest-construction behavior of birds changes easily as an adaptation to local circumstances. Instead, we now have a strong foundation for the study of the diversity of the social systems of swallows.

DNA analysis of slow-evolving (nuclear) genes has revealed some of the deepest roots of the evolution of modern birds. For example, chickenlike birds (Galliformes) and waterfowl (Anseriformes) are firmly positioned as being among the oldest modern birds (Cracraft et al. 2004; Figure 3–14, pages 70–71). The enigmatic Hoatzin is a remnant of an ancient basal lineage with no close living relatives, cuckoos included (G. Barrowclough, pers. comm.; Figure 3–15). One of the biggest surprises is that flamingos (Phoenicopteriformes) and grebes (Podicipediformes) appear to be each other's closest living relatives but with an ancient common ancestor (van Tuinen et al. 2001; Figure 3–16). This relationship was never included in past considerations of either group, given their entirely different morphologies.

FIGURE 3–15
Electrophoretic studies of proteins by Sibley and Ahlquist (1973) suggested that the Hoatzin might be related to *Guira* cuckoos, not to guans, as had been thought. But the relationships of this enigmatic species remain unresolved. Results of the latest DNA studies suggest that the Hoatzin represents an old basal lineage with no close living relatives. [*From original by E. Poole, courtesy of The Academy of Natural Sciences, Philadelphia*]

FIGURE 3–16 (A) The relationships of flamingos (Phoenicopteriformes) have long been debated, primarily about whether they are closer to waterfowl or to storks. (B) DNA comparisons suggest that flamingos are distantly related to grebes (Podicipediformes).

(A)



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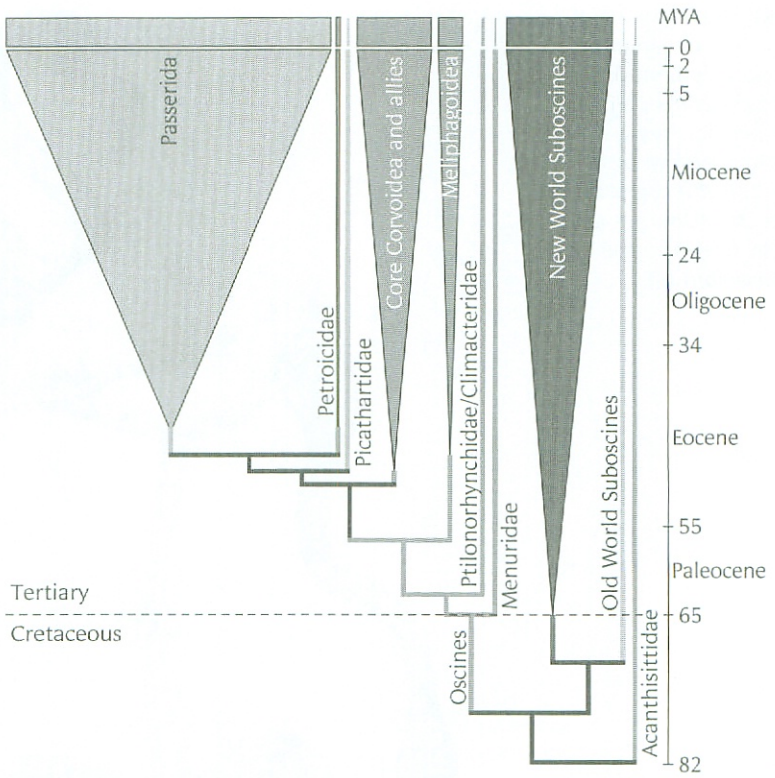


FIGURE 3–17 Phylogeny and diversification of songbirds (Passeriformes) based on two single-copy nuclear genes. The height of the bars on the right-hand edge of the branching diagram is proportional to the number of species in each clade. Projected divergence dates of clades in relation to the geologic time scale are based on assumptions of the rate of gene evolution, which are subject to criticism. [*After Barker et al. 2004*]

The new DNA technologies also reveal more details of the evolution of songbirds (Passeriformes) in the Tertiary, including their phylogeny and their biogeography (Barker et al. 2004; Figure 3–17). This single largest radiation of modern birds originated in ancient Australasia perhaps as early as the late Cretaceous, followed by repeated worldwide expansions of successful groups. Three species of New Zealand wrens (Acanthisittidae), which represent the oldest lineage of all, still persist in New Zealand. The so-called suboscine songbirds, which have simpler vocal-muscle arrangements than those of the oscine songbirds, split early into New World and Old World lineages. The New World suboscines—tyrant flycatchers, antbirds, and ovenbirds—became dominant members of the avifaunas of the New World tropics. The Old World suboscines—broadbills, pittas—did not. A host of Australasian families—lyrebirds (Menuridae), bowerbirds (Ptilonorhynchidae), honeyeaters (Meliphagidae), and others—evolved before the diversification of the two principal songbird clades—the Corvida and the Passerida.

Summary

The classification of the kinds of birds of the world helps ornithologists to communicate with one another and serves as a tool in the continuing study of avian evolutionary relationships. The species is the primary unit of biological classification.

Formal taxonomic classifications comprise a hierarchical series of inclusive categories that indicate the relationships among lineages. Orders, families, and genera are the principal taxonomic groupings of birds, all of which belong to the Class Aves.

Theoretically each taxon is monophyletic and consists of species more closely related to one another than to species in other taxa. In theory, the hierarchy of the classification and the evolutionary history of birds are the same.

The diversity of modern birds reflects historical patterns of speciation, extinction, and phyletic evolution. Conservative characters—attributes that do not change easily in the course of adaptation—enable ornithologists to decipher which groups of species have a common ancestor. Recognition of ancestral (primitive) versus changed (derived) character states aids in the reconstruction of the sequences of past evolutionary events.

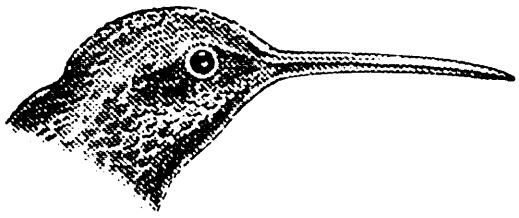
Convergence—the independent evolution of similar adaptations by unrelated species—can cause unrelated species to appear to be related. Cases of convergence can be revealed by detailed study of complex characters, such as the internal anatomy of the toes, and by biochemical evidence.

Two recent revolutions, cladistic analysis and biochemical technology, have infused a new vitality into the study of the phylogenetic relationships among species and among major groups of birds. Cladistic analysis sorts the polarities of primitive and derived characters. Biochemical comparisons of DNA compositions of species tend to confirm conclusions based on morphology, but they sometimes reveal unsuspected affinities and new patterns of adaptive radiation.

PART 2

FORM AND FUNCTION

CHAPTER 4



Feathers

Feathers are the most numerous, elaborate and diverse derivatives of the avian integument. [Stettenheim 2000, p. 461]

Feathers, the most distinctive feature of avian anatomy, are an extraordinary evolutionary innovation. Collectively referred to as plumage, feathers are unique structures of the skin. They provide insulation for controlling body temperature, aerodynamic power for flight, and colors for communication and camouflage. Modified feathers also perform secondary roles—in swimming, sound production, hearing, protection, cleanliness, water repellency, water transport, tactile sensation, and support.

This chapter covers feather structures and functions. First, we consider basic feather structure and its modifications, followed by a consideration of the major kinds of feathers in a bird's plumage, their growth, and their evolution. Highlighted next are the details of feather microstructure and pigmentation that make birds so colorful. Feathers also host bacteria and ectoparasites. Their suppression requires regular attention, including application of oily secretions of the preen gland. Finally, seasonal molts replace worn feathers with new ones, and they replace cryptically colored feathers with colorful ones or vice versa. A consideration of the relations of molts and plumages follows a review of the functions of plumage color patterns.

Feather Structure

Feathers consist mainly of beta-keratin, a fibrous protein polymer that forms microscopic filaments that have strong mechanical properties. Beta-keratins have some mechanical properties similar to those of the alpha-keratins found in the skin of all vertebrates, including humans and birds, but are an entirely unrelated group of proteins with very different molecular structure from that of the alpha-keratins. Beta-keratins are

unique to reptiles and birds. They make up most of the hard structures of reptilian skin and the leg scutes, claws, and beaks of birds. Feather keratins are a special class of beta-keratins that are characterized by a small deletion in their molecular sequence (Brush 1993).

The details of bird feathers have fascinated biologists for centuries; it is an enormous topic. We begin by reviewing the structure of a typical body feather, called a contour feather.

The primary features of a typical contour feather are a long central shaft and a broad flat vane on either side of this shaft (Figure 4–1). The hollow base of the shaft—the calamus, or quill—anchors the feather in a follicle below the surface of the skin. The rest of the shaft—the rachis—supports the vanes. Lateral branches off the rachis, called barbs, are the primary elements of vane architecture. Each barb consists of a tapered central axis, the ramus (pl. rami), with rows of smaller barbules projecting from both sides. A barbule consists of a series of single cells linked end to end; the cells may be simple or may bear projections called barbicels, some of which are elaborate and hooklike. Barbs and barbules form an interlocking, but flexible, planar surface.

Each vane of a typical body feather grades from a hidden, fluffy basal part, which provides insulation, to an exposed, cohesive outer part, which has a variety of functions (Figure 4–2). The barbules on the barbs at the base of the body feather are long, thin, and flexible and do not have barbicels. With their similarly thin, flexible parent barbs, they create a downy, or plumulaceous, feather texture. In contrast, the outer part of the vane is

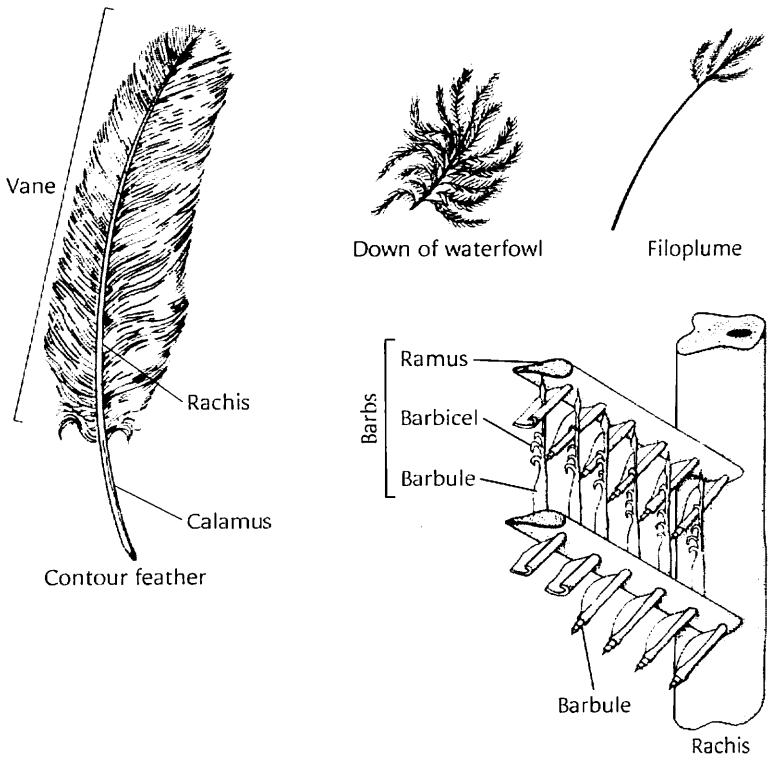


FIGURE 4–1 Structure of three kinds of feathers, with detailed structure of a typical contour feather.

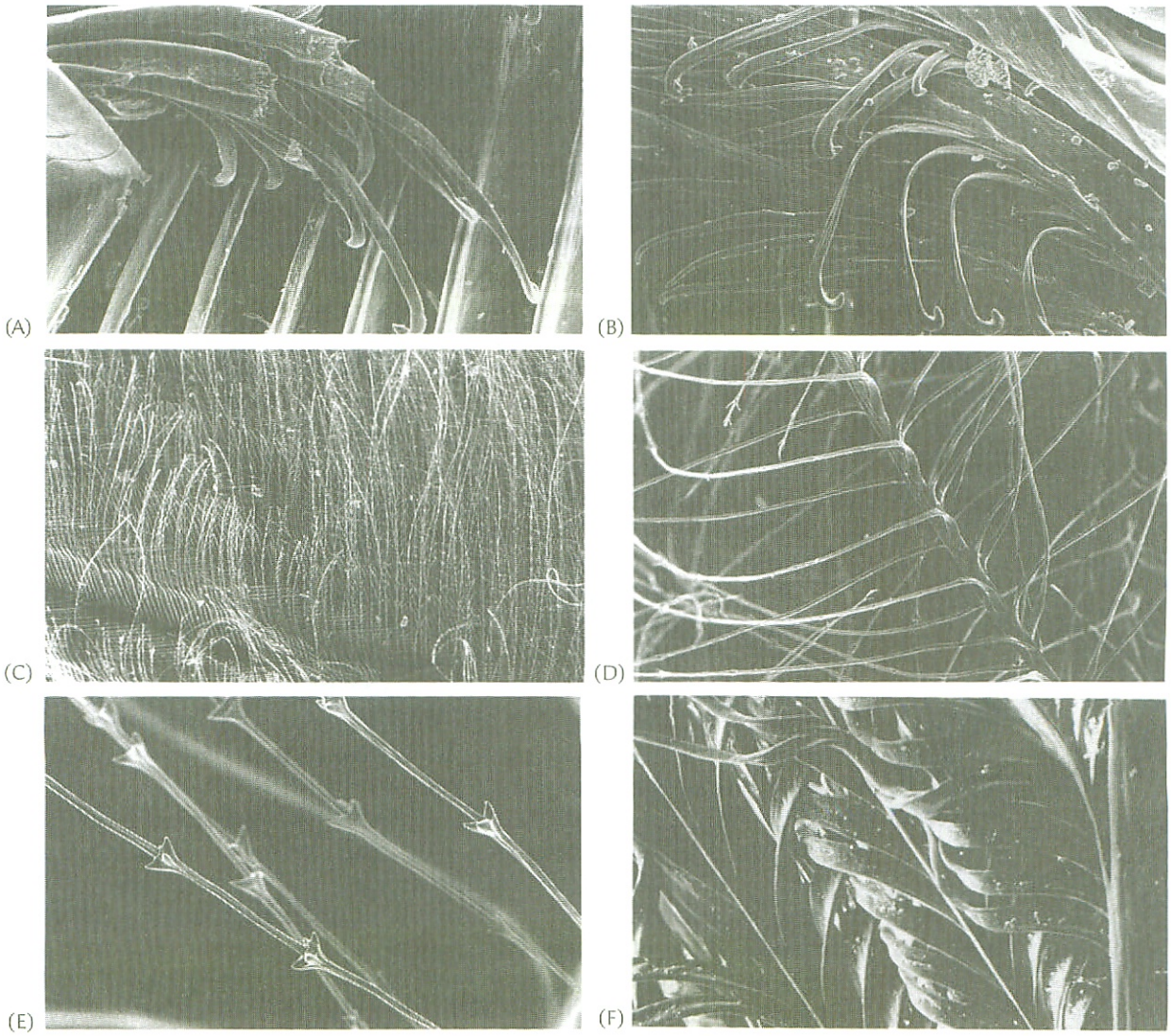


FIGURE 4–2 Scanning electron micrographs of feather structures: (A) Wild Turkey, tail feather. Oblique view of distal barbules with hooklets interlocking with proximal barbules. 358×. (B) American Crow, wing feather. Distal barbules, displaced to show hooklets. Behind them are more distal barbules showing other, unhooked projections. 406×. (C) Barred Owl, upper wing covert. Dorsal oblique view. The vertical filaments are the tips of the distal barbules, which are unusually long and project upward from the plane of the feather. This upward projection creates the velvety nap that quiets the airflow over the wings, producing the silent flight of most owls. 215×. (D) Domestic Goose, body down feather. Downy barb. The oblique thicker element is the ramus of the barb and the thinner elements are the barbules. Although the down appears grossly to be a bunch of fluff, magnification shows that the barbules are arranged in a regular manner. 130×. (E) Domestic Goose, body down feather. Barbules on a downy barb, showing projections at each node, called nodal prongs. These prongs are homologous to the hooklets and other projections on pennaceous barbules. They are thought to serve in keeping the downy barbs from becoming entangled, thereby creating the fluffy texture, but how they do so is not known. 325×. (F) Namaqua Sandgrouse, abdominal feather. The vertical element on the right is the rachis and the oblique elements are the rami of the barbs, bearing the coiled barbules that serve for holding water. 153×. [*Photographs courtesy of P. Stettenheim*]

a firmly textured, tightly interlocking, or pennaceous, structure. The cohesive structure of the outer vane is based on the interlocking arrangement of pennaceous barbules. Well-developed hooklet barbicels are present on the pennaceous barbules that form this part of the vane. Those barbules on the distal side of the barb—the side away from the base of the feather—have barbicels that grasp the next higher, inner barbules of the adjacent barb. In turn, barbicels, which can slide laterally along the next barb, are responsible for both the cohesion and the flexibility of the pennaceous vane.

The body feathers of some birds include a secondary structure—an afterfeather, or aftershaft—a mirror-image shaft and vane, attached to the same calamus. The barb and barbule structure of afterfeathers is typically plumulaceous, with rare exceptions. The afterfeather's primary function is to enhance insulation. Ptarmigans are grouse of high, cold alpine habitats. Providing essential insulation, the afterfeathers of the winter plumage of a ptarmigan are three-fourths as long as the main feathers. The afterfeathers of its summer plumage are much shorter.

Feathers are subject to striking modifications. Fusion of the developing barbs produces feathers that look like strips of plastic, as, for example, do the crown feathers of the Curl-crested Araçari, a small Brazilian toucan, and the central tail feathers of the Red Bird-of-Paradise. The "plastic" feathers of the bird-of-paradise function in courtship display, but why the araçari has such feathers is not known. The familiar Cedar Waxwing of North America is named for its waxlike wing-feather tips with fused, bright red terminal barbs. Vane shapes of display feathers range from long and pointed, like those on a rooster's neck (called hackles), to short and round, like those of the head feathers of small birds. The close spacing of large barbs with extra-long, curved barbicels produces water-repellent feathers in petrels, rails, and ducks. Conversely, the loss of these barbicels in cormorants and anhingas is an adaptation for diving. The loss of barbicels allows water to penetrate the plumage, soaking it and reducing buoyancy but requiring air drying of the feathers after a swim. Coiled barbules on the belly feathers of sandgrouse help to transport water (Box 4–1).

BOX 4–1

DESERT SANDGROUSE CARRY WATER IN MODIFIED FEATHERS

The sandgrouse of African deserts commute at dawn and dusk to the nearest water hole to quench their own thirst and to get water for their young, which remain flightless at nests as far as 30 kilometers away (Cade and Maclean 1967). At the water hole, male sandgrouse soak their belly feathers, which are modified to hold water in flight. Flattened and coiled barbules on the inside surface of the feathers (see Figure 4–2F) have hairlike extensions that absorb and hold water for transport back to the young. Upon return, the male adopts an upright watering posture, which attracts the young from their hiding places near the nest. The young drink by squeezing the wet elongate feathers in their bills. The chicks glean only from 10 to 18 milliliters of the 25 to 40 milliliters of water soaked up each time the parent visits the water hole.

Vaned Feathers

The most conspicuous feathers are called vaned feathers. They include the smaller contour feathers that cover the body surface and the larger flight feathers of the wings and tail. The smooth overlapping arrangement of vaned feathers reduces air turbulence in flight. The tiny, flat contour feathers that cover a penguin's body create a smooth, almost scaly, surface that reduces friction during swimming.

The flight feathers of the wing, called remiges (sing. remex), are large, stiff, pennaceous feathers (Figure 4–3). They primarily serve aerodynamic functions and have little importance in insulation. Rows of smaller feathers, called coverts, overlap the bases of the remiges and cover the gaps between them. The long shafts of the outer (distal) remiges—the primaries—attach to the bones of the hand and the second digit. These feathers

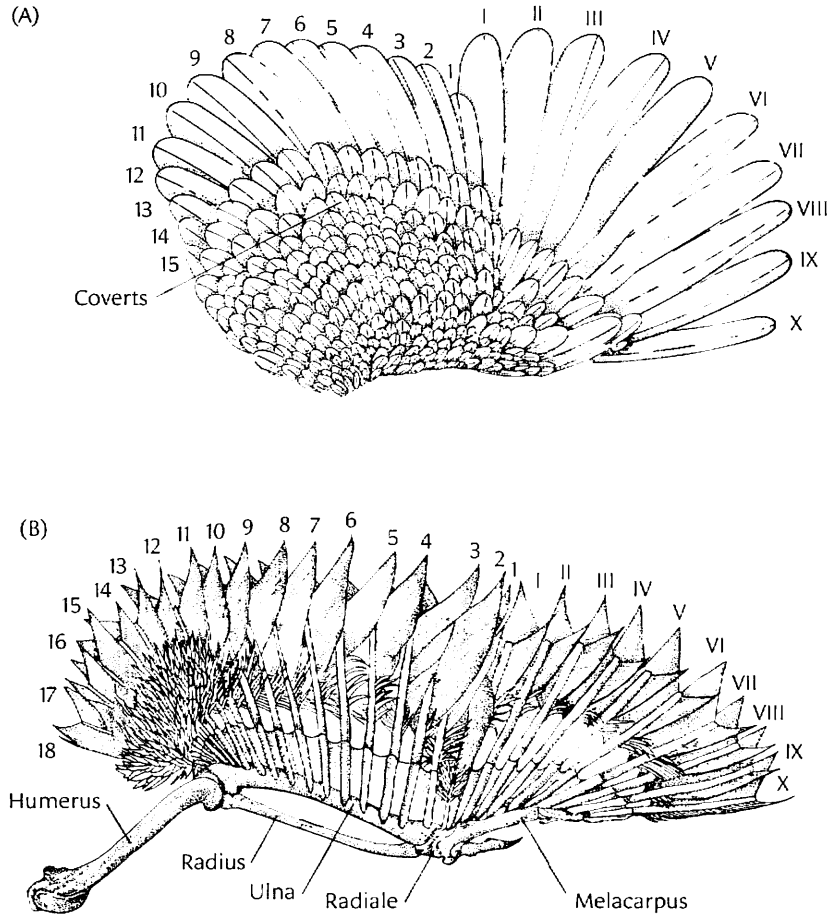


FIGURE 4–3 Dorsal view (A) of the extended left wing of a White Leghorn Chicken and (B) of the skeletal attachments of the primaries and secondaries of the same wing. Primary remiges are numbered I to X; secondary remiges are numbered 1 to 15 in part A and 1 to 18 in part B. The ends of the feathers have been omitted in part B. [*After Lucas and Stettenheim 1972*]

provide forward thrust on the downstroke of the wing during flight. Flight-feather vanes are asymmetrical, presenting a narrow, leading (forward) edge vane that cuts the air. Most birds have 10 primaries; storks, flamingos, grebes, and rheas have 11; ostriches have 16; and some songbirds have 9. The flightless kiwis have only 3 or 4 primaries.

Specialized barbules, called friction barbules, are found on the inner vanes of the outer (primary) wing feathers. Friction barbules have broad, lobed barbicels that rub against the barbs of overlying feathers, thereby reducing the slippage and separation of feathers during flight. The longest friction barbules are found in the central part of the inner vane.

Silent flight, which enables an owl to surprise prey, results in part from two special structural features that muffle feather sounds (see Figure 4–2C). The barbs on the leading edges of the owl's primaries are long, curved, well-separated structures that reduce air turbulence. The unusually long filamentous tips of some barbules also help minimize the rubbing of overlapping feathers and create a soft, slightly fuzzy feather texture. Nightjars have a similar soft feather texture.

Because flight efficiency is directly linked to the structure of the primaries, major structural modifications of these feathers are uncommon. The narrow outer primaries of the male American Woodcock, which produce trilling noises during courtship flights, are an exception. The modified primaries of flightless cassowaries consist only of 28-centimeter-long extensions of the hollow tubular calamus. These strong spinelike structures protect a cassowary's flanks from abrasive vegetation. During the breeding season, long extensions of the second primaries of male Standard-winged Nightjars grow out and are used in courtship (Figure 4–4). The

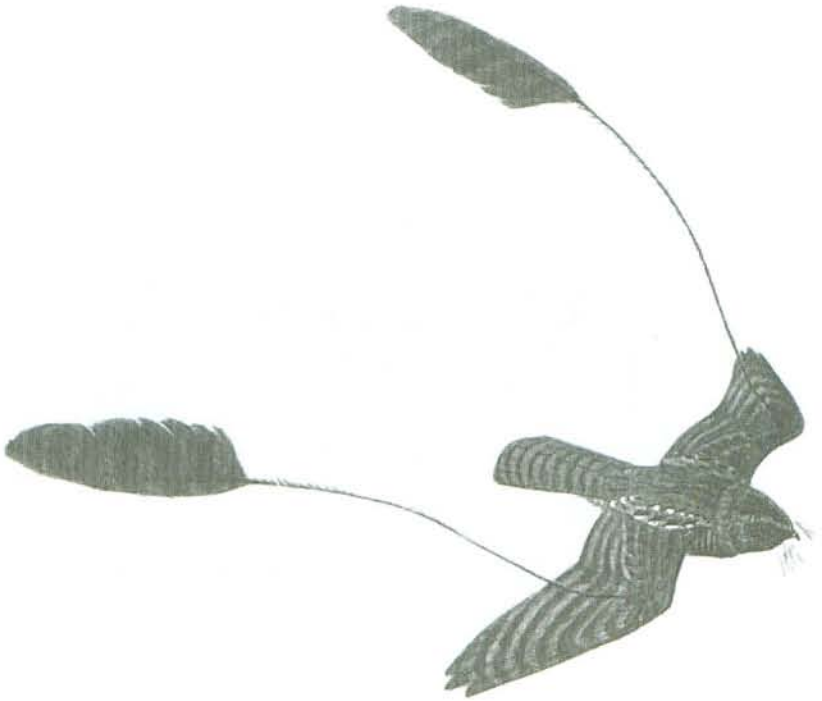
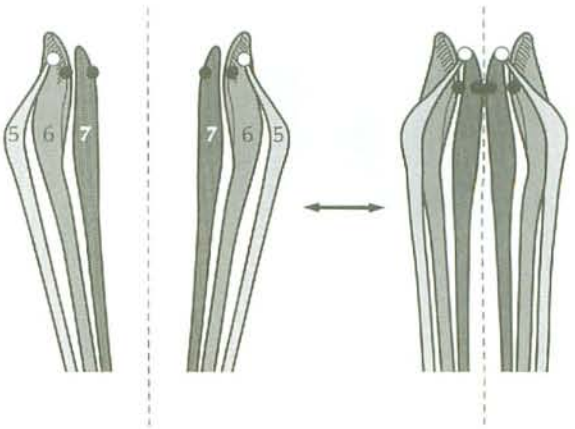


FIGURE 4–4 The "standards" of the Standard-winged Nightjar are highly modified primaries, which are dropped shortly after courtship has been completed.

BOX 4–2

THE BIRD THAT CALLS LIKE A CRICKET

Back in 1871, Darwin himself called attention to the thickened clublike shafts of the secondaries of the Club-winged Manakin as an example of how sexual selection could lead to the production of mechanical sounds in courtship displays (see Figure 12-12). The mechanical sounds from the wings of this species substitute for the vocal sounds of other manakins (Bostwick and Prum 2003). Recent studies using high-speed video of the rapid-fire wing claps of this species revealed exactly how the shafts produce the courtship sound "tick-tick-ting" (Bostwick and Prum 2005). The mechanism is unique among birds and similar to the production of chirps by crickets (see the illustration). The fifth secondary acts as a "pick" that rubs back and forth across the ribbed surface of the adjacent sixth secondary when the manakin snaps its wings over its back. The rubbing of the pick causes the hollow clublike shafts of the sixth and seventh secondaries to resonate and produce the "ting" as a sustained violin-like note.



Graphical illustration of how the tip of secondary 5 (the pick) moves across the surface of enlarged secondary 6's (the file) of the left and right wings. The mechanical impulses that result sustain the resonance sounds of the shafts of secondary 6 and probably secondary 7. Relative motion of the pick and file is shown by the white and black circles, respectively.

nightjars are said to discard the extensions by biting them off, but this notion is unverified.

The inner (proximal) flight feathers of the wing—the secondaries—attach to the ulna wing bone (see Figure 4–3). Numbering from 6 in hummingbirds to 19 in some owls, and 40 in albatrosses, the secondaries form much of the inner wing surface. In some species, they have been modified for display purposes. For example, the broad, flaglike inner secondaries are essential for courtship in the Mandarin Duck. A quite different kind of modification for producing mechanical courtship sounds are the thickened, clublike feather shafts of the central secondaries of the Club-winged Manakin, a tiny denizen of the thick undergrowth of rain forests in South America (Box 4–2).

The flight feathers of the tail, called rectrices (sing. rectrix), attach to the fused caudal vertebrae, or pygostyle. The usual 12 rectrices function primarily in steering and braking during flight (Figure 4–5). Among the exceptions are anis and grouse with 18 tail feathers and snipe with 24. Rachises vary from thin and flexible, like those in the display tail feathers of some tropical hummingbirds, to stiff rods, like those of the bracing tail feathers of woodpeckers. The elaborate tails of birds-of-paradise

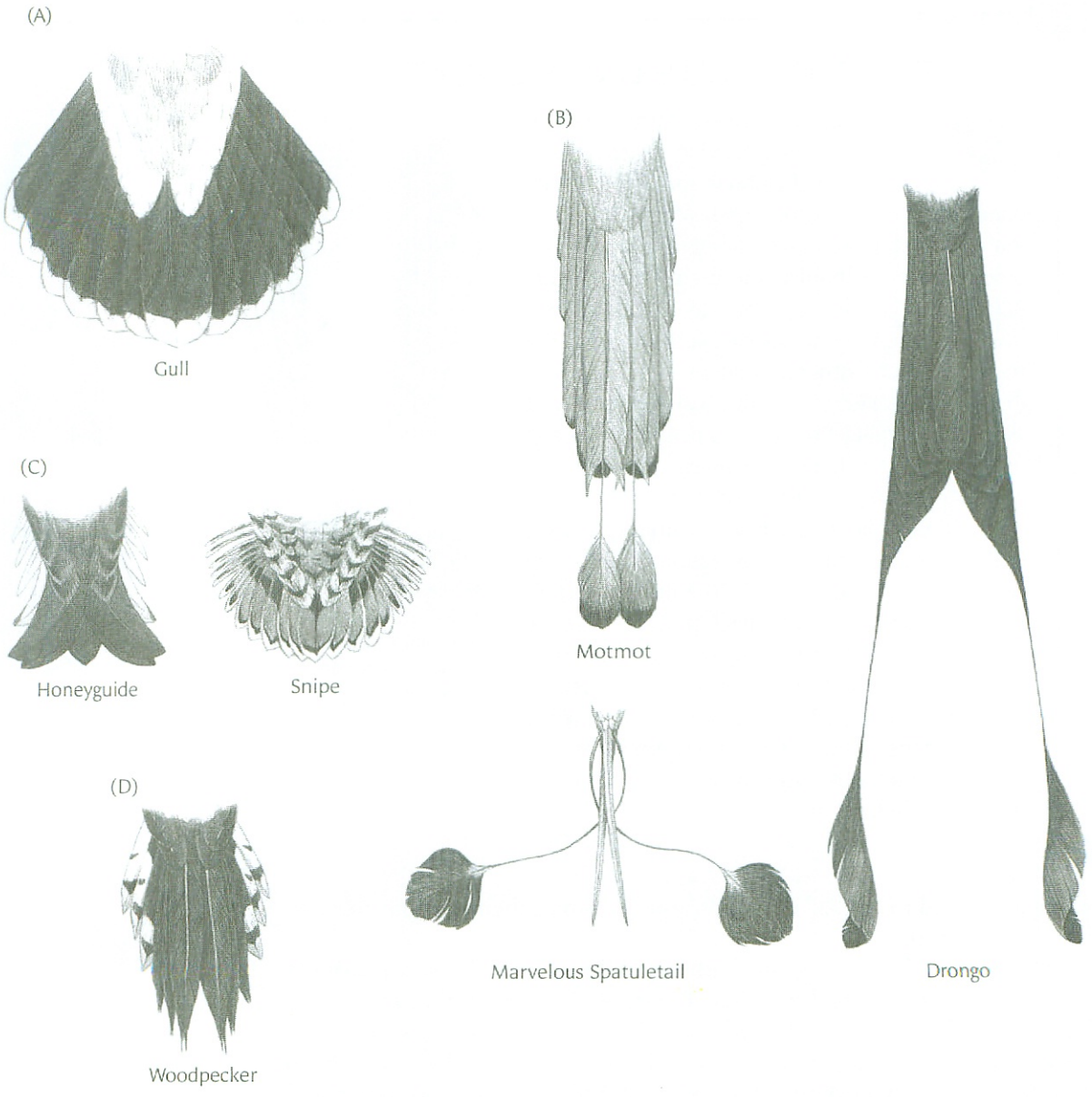


FIGURE 4–5 Tail feathers and their modifications: (A) unmodified tail of gull; (B) racquet-shaped tail feathers of a motmot, a drongo, and a hummingbird (Marvelous Spatuletail); (C) sound-producing tails of a honeyguide (Lyre-tailed Honeyguide) and a snipe; and (D) supporting tail of a woodpecker.

and some hummingbirds (see Figure 4–5, Marvelous Spatuletail) serve primarily in display and can be a handicap in flight. Some motmots, drongos, kingfishers, and hummingbirds have racquet-shaped rectrices with bare shafts and terminal vaned sections. The circular tail tips of a male King Bird-of-Paradise are tight whorls of rachises and inner vanes (see Figure 1–1). Tail feathers are also modified for sound production—for example,

in some snipes—and for bracing support in creepers, woodpeckers, woodcreepers, swifts, and penguins.

Downs, Bristles, and Other Kinds of Feathers

Unlike firm-vaned feathers, down (plumulaceous) feathers are soft and fluffy (see Figure 4–1). The down feathers of chicks and those of adult birds, called definitive down, vary from thick, continuous distributions to restricted distributions. Down feathers provide excellent natural, lightweight thermal insulation. A down feather typically lacks a rachis, but, as always, there are exceptions, including the down feathers of waterfowl. On most birds, flexible plumulaceous barbs and barbules extend directly and loosely from the basal calamus. Downy barbules entangle loosely, trapping air in an insulating layer next to the skin.

Semiplumes are intermediate in structure between down and contour feathers. They enhance insulation, fill out the aerodynamic contours of body plumage, and serve as courtship ornaments (Box 4–3). A semiplume has a large rachis with loose plumulaceous vanes. Some are close to down in structure, whereas others more closely resemble contour feathers. Semiplumes are distinguished from down feathers by the length of their rachises, which are always longer than the longest barb. Semiplumes are usually hidden from view at the edges of the contour feather tracts (see page 101).

Filoplumes are hairlike feathers that monitor the movement and position of adjacent vaned feathers (see Figure 4–1). Distributed inconspicuously throughout the plumage, they are most numerous near mechanically active, or movable, feathers; each flight feather may have from 8 to 12 filoplumes. They extend beyond the contour feathers of songbirds—particularly on the back of the neck, a region called the nape. A filoplume consists of a fine shaft, or rachis, that thickens distally, ending in a terminal tuft of one to six short barbs with barbules. Disturbance of a filoplume's enlarged tip is magnified and transmitted by the long, thin shaft to sensory corpuscles at its base, which then signal the muscles at the base to adjust the feather's position. Filoplumes associated with the flight feathers aid aerodynamic adjustments; those in association with contour

BOX 4–3

THE DISPLAY PLUMES OF EGRETS NEARLY CAUSED THEIR EXTINCTION

The breeding display plumes of the Great Egret and the Snowy Egret were coveted for human display as well. These large semiplumes once commanded a high price for use in ladies' hats of the highest fashion. The resulting slaughter of egrets in their breeding colonies nearly caused their extinction early in the twentieth century. Concerned citizens rallied to the cause of bird conservation with an unprecedented outcry and founded the National Audubon Society, which adopted the egret as its emblem. Laws were passed to protect the egrets, which recovered at first in guarded Audubon sanctuaries.

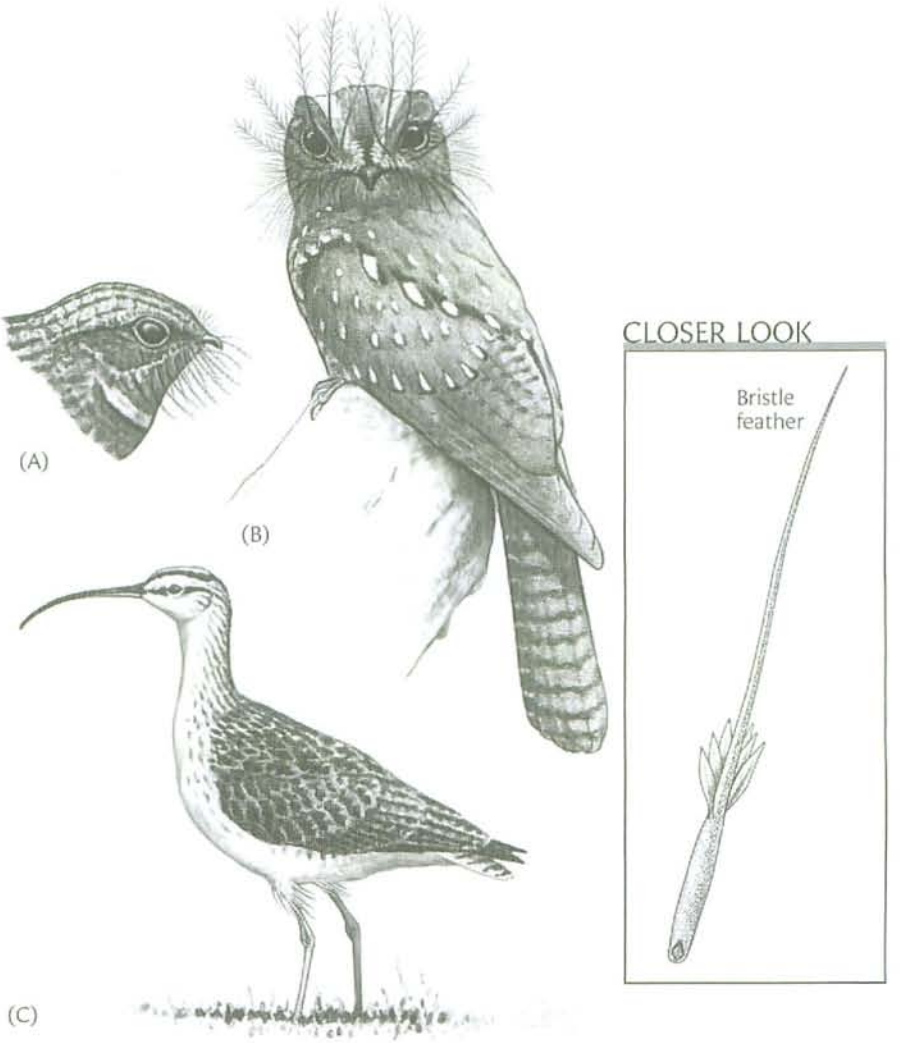


FIGURE 4–6 Bristles. (A) Whip-poor-will has well-developed bristles about the mouth. (B) Australian Owlet-Nightjar has elaborate bristles and semibristles around its bill. (C) An exception to the usual head locations of bristles are those on the knees of the Bristle-thighed Curlew.

feathers also may help to monitor airspeed. Filoplumes are absent in penguins and in flightless birds such as ostriches. The long, broad-at-the-base, white display filoplumes of sagegrouse extend from 5 to 10 centimeters beyond the neck feathers (Schroeder et al. 1999).

Bristles (Figure 4–6) are specialized feathers with both sensory and protective functions. Corresponding to their sensory functions, bristles, like filoplumes, have sensory corpuscles at their bases. Bristles are simplified feathers that consist only of a stiff, tapered rachis with a few basal barbs. Semibristles are similar but have more side branches. Except for those on the knees of the Bristle-thighed Curlew and on the toes of some owls, bristles are found almost exclusively on the heads of birds. The facial feathers of raptors tend to be simplified to bristles and semibristles, which are easier to keep clean than are fully vaned feathers. This condition reaches an extreme in the carrion-eating vultures, which have bare heads with scattered bristles. The eyelashes of such birds as ostriches, hornbills, rheas, and cuckoos consist of protective bristles, as do the nostril coverings of

woodpeckers, jays, and crows. Most aerial insect-eating birds have bristles and semibristles around their mouths. The semibristles around the mouths of nightjars and owlet-nightjars are especially well developed, acting not only as insect nets, but possibly also as sensors of tactile information, in much the same way that a cat's whiskers do.

A dustlike substance made up of keratin particles that are 1 micrometer in diameter, resembling talcum powder, is present on the contour feathers of many birds. Special feathers called powderdowns, dispersed throughout the feather coat, continuously slough this powder, from the surface of their barbs. Powderdown feathers grow in dense, distinctly arranged patches on birds such as herons and the unique Cuckoo Roller of Madagascar and Kagu of New Caledonia. The still-disputed functions of powderdowns may include the waterproofing of feathers.

Feather Growth

Although a bird can change the position, visibility, and function of its plumage, it cannot change the structure of an individual feather. Feathers are dead structures. After they are fully grown, feathers cannot change color or form except through fading or abrasion. No nerves, muscles, or blood vessels lie beneath the outer surface of an exposed feather. The only mechanism for damage repair is the replacement of the whole feather. Except for the accidental loss of feathers and their immediate regrowth, feather replacement, or "molt," takes place regularly with age and with season.

New feathers grow from specialized pockets of epidermal and nourishing dermal cells called follicles (Figure 4–7). At the base of a follicle is

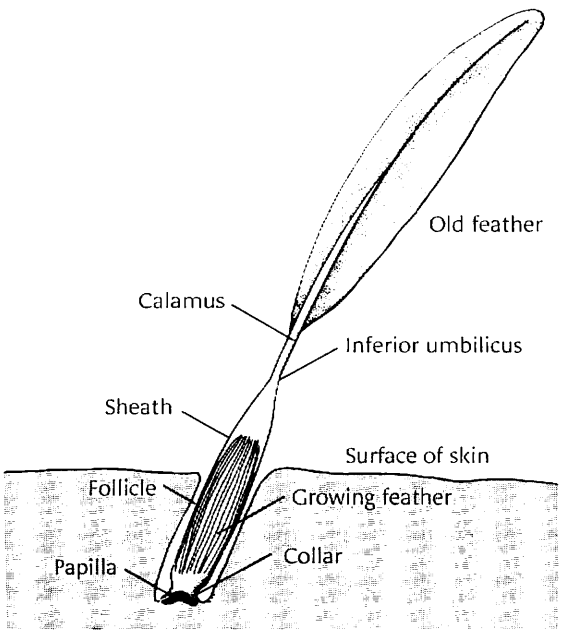


FIGURE 4–7 A new feather, growing from a papilla and collar in the follicle, pushes out the old feather. [*After Watson 1963*]

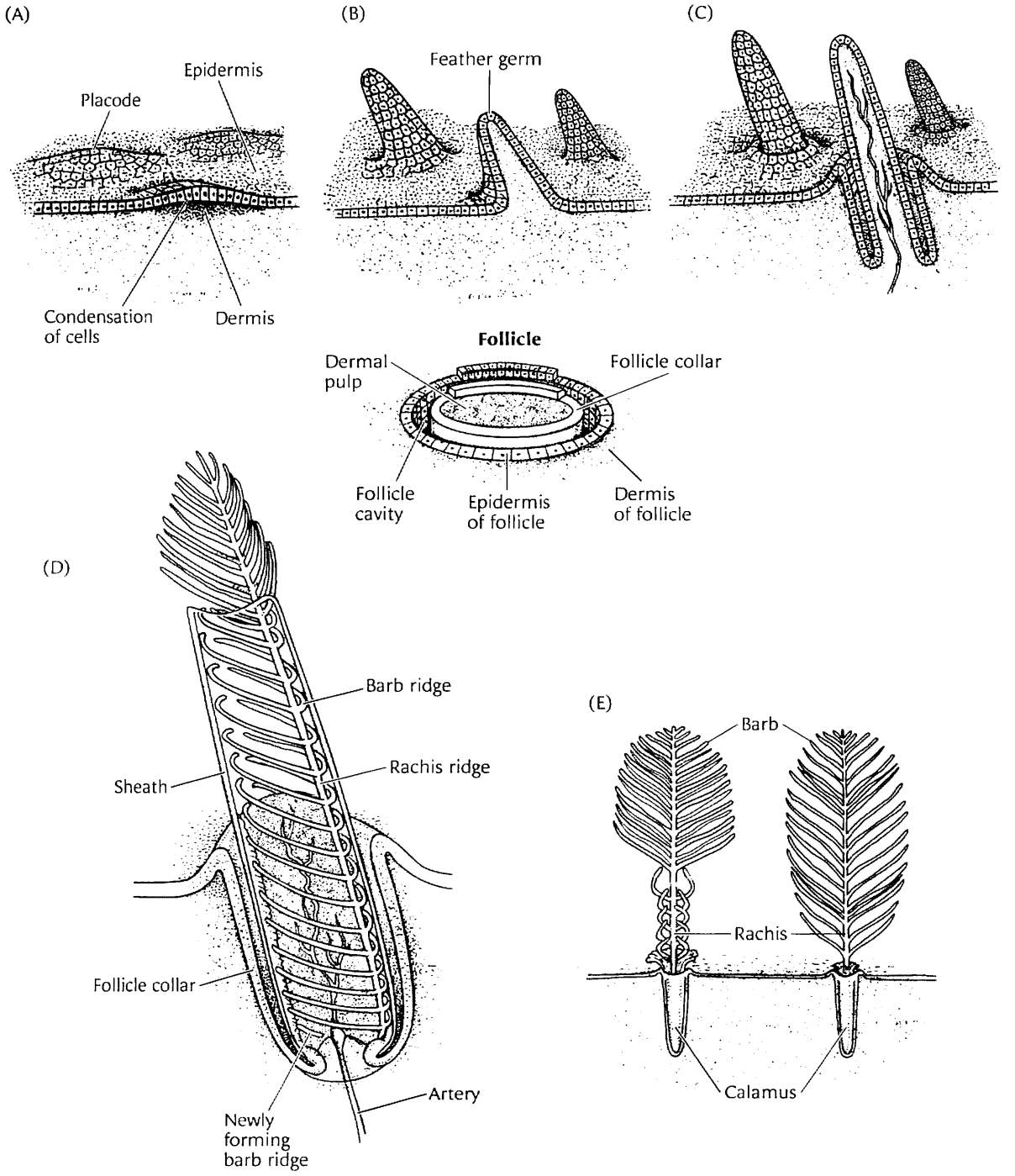


FIGURE 4–8 Feather growth and development. (A) Feather growth begins with a thickening of the epidermis, the *placode*, over a condensation of cells in the dermis. (B) The placode elongates into the tubular feather germ. (C) Cells proliferate in a ring around the feather germ to create the follicle (detail below). Production of new keratinocyte cells in the follicle collar push older cells up and out to create the tubular feather. (D) The outermost layer becomes the sheath, whereas the inner layer divides into a series of barb ridges that develop into the barbs of the feather. (E) The feather emerges and unfurls from the sheath into its final shape. The follicle collar forms the calamus at the base of the feather. [*After Prum and Brush 2003*]

the follicle collar, a persistent ring of feather stem cells that divide to produce the cells that will become all the feathers of that follicle. In the life of a bird, the same follicle will produce feathers of strikingly different forms, including the first natal down and contour feathers. In follicles that produce bilaterally symmetrical feathers, such as flight feathers, the ring of stem cells tilts toward the side where the quill arises; but, in radially symmetrical feathers, such as down, the ring of stem cells is horizontal (Yue et al. 2005). In the Ruff (see Figure 12–17), the same follicles produce the elaborate display plumage used during the breeding season and the small, drab feathers of the nonbreeding plumage.

A new feather begins to grow when the follicle collar begins to divide and produce new feather cells, pushing the previous feather out of the follicle. As new cells divide at the base, the tubular feather gradually emerges from the skin. The dermal papilla develops into the central pulp, which provides nourishment for the growing cells and supports the delicate epidermal cylinder. All feathers are variations of this initial tube (Figure 4–8).

The epidermal cells of the growing feather use signaling proteins to coordinate their differentiation into the various feather parts (Harris et al. 2002). The outermost layer of cells becomes the sheath, which falls off when feather growth is complete. The intermediate cells become the barb ridges that form the major branches of the feather vane. The barbules grow from horizontal rows of cells in the periphery of the barb ridges. Fusion of barb ridges on the dorsal side of the tube then forms the rachis ridge, which becomes the feather shaft.

As the feather primordium emerges from the skin, the epidermal cells begin to produce beta-keratin. Eventually, these cells fill entirely with the insoluble keratin, become completely cut off from nutrients, and die. The sheath then cracks and falls off, and the tightly bound barbs uncoil and expand to create the feather vane. The final undifferentiated tubular calamus remains inserted in the follicle until the next feather grows in. The pulp, the core of living cells and blood vessels, is then resorbed by the follicle. The only evidence remaining of this early life-support system is a small hole at the end of the shaft, known as the inferior umbilicus.

The follicle grips the feather at the calamus by a combination of muscular tightening and friction. Substantial force—from 500 to 1000 grams for a single body feather of the average chicken—is required to pull a feather from this grip. The tight grip of follicle muscles controlled by the autonomic nervous system may relax when a bird becomes frightened. The resultant loss of feathers is known as fright molt. Nightjars, for example, easily drop their feathers when disturbed.

Evolution of Feathers

The details of feather growth have been used to support a developmental theory of the evolution of feathers (Prum 1999). The complicated

process of the growth of a vaned feather implies that feathers must have evolved through a series of stages from simple to more complex. Each hypothesized stage was characterized by a new (evolutionarily novel), more advanced mechanism of feather growth, a highlight of the new scientific discipline "Evo Devo" (Carroll 2005).

The process of feather growth consists of five distinct stages. Each probably required a new mechanism of growth or a developmental novelty as feathers evolved their definitive form (Prum 1999; Figure 4–9). First in the series of evolutionary steps was the origin of an undifferentiated collar (stage I) followed by the formation of barb ridges (stage II), helical displacement of the forming barb ridges (stage III), differentiation of barbule structures (stage IV), and, finally, diversification of barbule structure and the positions of barbs (stage V). This model predicts that feathers were an undifferentiated cylinder at first (stage I), then a tuft of unbranched barbs (stage II), followed by a simple two-sided feather (stage III), a vaned, pennaceous feather structure (stage IV), and, ultimately, a diversity of feather structures that included aerodynamic functions (stage V).

Evidence in support of the developmental model of the evolution of feathers comes from the observation that feathers corresponding to each of the hypothesized stages are found on modern birds. For example, the cassowary wing feather is a simple tube that conforms exactly to the predictions of stage I. These modern feathers are secondarily simplified, but they demonstrate the capacity of feather follicles to produce all of the hypothesized morphologies.

Additional evidence in support of the developmental model comes from the molecular details of feather development. The same systems of signaling genes have been repeatedly co-opted, or reutilized, in the development of novel feather morphologies (Harris et al. 2002). These molecular data support the cause-and-effect cascade of developmental events in feather growth, and they corroborate the original hypothesis of a relation between the events in feather growth and feather evolution.

The known feathers of theropod dinosaurs also appear to fit the predicted early stages of the developmental model (Prum and Brush 2002). Specifically, there is good evidence that downy feathers (stage II) evolved in theropod dinosaurs before feathers with a planar vane (stage III or IV). Although some have disputed the homology of these structures to avian feathers (Feduccia 2002), definitive evidence of modern feathers on some raptor dinosaurs (e.g., *Microraptor*) is compelling.

The dramatic discovery of a variety of both primitive and completely modern feathers on numerous theropod dinosaurs, including the basal relatives of *Tyrannosaurus rex*, demonstrates that feathers first evolved in bipedal, terrestrial, meat-eating theropod dinosaurs before the origin of birds and before the origin of avian flight (see page 34). These discoveries suggest that birds are no longer the only feathered animals and that the biology of many familiar dinosaurs may be drastically different from what we once thought.

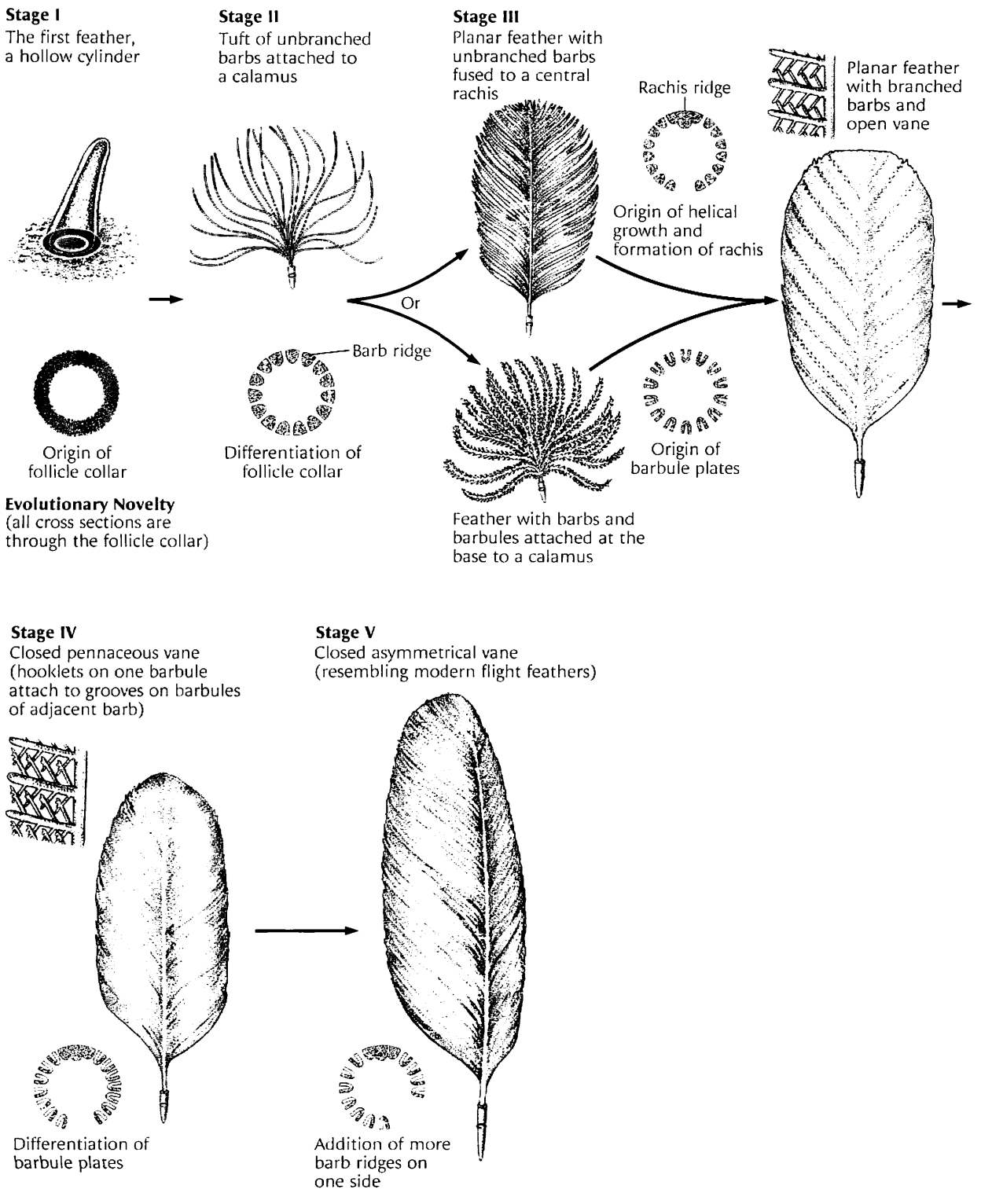


FIGURE 4–9 Evo Devo: The five stages in the evolution of feathers as an evolutionary novelty. This hypothesis corresponds to the key steps in the growth and maturation of modern feathers in living birds. [*After Prum and Brush 2003*]

Feather Colors

The stunning colored plumages of birds are one reason for their popular appeal. Male Painted Buntings of the southeastern United States sport patches of brilliant reds, greens, and blues. The tiny Many-colored Rush-Tyrant of South America features red, orange, blue, green, yellow, black, and white; locally, it is called *Siete Colores*, meaning "seven colors." At the other extreme are drab gray olive birds, including many flycatchers of North and South America and the leaf warblers *(Phylloscopus)* of Europe and Asia.

Feather colors come in all shades, hues, and tints, owing to biochrome pigments deposited in the barbs and barbules and to nanometer-scale features of the feather structures. Biochrome pigments are naturally occurring chemical compounds that absorb the energy of certain wavelengths of light and that reflect the energy of other wavelengths to produce the observed colors. Structural colors result from the physical alteration of the components of incident light. Pigments and structure often operate together.

Biochrome Pigments

The three major categories of feather pigments are melanins, carotenoids, and porphyrins. Melanins produce earth tones—grays and blacks, browns, and buff colors. Carotenoids produce bright yellows, oranges, reds, and certain blues and greens, except in parrots (see page 96). Porphyrins are responsible for particular bright brown and green feather colors and a unique magenta.

With the exception of albinos, almost all birds have some melanin pigment in their feathers. Melanin pigment is synthesized from the amino acid tyrosine by mobile pigment cells called melanoblasts, which creep about in the inner (dermis) layer of the skin. Under the direction of genes that encode the melanocortin receptor, melanocytes manufacture and insert melanin granules into specific cells that are destined to become particular barbs and barbules. Periodic deposition into the embryonic feather structures during development produces subtle color patterns such as barring or speckling (see Prum and Williams 2002 for advanced models of this process). The density of melanin deposition defines shades of brown or gray.

Two kinds of melanin prevail in bird feathers. Eumelanins are large, regularly shaped, blackish granules that produce dark brown, gray, and black. Phaeomelanins are irregularly shaped, reddish or light brown granules that produce tans, reddish browns, and some yellows. Color patterns often correspond to the predominance of either eumelanins or phaeomelanins. In the plumage of the Gray Catbird, for example, eumelanins produce the lead-gray color of most of the plumage, but phaeomelanins produce the rusty color of the undertail coverts.

Melanins perform many functions. The extra keratin associated with melanin makes the feather more resistant to wear (Burtt 1979). Dense melanin concentrations in the black wing tips of high-speed aerial species,

such as gulls and gannets, reduce the fraying of those feathers. Melanins help protect the feathers of desert species from sand abrasion.

Melanins also increase a feather's resistance to degradation by bacteria that reside in feathers (Goldstein et al. 2004). The ubiquitous soil bacterium *Bacillus licheniformis* secretes an enzyme that erodes the beta-keratin matrix of the feather. Black feathers with melanin suffer less erosion than do white feathers, which lack melanin. This finding helps to explain why birds of wet climates tend to be dark colored (Burtt and Ichida 2004; Shawkey and Hill 2004). Better camouflage in darker, wetter habitats is the traditional explanation. But birds in wetter climates also bear higher densities of bacteria in their plumage, which would favor higher levels of feather melanin to increase resistance to destructive bacterial enzymes. In addition, melanins absorb radiant energy, which aids thermoregulation (see Chapter 6). There is speculation that melanin granules promote the drying of damp feathers by absorbing and concentrating radiant heat in the feather microstructure (Wunderle 1981). If true, this activity would supplement the advantages of resistance to bacteria and of camouflage—reasons favoring increased melanin deposition in wetter climates.

Carotenoid pigments are responsible not only for most bright red, orange, and yellow colors but also for some purple and ultraviolet colors. They are derived from a bird's diet and signal its individual qualities (Box 4–4). After their assimilation, they can be modified and used as pigments in many ways. Carotenoid pigments metabolized in the follicle itself accumulate in droplets of lipid in the cells of growing feathers and are then left

BOX 4–4

BRIGHT RED MARKS THE BEST MALE HOUSE FINCHES

The male House Finch varies in plumage color from bright to pale red or even yellow orange. With a series of elegant experiments, Geoffrey Hill (2002) demonstrated not only that the plumage color of the male House Finch is related to diet, but also that females prefer brightly colored males to dull-colored males.

High-quality males apparently have intrinsically superior foraging ability and better access to carotenoid-rich foods that brighten their colored badges. Both the intensity and the extent of red carotenoid pigmentation in the plumage are due to the carotenoid pigments that they eat while they are replacing their feathers during the annual molt; these finches cannot use carotenoids stored in advance of the molt to achieve a brighter plumage.

Because bright red pigmentation serves as an accurate badge of male quality, the female House Finch uses the red color badge to pair preferentially with the best males. Brightly colored males are better providers for their families: they bring more food to their females during incubation and to their nestlings. Females paired with dull-colored males more often abandon the breeding effort, apparently because of inadequate provisioning by their mates. Bright red males also survive the winter better than dull-colored males do and thus are available for more than one breeding season.

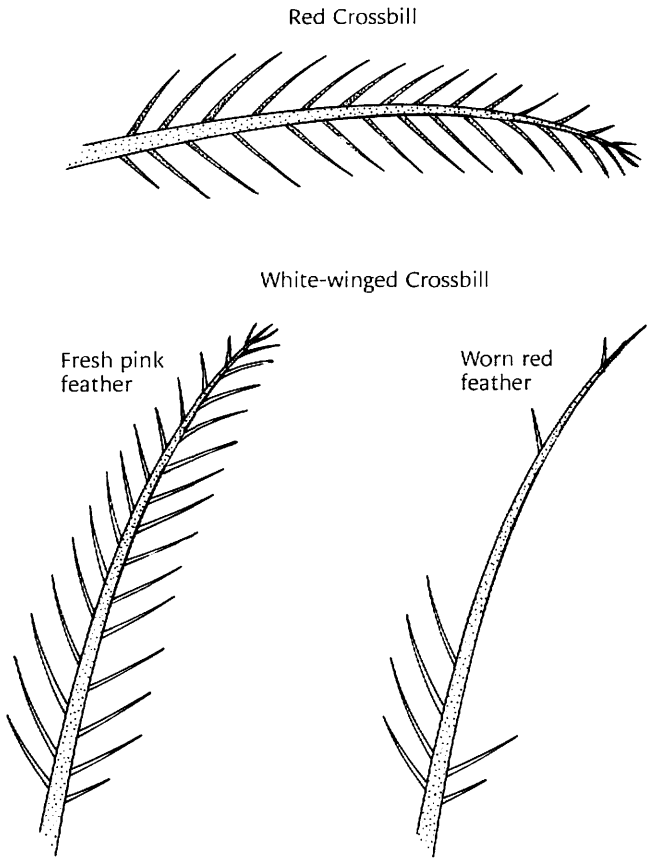


FIGURE 4–10 Red carotenoid pigment (stippling) is deposited in both the barbs and the barbules of feathers of the Red Crossbill but in only the barbs of the feathers of the White-winged Crossbill, leaving the barbules clear. The feathers of the Red Crossbill are deep brick red, whereas those of the White-winged Crossbill are pink. The White-winged Crossbill plumage reddens as the unpigmented barbules wear off.

embedded in the barbs and barbules (Figure 4–10) when the natural fat solvents disappear during the last stages of keratinization (McGraw 2004). They also are often stored in egg yolk, body fat, and the secretions of oil glands.

The bright red feathers of parrots are not colored by carotenoid pigments. Rather, parrots produce their rainbow of red, orange, and yellow colors from a special set of lipochrome pigments called psittacofulvins, which they manufacture in the growing feather (McGraw and Nogare 2005).

Porphyrins are related chemically to iron-containing hemoglobin and liver bile pigments. They show intense red fluorescence under ultraviolet (UV) illumination. Porphyrins are present in the reddish or brown feathers of at least 13 orders of birds, notably owls and bustards. These pigments, however, are found primarily in new feathers, because they are chemically unstable and easily destroyed by sunlight. The best-known avian porphyrin pigment contains copper instead of iron. This pigment—

called turacin or uroporphyrin III—produces the bright magenta in the wings of the crow-sized turacos of African forests (see Figure 1–16F).

Chemically related to turacin is another unusual copper porphyrin pigment called turacoverdin, which produces the bright green colors of a few birds (Dyck 1992). Most of the green colors of birds result from combinations of yellow pigments and structural blue, or iridescence (see next section). Olive green colors usually result from combinations of melanins and carotenoids, one in the barbs and the other in the barbules. Turacoverdin creates the true green colors of turacos. It is also responsible for the green back and wing feathers of the Crested Partridge and the Blood Pheasant and for the green wings of the Wattled Jacana. Porphyrin pigments, however, are not responsible for the green head feathers of the Common Eider, which await chemical analysis and perhaps the discovery of a new pigment.

Structural Colors

Many of the brightest feather colors—rich parrot greens, shimmering bluebird blues, and explosive hummingbird iridescences—are structural colors that result from the physical alteration of incident light. Bright skin colors also may be structural (Box 4–5). In general, white is a structural color produced by the backscattering of all light wavelengths. In contrast, the backscattering of a specific subset of visible wavelengths produces structural colors of specific hues (e.g., blue, green, or red). This process, called coherent scattering or constructive interference, takes place by light waves bouncing off the interfaces of nanometer-scale structures in the bird feathers. The spatial periodicity of the structures creates predictable differences in the distance traveled by the scattered light waves. Most

BOX 4–5

STRUCTURAL COLORS OF BIRD SKIN AND EYES

Structural colors are prominent not just in the feathers of birds, but also in the skin and eyes of many birds. Structurally colored blue or green skin is known in at least 50 families of birds (Prum and Torres 2003). The structural colors of bird skin are produced by coherent scattering, or constructive interference, of light waves from arrays of parallel collagen fibers in the skin. The size and spacing of the fibers produces colors of various hues ranging from deep ultraviolet and blues to greens, yellows, and orange.

Dark blue skin colors tucked in next to the fleshy green eyebrows of the Velvet Asity, a species found only on Madagascar, reflect strongly in the near ultraviolet (Prum et al. 1999a). Ultraviolet structural colors are now known from the skin of the tragopans, Bulwer's Pheasant, Blue Coua, and Toco Toucan.

The colors of the irises of bird eyes are produced by a very complex mixture of carotenoid and pterin pigments and structural colors produced by iridophores (Oliphant 1987). Iridophores are pigment cells that include arrays of pigment crystals, and they are responsible for the structural colors of amphibian and reptile skin. In birds, they remain only in the iris and may have been lost elsewhere with the evolution of feathers.

wavelengths are scattered out of phase—that is, the peaks and troughs of the waves do not line up—and the waves cancel each other. The few waves that travel a complete return cycle will be in phase; by lining up, the peaks and troughs of these waves combine to produce a bright light of that wavelength. Arrays with larger periodicities will produce longer-wavelength, or redder, colors; those with smaller periodicities will produce shorter-wavelength, or bluer, colors.

Three different classes of structural features produce the structural colors of feathers (Prum et al. 1999b). First is the incoherent reflectance of all visible wavelengths from unpigmented feathers producing white when light scatters off cellular air bubbles. The Rock Ptarmigan has evolved large, irregularly sized air bubbles in the barbules that increase the magnitude of light scattering to match the brilliant white snow (Dyck 1979).

Coherent light scattering from arrays of melanin granules, called melanosomes, in the feather barbules produces a second class of structural colors (Figure 4–11). Melanin granules arranged in regular layers create iridescent colors that change hue with angle of observation or illumination.

Some birds have evolved air-filled melanin granules that make brighter colors than than do solid melanin granules. For example, from 7 to 15 layers of hollow, air-filled, pancake-shaped melanin granules produce the brilliant colors of hummingbirds. The intense metallic green colors of trogons and quetzals are made by hexagonal arrays of air-filled, capsule-shaped melanin structures. These structures must be regularly and precisely spaced to within 10 nanometers or the color produced will be observably different to another bird.

The third class of structurally colored feathers includes the noniridescent colors produced by air-filled cavities within the keratin of the medullary cells of the feather barb rami. Examples of these structural colors are found in the Blue Jay, the Eastern Bluebird, and the tropical Plum-throated Cotinga. These colors are produced by the same physical mechanism as that producing the iridescent barbule colors—coherent scattering—but they lack iridescence because the air bubbles are not organized in any laminar or crystalline order. Thus, these arrays tend to backscatter the same hue regardless of the angle of observation.

Pigments combine with structural colors to produce additional colors. The wild Budgerigar, for example, is green because of an association of yellow (probably psittacofulvin) pigment with structural blue. Mutant parakeets are blue rather than green because a single recessive gene blocks yellow pigment deposition. If the pigment is red rather than yellow, violet or purple results, as in the Pompadour Cotinga (Brush 1969). Structural blue from the barbs plus red pigment in the barbules is responsible for the purple head feathers of the Blossom-headed Parakeet.

Ultraviolet Reflectance

The feather colors of birds, especially blues and violets, are rich in UV reflectance. The powerful blue color of the male Eastern Bluebird and Western Bluebird *(Sialia)* includes strong UV components, produced by

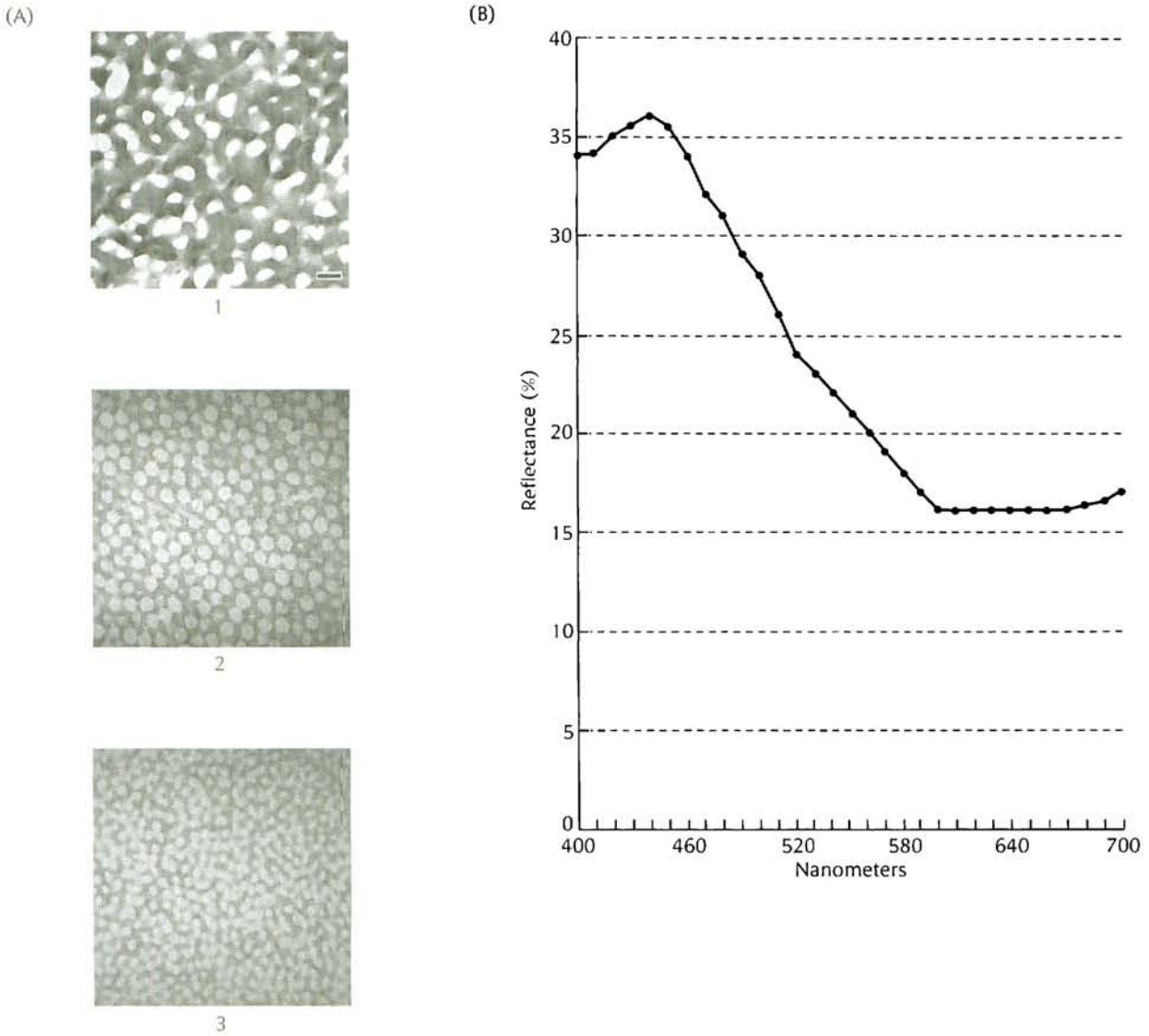


FIGURE 4–11 Coherent light scattering. (A) Transmission electron micrographs of the spongy medullary keratin matrix from (1) green feather barbs of a Budgerigar parakeet; (2) blue back feather of a Spangled Cotinga; and (3) blue back feather of an Asian Fairy-bluebird. The white spaces are air; the gray spaces are the beta-keratin of the feather. (B) Reflectance spectra from the barbs of a Budgerigar. [*From Prum et al. 1999b*]

coherent light scattering by the medullary nanostructures of the barb. The difference between the bright color of male bluebirds and the more subdued color of females corresponds directly to the thickness of the spongy layer of barbs responsible for coherent light scattering and the details of its internal nanostructure, such as the size of the air spaces (Shawkey et al. 2003). Most, but not all, UV colors are structural; some carotenoid pigments also have significant UV reflectance.

Such UV reflectance, as well as differences between sexes, appears to be a general and ancestral feature of bird-feather coloration, not an occasional oddity. Almost all of 312 species surveyed, belonging to 142 bird families, have significant amounts of UV in their color spectra (Eaton and Lanyon 2003). All-white birds, such as the sheathbills of Antarctica (Chionidae), lack UV reflectance. The only other taxonomic group in this survey that lacks UV coloration is the Rhea of South America.

The importance of UV reflectance to bird biology and behavior has been overlooked until recently, largely because humans can't see UV wavelengths. But birds can; they have a fourth, UV-sensitive cone in their retinas, which humans lack. For example, the brilliant carotenoid color of the Scarlet Ibis looks red to humans, but it also has a substantial UV reflectance that is visible to birds. So, to birds, this color resembles a type of purple that combines red and ultraviolet and appears very different from the pure red hue that humans see.

Sexes of birds that appear the same in colors visible to us may differ dramatically in the UV patches that influence mate choice, with consequences. Brighter male bluebirds are better mates. They pair earlier, feed young more often, and fledge more young than do males with weaker ultraviolet sheens (Siefferman and Hill 2003). Previously unrecognized differences between species are being discovered. Two extremely similar species of mountain tanagers (Black-chinned and Blue-winged) of the Andes of South America differ in the presence versus the absence of a strong ultraviolet band on their backs (Bleiweiss 2004). The difference is accurately related to which populations are reproductively isolated and which are not.

Genetic Control of Feather Color

Except for those of chickens, little is known about the genetic control and inheritance of feather colors (Buckley 1987). The presence, absence, and pattern of deposition of particular pigments is often controlled by genes that segregate and recombine in predictable combinations, just as the genes that control blue eyes versus brown eyes in humans do. Analogous to human eye colors are alternative plumage colorations, called color phases, in birds. The Gouldian Finch, a brightly colored Australian species commonly kept as a cage bird, comes in red-faced, black-faced, and yellow-faced color phases. Genetic color morphs are widespread among bird species. They include dark-colored versus white phases of herons, seabirds, and geese; rusty versus gray phases of owls and nightjars; black versus pied phases of oystercatchers and passerine songbirds; and buffy versus grayish downy chick colors of swans, geese, and terns.

The Feather Coat

The feather coats of most birds consist of thousands of feathers. A Tundra Swan has roughly 25,000 feathers, of which 20,000 (80 percent) are on its head and neck (Wetmore 1936). Songbirds typically have from 2000 to 4000 feathers, of which 30 to 40 percent are on the head and neck.

The lightness of a single feather belies the total weight of a bird's feather coat. In general, on the basis of comparisons of weights of feathers and prepared skeletons of 142 birds of 57 species, the feather coats of birds weigh about twice as much or more than their dried bones, with a wide range of values (R. C. Banks, pers. comm.). The plumage of a Bald Eagle weighs about 700 grams, more than twice as much as its skeleton (272 grams) (Brodkorb 1955), and between 17 and 20 percent of its total adult body mass.

Although feathers cover the entire body of a bird, they are not attached to the skin evenly or uniformly in most birds. Rather, feather attachments are grouped in dense concentrations called feather tracts or pterylae, which are separated by regions of skin with few or no feathers, called apteria. The feather tracts themselves are not evident without close examination, because the feathers spread out from them to cover the entire body. The nine major feather tracts (Figure 4–12) are subdivided into as many as 100 separate groupings, which distinguish avian taxa. The study of these arrangements is called pterylosis.

The functional significance of feather tracts and apteria has not yet been established. For years, ornithologists doubted that they had functional

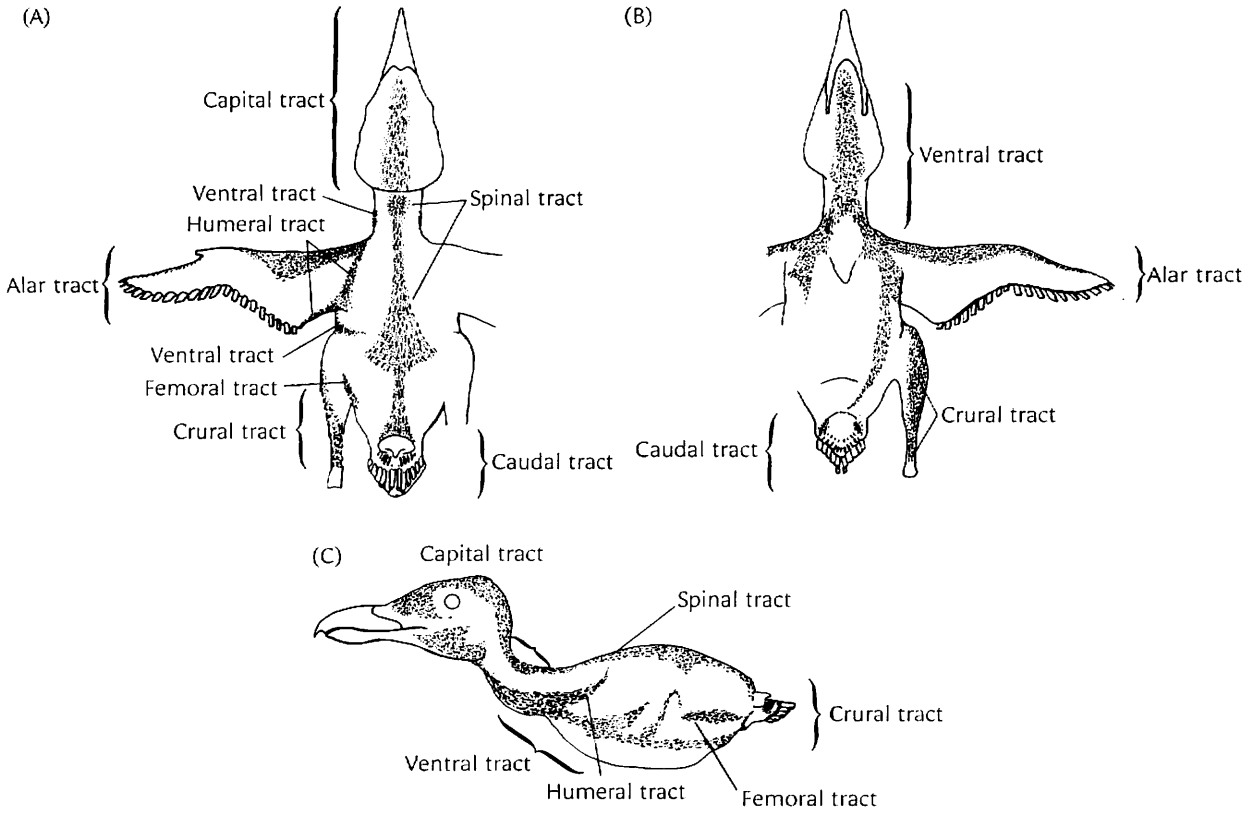


FIGURE 4–12 The nine major feather tracts, or pterylae, of a Loggerhead Shrike. Bare or nearly featherless areas between the tracts are called apteria. (A) Dorsal view. (B) Ventral view. (C) Lateral view. [*After Van Tyne and Berger 1976*]

significance and hence were good taxonomic characters (P. Stettenheim, pers. comm.). The apteria probably facilitate the movement of skin and feathers. They also facilitate heat loss during flight, perhaps their most important function (see Chapter 6): penguins lack them. The bases of adjacent follicles are linked by an elaborate network of tiny muscles. The muscles not only raise and lower the feathers but also, in some cases, twist them or pull them closer together. In short, they are capable of quite a range of movement. Temperature regulation and display are probably among the most common reasons why feathers are moved, but they are not the only ones. Other reasons include to adjust buoyancy, wing surface, or tactile sensations.

Feather Care

Daily care of feathers is essential. Feathers are inert and do not have an internal system of nourishment and maintenance. They would become brittle with age and exposure were it not for regular applications of the waxy secretions of the uropygial gland, or preen gland, located on the rump at the base of the tail. This gland, which is found in most birds, evolved as an essential accessory to feathers. Most preen glands are bilobed structures with a small tuft of downlike feathers encircling the glandular orifices of a well-differentiated papilla (Figure 4–13).

The preen gland secretes a rich oil of waxes, fatty acids, fat, and water, which, when applied externally with the bill, cleans feathers and preserves feather moistness and flexibility. Regular applications of the secretion to the plumage sustain its functions as an insulating and waterproofing layer. The largest preen glands are found in birds that swim, dive, or rest on water, such as petrels, pelicans, ducks, and grebes (Johnston 1988). Whether their secretions are essential for keeping feathers dry and pliable and for maintaining buoyancy remains to be verified. The water repellency of penguin feathers depends chiefly on the fine structure of the barbs, not on the uropygial secretion (Kostina et al. 1996).

The waxy secretions of the preen gland also help to regulate the bacterial and fungal floras of feathers. Certain preen-gland lipids protect feathers against fungi and bacteria that digest keratin, thus influencing both insulation and color (Shawkey et al. 2003). Others may promote the growth of nonpathogenic fungi and discourage feather lice. Such chemical hygiene is among the most important functions of preen-gland secretions. The foul-smelling preen-gland secretions of hoopoes and wood hoopoes of Africa may also repel mammalian predators.

Living among the feathers themselves are unique and diverse bird parasites, including chewing lice, louse flies, and feather mites (Proctor and Owens 2000; Figure 4–14). These parasites have been with birds for a long time: the fossil record includes a 44-million-year-old bird louse with feathers in its gut (Wappler et al. 2004). Chewing lice, or mallophaga, feed on the feathers themselves as well as on blood or tissue fluids. As many as 12 species may inhabit the plumage of one bird, with each species

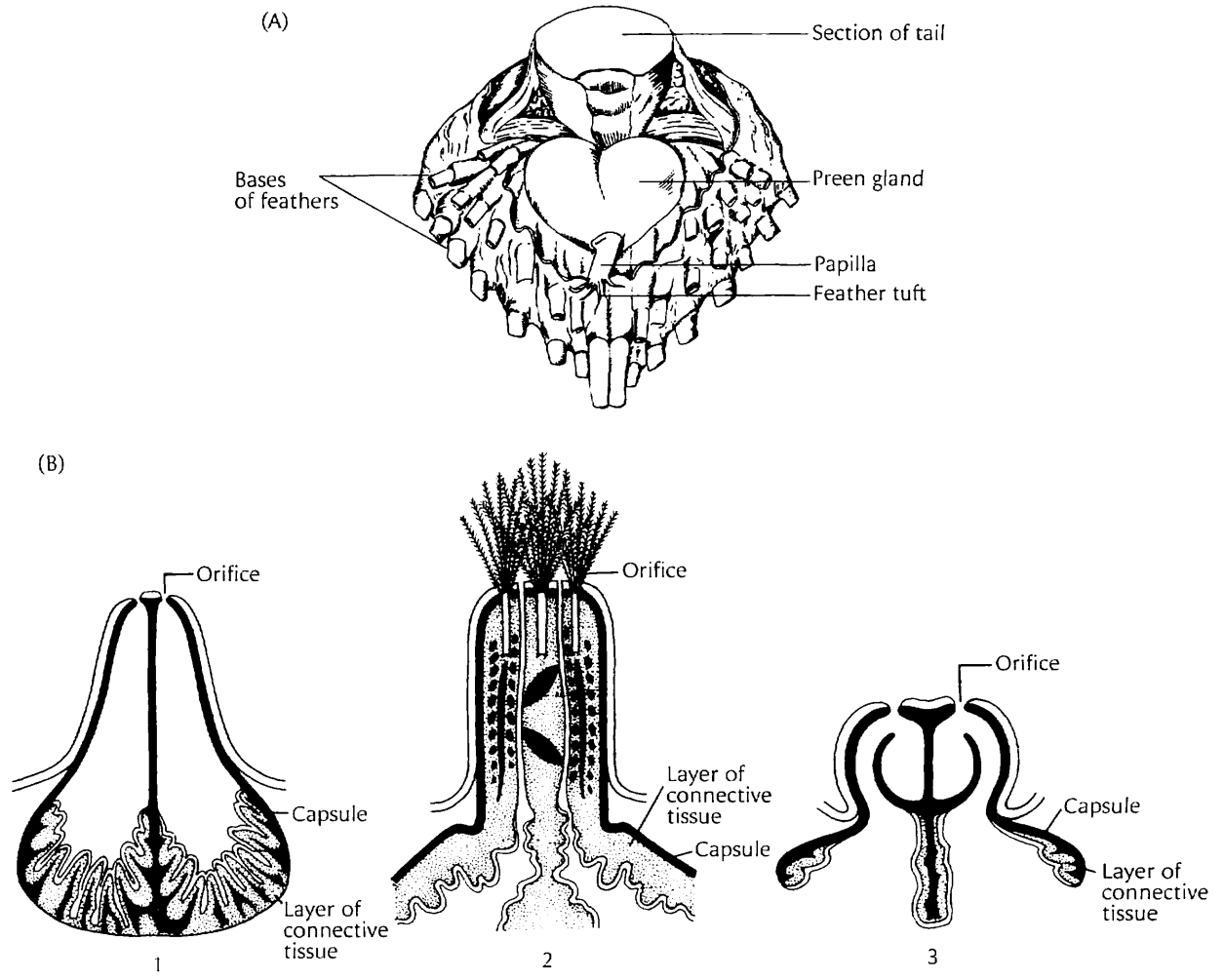


FIGURE 4–13 At the base of the tail on the lower back of most birds is the preen gland, which produces oily secretions that are essential for feather care. (A) Dorsal view of the gland and its environment on a White Leghorn Chicken. (B) Details of papilla: (1) delicate type; (2) compact type; (3) unique passerine type. [*(A) After Lucas and Stettenheim 1972. (B) Adapted from Jacob and Ziswiler 1982*]

specializing on different kinds of feathers or parts of the body. Louse flies are flat, tough, clawed, bloodsucking flies specialized for living in the feathers of birds and the fur of mammals. More than 150 species are known to parasitize birds. Louse flies are the principal vectors of blood parasites and aid the transport of chewing lice and feather mites from one host to another. Feather mites live their entire life cycles on their avian hosts and include many species specialized for particular feather microhabitats. Some live on the feather surfaces; others live inside the feather shaft.

Feather-chewing parasites damage the structural integrity of feathers, reducing both winter survival and the attractiveness of male pigeons, for example, to females (Clayton 1990, 1991; see Figure 4–14). Feather damage

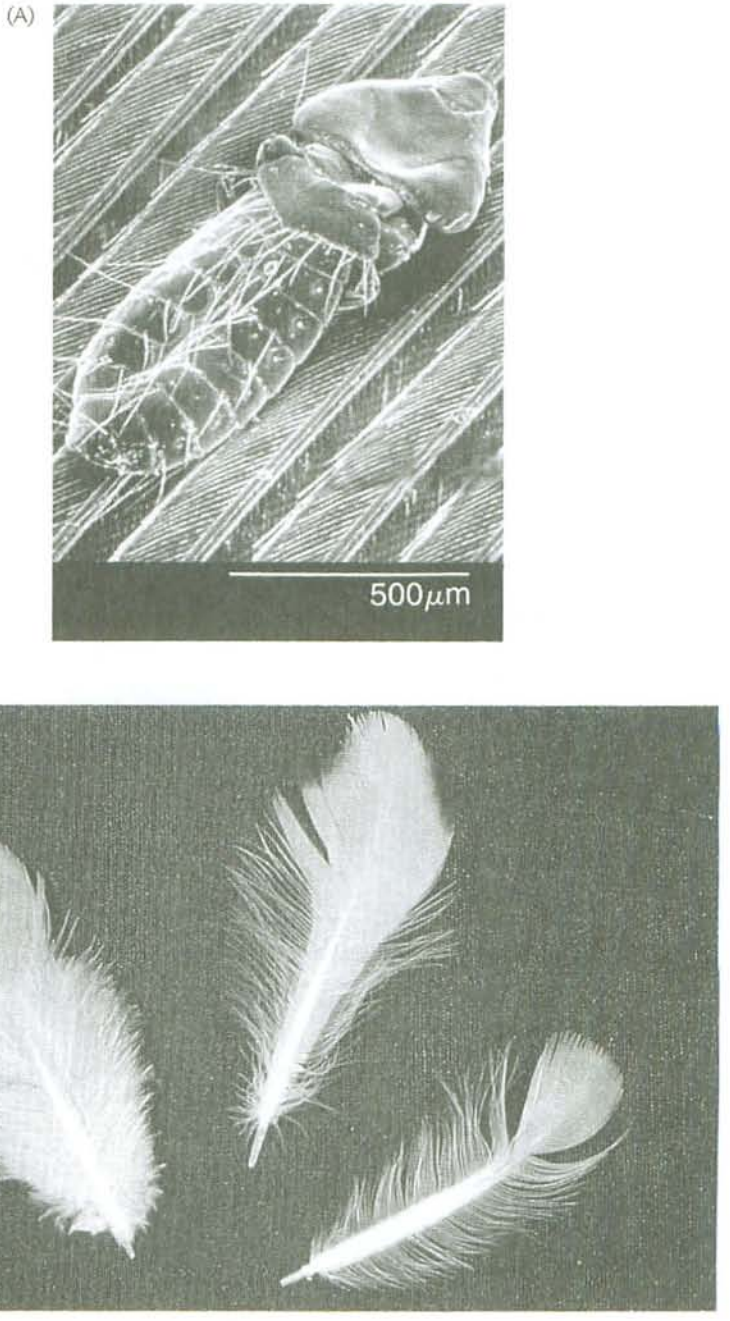


FIGURE 4–14 (A) Scanning electron micrograph of a chewing louse (*Philopterus* sp.) on a host's feather. (B) Damage to abdominal contour feathers done by feeding lice: (*left to right*) no damage, average damage, and severe damage. Only the basal downy region and the barbules of the basal and medial regions of a feather are consumed, never the distal region. The barbs and shaft are not damaged, apparently because they are too large to ingest. [*From Clayton 1990, courtesy of D. Clayton and K. Hamann*]

reduces the insulating quality of feathers and thereby causes metabolic heat production to increase by as much as 8.5 percent (Booth et al. 1994).

Birds may preen their feathers as often as once an hour while resting. They systematically rearrange their plumage with their bills and reposition out-of-place feathers. They also draw the long flight feathers individually and firmly through the bill to restore the vane's integrity and to remove parasites. Birds groom and delouse head and neck feathers by vig-

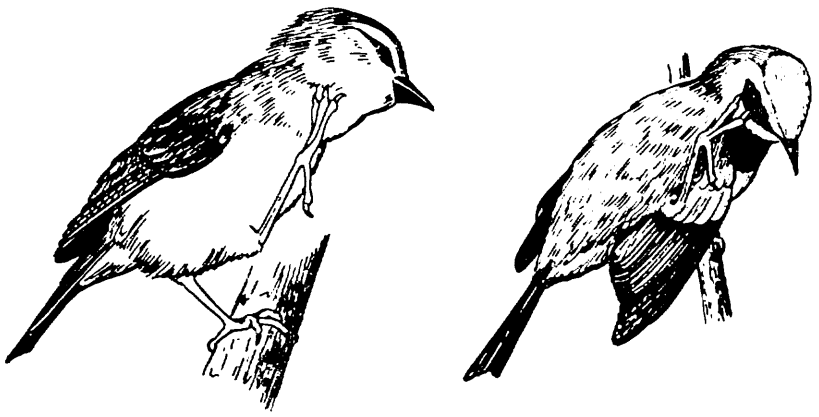


FIGURE 4–15 Head-scratching techniques. (A) Tennessee Warbler scratching directly, with foot under the wing. (B) Golden-winged Warbler scratching indirectly, with foot over the wing. [*From Burtt and Hailman 1978*]

orous scratching. Herons, nightjars, and barn owls have miniature combs on their middle toe claws that are used in grooming. Most birds scratch their heads directly, reaching up under the wing with a foot, although some scratch indirectly, over the wing (Figure 4–15). The advantage of one method over the other is not apparent but may be due to phylogenetic relationships. Crippled and one-legged birds cannot scratch their heads properly and, as a result, accumulate large, uncontrolled populations of lice on their heads.

Until recently, birds were thought to lack poisonous chemical defenses, such as those of some brightly colored frogs and insects. However, certain New Guinea forest birds—the three species of shrike-thrushes called pitohuis—are toxic. Jack Dumbacher and his colleagues (1992) discovered that the skin and feathers of pitohui shrike-thrushes contain a deadly alkaloid neurotoxin. The Hooded Pitohui, in particular, carries large amounts of poison. Indigenous New Guinea peoples knew that pitohuis made them sick if eaten without special preparations. The feather poisons of pitohuis, some species of which are bright rusty orange and black in color, are similar in chemical structure to the batrachotoxins of the deadly arrow poison frogs of South America. Still needed are the answers to several key questions. Do birds produce this poison or acquire it in their diet, perhaps from small beetles known to have high concentrations of this toxin (Dumbacher et al. 2004)? Either way, how do they keep from poisoning themselves when they preen? What are the benefits, if any, of carrying these potent toxins?

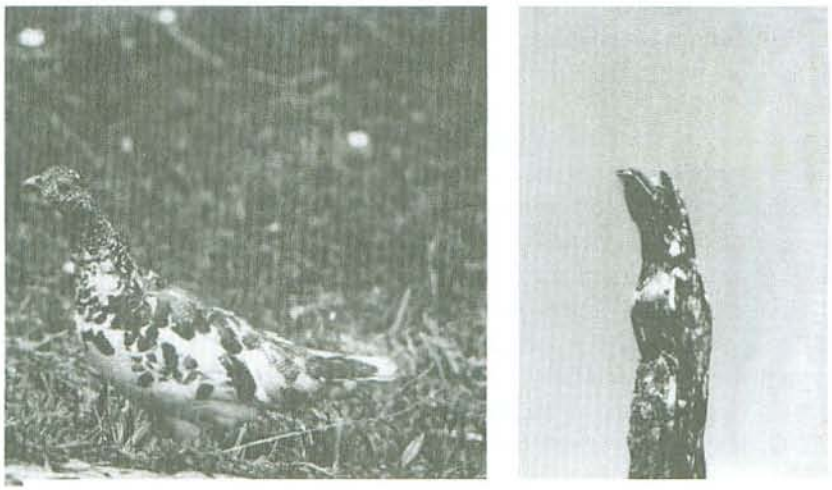
Plumage Color Patterns

Plumage colors, the great composite of individual feather colors, vary in hue from drab to bright and in pattern from cryptic (concealing) to bold.

Concealment is the first role of bird color patterns, not just of those that are obviously cryptic, but also of many bold or bright patterns that match a bird's usual environment. Ptarmigan are nearly pure white in winter, when they blend with the mountain snows. In spring, when patches of snow remain on the alpine meadows, the birds are white and brown (Figure 4–16A). In summer, when herbs and lichen cover the rocks, ptarmigan are finely barred black and brown. Woodcocks and Whip-poor-wills resting on a forest floor of dead leaves are invisible to us. Parrots disappear among the greens of tropical leaves and the reds of tropical flowers. The American Bittern points its bill skyward, aligning its body contours and the stripes on its breast with the surrounding vertical marsh grasses. The wood-colored Common Potoo of tropical America conceals itself by assuming the posture of a dead stump (Figure 4–16B).

Some bold color patterns reduce the contrast between a bird's shape or outline and its background. The double breast bands of the Killdeer, a small plover, are a classic example of a disruptive pattern. The bands visually separate the outline of its head from that of its body. To be most effective, the contrast between disruptive patches on a bird's body should be as great as that between the bird and its background. The finely patterned summer plumage of a ptarmigan blends with the finely patterned alpine grasses and lichens, and the boldly patterned plumages of the arboreal wood warblers of North America blend with the small leaves, branches, and lighting of trees.

Abbott Thayer and his son Gerald (1909) were the first to identify the principle of countershading in concealment. Lower reflectivity of the dark dorsal surface of a bird interacts visually with contrasting light un-



(A) (B)

FIGURE 4–16 Plumage coloration provides excellent camouflage. (A) The White-tailed Ptarmigan blends into an alpine meadow. (B) The Common Potoo looks like a dead stump. [*(A) Courtesy of A. Cruickshank/VIREO. (B) Courtesy of J. Remsen/VIREO*]

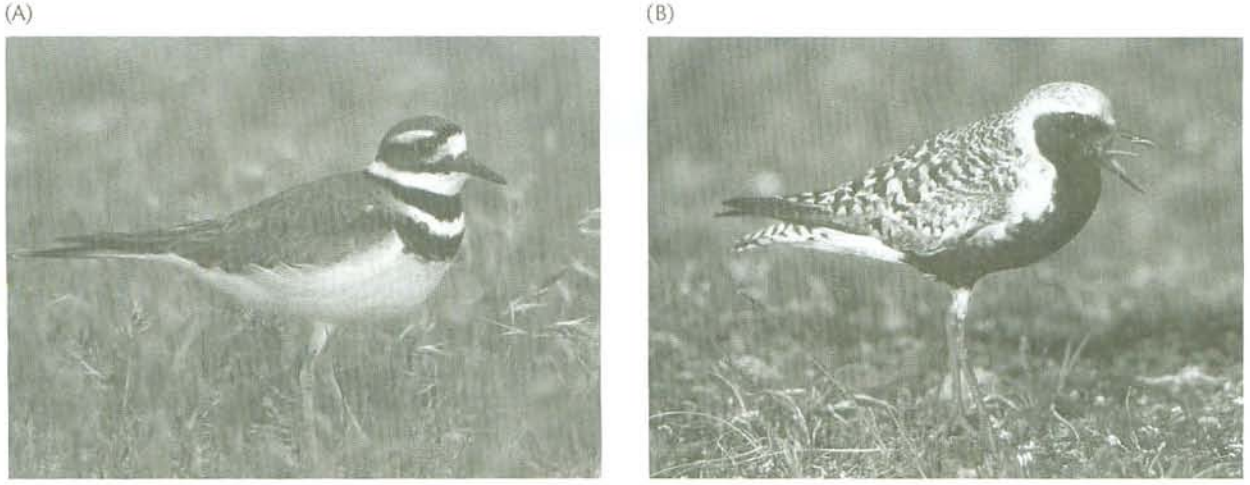


FIGURE 4–17 (A) The plumage pattern of a Killdeer (a plover) combines countershading, the achromatic reflectance of substrate by white underparts, disruptive head and breast markings, and breast bands that help match horizontal breaks in the shoreline or horizon. (B) The breeding plumage of a Gray Plover is an example of reverse countershading. [*(A) Courtesy of A. Morris/VIREO. (B) Courtesy of Doug Wechsler/VIREO*]

dersides to disguise its outline, helping it to match its background. The value of contrast increases with the intensity of illumination from above. Open-country birds, such as plovers, have strongly contrasting colors on their upper and lower surfaces (Figure 4–17A). White underparts work particularly well as a neutral (achromatic) reflector that takes on the hue of the nearest surface.

The advantages of bold color patterns for visual display during the breeding season can supplement or take precedence over the need for concealment. Whereas countershading enhances concealment, reverse countershading (white upperparts and dark underparts) renders the breeding male Spectacled Eider, Bobolink, and Gray Plover strikingly conspicuous (Figure 4–17B).

The signal values of plumage patterns are many (Figure 4–18). The uniform coloration of the all-red male Northern Cardinal enhances its outline and renders it more conspicuous than would a mixed color pattern; the crest probably enhances this effect. Contrasting edges enhance striking signal patches, such as the white crest of a Hooded Merganser, the orange crown stripe of a Golden-crowned Kinglet, or a Mallard's blue wing patch. Unusual shapes, especially those that are geometrically regular, such as the triangular white wing patches of an adult Sabine's Gull or the rectangular wing patches of ducks, are highly visible because they do not normally match the elements in a natural background. Regular repetition, such as in the tail spots of a Yellow-billed Cuckoo or the head stripes of a White-crowned Sparrow, achieve similar conspicuous results.

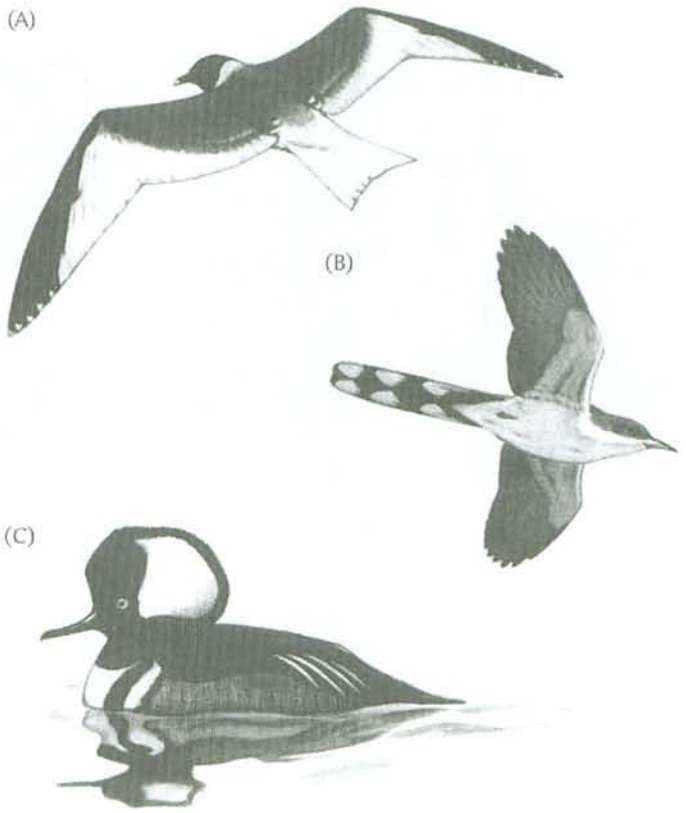


FIGURE 4–18 Conspicuous plumage signal patterns: (A) triangular wing pattern of an adult Sabine's Gull; (B) repeated white tail spots of a Yellow-billed Cuckoo; (C) outlined crest of a male Hooded Merganser.

Molts and Plumages

Every bird goes through a series of plumages, or feather coats, in its lifetime. Accidental feather loss triggers the growth of replacement feathers, but feathers are typically replaced in a comprehensive way, both seasonally and with age. The first natal down plumage may consist of a few scattered down feathers—the psilopaedic feather coat found on most hatchling land birds—or it may be a dense, fuzzy covering, termed ptilopaedic, like that of ducklings and chicks. The fragile down feathers rarely last more than a week or two. A more substantial set of downy or vaned feathers then replaces them. In loons and penguins, the second generation of down grows from the follicles of the first generation, pushing the old ones out. In hawks and waterfowl, the second coat of down grows from a different set of follicles.

Most birds have only one coat of natal down, which is pushed out of its follicles by incoming juvenal pennaceous feathers in the first weeks of life. Wisps of down may remain attached for a time to the new feathers. A baby bird's first set of wing and tail feathers appears at this time and grows rapidly in preparation for flight. As the young bird—now called a

juvenile—approaches independence, it exchanges parts of its juvenal feathers for new plumage.

Immature or adult plumage replaces the juvenal plumage of most of the feather coat, although not always that of the wings or tail. The young American Robin, for example, begins in midsummer to replace its spotted juvenal plumage with unspotted adult plumage (Figure 4–19). The first wing feathers remain. A few months later, its original flight feathers will propel the young robin on its first migratory flight. The bird will not molt again until it is just over one year old.

An adult bird typically molts after breeding, replacing its entire plumage. It may keep its new set of feathers for 12 months or it may replace some plumage before nesting the following year, converting somber camouflage plumage into brightly colored plumage for territorial display. Feathers of species that retain their plumage a full year may change in appearance because of wear. The Common Starling, which is spotted in the winter, loses its spots as the feather tips wear off; by spring, it is sleek and glossy. Meadowlarks also wear off the buffy feather tips of their winter plumage, exposing bold black and yellow underparts in the spring.

FIGURE 4–19 The spotted plumage of a juvenile American Robin, with residual tufts of down still attached to incoming head feathers.

Terminology

The terminology of molts and plumages relates a particular molt to the incoming generation of feathers, because feather loss is a passive result of the growth of new feathers (Humphrey and Parkes 1959). Additionally, the plumage that is renewed after breeding is considered the main component, or the "Basic" plumage, of the annual cycle of plumages, and breeding adornments are considered temporary additions, or "Alternate" plumages. Some ornithologists prefer other terms for molts and plumages (Howell et al. 2003; Jenni and Winkler 2004).

Consider the plumages of a male Scarlet Tanager, which wears an olive green Basic plumage in fall and winter and a bright red Alternate plumage in spring and summer. The plumage of a male Scarlet Tanager at any given time actually comprises a series of feather generations that bear testimony to the bird's age and the time of its last molt (Table 4–1). In its first month, a juvenile male Scarlet Tanager is olive green with olive brown wing feathers and streaked underparts. The first Prebasic molt in July and August produces the Basic 1 plumage, which resembles that of its unstreaked, olive green mother, except for black wing coverts that identify it as a male. In less than a year, this male tanager will undergo the Prealternate 1 molt, which replaces most of its olive green body plumage with red orange. Molting males appear with peculiar mosaics of differently colored old and new feathers: green, yellow, and orange. Even when fully red orange in May, the young tanager still has the olive brown wings that signal its first-year status; adult males have black wing feathers.

In its second fall, the male tanager undergoes the Prebasic molt of its entire plumage, replacing red orange body feathers with olive green winter, or Basic 2, plumage and replacing its olive brown wing feathers with jet black feathers. In the following spring, the Prealternate molt replaces winter plumage with a bright red breeding plumage. The maturing tanager now resembles other adult males and proceeds through regular cycles of Prebasic molt into camouflaged Basic plumage after breeding and

TABLE 4–1 Plumages and molts of a male Scarlet Tanager

Age	Molt	Plumage	Color*
0–1 month	Prejuvenal molt	Juvenal plumage	Green and brown
1–3 months	First Prebasic molt	Basic 1	Green and brown
8–10 months	First Prealternate molt	Alternate 1	Red and brown
1+ years	Second Prebasic molt	Basic 2	Green and black
1+ years	Second Prealternate molt	Alternate 2	Red and black

*Body and wings.

Prealternate molts into brightly colored Alternate display plumage before breeding.

The comparative study of molts and plumages reveals that some species, such as the American Robin and Common Starling, undergo only a single annual molt, whereas others, such as the Scarlet Tanager, have extra seasonal molts (Pyle 1997). One complete molt a year was probably the primitive pattern from which more complex molt patterns evolved, and it continues to be the typical pattern. Gradual feather replacement imposes the least metabolic stress on an individual bird, and a yearly molt is sufficient to offset normal rates of feather wear.

Multiple molts have proved advantageous for some birds as aids to seasonal display or as adaptations to severe feather wear or infestation by parasites. For example, in deserts, where wind and sand rapidly destroy feathers, some African larks molt completely twice a year. European larks, which suffer less abrasion, molt only once a year. Species that live in coarse grass habitats, such as the Bobolink (Figure 4–20) and Saltmarsh Sparrow, also may molt twice a year. Shedding parasites is one apparent result of the double molt in the Saltmarsh Sparrow. It has fewer feather parasites than the Seaside Sparrow, which lives in the same marshes but molts only once a year.

A few birds molt three or four times a year, but the extra molts are only partial ones. The Ruff, a large shorebird with an unusual lek mating system (see Figure 12–17), produces a variety of striking male breeding

FIGURE 4–20 Bobolinks molt completely twice a year. The male changes from a brown streaky plumage like that of the female in the winter (*left*), to a bold black-and-white plumage (*right*) in the spring.

plumage in stages. Ruffs undergo a standard Prebasic molt in the fall to assume a brown camouflaged winter plumage; a Prealternate molt in the spring, which produces most of its breeding plumage; and then a third supplemental molt, which produces the "ruff," which varies in color from white to rust to black and many combinations of these colors. The same set of follicles generates feathers of different types in the successive molts. To match their camouflage to the seasonal changes in the tundra, ptarmigan have three partial molts a year, and some populations of the Willow Ptarmigan have four.

Whereas geese have simple annual molt and plumage cycles, many ducks of the northern temperate regions have more unusual sequences in which the Prealternate molt starts before the fall Prebasic molt finishes. After they breed, drakes undergo a rapid Prebasic molt that often includes simultaneous loss of all flight feathers, rendering them flightless and vulnerable for several weeks. The Basic plumage that follows is a camouflaged, hen-colored "eclipse" plumage. Then an early Prealternate molt produces the drake's handsome breeding (Alternate) plumage in time for courtship and pair formation during the early winter.

Sequences of Feather Replacement

Molts of most birds follow a regular sequence within each feather tract. The usual sequence for the primary flight feathers, for example, is from the innermost primary outward to the last feather of the wing tip. In contrast with groups such as the ducks that become flightless because they molt all their flight feathers at the same time, regular and symmetrical sequences of flight-feather replacement help to maintain flight ability. The staggered replacement of the primaries and secondaries of the wings produces only small, temporary gaps in the wing surface and only a small reduction in flight power.

Like the flight feathers of the wing, tail feathers typically molt centrifugally from the innermost pair to the outermost pair, with some exceptions. Large Asian partridges called snowcocks use the 20 rectrices of their enormous tails for additional aerodynamic lift in sailing across steep ravines. Snowcocks have a pattern of tail molt that differs from that of other partridges: it starts in the middle of each side of the tail and proceeds slowly in both directions, a process that aids flight across deep mountain valleys. The extended display primaries of male Standard-winged Nightjars, mentioned on page 84, emerge last, out of normal sequence, apparently because they are a liability in flight.

The flight of birds, from the roles of feathers on the wings to the specialized flight abilities of different species, is the topic of the next chapter.

Summary

The avian feather is a unique structure that is versatile in form and function. Feathers provide insulation, which enables birds to maintain a high

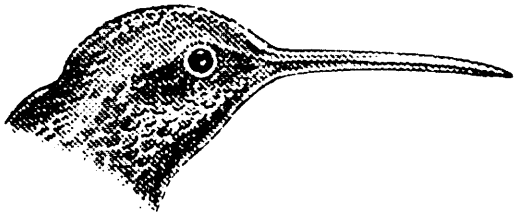
body temperature; they are essential for flight and serve in visual communication and camouflage. Modified feathers aid in swimming, sound production, protection, cleanliness, water repellency, water transport, tactile sensation, hearing, and support of a bird's body.

The basic structure of a body, or contour, feather consists of a stiff, central rachis with side branches called barbs and secondary side branches called barbules. The interlocking system of barbs and barbules forms a flexible but cohesive flat surface called the vane. Loose barbs and barbules at the base of the feather enhance insulation. Other major kinds of feathers include the flight feathers, down feathers, semiplumes, filoplumes, bristles, and powderdown. The tough, inert molecules that form the feather are a unique form of beta-keratin.

Feather coloration is controlled by carotenoid and melanin pigments, which are deposited in the barbs and barbules, and by the interactions of light with nanostructures in the feathers. Coherent light scattering by nanostructures of the barb is responsible for most of the blue and green colors of bird feathers. Iridescent colors result from reinforcement of certain wavelengths of light reflected by special layers of pigment granules. Ultraviolet reflectance by feathers, which is proving to be ubiquitous, enables birds to see plumage color differences that humans cannot see.

The entire feather coat consists of thousands of individual feathers, which are arranged in groups called tracts. Linking the bases of adjacent feathers is a system of tiny muscles that control feather position. The feather coat of a bird typically weighs two to three times as much as its skeleton. The entire feather coat is replaced at least once a year in regular molts. Partial molts may supplement the main annual molt to produce composite plumages.

CHAPTER 5



Flight

The pure acrobatic ability of birds far exceeds that achieved by the most sophisticated aircraft. [Dial 1994, p. 301]

Flight is the central avian adaptation. Yet birds do not merely fly. They are masters of the fluid that is air, just as fishes are masters of the fluid that is water. Birds can hover in one place, dive at breathtaking speeds, fly upside down and backward, and soar for days on end. Birds are one of nature's finest locomotor experiments (Dial 1994). Our best aircraft are inferior by a large margin.

Basic bird flight has many components—taking off, maneuvering, stabilizing positions, and landing—each of which is complex in its own right. Flight requires rapid and constant adjustments of the wings and tail. The sensory system sends information from thousands of individual feathers in a bird's plumage (see page 87) to the flight-control center in the brain and neural receptors throughout the body (Dial 1994; see page 200).

Flight is expensive in regard to short-term energy output but makes up for that investment in regard to cost per unit distance covered. Flight is the most economical form of locomotion: it costs less energy to fly 1 kilometer than to walk, run, or swim the same distance. A 10-gram bird in flight, for example, expends less than 1 percent of the total energy required by a 10-gram mouse to run the same distance. The high short-term costs of flight, however, favor efficient designs of a bird's wings as well as its skeleton.

This chapter first considers the elementary aerodynamic principles of flight, including the role of wings as airfoils, the phenomenon of lift, and the countering forces of thrust and drag. Different modes of flight—the gliding flight of soaring birds and the hovering of hummingbirds—help to illustrate these principles. The fundamentals of flapping flight follow, including the role of leading-edge vortices in generating lift. Then we review the anatomy of avian flight, particularly the skeleton and the highly developed breast muscles that power flight. Flightless birds also highlight the adaptations and tradeoffs required for flight. Some diving birds (such

as penguins) have traded aerial flight for underwater flight with the use of highly modified flipperlike wings.

Elementary Aerodynamics

To stay aloft, birds must overcome the forces of gravity and drag by generating equal and opposite forces—lift and thrust. Lift is the upward air-pressure force that counters the downward force of gravity, expressed as a bird's weight. Thrust is a forward force that counteracts the slowing influence of the forces of turbulence and friction, collectively called drag. When these four forces—weight, lift, drag, and thrust—are in dynamic balance, a bird maintains level flight at a constant speed. Unlike airplanes, which generate lift with wings and thrust with engines, birds use their wings to do both (Figure 5–1).

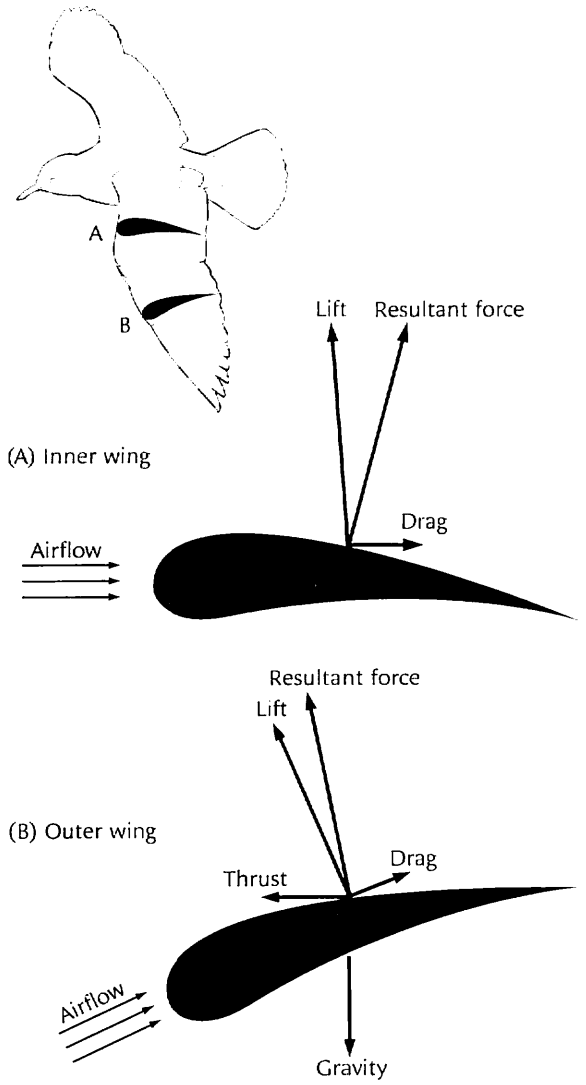


FIGURE 5–1 Aerodynamic forces on two cross sections of the wing of a gull. The upward force of lift counteracts gravity. The forward force of thrust counteracts the slowing force of drag created by friction and by air turbulence. The airfoil of the inner wing (A) generates mostly lift. The different orientation (angle of attack) of the outer wing (B) generates both thrust and lift. [*After Burton 1990*]

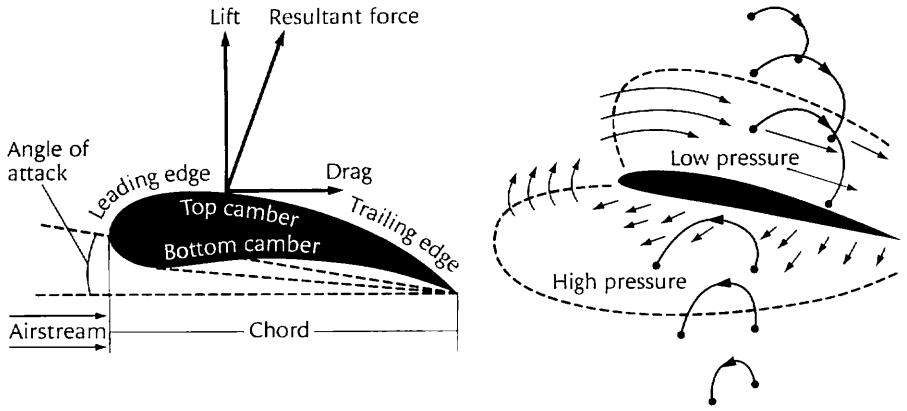


FIGURE 5–2 Functional anatomy of the airfoil. (A) Dimensions and their terminology. (B) The streamlined, asymmetrical shape of an airfoil produces lift by reducing pressure on the upper curved surface relative to that on the lower surface. Faster and more complicated airflow patterns on the upper surface reduce pressure there and contribute to the production of lift. Downward deflections of the airstream produce an opposite, upward-directed physical force. [*After Burton 1990; Long 1999*]

The wings of birds produce lift by the passage of the airstream across their surfaces, usually by forward movement into the airstream. Even a stationary wing, however, generates lift in a wind; for example, an albatross with outstretched wings will rise gently into a strong wind. In the simplest sense, the wings function as airfoils with properties like those of the wings of airplanes. The upper surfaces of an airfoil are curved more strongly than the lower surfaces, producing a curved structure that tapers posteriorly. The orientation, or angle of attack, of the airfoil with respect to the passing airstream, called "relative wind," produces the net upward force called lift. The angle of attack is defined as the angle between the direction of the airstream and the straight chord line connecting the leading and trailing edges of the airfoil (Figure 5–2A). The amount of lift generated must balance a bird's weight to sustain level flight.

Airfoils produce lift by altering the circulation of air around them, deflecting some of it downward, and by increasing the speed of airflow at the upper surface relative to its speed at the lower surface of the airfoil (Anderson and Eberhardt 2001; Kunzig 2001; see Figure 5–2B). Several components of the alteration of air circulation by the airfoil contribute to the production of lift.

Differential airspeeds across the airfoil produce lift, in part, as an expression of the Bernoulli principle. In brief, fast-moving air imparts less pressure against an adjacent surface than does slower-moving air, causing a net force upward in regard to the paired surfaces of an airfoil. The air deflected upward by the leading edge of the airfoil and then by its own inertia straight backward produces a space of lower pressure above the upper surface. Air rushes, or accelerates, from the high-pressure area ahead of the airfoil, and below it, into the low-pressure space being swept out

above and behind the airfoil. The direction of this movement is toward the trailing edge of the airfoil. As a result, air flows faster over the top of the airfoil than below it, creating a net upward force. If you were to blow gently over the upper surface of a piece of tissue paper, the tissue would rise or straighten out because of the net upward pressure on the lower side. The unequal pressures that develop as air flows over the surfaces of a bird's wing have the same effect. This effect is the classic explanation of lift. But the Bernoulli effect is just a small part of the circulation pattern generated by the airfoil and of the creation of the net upward force called lift.

New analyses of the aerodynamics of avian flight suggest that the primary function of the wing as an airfoil is to move air downward (Long 1999; Videler 2005). First, the leading edge of the airfoil and its tilted undersurface push into the air ahead of them, creating high pressure ahead of the wing and below it. The asymmetrically curved shape of the airfoil directs the airstream as a whole downward. Elementary physics (Newton's third law) tells us that, for every action, there is an equal but opposite reaction. The downward deflection of air by the airfoil, therefore, produces opposite upward forces of lift. In addition, the curved upper surface of the airfoil deflects some air particles upward at first, then backward, and finally downward in a slowing spiral motion toward the trailing edge of the wing. Their final downward trajectory adds more upward lift.

The amount of lift increases with airspeed and with the volume of air deflected, which in turn is a function of wing area. When a large bird, such as a gull or albatross, stands on the edge of a cliff facing into the wind, the flow of air across its outstretched wings generates lift. The amount of lift increases by the square of the velocity of the airstream. If the wind is strong enough, the bird rises effortlessly into the air. In still air, the seabird must jump off the cliff with wings outstretched. As the bird drops, airspeed increases, producing lift and, with it, flight. Birds that do not launch themselves from cliffs or trees may generate the initial forward thrust by running as they take off. Loons and some ducks run over the water until they become airborne.

The orientation, or angle of attack, of a wing in a current of air affects the generation of lift (Figure 5–3). More lift is generated as the pitch of the wing rotates clockwise, increasing the angle of attack and consequently the downward deflection of air. If the angle of attack is too great, however, the airstream no longer follows the streamlined surfaces of the airfoil. Instead, the air separates from the surface, then swirls upward and forward from the rear edge of the wing. The negative force called drag increases with the disruption of the airflow. Increased drag blocks the backward flow of air over the upper surface and causes a loss of lift, or a stall. When landing, a pilot purposely stalls an airplane by increasing the angle of attack of the wings just before the wheels touch the runway. Birds, too, adjust the angle of their wings to stall just before landing.

Slots between adjacent flight feathers aid in the fine control of the air moving over the wing surface and thereby aid in the extraction of lift-producing energy. Slots are cracks or holes through which air squeezes. Air forced from beneath the wing through a slot expands on the upper

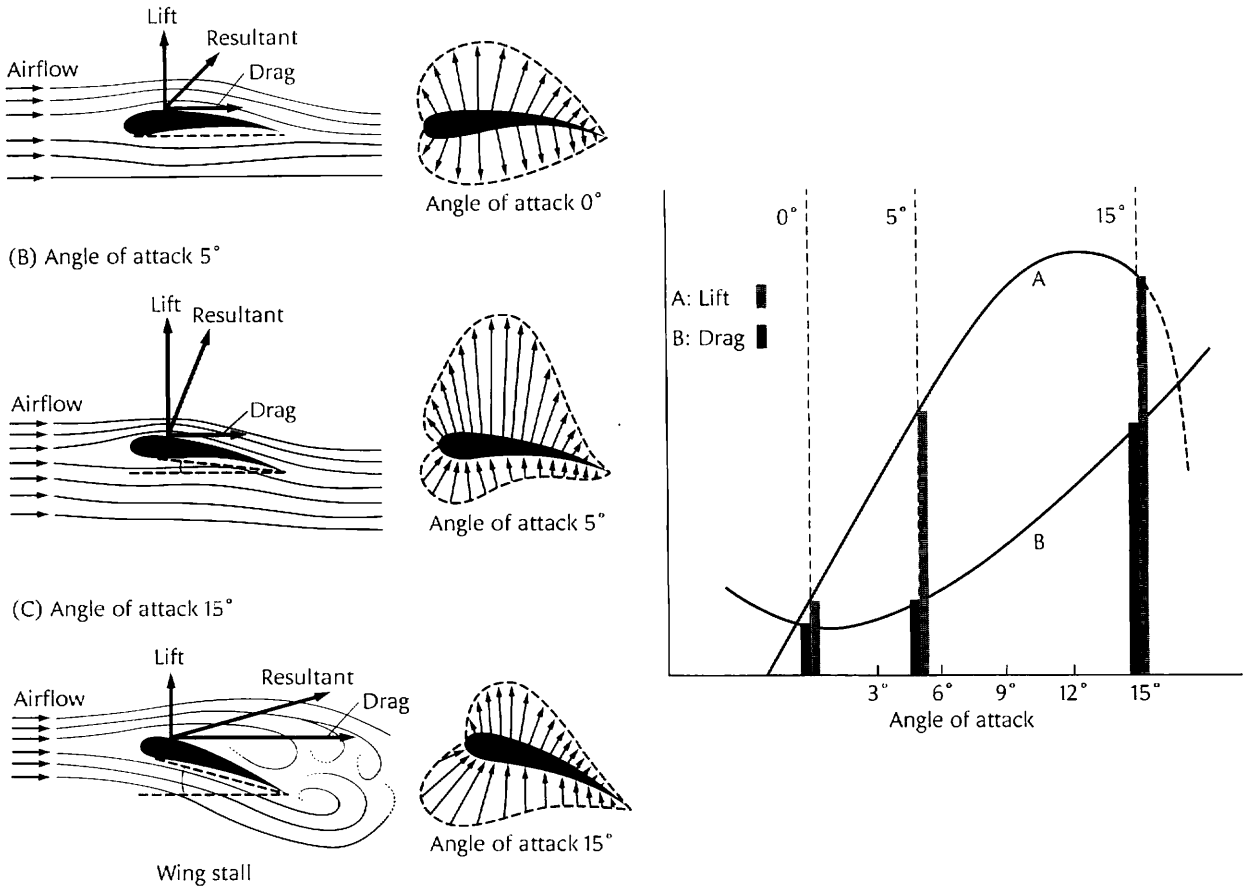


FIGURE 5–3 The angle of attack affects the balance of aerodynamic forces on the wing. The angles of attack illustrated are (A) 0, (B) 5, and (C) 15 degrees. Increasing the angle of attack by 5 degrees from a horizontal position increases lift, but increasing the angle by only 15 degrees causes the airstream to separate from the upper surface of the airfoil, which increases turbulent airflow, or drag, and severely reduces lift. Higher angles of attack will cause a loss of lift and the bird or airplane to stall. [*After Burton 1990*]

side, reducing the pressure there and increasing lift. The wing tips of many soaring birds include slots between the ends of the primary feathers (Figure 5–4). In effect, the slots permit the primaries to act as individual "winglets," reducing drag at the wing tip by redistributing the air turbulence horizontally and vertically. Some slots also control the flow of air over the airfoil to maintain some lift at slow speeds or at high angles of attack when a bird is stalling. The extended alula, or bastard wing, creates a slot at the leading edge of the wing that keeps airflow bound to the wing (Figure 5–5). This adjustment helps especially during landing and takeoff, when forward thrust is minimal and extra lift is essential to prevent stalls. Modern aircraft have these same sorts of slots in the front of the wing, which you can sometimes see opening on landing.

FIGURE 5–4 Slots reduce induced drag at the wing tip, aid fine control of airflow over the wing surface, and prevent stalling at slow airspeeds. Soaring birds such as the Turkey Vulture shown here have well-developed slots between the tips of the primary wing feathers. Slight adjustment of the primaries and their associated slots control a vulture's speed, lift, and aerial position as it searches the terrain for carcasses. [*A. Morris/VIREO*]

Any slight air turbulence or friction between the air and a bird's body and wing surfaces reduces lift through the opposing force of drag. The thin leading edges of the wings minimize friction, or profile drag. Similarly, the thin leading edge of a Frisbee makes it is easier to throw than a soccer ball. Friction, and therefore profile drag, increases with airspeed. Thus, it is harder to throw a Frisbee or a soccer ball or to fly into a strong wind with high airspeeds than it is to throw or fly into a light wind. Conversely, turbulence, or induced drag, decreases at faster airspeeds as air flows more smoothly over the wings.

Forward thrust provides the power to overcome the slowing effects of drag on airspeed. Propellers and jet engines provide thrust for airplanes. The downbeat of the wing stroke provides thrust for most birds. In keeping with Newton's second law of motion, thrust force equals mass (amount of air moved) times velocity (rapidity of the wingbeat). Similarly, a canoe paddle generates forward thrust by pushing water, instead of air, backward. The total thrust required to overcome the effects of drag is the sum of the thrusts required to overcome profile drag and induced drag. These two components of thrust are therefore called profile power and induced power, respectively.

Total flight-power requirements vary in a parabolic relation to flight speed, because induced power decreases as profile power increases (Figure 5–6). The energy cost of flying is least at intermediate speeds and

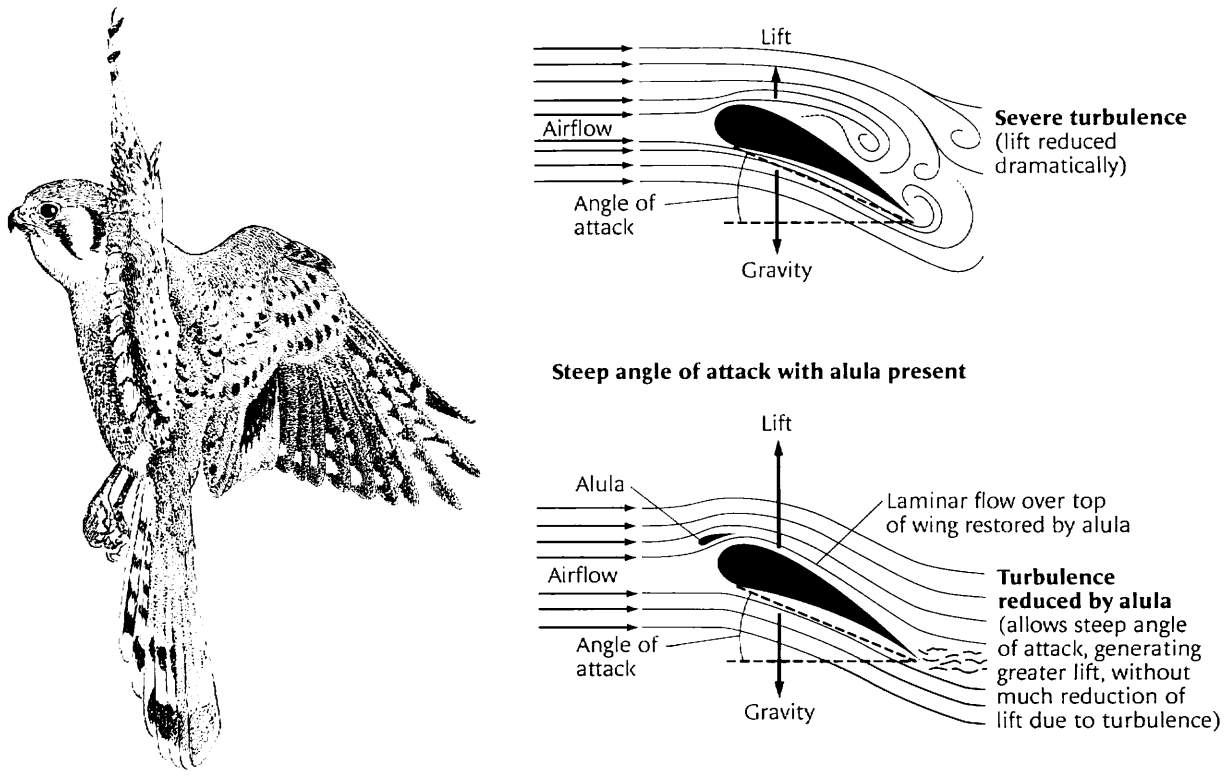


FIGURE 5–5 The slot created by the extended alula keeps the airflow close to the wing during takeoff and landing. [*After Able 2004*]

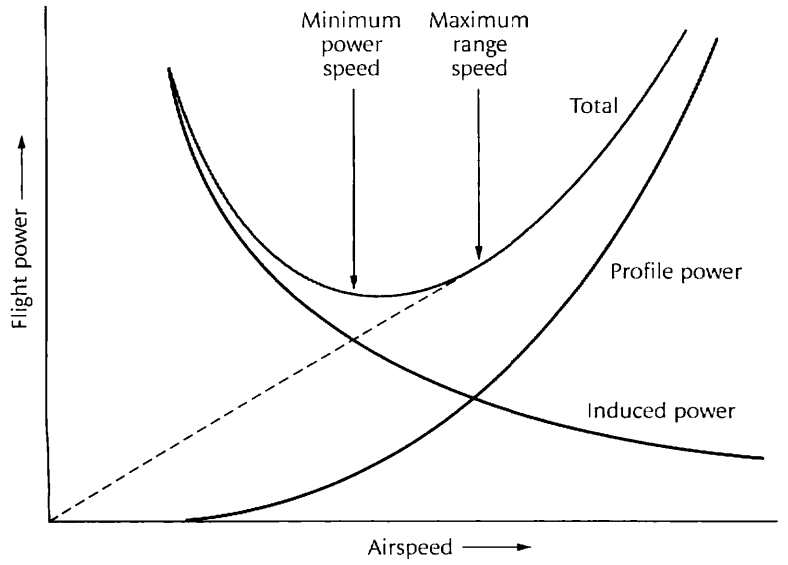


FIGURE 5–6 Total flight-power requirements are the sum of profile power (which increases with speed) and induced power (which decreases with speed). This sum bears a parabolic, or U-shaped, relation to airspeed. The total is least at minimum power speed, or the bottom of the parabola. The power required to fly a unit distance is least at the maximum range speed, which is defined by the lowest-value intersection of the (broken) line drawn from the origin (zero speed, zero power). [*After Alexander 1992*]

BOX 5–1

PEREGRINE FALCONS: SPEED STOOPING

The Peregrine Falcon (see Figure 21–9) achieves breath-taking speeds when diving, called stooping, on its aerial prey. Stoops are executed at angles ranging from 30 to 60 degrees, sometimes starting at more than 1500 meters from the prey and dropping from 450 to 1080 meters in altitude (White et al. 2002). Calculations of their airspeed by stationary observers range from 160 to 440 kilometers per hour (96–264 miles/hour). Arguably, the most direct measurements are those by a free-falling parachutist who accompanied his trained falcons in dives from 3670 meters, or 12,000 feet (Franklin 1999). At 240 kilometers per hour (144 miles/hour), the stooping falcon tucked in its wings and extended its shoulders to assume a diamond shape. At higher speeds (320 kilometers/hour, or 200 miles/hour), the falcon elongated and streamlined its shape to the maximum by pulling its wings in close to its body and extending its head. Keeping an eye fixed on the target prey while diving at such speeds is challenging, in part because the falcon's acute vision is to the side, not straight ahead. Turning the head would increase drag and slow the bird down. So the falcon instead adopts a spiral path that keeps its head straight and the prey in sight slightly to the side. Better aerodynamics of the body orientation more than compensate for the longer stoop path (Tucker et al. 2000).

greatest at low and high speeds. Hovering in one place with no airspeed is an energetically expensive mode of flight; flying very fast also is expensive. Birds tend to fly at their minimum power speeds (30–60 kilometers per hour), which minimize the rate of fuel use and maximize the time airborne (Rayner 1985a).

Birds do not always strictly adhere to flight speeds that minimize power costs (McLaughlin and Montgomerie 1990; Bruderer and Boldt 2001). Hummingbirds, for example, hover expensively in front of flowers to extract nectar, and they fly fast to beat competitors to nectar-filled flowers (Gill 1985). Peregrine Falcons dive on prey at breath-taking speeds (Box 5–1). Additionally, a bird should fly faster than its minimum power speed to achieve the maximum flight range with a given amount of fuel because the added momentum carries it farther for the same total power investment. Flight at this maximum range velocity is most characteristic of long-distance migrants, such as geese (Box 5–2). Migrating Common Swifts travel at about 40 kilometers per hour, close to their predicted maximum range velocity. In contrast, while feeding, Common Swifts cruise slowly at only 23 kilometers per hour, close to their predicted minimum power speed.

Kinds of Flight

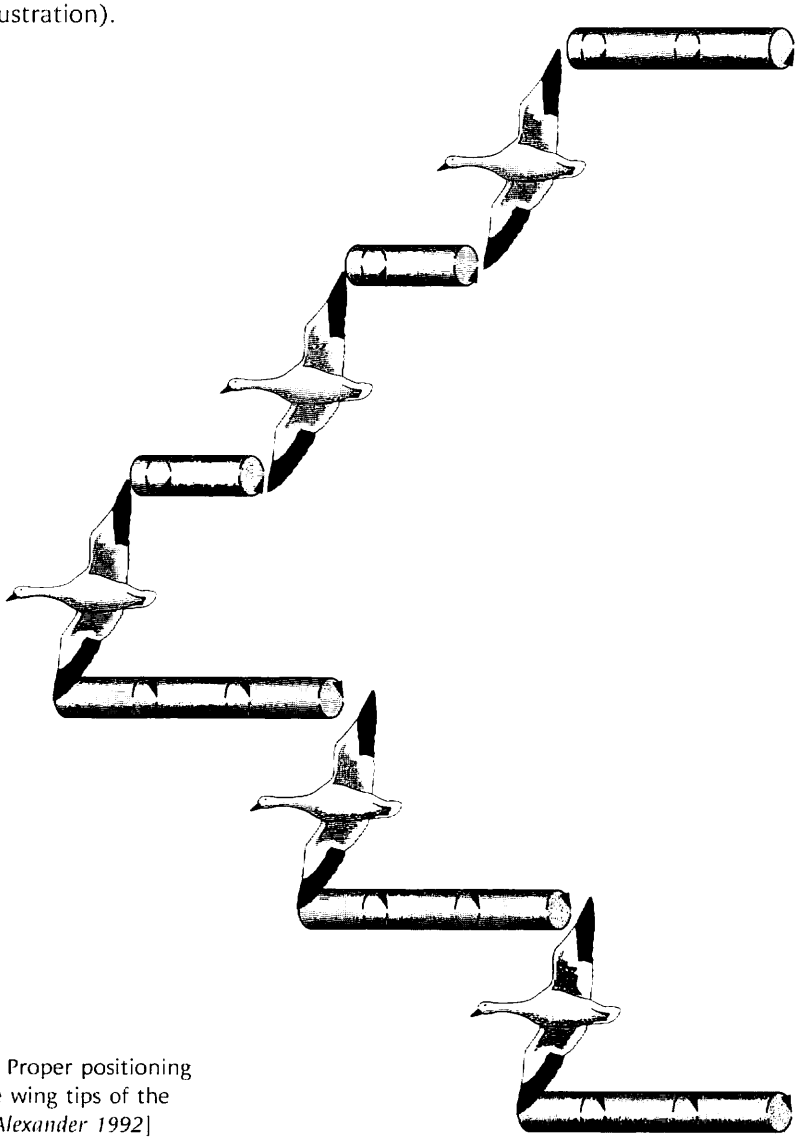
Beyond the basics, birds have exploited an extraordinary range of specialized modes of flight. Simple aerodynamic models and comparisons with airplanes do not always accurately apply to the dynamics of actual flight. Small birds, particularly, use varied forms of flapping flight that reduce

BOX 5–2

FLYING IN FORMATION

Flying in formation helps to save energy, especially in large or heavy birds, such as geese, with small wings relative to their mass (Badgerow 1988; Alexander 1992). By flying just off the wing tip of the preceding bird, each goose cancels some of the air turbulence at its own wing tips, which reduces induced drag and saves energy. In the familiar "Vee" formations of migrating geese, each individual bird flies off and behind the wing tip of the bird in front of it (see illustration).

The energetic advantage of formation flight could be as high as 50 percent. Direct measures of the energy output of pelicans trained to fly in formation proved that they use from 10 to 14 percent less energy in flight formation, partly because the group's airstream allows those in back to glide more than the leaders can (Weimerskirch et al. 2001).



"Vee" formation of migrating geese. Proper positioning relative to the air currents from the wing tips of the preceding bird saves energy. [*After Alexander 1992*]

profile drag and that level power costs in relation to airspeed. In this section, we start with simple forms of flight—soaring and gliding—and proceed to features of complex flapping flight.

Soaring, or Gliding, Flight

The soaring flight of vultures and many other birds illustrates how the forces of weight, lift, and drag work in this simplest form of flight. Without flapping their wings to apply forward thrust, soaring vultures gradually lose altitude in still air—that is, they "sink"—because of drag. Glider airplanes also sink at predictable rates that take into account their airspeed and wing dimensions. Sink rates are lowest when drag is lowest, at intermediate flight speeds. Soaring birds and gliders both counter their inevitable descent by taking advantage of rising air. The two principal ways of doing so are called thermal soaring and slope soaring.

Thermal soaring exploits columns of warm air that rise when the ground is heated by the sun (Figure 5–7). The soaring bird circles upward within the column of rising air and then glides to the base of an adjacent thermal. The bird continues to fall relative to the air, but air rises in thermals at the rate of approximately 4 meters per second, which easily offsets a sink rate of 1 to 2 meters per second. Colin Pennycuick (1972) pioneered the study of the gliding flight of birds by following vultures that commuted from their roosts to feeding grounds out on the Serengeti Plain of East Africa. He did so from his own plane, a motorized glider that could simulate the flight of the vultures but that could also generate thrust when necessary. The vultures could travel 75 kilometers by using only six thermals that rose to heights of 1500 meters. Migrating hawks, such as the Broad-winged Hawk in eastern North America, also use thermals, a practice that allows them to cover long distances with maximum economy. Flocks of Broad-winged Hawks, called "kettles," rising in air

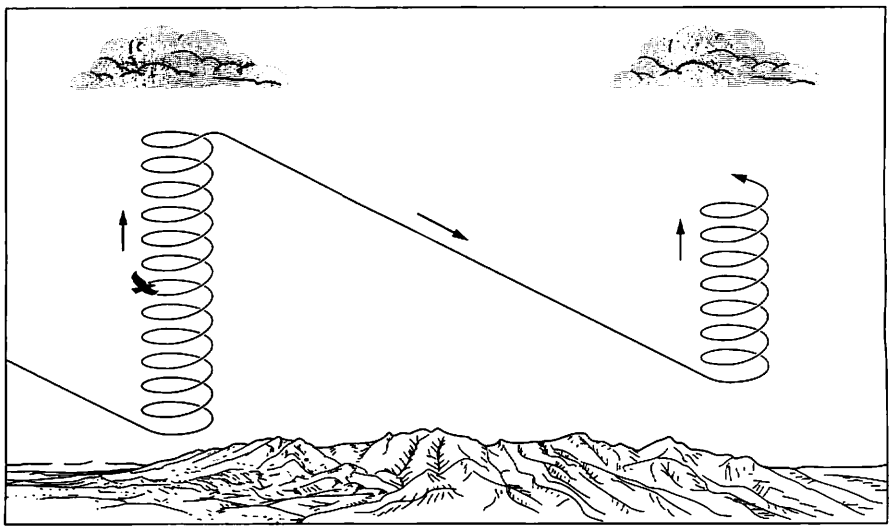


FIGURE 5–7 Use of thermals by a gliding vulture to counteract sinking. [*After Pennycuick 1973*]

thermals as well as wind deflected upward by the ridge, are a special attraction at famous hawk-watching locations, such as Hawk Mountain in eastern Pennsylvania.

Slope soaring exploits a different kind of rising air—namely, the air that is deflected upward when it hits a terrestrial ridge or ocean wave. Migrating hawks soar along ridges and gulls hang effortlessly behind boats or above the ocean beach by riding the deflected air currents. Seabirds, such as the long-winged albatrosses, can cruise expertly along to the windward sides of large wave crests. If the line of the wave crest is not in the intended direction of travel, the albatross can fly into a head wind by alternately rising off the crest of a wave and gliding at an angle to an adjacent wave. This so-called dynamic soaring takes advantage of the layers of different wind speeds above the ocean. The albatross accelerates downward from the fast-moving, upper air layers into the slower-moving, lower air layers; then, they swing upwind. As they lose speed and lift, they bank again into the fast-moving, upper air layers.

Flapping Flight

Gliding flight minimizes the use of powered thrust to overcome the negative effects of drag. Flapping flight, on the other hand, adds thrust to the controlling forces. Each primary flight feather functions as an airfoil, as can the wing itself. When these airfoils change their orientations downward from the horizontal, a part of the upward lift that they generate changes into forward thrust. This principle is illustrated by the performance of the rotating blades of a helicopter. Each blade is an airfoil positioned at the best angle of attack relative to the sweep of the rotor. When the blades rotate in a horizontal plane, air is deflected directly downward to generate lift that offsets the weight of a hovering helicopter. By tilting the rotor forward, the blades drive air backward as well as downward, thereby imparting forward thrust and causing the helicopter to move forward (Figure 5–8).

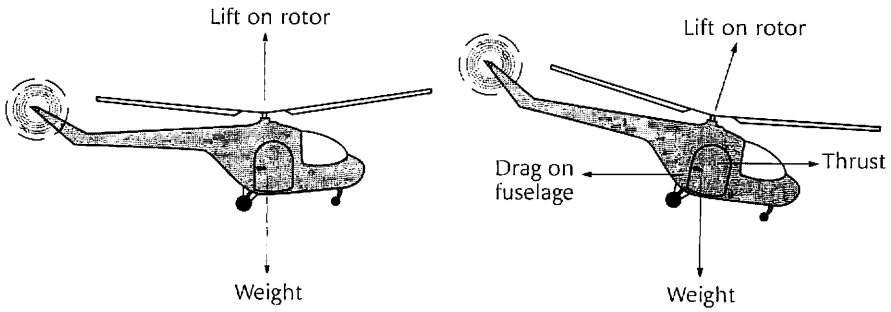


FIGURE 5–8 Hovering (*left*) and forward (*right*) flight of a helicopter. When the blades of the rotor rotate in a position that is horizontal to the ground, the lift that they generate balances the downward pull of gravitation, called weight. Tilting the rotor directs some of the lift in a forward direction, called thrust, and generates negative forces, called drag.

The wings of birds also act like large propellers, with some accessory propellers in the wing tip and with some distinction between the contribution of the inner wing and that of the outer wing (see Figure 5–1). In the outer half of the wing, each primary functions as a smaller, separate airfoil; together they can produce forward thrust, as does the propeller of an airplane. To produce forward thrust, the airfoils of propellers and of primaries move vertically rather than horizontally through the air. As the leading edge of the primary slices the air column during the downstroke, the net pressure on the back surface pushes the feather forward. Control of the angle of attack of each primary by tendons and muscles, as well as by the natural responses of the flexible vanes to air pressure, results in a continuously integrated system of feather positions through the wing stroke. The forward forces of thrust produced by the propeller-like primaries are transferred to the inner wing, the horizontal movement of which generates lift. The result is forward flight.

The same principles apply to the wing action of hummingbirds, which among vertebrates sustain the highest known levels of oxygen consumption and muscle-power output while hovering (Chai and Dudley 1995). In his pioneering analyses of bird flight, Crawford Greenewalt (1960a) took high-speed movies of hummingbird flight and then studied them at slow speeds to discover how hummingbirds achieve their remarkable control. He concluded that hummingbird flight resembles that of a helicopter or, more precisely, a novel combination of airplane and helicopter in which the propellers rotate about a horizontal axis to produce various combinations of lift and forward thrust. Greenewalt describes the action thus:

> In hovering flight the wings move backward and forward in a horizontal plane. On the down (or forward) stroke the wing moves with the long leading edge forward, the feathers trailing upward to produce a small, positive angle of attack. On the back stroke the leading edge rotates nearly a hundred and eighty degrees and moves backward, the underside of the feathers now uppermost and trailing the leading edge in such a way that the angle of attack varies from wing tip to shoulder, producing substantial twist in the profile of the wing. [Greenewalt 1960a, p. 233]

A hummingbird can move forward or backward from stationary hovering, just by changing the direction of the wingbeat, because every angle produces a different combination of lift and thrust. Forward velocities increase as the wings beat in an increasingly vertical plane. This rotation of the wing is made possible by the unusual structure of the humerus and its articulation with the pectoral girdle. The secondaries of a hummingbird's inner wing are short, and the outer primaries are elongated to form a single, specialized propeller. The complete stroke of the wing tip describes a figure-eight pattern, which includes a powered up-

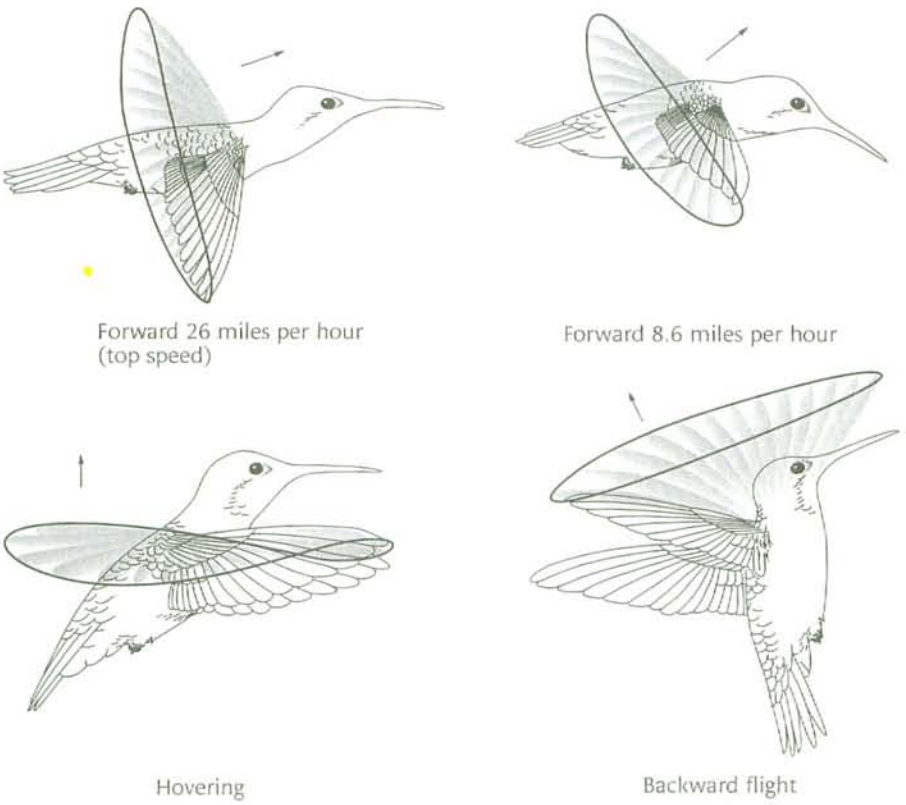


FIGURE 5–9 Hummingbird wing motions. In forward flight, the wings beat vertically to generate forward thrust. In hovering flight, the wings beat horizontally in the pattern of a flattened figure eight. To fly backward, the hummingbird tilts the angle of wing action to create rear-directed thrust. [*After Greenewalt 1960a*]

stroke as well as downstroke (Figure 5–9). The upstroke generates only one-third of the power generated by the downstroke, not the same amount, as was believed for many years (Warrick et al. 2005).

Like the wings of insects, the wings of birds and their controlling musculature oscillate mechanically with intrinsic elasticity (Greenewalt 1960b). The wings of a Ruby-throated Hummingbird, for example, beat at an essentially constant rate of 53 strokes per second. The durations of the upstroke and downstroke are equal. The wingbeat rates of various species of hummingbirds and most other birds decrease predictably with increasing wing length, as oscillation theory predicts. These observations have important implications for the neuromuscular basis of avian flight. After the wingbeat rate has reached its natural oscillating frequency, the nerves and muscle fibers responsible for sustaining the rhythm need to fire perhaps only once every four beats, like a child on a swing with only an occasional push by the parent.

Birds in flight control lift and thrust in complex, rapid, and continuous patterns (Warrick et al. 1998). No aircraft approaches the average

TABLE 5–1 Birds compared with airplanes

Statistic	Plane (type)	Bird (species)
Travel speed (body lengths/second)	32 (supersonic SR-1)	75 (Common Pigeon) 120 (Common Starling) 140 (swifts)
Roll rate (degrees/second)	720 (A-4 Skyhawk)	5000 (Barn Swallow)
G forces allowed	4–5 (general aircraft) 8–10 (select military aircraft)	10–14 (many species) Note: Hundreds of times per day

From Dial 1994.

bird's acrobatic maneuverability (Table 5–1). Slow-motion photographs of birds during takeoff, aerial maneuvers, chases, and landings reveal the precise changes in wing position that control body orientation and airspeed (Figure 5–10). Birds rarely crash. Even more important than the integration of lift and thrust is the independent control of each wing. Asymmetrical wing actions enable a bird to steer, turn, and twist. By flapping with one wing oriented forward and the other wing oriented backward, the bird can execute an abrupt turn. Setting the wings in a partly folded position reduces the amount of lift, controlling the loss of altitude gradually while gliding. By setting one wing back farther than the other, the bird adds curvature to its glide path.

About 50 different muscles control the wing movements. Some muscles fold the wing; others unfold it. Some pull the wing upward, others

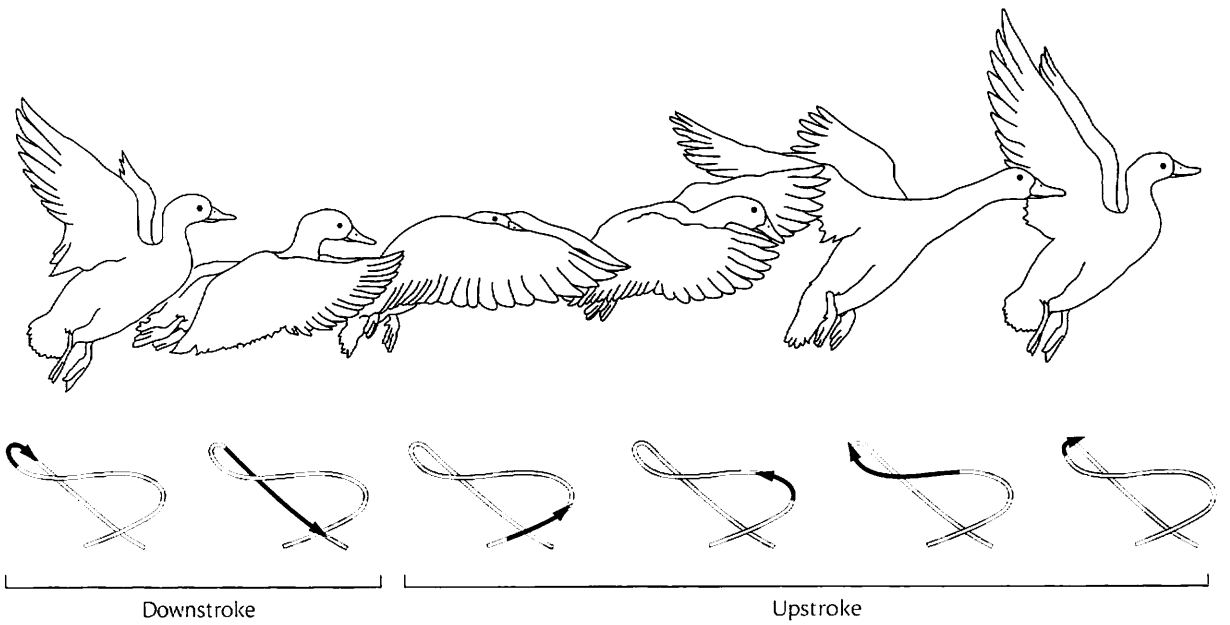


FIGURE 5–10 Complete wing stroke of the duck. Black arrow sections trace the movement of the wing tip through the wing stroke. [*After Burton 1990*]

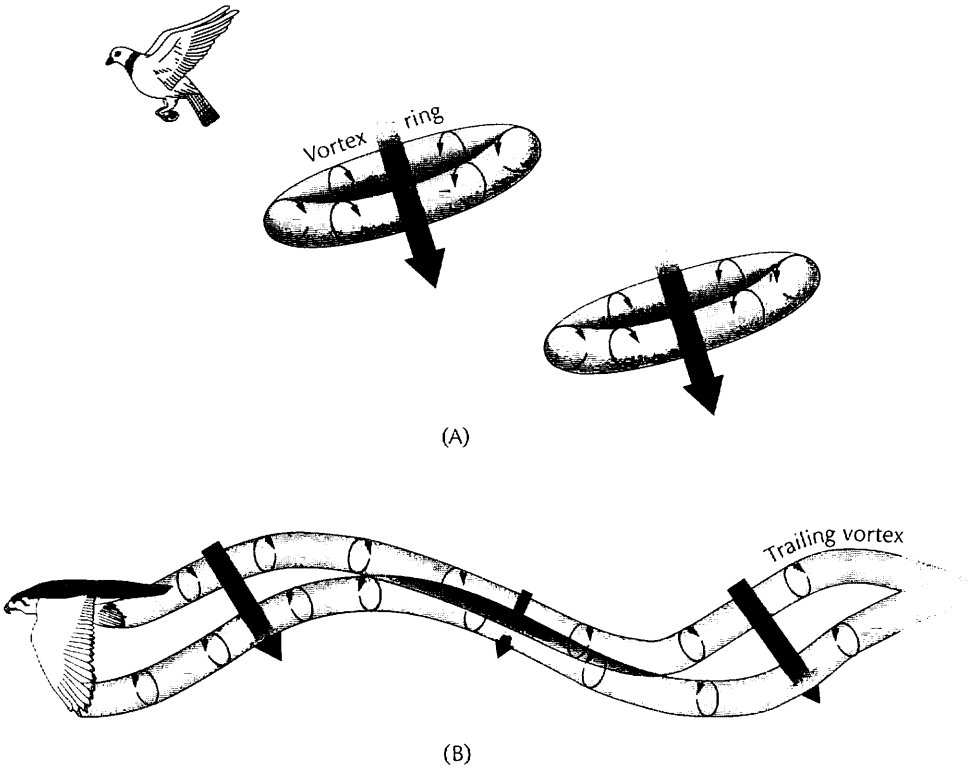


FIGURE 5–11 Wingbeats leaving trailing currents of swirling air. (A) The powered downstroke of slow-flying pigeons produces doughnut-shaped patterns of air currents called vortex rings. (B) The pattern of vortices trailing behind a fast-flying kestrel with continuously integrated powered downstrokes and recovery upstrokes. [*After Alexander 1992*]

pull it down, and still others adjust its orientation. In most small birds, only the downstroke is the power stroke. Little lift is achieved on the recovery stroke, during which the primaries are separated to minimize air resistance. Powered downstrokes followed by simple recovery strokes produce doughnut-shaped rings of turbulent, swirling air, called vortex rings, in the wake of the flying bird (Rayner 1988; Figure 5–11). The forces of lift and thrust on the wing are continuously integrated during the normal wingbeat. The conversion of the trailing vortices from doughnut-shaped rings into continuous streams in fast flight is due to the integration of forces from the wings' downstrokes and upstrokes. These trailing vortices, however, must be left behind in a controlled fashion: flapping too slowly causes the turbulence to backlash; flapping too fast causes interference of the turbulence with the next upstroke. As a rule, birds increase their airspeed, not by beating their wings faster, but, instead, by increasing the amplitude and orientation of their wingbeats to achieve greater thrust (Tobalske and Dial 1996).

One number, the Strouhal number, defines optimum rates of wing (or tail) motions to effect flight efficiency (Taylor et al. 2003; Whitfield 2003).

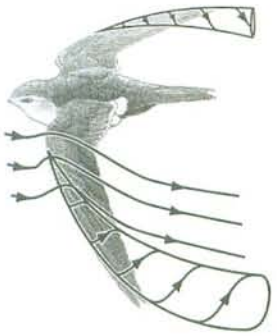


FIGURE 5–12 Conical leading-edge vortices create lift on the tapered wings of swifts by deflecting the oncoming airstream downward. The expanded area indicates the downwash that generates lift. Leading-edge vortices first appear off the wrist and continue to be generated along most of the length of the narrow wings but move inside and upward and then behind the wing tip itself. [*After Videler et al. 2004*]

Simply multiply wing-stroke speed times body size, and divide by forward speed. Birds, as well as bumblebees, bats, and locusts, all operate most efficiently at the predicted Strouhal numbers from 0.2 to 0.4. So do swimming animals from fish to whales.

Adding to the acrobatic abilities of aerial birds such as swifts and hummingbirds are recently discovered sources of lift on the outer wings, called leading-edge vortices (Videler et al. 2004; Muller and Lentink 2004; Warrick et al. 2005). Already known as a fundamental of insect flight, leading-edge vortices may also play a major aerodynamic role in bird flight. The sharp leading edges of the wings of swifts, for example, spawn a swirl of air that can aid flight if it is stabilized and channeled to best effect. By sweeping their wings backward in gliding flight, birds can convert the leading-edge vortex into a tiny tornado at the wing tip (Figure 5–12). Low pressures in the core of the vortex tornado suck the wing tip upward or forward, depending on its orientation. The small, swept-back wings of supersonic fighter jets exploit the same aerodynamic effects. The leading-edge vortices add lift in variable wind speeds and even at low angles of attack. Changing wing positions changes their immediate effect, which enables swifts to turn quickly to catch insects.

Landing on elevated or arboreal perches, particularly, requires exceptional control of flight trajectory. Birds are unique among flying vertebrates in the way that they land (Caple et al. 1983, 1984). Aerial species such as bats, flying squirrels, and certain lizards make contact with their forelimbs and then rotate their bodies downward until the hind feet touch the landing surface (Figure 5–13). Variations exist, but only birds rotate their centers of mass upward to stall directly over the landing site.

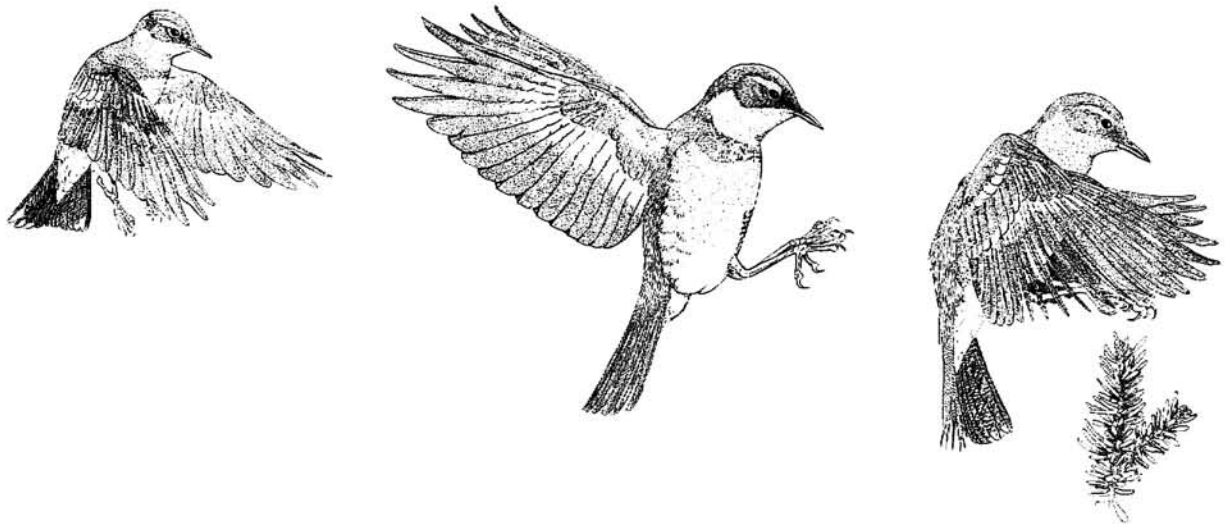


FIGURE 5–13 Varied Thrush landing on a tree stub. Note the forward extension of the feet as the thrush controls the final touchdown. [*After Able 2004*]

Supplementing the wings are the tail's contributions to flight, which may be minimal in species with small tails but substantial in other species. Tails help to control flight position and stability as well as aid steering and braking. Tails also add lift by improving airflow over the wings, especially at slow speeds, and by reducing turbulence as air passes over the body. This contribution may be more important in young birds that are learning to fly than in skilled adults. Immature raptors, in particular, tend to have longer tails than those of adults. The size difference (as much as 15 percent) is most pronounced in short-tailed eagles such as the Bateleur of East Africa, as well as in the familiar Red-tailed Hawk of North America. Corresponding to the increased lift, immature raptors have a more buoyant flight than do adults. Extra lift apparently reduces the chance of injury when they strike prey and facilitates their mastery of early flight and hunting skills (Amadon 1980).

Intermittent Flight

Many birds alternate regular bouts of flapping flight with short periods of nonflapping flight. Cooper's Hawks and Black Vultures, for example, flap several times and then glide, appropriately called flap gliding. Finches and woodpeckers rise and fall as they alternate flapping and nonflapping sequences in their characteristic flap-bounding flight. These two main categories of so-called intermittent flight both reduce a bird's power costs. They are distinguished by wing positions—wings extended in gliding versus wings folded, or flexed, in bounding—and by their advantages at different flight speeds. Flap gliding reduces predicted costs at slower airspeeds, especially those below minimum power speed (Rayner 1985b). Conversely, flap bounding reduces predicted costs at fast speeds, especially at or above maximum range velocity. Experiments in wind tunnels support these predictions. Mid-sized species such as the Common Starling shift from flap gliding at slow airspeeds to flap bounding at high airspeeds (Tobalske 1995). The two modes of intermittent flight also scale differently with respect to body size. Flap gliding is favored in large birds, whereas flap bounding works best in small and mid-sized birds. The European Green Woodpecker is the largest species (176 grams) known to employ flap bounding (Tobalske 1996).

Wing Sizes and Shapes

Flight speeds, gliding ability, aerial agility, and energy consumption all depend on the size and shape of a bird's wings (Figure 5–14). The costs of flight are determined by the relation between a bird's total wing area and its body mass—that is, how much mass, in grams, must be carried by each unit area of wing surface. The relation between wing area and body mass, called wing loading, is given in grams per square centimeter of wing-surface area. Some birds have small wings relative to their body mass, and thus high wing loadings. Other birds have proportionately large wing

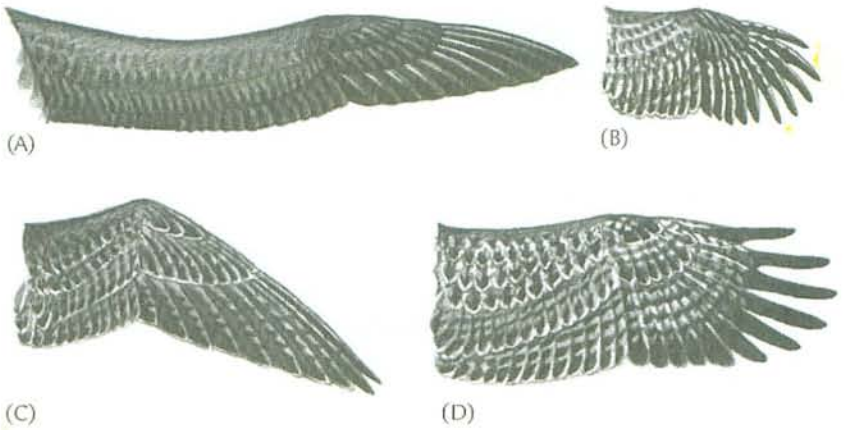


FIGURE 5–14 Flight abilities vary with the shape of bird wings. (A) Long, narrow wings, such as those of an albatross, are best for high-speed gliding in high winds. (B) Short, rounded wings, such as those of a grouse, permit fast takeoffs and rapid maneuvers. (C) The slim, unslotted wings of falcons permit fast, efficient flight in open habitat. (D) Slots in wings of intermediate dimensions increase the lift and gliding ability of buteos.

areas, and thus low wing loadings. The Thick-billed Murre, a species of auk that spends much of its time swimming and diving, has small wings and high wing loadings (2.6 grams/square centimeter). The murre and other diving birds—loons, grebes, and diving ducks—with high wing loadings must run over the water, flapping their wings to gain enough lift for flight. In contrast, the large-area wings of similar-sized raptors, such as the Red-tailed Hawk, translate into low wing loadings that allow prolonged soaring. Songbirds tend to have large wings for their body mass and, consequently, low wing loadings of about 0.1 to 0.2 gram per square centimeter, allowing frequent launches and active maneuverable flight at relatively low cost.

Wing dimensions also affect lift and drag forces and, as a consequence, mode of flight. The long, narrow, pointed wings of albatrosses, falcons, and swallows have a high lift-to-drag, or so-called aspect, ratio. They are adapted to efficient soaring and open-country flying at fast speeds. The long, narrow wings of albatrosses, for example, produce more lift than do shorter, broad wings of equal total area because the leading edge of a wing produces the most lift; the rear half of a wing produces the least. Thus, long, high-lift wings enable Turkey Vultures to begin soaring early in the day. In contrast, their short, rounded wings force Black Vultures to wait for the assistance of rising warm-air currents until they can soar without expensive flapping. In addition, induced drag, or turbulence, declines as wing length increases. Long, narrow wings separate the wing tips where turbulence is greatest. Although long, narrow wings are best for gliding and fast open-country flying, they sacrifice maneuverability. Thus aerial birds typically have long, pointed wings, whereas species living in dense vegetation have short, rounded wings. A falcon's pointed wings serve it

well in high-speed chases in open country, whereas a Sharp-shinned Hawk's short, rounded wings enable it to chase small birds through dense vegetation.

Short, rounded wings have a low aspect ratio. They are best for maneuvering flight and explosive takeoffs that require fast wingbeats. Wrens have short, rounded wings. Their rapid wingbeats enable them to maneuver amid seemingly impenetrable networks of branches and vines. The short, rounded wings of quail and pheasants permit short bursts of rapid acceleration, enhancing their chances of escaping predators.

The Skeleton

The skeleton of a bird is uniquely structured for flight (Figure 5–15; see also Figure 1-3). Fusions and reinforcements of lightweight bones make the avian skeleton both powerful and delicate. Unusual joints not only make flight motions possible but also brace the body against the attendant stresses. The skeleton strategically supports the large muscles that provide the power for flight.

In cross section, many bird bones are light, air-filled structures unlike the dense, solid bones of many terrestrial animals. The hollow, long bones

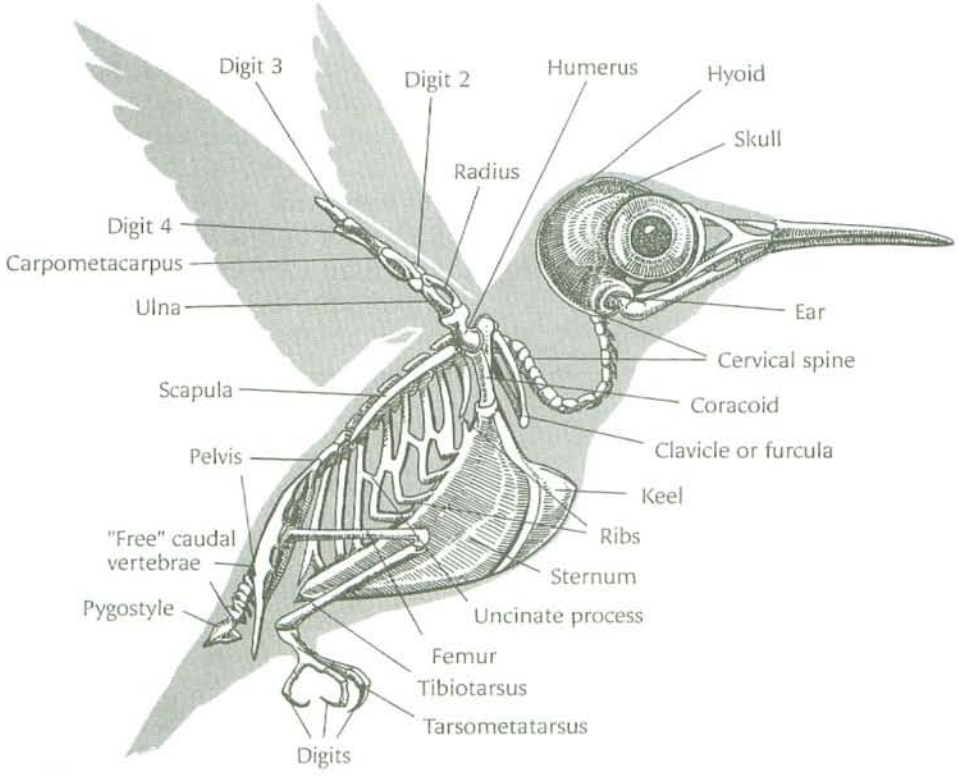


FIGURE 5–15 Major features of a hummingbird skeleton. [*After Tyrrell and Tyrrell 1985*]

of the wings may be strengthened further by internal struts. Instead of a heavy, bony jaw filled with dense teeth, birds have a lightweight, toothless bill. The huge bills of toucans, being hollow, are not the burden they seem.

Despite these adaptations for reduced mass, the bird skeleton withstands the strains imposed by flight. The thorax is more rigid and better reinforced than that of a reptile. The hinged, bony ribs frame a strong bridge between the backbone and the breastbone but allow expansion for breathing. Horizontal bony flaps, called uncinate processes, extend posteriorly from the vertical upper ribs to overlap the adjacent ribs and reinforce the rib cage. The sternum, or breastbone, typically has a large keel, or carina, that anchors the major flight muscles. A bird's flying ability increases with the size of its keel; some flightless birds lack the keel completely.

The flight muscles act in concert with the bones of the pectoral girdle, which include, on each side, the coracoid, scapula, and furcula (Figure 5–16). On top of the rib cage are the long, saberlike scapulae, each of which joins to the coracoid and furcula (Box 5–3). This triangular system of struts resists the chest-crushing pressures created by the wing strokes during flight. An acute angle between the scapula and the coracoid increases the potential exertion force of the dorsal elevator muscles, which help to pull the humerus, or upper wing bone, upward. This angle is oblique in flightless birds.

The avian wing is a modified forelimb. The humerus, ulna, and radius are homologous to the limb bones of other vertebrates. Large surfaces at the joints between the limb bones allow the resting wing to fold neatly against the body. These elaborate joints also permit the wing to change positions and angles during takeoff, flight, and landing. When outstretched, these joints are strong enough to withstand the wrenching forces created during wing strokes.

The fused hand and finger bones help to provide strength and rigidity in the outer wing skeleton. Most of the wrist bones—the carpals and metacarpals—are fused into a single skeletal element called the carpo-

BOX 5–3

THE FURCULA IS A FLEXIBLE, ELASTIC SPRING

In most birds, the furcula, or wishbone of the holiday dinner turkey, is a fused pair of clavicles, or "collar bones," and serves as a strut, or spacer, between a bird's shoulders. X-ray movies of flying Common Starlings reveal that, in flight, the furcula can act as an elastic spring (Jenkins et al. 1988; Pool 1988). With each beat of the wing, the upper ends of the furcula spread widely, becoming as much as 50 percent wider than the normal resting width, and then contract. The furcula repeats this cycle of wide elastic expansion and contraction from 14 to 16 times a second in synchrony with the starling's wingbeats. Exactly how the spring action of the furcula aids flight is unclear, but it may enhance respiratory performance by pumping air through the air sacs (see Chapter 6). Because it functions as a rapidly vibrating spring, the wishbone "may be one of the most dynamic skeletal units in the vertebrate world" (K. Dial, in Pool 1988).

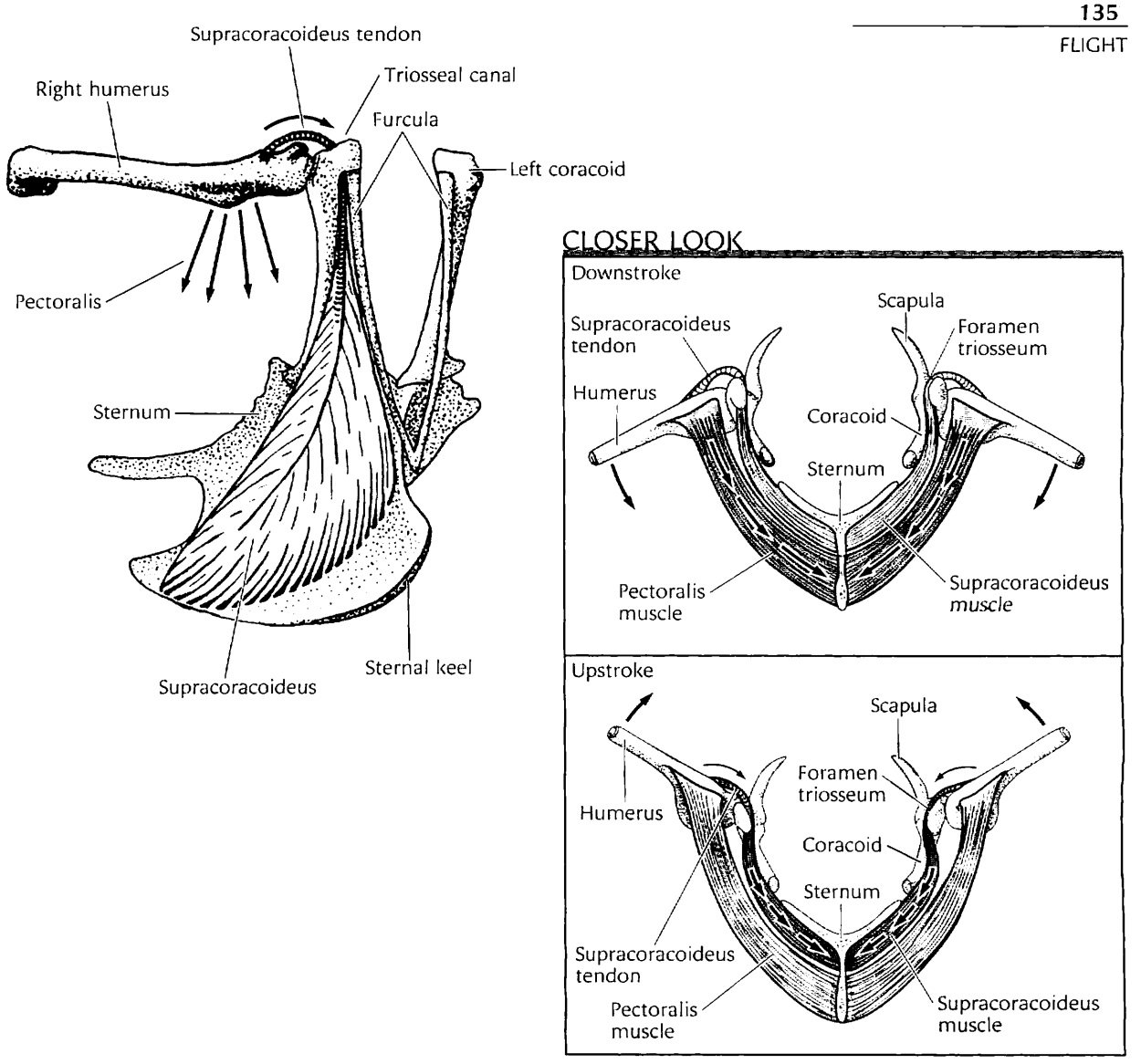


FIGURE 5–16 Right front view of the pectoral girdle and sternum of a pigeon. The ventrally located supracoracoideus muscle raises the wing by means of a pulleylike tendon that passes to the dorsal surface of the humerus through the triosseal canal between the furcula and the coracoid bones, plus the scapula (illustrated in Closer Look). The curved arrow indicates the action of this tendon. The pectoralis muscle, which has been removed in this drawing but is shown in the Closer Look, inserts onto the lower side of the humerus and pulls the humerus downward, as indicated. [*From George and Berger 1966; "Closer Look" after Able 2004*]

metacarpus. There are only 2 free carpals in the avian wrist, far fewer than the 10 or more in most vertebrate wrists. The hand itself includes three digits, rather than the five found in most tetrapods. The alula, or bastard wing, originates from the first digit, the thumb, and moves independently

of the rest of the wing tip. Within the wing itself are powerful tendons and compact packages of tiny muscles that control the subtle details of wing position.

Flight Muscles

The two great flight muscles—pectoralis and supracoracoideus—originate on the keeled sternum and insert onto the expanded base of the humerus. Their ventral positions help to lower a bird's center of gravity in flight.

The pectoralis muscle complex accounts for as much as 35 percent of a bird's total body weight. Contraction of this muscle pulls the wing down in the power stroke. Different sections of this architecturally complex muscle enable takeoff, level flight, and landing. The pectoralis muscle attaches to the furcula and to the strong membrane between the coracoids and the furcula. It also attaches to the peripheral parts of the sternum, including the outer part of the keel. In tree-trunk-climbing birds with shallow keels, such as woodcreepers, the pectoralis muscle spreads thinly over the rib cage for attachment.

The supracoracoideus muscles lift the wings on the recovery stroke (see Figure 5–16). The supracoracoideus muscles are typically smaller than the pectoralis muscles. From each of these muscles positioned ventrally in the sternum, a strong tendon passes upward and forward through the triosseal canal (formed by the junction of the coracoid, scapula, and furcula) and inserts onto the dorsal side of the base of the humerus. The dorsal insertion of this tendon enables the ventrally located supracoracoideus muscles to raise the wing, as if by a pulley. The supracoracoideus muscles power the rapid initial wingbeats that are essential for clearing the ground quickly upon takeoff and achieving a minimal airspeed. A pigeon is unable to take off from the ground if its supracoracoideus tendons are cut experimentally (Sy 1936). Once launched and airborne, however, pigeons can fly without functional supracoracoideus muscles because the smaller dorsal elevator muscles can handle the less demanding recovery strokes of the wings during sustained flight.

Hummingbirds use the upstroke of the wing as a propelling power stroke rather than as a recovery stroke. Logically, the supracoracoideus of hummingbirds is five times as large relative to body size as that of most other birds. It is half the size of the pectoralis muscle and constitutes 11.5 percent of total body mass, more than in any other bird. The supracoracoideus muscle is also unusually large in penguins, whose flippers propel them forward with a powered upstroke as well as downstroke.

Muscle-Fiber Metabolism

The power for flight derives from the metabolic activity in the cellular fibers of flight muscles, some of which have an extraordinary capacity for aerobic metabolism. Certain muscle fibers are suited to specific modes of

flight. Red and white fibers are the extremes of the variation, but intermediate fiber types exist.

Sustained flight power derives from a high concentration of red muscle fibers in the flight muscles. The sustained contraction power of red muscle fibers results from the oxidative metabolism of fat and sugar, which is termed aerobic respiration. These narrow fibers have high surface-to-volume ratios and short diffusion distances, which aid the uptake of the oxygen required for aerobic metabolism. They also contain abundant myoglobin, mitochondria, fat, and enzymes that catalyze the chain of metabolic reactions known as the Krebs cycle. Experimental studies of extracts from pigeon breast muscle, which is rich in red fibers and the associated enzymes, have contributed to our present knowledge of aerobic metabolism. The aerobic capacity of the flight muscles of small songbirds and small bats is at the highest level known for vertebrates.

Few birds have muscle that consists entirely of red fibers. Rather, blends of different fibers that combine long-term endurance in flight with short-term power are typical of most birds. White muscle fibers provide this short-term power through anaerobic metabolism, which does not require oxygen. Unlike red fibers, they contain little myoglobin, few mitochondria, and a different set of enzymes. The white fibers are capable of a few rapid and powerful contractions, but they fatigue quickly as lactic acid—a product of anaerobic metabolism—accumulates. The light meat of the breast muscles of domestic fowl and grouse consists primarily of narrow, white muscle fibers, the source of power for explosive takeoff. The short-term power of white muscle fibers is useful as well for fast turns and evasive actions in flight, but the birds tire easily and cannot fly long or far.

Flightless Birds

Not all birds fly. Besides the ratites (e.g., ostriches and cassowaries), there are flightless grebes, pigeons, parrots, penguins, waterfowl, cormorants, auks, and rails. The original faunas of remote predator-free islands, such as the Hawaiian Islands in the Pacific Ocean and the Mascarene Islands in the Indian Ocean, included a host of flightless birds: geese, ibises, rails, parrots, and the extinct Dodo (see Box 21–1). If flight and mobility are so clearly advantageous to the majority of birds, why are some birds flightless? The answer lies largely in the costly development and maintenance of the anatomical apparatus required for flight. An enlarged, keeled, calcified sternum and large pectoralis muscles, for example, are expensive to produce. Their maintenance also requires much energy. In the absence of advantageous uses, such as the need to fly from predators, natural selection favors reduced investment in the material and energy for flight (McNab 1994). Rails often evolve flightless forms on islands where predators are absent (Olson 1973). Rails also typically delay until they are nearly full grown the addition of calcium to the (cartilaginous) sternum,

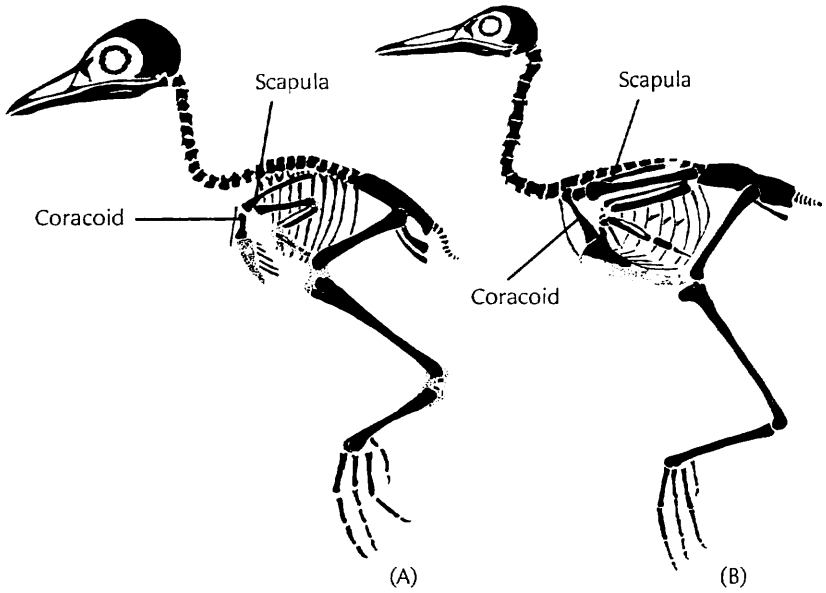


FIGURE 5–17 Skeletons of the King Rail, a flying rail, at (A) 17 days and (B) 47 days after hatching (size reduced so that femur lengths in the two drawings are equal). Stippled areas represent cartilage. Note the obtuse angle formed by the articulation of the scapula and coracoid in the younger form and the acute angle in the older form. [*From Olson 1973*]

strengthening it into a bony structure that supports flight (Figure 5–17). Simple postponement of this conversion would lead to flightlessness. In the fossil record, evolutionary reduction of the sternal keel and the mass of flight muscles is, in fact, a first sign of reduced flying ability. The angle between the scapula and the coracoid also becomes more obtuse, and ultimately the wing bones become smaller. The flightless kiwis of New Zealand, for example, have only vestigial wings.

Other routes to the evolution of flightlessness are seen in specialized diving birds. Foot-propelled divers, such as loons, grebes, and cormorants, have evolved powerful legs and feet that function as paddles. If evolution favors hindlimbs for locomotion, wings and associated pectoral development may regress and render a diving bird nearly or completely flightless. Extreme cases are those of the flightless Titicaca Grebe of Lake Titicaca, Peru, and the Flightless Cormorant of the Galápagos Islands (Figure 5–18). Reduced-sized wings trap less air, thereby reducing buoyancy that interferes with diving.

Penguins, which are wing-propelled divers, represent another route to flightlessness in specialized diving birds. Their wings propel them through water rather than through the air; their feet act as rudders rather than as paddles. The evolution of such forms has occurred not only in penguins but also among the auks in the Northern Hemisphere.

The evolution of wing-propelled divers from flying birds proceeds through an intermediate state in which wings are used for both underwater propulsion and aerial flight. Diving petrels represent the inter-

FIGURE 5–18 Flightless Cormorant drying its little wings after swimming. This species retains an ancestral behavior that is typical of other, flighted species of cormorants, which must dry their water-soaked flight feathers after a swim in order to fly (see page 81). [*Michael Gore/Frank Lane Picture Agency/CORBIS*]

mediate stage in the evolution from flying petrels to flightless penguins. Auks, such as the Razorbill, with dual-purpose wings, represent the intermediate stage in the evolution of specialized divers from flying ancestors to the flightless Great Auk of the North Atlantic. The progressive specialization of wing skeletal structure is evident in the changes from the slim wing bones of a gull through shorter and heavier bone structures to the broad, flat wing skeleton of a penguin's flipper (Figure 5–19).

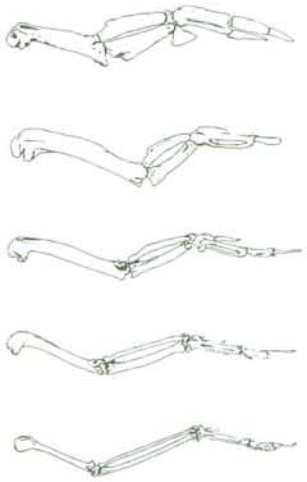


FIGURE 5–19
Modifications of the wing skeleton in wing-propelled diving birds: (*bottom to top*) an aerial gull, an auk, the flightless Great Auk, an extinct penguinlike auk, and a penguin. [*From Storer 1960*]

Summary

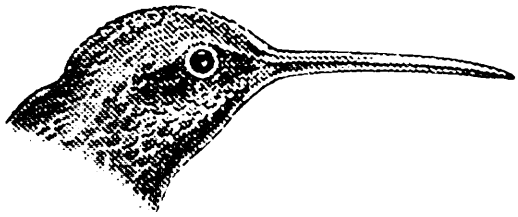
Structural adaptations for flight dominate avian anatomy. Fusions and reinforcements of lightweight bones are among the adaptations of the avian skeleton for flight. Of particular importance are the keeled sternum, which supports the powerful pectoralis and supracoracoideus flight muscles, and the strut-like arrangement of the pectoral girdle. The tendons of the ventrally located supracoracoideus muscles pass through the triosseal canal to dorsal insertions on the humerus. The red fibers of avian flight muscles have an extraordinary capacity for aerobic metabolism and sustained work.

The form of the wing and of the individual flight feathers is that of an airfoil, which generates a force called lift as air passes over and is

deflected downward by the asymmetrical surfaces. Control of flight is achieved through changes in wing and wing feather positions and through the use of slots between feathers. Gliding birds exploit rising air currents, both heated thermals and slope-deflected air, to gain altitude without the exertion of flapping. Hummingbirds achieve extraordinary maneuverability in flight by beating their wings at different angles in a figure-eight pattern that includes a powered upstroke as well as a powered downstroke. Flight power requirements are least at intermediate flight speeds, but birds often fly faster or slower than this speed to maximize distances traveled or to feed. Particular wing shapes adapt birds to specific modes of flight because they influence the penalties of induced and profile drag relative to the wing's ability to generate lift and thrust. Long, narrow wings sacrifice maneuverability for high-speed flight with low drag. Birds are the only vertebrates that can land with precision on elevated or arboreal perches.

Some birds have become flightless, particularly on remote islands that lack mammalian predators. Delayed ossification of the sternum in rails predisposes them to the evolution of flightlessness. Specialized diving birds rely either on hindlimb locomotion or wing-propelled underwater locomotion. Extremes of both kinds of diving birds have lost the power of flight. Penguins, for example, have flipper-like wings.

CHAPTER 6



Physiology

Weight for weight, birds eat more food, consume more oxygen, move more rapidly, and generate more heat than any other vertebrates. [Welty 1982, p. 130]

Feathers and flight are conspicuous features of birds. Less conspicuous, but just as fundamental, are the internal systems of metabolism and excretion—collectively called physiology. These systems sustain daily activities and adapt individual birds to their particular environments, hot or cold, wet or dry.

The advanced physiology of birds provides both power and endurance. Power and endurance derive from the maintenance of high body temperatures. One advantage of high body temperatures is that activity is unconstrained by low ambient temperatures. Birds are fully active in the early morning cold, in midwinter, and in the high mountains. In turn, high body temperatures demand much energy and water, two resources that often are in short supply. Adaptations for heat loss and water economy, as well as heat conservation, enable birds to live in extreme and seasonal environments.

This chapter focuses on the fundamentals of avian physiology—metabolism, temperature regulation, feeding and digestion, and water economy. Birds maintain a delicate physiological balance of the conflicting needs for temperature regulation, activity, and water economy. Supporting the demands of sustained aerobic metabolism is a unique and highly efficient respiratory system coupled to a powerful heart and circulatory system. The high body temperatures of birds require active control of heat exchange with the environment to conserve energy in cold environments and to lose heat in hot environments and in flight. Specialized bills and digestive systems garner the required energy and nutrition from the environment. Also essential are water reserves required for heat loss through evaporative cooling as well as the excretion of electrolytes. Metabolic water is an important source of these reserves.

Physiological constraints influence all aspects of a bird's life. Later chapters treat additional features of avian physiology related to migration, reproduction, stress, disease resistance, and the hormonal control of behavior.

The High Body Temperatures of Birds

The physiology of birds, specifically their metabolism, relates directly to the maintenance of a high body temperature through the production of metabolic heat, or endothermy. Most birds, large and small, in the frigid Arctic and in the hottest deserts, keep their core body temperature higher than the surrounding air, at about 40°C. High body temperatures enhance intrinsic reflexes and powers. They enable birds to be active, fast-moving creatures. In animals generally, the rates of physiological processes increase with body temperature. For example, the transmission speed of nerve impulses increases 1.8 times with every 10°C increase in temperature. The speed and strength of muscle-fiber contractions triple with each 10°C rise in temperature.

The maintenance of high body temperatures through endothermy, however, is energetically expensive; birds consume from 20 to 30 times more energy than do similar-sized reptiles. The maintenance of high body temperatures also risks lethal overheating. Above 46°C, most proteins in living cells are destroyed more rapidly than they are replaced (Figure 6–1), causing potentially fatal changes in the chemistry of the brain.

Even more important than the benefits of endothermy for speed or strength are those for endurance (Rubin 1995). Warm amphibians and reptiles can escape or strike with lightning speed but are quickly exhausted. Some birds fly for hours or days. Increased aerobic metabolism and insulation were among the major changes that accompanied the evolution of reptiles into birds. These changes made possible regulated high body temperatures and the many advantages of dependable rates of muscle function. Higher activity levels coupled with greater endurance opened a new range of ecological opportunities for birds. However, challenges accompany the benefits. The high metabolic demands of temperature regulation and of the daily activities of birds require extraordinary delivery rates of energy and oxygen to the body's cells as well as the rapid removal of

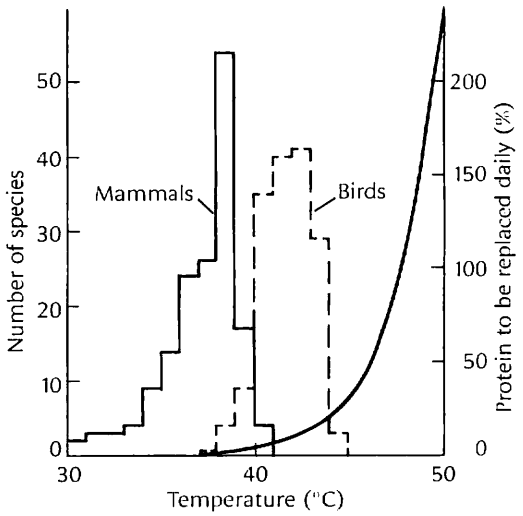


FIGURE 6–1 Birds and mammals regulate their body temperatures to be just below temperatures that destroy body proteins. Shown here are the body temperatures of many bird and mammal species. The curved line represents the rate of protein replacement as a function of body temperature.

poisonous metabolic waste products. Efficient respiratory and circulatory systems help to meet these demands and to keep a bird's body chemistry in balance.

The Respiratory System

The respiratory system of birds is different in both structure and function from the respiratory system of mammals. Avian lungs are small, compact, spongy structures molded among the ribs on either side of the spine in the chest cavity. The dense tissues of avian lungs weigh as much as the lungs of mammals of equal body weight but occupy only about half the volume. Healthy bird lungs are well vascularized and light pink in color.

Avian lungs are unique in that the air flows in only one direction, rather than in and out as in other vertebrates. How do birds control the air so that it flows through their lungs when they can only inhale and exhale through one trachea? The solution is a surprising combination of unique anatomical features and the manipulation of airflow. Supplementing the lungs is an elaborate system of interconnected air sacs, not present in mammals (Figure 6–2). Conversely, birds lack a diaphragm, the

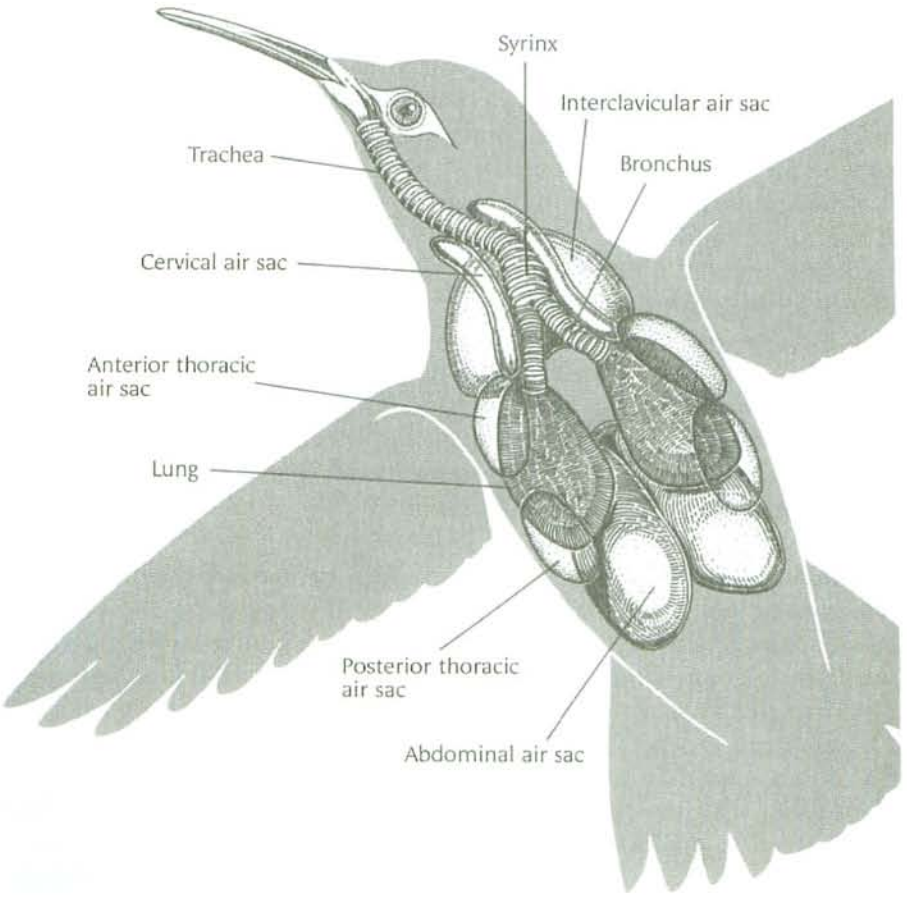


FIGURE 6–2 Positions of the air sacs and lung in a bird's body. [*After Tyrrell and Tyrrell 1985*]

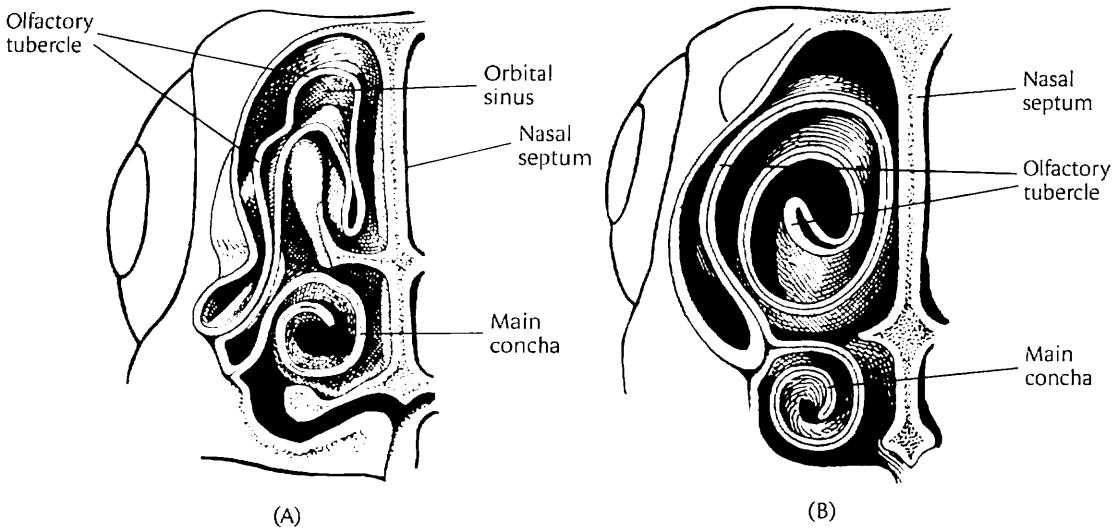


FIGURE 6–3 Cross sections of the nasal cavities of (A) a Northern Fulmar and (B) a Turkey Vulture, showing the elaborate folds, called conchae, that cleanse and heat inhaled air, remove water from exhaled air, and provide lots of surface area for olfactory receptors in some species. [*Adapted from Portmann 1961*]

muscle between chest and abdomen that causes mammalian lungs to inflate (inhale) and deflate (exhale). Instead, birds inhale by lowering the sternum, which enlarges the chest cavity and expands the air sacs. Contraction of the sternum and ribs compresses the air sacs, pushes fresh air from them through the lungs, and exhales the air (see below for complete sequence of air movements).

Most birds inhale air through nostrils, or nares, at the base of the bill. A flap, or operculum, covers and protects the nostrils in some birds, such as diving birds that must keep water from entering their nostrils and flower-feeding birds that must keep pollen out. Inhaled air passes into paired chambers (Figure 6–3). Each nasal chamber has elaborate folds, called conchae (sing. concha), that increase the surface area over which air flows. The surfaces of the conchae cleanse and heat the air before it enters the respiratory tract. Olfactory tubercles sample (smell) its chemistry. The conchae are also well supplied with nerves and a network of blood vessels—rete mirabile—that help to control the rate of heat loss from the body.

Inhaled air moves next down the trachea, or windpipe, which divides into two bronchi and in turn into many subdividing stems and branches in each lung (Figure 6–4). Most of the lung tissue comprises roughly 1800 smaller interconnecting tertiary bronchi. These bronchi lead into tiny air capillaries that intertwine with blood capillaries, where gases are exchanged.

Inhaled air proceeds through two respiratory cycles that, together, consist of four steps. Most of the air inhaled in step 1 passes through the primary bronchi to the posterior air sacs (Figure 6–5). In step 2, the exhalation phase of this first breath, the inhaled air moves from the posterior air sacs into the lungs. There, oxygen and carbon dioxide (CO_2) exchange

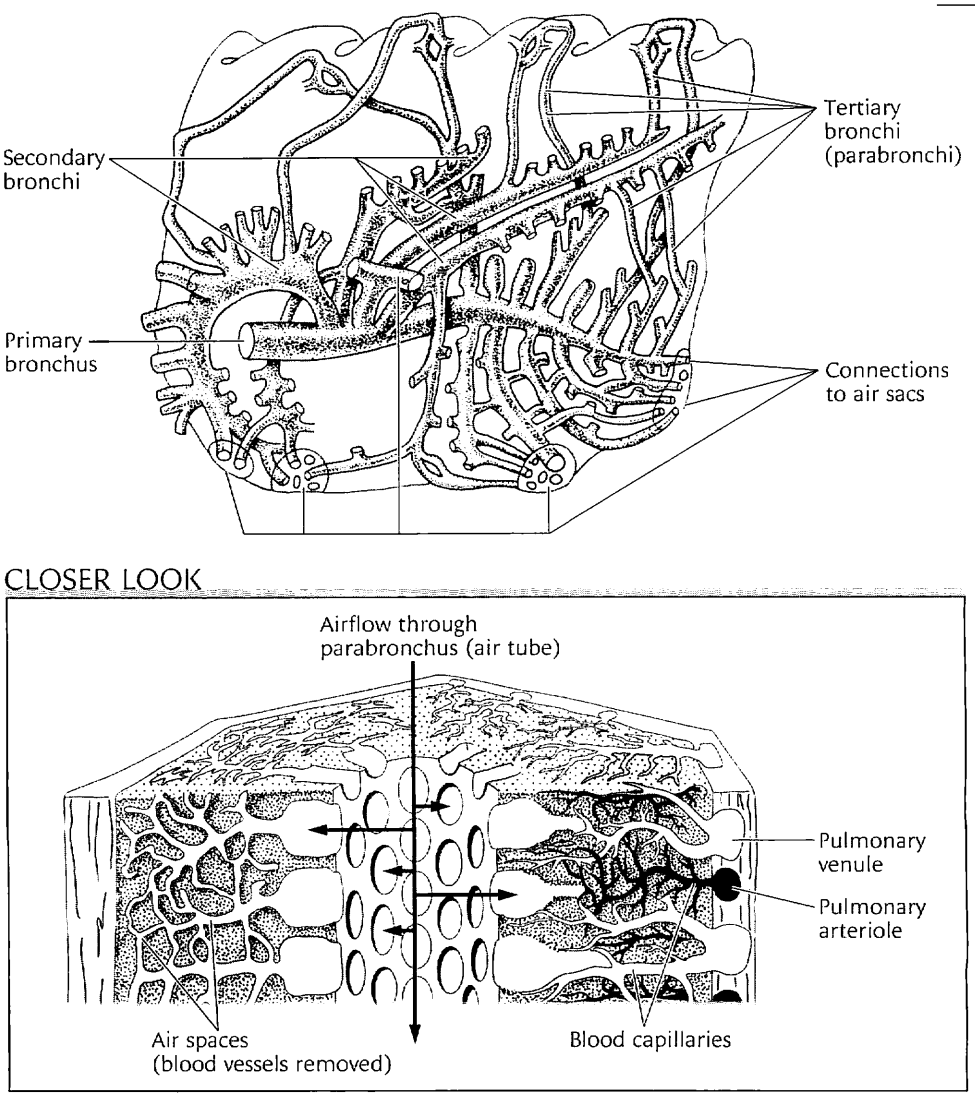


FIGURE 6–4 Interconnecting bronchial tubules form the internal structure of a bird's lung. Tertiary bronchi, or parabronchi, and fine air capillaries constitute most of the lung tissue. [*After Lasiewski 1972; "Closer Look" Evans and Heiser 2004*]

takes place as inhaled air flows through the air-capillary system. The next time that the bird inhales, step 3, the oxygen-depleted air moves from the lungs into the anterior air sacs. The second and final exhalation, step 4, expels CO_2-rich air from the anterior air sacs, bronchi, and trachea back into the atmosphere.

This series of four steps maximizes contact of fresh air with the respiratory surfaces of the lung. Most importantly, a bird replaces nearly all the air in its lungs with each breath. No residual air is left in the lungs during the ventilation cycle of birds, as it is in mammals. By transferring more air and air higher in oxygen content during each breath, birds achieve a more efficient rate of gas exchange than do mammals.

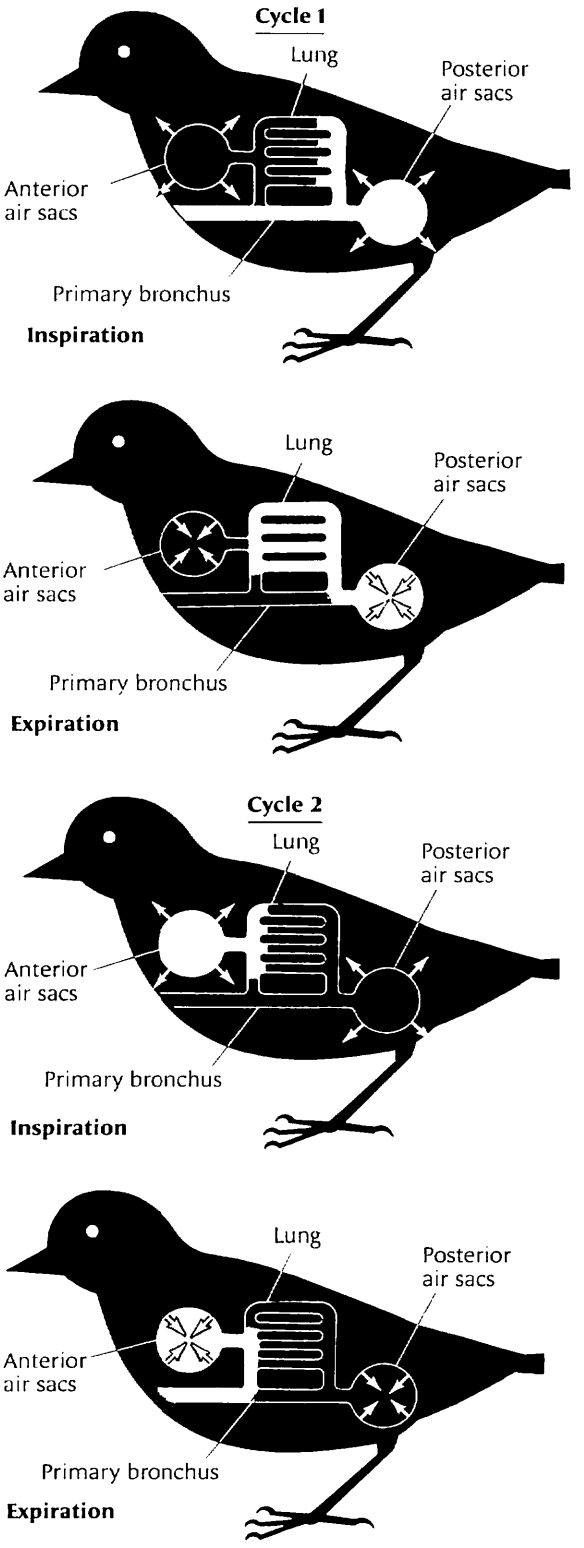


FIGURE 6–5 The unidirectional movement of a single inhaled volume of air (shown in white) through the avian respiratory system. Two full respiratory cycles—inspiration, expiration, inspiration, and expiration—are required to move the gas through its complete path. This diagram does not show the tracheal connection from the main bronchi to the mouth. [*After Schmidt-Nielsen 1983*]

The air-sac system is an inconspicuous, but integral, part of the avian respiratory system (see Figure 6–2). The number of air sacs varies from 6 in weavers and 7 in loons and turkeys to at least 12 in shorebirds and storks; most birds have 9. The paired cervical sacs located in the neck are perhaps the most visible: they inflate as the large red sacs on the necks of displaying male frigatebirds and the yellow neck sacs of strutting Sage Grouse (see Figure 3–14).

Air sacs are thin-walled (only one or two cell layers thick) structures that extend throughout the body cavity and into the wing and leg bones. Supporting their ancestral relationship to birds, theropod dinosaurs also had pneumatized arm and leg bones (Prum 2002). The air sacs connect directly to the primary and secondary bronchi and, in some species, connect indirectly to parabronchi. The air sacs make possible the continuous, unidirectional, efficient flow of air through the lungs. They not only help to deliver the huge quantities of oxygen needed, but also help to remove the potentially lethal body heat produced during flight. Inflated air sacs also help protect the delicate internal organs during flight. Air pressure from the single interclavicular sacs is essential for vocal sound production (see Chapter 8).

During flight, expansions and contractions of the furcula, or wishbone, complement the movements of the sternum that help to pump air through the respiratory system (Jenkins et al. 1988). High-speed x-ray movies of Common Starlings flying in a wind tunnel revealed that the wishbone bends outward during the wings' downstroke and then recoils inward on the upstroke. It expands outward to almost 50 percent more than its resting width and does so with each wingbeat (see Box 5-3).

The wingbeat cycle itself has a major effect on respiration. It affects the breathing patterns and internal air pressures of Black-billed Magpies flying in a wind tunnel (Boggs et al. 1997). Specifically, changes in air pressure in the air sacs and in tracheal airflow correspond directly to the three wingbeat cycles that accompany each respiratory cycle (Figure 6–6). Coordination of the phases of wingbeat and respiratory cycles minimizes interference and actually assists respiration.

Rates of breathing vary with activity and size; they decrease in larger birds. A resting 2-gram hummingbird breathes about 143 times a minute,

BOX 6–1

BIRDS HYPERVENTILATE WITHOUT SEVERE PENALTY

Rapid breathing during exercise or at high, oxygen-poor altitudes expels large amounts of carbon dioxide. Loss of carbon dioxide increases the alkalinity of the blood (normally the pH lies between 7.3 and 7.4), which causes blood vessels to constrict, severely reducing the flow of oxygen-rich blood to the brain. In mammals, blood flow to the brain may drop from 50 to 75 percent during such hyperventilation, an effect that causes fainting and, sometimes, death. Remarkably, for reasons that remain unknown, blood flow does not drop in birds even at pH 8, which would kill a mammal (Grubb et al. 1978, 1979). Without this safeguard, birds would be unable to fly at high altitudes.

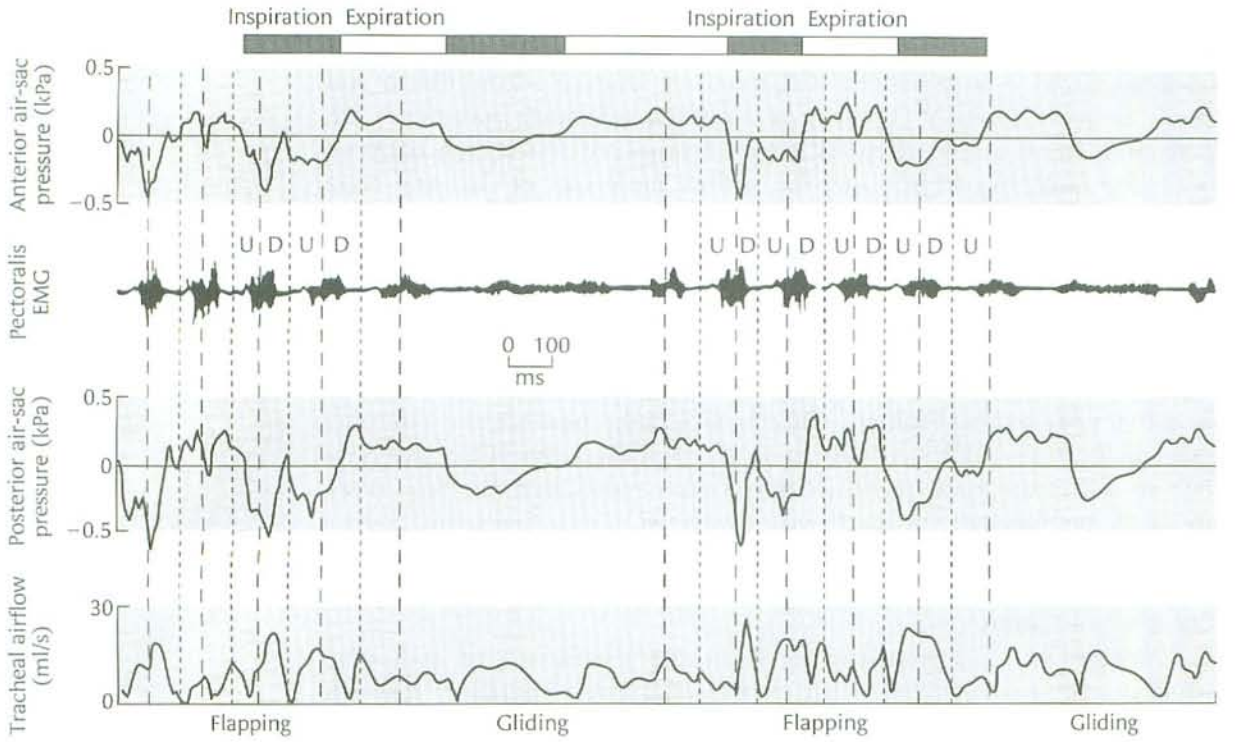


FIGURE 6–6 Air-sac pressures and tracheal airflow during flight of a Black-billed Magpie. There are three cycles of wingbeats in each respiratory cycle of inhalation and exhalation. Electrical activity in the pectoralis muscle indicates flapping versus gliding wing actions. In flapping flight, the upstroke of the wing coincides with increases in air-sac pressure and decreases in tracheal airflow. Abbreviations: U, upstroke; D, downstroke; EMG, electromyogram. [*After Boggs et al. 1997*]

whereas a 10-kilogram turkey breathes only 7 times a minute. In flight, birds meet the increased oxygen demand by increasing their ventilation rates to 12 to 25 times their normal resting rates (Box 6–1).

The Circulatory System

The high metabolic rates of birds require rapid circulation of high volumes of blood between sites of pickup and delivery of metabolic materials. The circulatory system delivers oxygen to the body tissues at rates that match use and simultaneously removes carbon dioxide for exhalation. It also delivers fuel in the form of glucose and elementary fatty acids and removes toxic waste products for excretion. The demands on the avian circulatory system are far greater than those on the systems of reptiles and exceed those of most mammals.

Like mammals, birds have a double circulatory system and a four-chambered heart (Figure 6–7). Avian hearts are on average 41 percent larger than those of mammals of the corresponding body size, the differ-

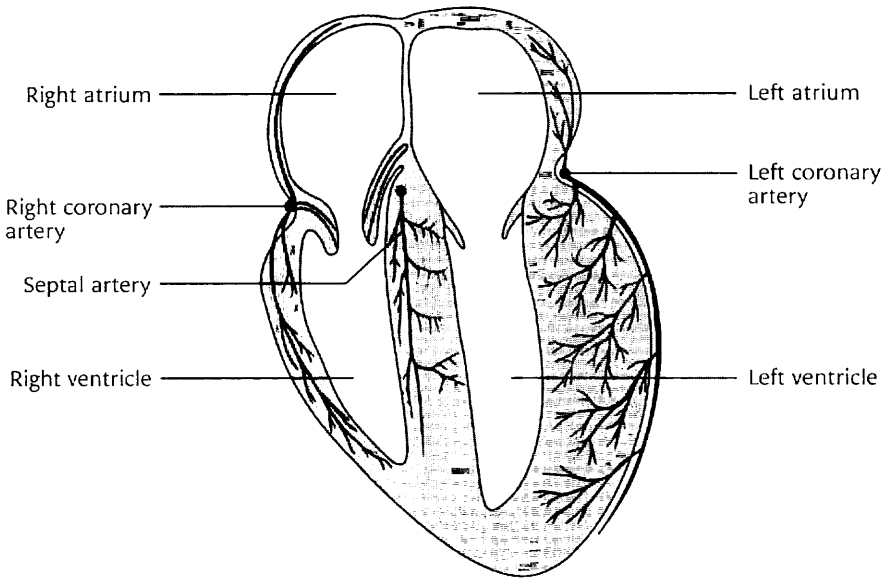


FIGURE 6–7 The large, four-chambered bird heart supports efficient oxygenation of blood. [*From Jones and Johansen 1972*]

ences being most pronounced between small birds and small mammals (Bishop 1997). The heart accounts for 2 to 4 percent of the total mass of a hummingbird; few small mammals have heart masses greater than 1 percent of their mass. Normal resting heart rates in medium-sized birds range from 150 to 350 beats per minute; they average about 220. Heart rates of small birds are higher than those of large birds and exceed 1200 beats per minute in small hummingbirds.

The performance of the heart is measured in terms of cardiac output—or the rate at which the heart pumps blood into the arterial system. Defined as "heart rate times stroke volume (the volume of blood pumped with each contraction) from one ventricle," cardiac output averages from 100 to 200 milliliters of blood per kilogram of mass per minute in birds. Major organs—the heart, liver, kidneys, and intestines—receive large percentages of the cardiac output, averaging from 8 to 10 percent each. The brain and eyes are next in line, receiving 3 and 4 percent, respectively. When a bird flies or swims, cardiac output allocations to the flight and leg muscles, respectively, increase dramatically.

Although bird hearts beat more slowly at rest than do the hearts of similarly sized mammals, their larger stroke volumes create comparable cardiac outputs. Not only is the avian heart larger, but its ventricles empty more completely than do those of mammals on each contraction. At high heart rates, ventricles fill more completely between contractions. The avian ventricles are also made up of more muscle fibers than is the mammalian ventricle. Each fiber (cell) is thinner than mammalian heart-muscle fibers and contains more mitochondria—energy-producing organelles that depend on the supply of oxygen. The thinness of avian heart-muscle fibers

speeds the transfer of oxygen and increases the capacity for aerobic work and endurance at high activity levels.

The high-performance features of the avian heart have their costs. The high tension of avian heart muscles and the strength of the ventricular contractions lead to high arterial blood pressures. Extremes as high as 300 to 400 millimeters of mercury are known in some strains of domestic turkeys—the maximum known for any vertebrate. A blood pressure of 150 millimeters of mercury is high for a human. Not surprisingly, aortic rupture is a common cause of death in these turkeys, which are raised on high-fat diets for weight gain.

Metabolism

Metabolic rates change rapidly with different levels of activity, dropping to a minimum when a bird sleeps or rests and rising to a maximum during flight. Intermediate rates of metabolism support the regulation of body temperatures during periods of cold or heat stress. The total daily energy budget of a bird is the sum of these varied expenditures (Figure 6–8A).

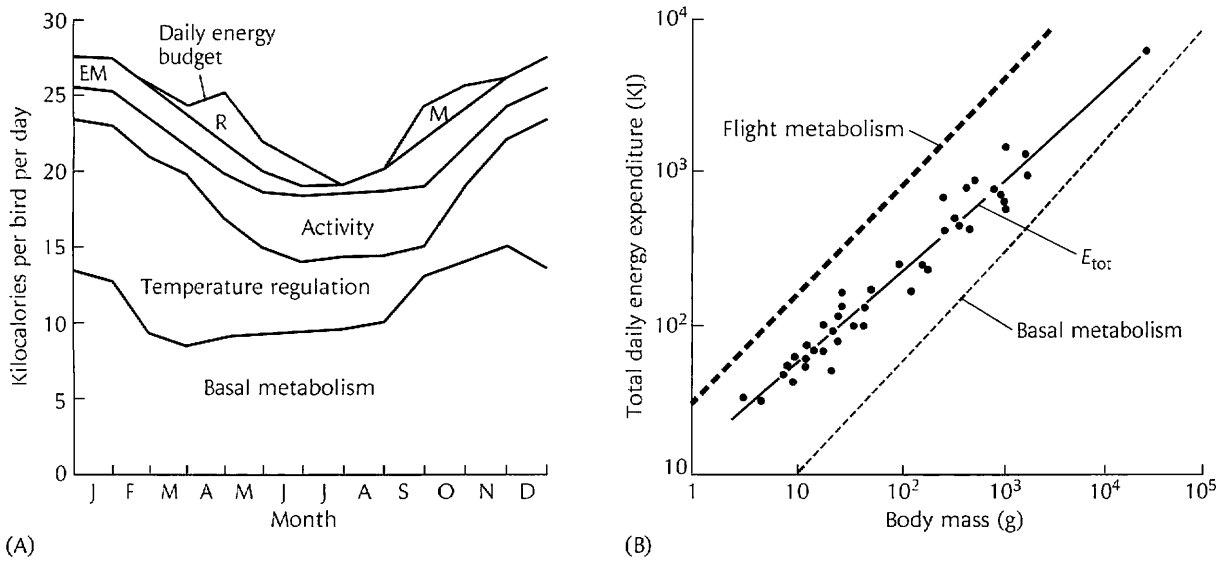


FIGURE 6–8 (A) Model of seasonal variation of energy expenditure (in kilocalories) of a small temperate-zone bird. The total daily energy budget varies monthly as the sum of different expenditures. Abbreviations: EM, existence metabolism; R, reproduction; M, migration. (B) Metabolism and daily energy expenditures typically increase with body size. The slope of this fundamental physiological relation—the increase in basal metabolism with increased mass—is predictably from 0.72 to 0.73 for different-sized birds, as well as for different-sized mammals. Large birds expend less energy per gram of mass than do small birds. Total daily energy expenditures (E_{tot}, in kilojoules) do not increase as fast with increasing body size as does basal metabolism, possibly because small birds are more active than large birds. Energy expenditures of birds during flight—flight metabolism—vary from 2 to 25 times as high as basal metabolic rate. [*(A) After Blem 2000; (B) after Walsberg 1983*]

The following discussions proceed from the minimum, or basal, metabolism to the ways in which birds regulate their body temperatures during cold and heat stress.

Basal Metabolism

Even resting birds use energy. Carefully controlled measurements of the minimal metabolic requirements of resting birds fasting at nonstressful, or thermoneutral, temperatures give estimates of what is called basal metabolism or, sometimes, standard metabolism to acknowledge experimental controls of this measurement. All birds have high basal metabolic rates (BMRs) relative to most vertebrates. Basal metabolism relates directly to mass, but not in a 1:1 relation (Figure 6–8B). An 8-kilogram bustard is 100 times as large as an 80-gram falcon, but it expends only 30 times as much energy per unit of time. Just as the surface area of a sphere relates to its volume, large birds have less surface area per unit of volume than do small birds. Thus, a large bird cannot lose heat as fast as a small bird, because it has less surface area per gram of heat-generating tissue. If an ostrich's tissues produced heat at the same rate as a sparrow's tissues, the ostrich would not be able to dissipate heat fast enough from its body surfaces and would boil inside.

Activity Metabolism

A bird usually spends only a fraction of its day at its basal metabolic level—that is, when resting and fasting. Most of its time is spent, instead, in activities that require the expenditure of more energy and the use of more oxygen. The simple digestion of a meal, the slight muscle actions associated with awareness and attention, or the powering of a strenuous sprint or vertical takeoff all increase energy expenditures. Just being awake and resting increases metabolic rate by 25 to 80 percent above the basal rate. Metabolic costs increase more with exertion. Swimming Mallards, for example, increase their metabolism 3.2 times BMR at their most efficient (and preferred) speed and 5.7 times BMR when they swim as fast as they can (Prange and Schmidt-Nielsen 1970).

Matthew Bundel and his colleagues (1999) trained Greater Rheas—large, flightless, South American relatives of the ostrich—to run on an inclined treadmill while wearing clear plastic hoods to measure their oxygen consumption. It took two years to train them to run just as fast as they could to stay in the same place, which would have pleased the Red Queen of *Through the Looking-Glass*. Their aerobic metabolism peaked at 36 times minimum resting rates (not BMR) at an uphill running speed of 4.0 meters per second (14.4 km/s). At faster paces, they relied increasingly on lactate-producing anaerobic metabolism for running energy. The rhea's increase in aerobic metabolism, or aerobic scope, exceeded that reported for most mammals, including powerful running mammals such as

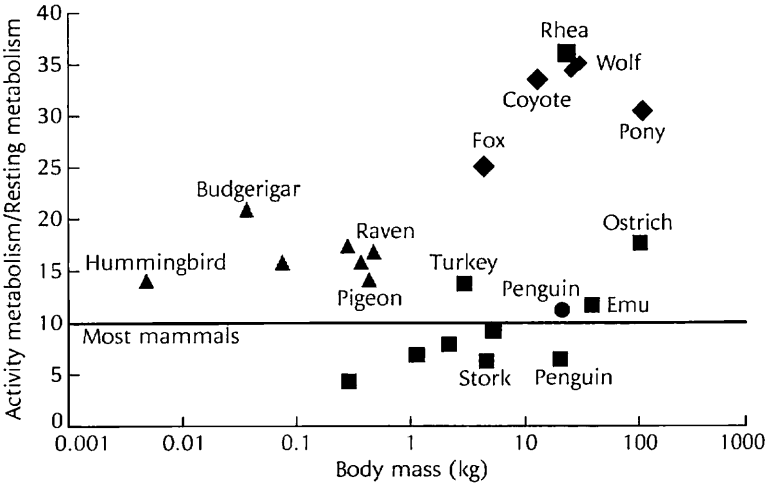


FIGURE 6–9 Increases in activity metabolism above resting minima for rheas and athletic mammals at the aerobic maximum and for other birds at the highest rates available. Metabolic rates are expressed as the ratio of activity metabolism to resting metabolism, or the factorial increase of activity metabolism. Triangles, flying birds; squares, running birds; circles, swimming birds; diamonds, running mammals. [*After Bundel et al. 1999*]

wolves and horses (Figure 6–9). More broadly, birds appear to have double the aerobic scope of mammals.

Birds in flight sustain high levels of aerobic metabolism. Small birds in flight can operate at 10 to 25 times their BMRs for many hours, whereas small mammals can sustain an activity level of metabolism of only 5 to 6 times their BMRs (Bartholomew 1982). Estimates of flight metabolism range from 2.7 to 23 times BMR, with variations due to flight mode, flight speeds, wing shape, laboratory constraints, or a combination of them (Blem 2000). Low values of flight metabolism are obtained for swallows and swifts in partly soaring flight, and high values are obtained for finches and hovering hummingbirds.

Temperature Regulation

A bird's thermal relations with its environment are critical to its survival. Endothermy itself is part of a dynamic relation between internal heat production and heat lost to the external environment. Heat is an inevitable result of the inefficiency of biochemical reactions and so is a direct product of metabolism. Rates of heat production or loss are expressed in watts or joules per hour—the average student at rest produces heat at the same rate as does a 100-watt lamp.

In special situations (e.g., in a nest hole or a burrow free of wind, in which wall temperature equals air temperature), ambient air temperature provides an accurate index to the rate of heat loss or heat gain; but, in more realistic environments, in which the sun shines and the wind blows, a bird's thermal relation with its environment becomes a complex function of the intensity of radiation and convection.

Bird-feather coats are among the best natural, lightweight insulations. Reduced feather insulation increases metabolism. The abnormal feathers of frizzled chickens (Figure 6–10), for example, provide little insulation. Their resting metabolism and the rate of heat loss are twice those of normal chickens at 17°C (Benedict et al. 1932). Contour feathers in the plumage contribute to a bird's insulation, but the down feathers underneath the contour feathers are the primary sources of insulation. Thus, arctic finches have dense down, whereas tropical finches do not.

Insulation increases with the amount of plumage. Some birds enhance their insulation during cold seasons by molting into fresh, thick plumage. Nonmigratory House Sparrows, for example, increase plumage weight 70 percent, from 0.9 gram of worn plumage per bird in August to 1.5 grams

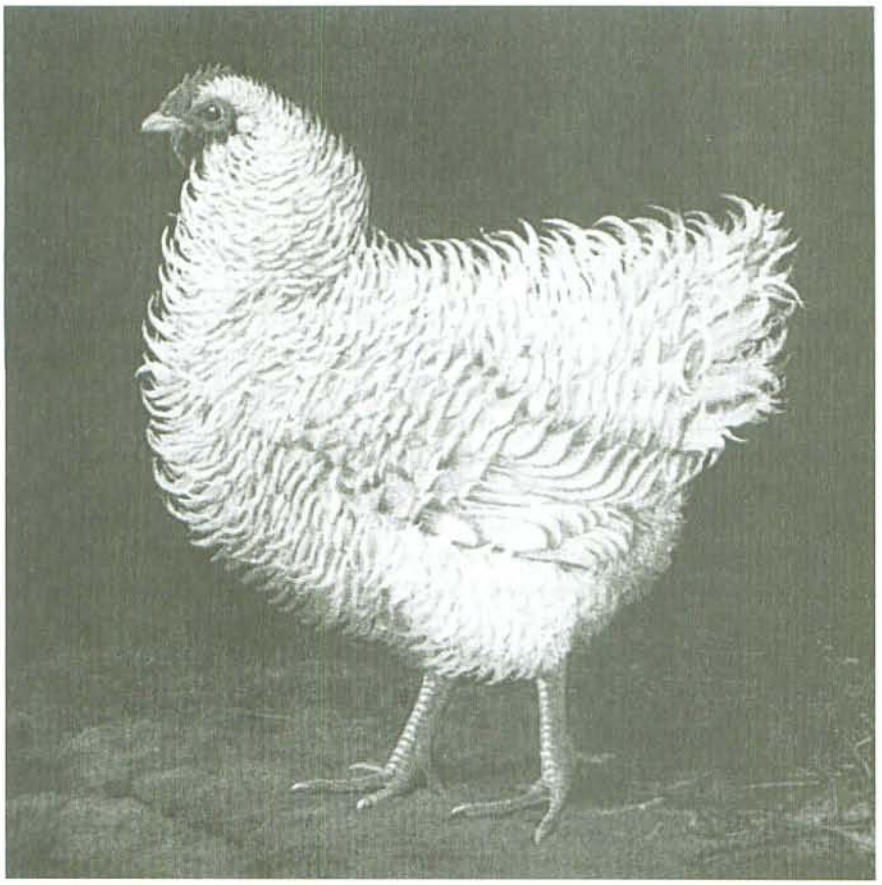


FIGURE 6–10 "Frizzled" chickens have high metabolism rates because their abnormal plumage does not provide as much insulation as that of normal chickens. The following description appeared in *Ornamental and Domestic Poultry* (Edmund Saul Dixon 1848, p. 344): "It is difficult to say whether this be an aboriginal variety, or merely a peculiar instance of the morphology of feathers; the circumstance that there are also Frizzled Bantams would seem to indicate the latter case to be the fact. Schoolboys used to account for the up-curled feathers of the Frizzled Fowl, by supposing that they had come the wrong way out of the shell."

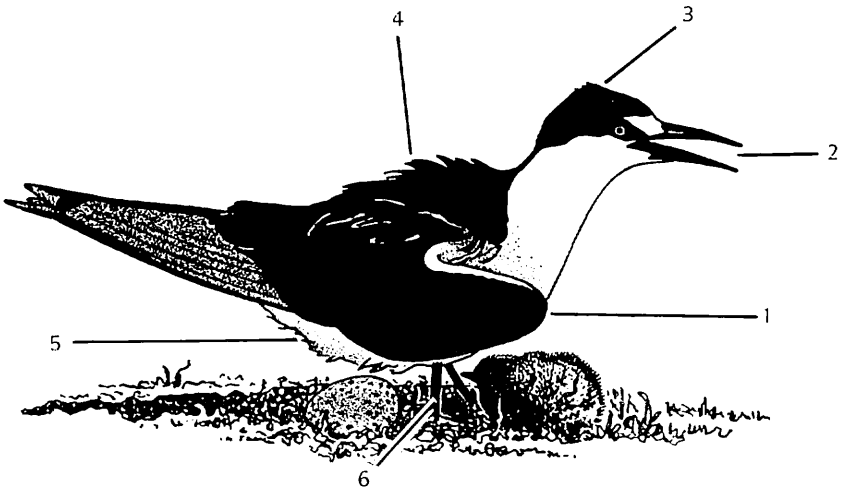


FIGURE 6–11 The Sooty Tern, a bird that is subject to great heat stress at the nest. On a hot day, the bird uses a variety of heat-dissipating mechanisms: (1) exposing the bend of the wing, (2) panting, (3) ruffling crown feathers, (4) ruffling back feathers, (5) wetting abdomen periodically, and (6) exposing the legs. [*From Drent 1972*]

of fresh plumage in September (Lowther and Cink 1992). Seasonal adjustments in insulation are less pronounced in tropical birds and in migratory species that escape major shifts in environmental temperatures.

Birds adjust the positions of their feathers to enhance either heat loss or heat conservation. Fluffing the feathers in response to cold creates more air pockets and increases the insulation value of the plumage. Additional heat savings come from tucking the bill under the scapula feather tract and reducing exposure of the legs. Holding the wings out from the body and extreme elevation of the back, or scapular, feathers enhance heat loss by exposing the bare apterial skin to convection. Tropical seabirds that nest in the open sun often elevate their plumage to avoid overheating (Figure 6–11).

Dark pigmentation aids temperature regulation by absorbing the energy-rich short wavelengths of the solar spectrum. Light-colored plumage reflects, rather than absorbs, more of the impinging radiant energy than does dark plumage. The Greater Roadrunner erects its scapular feathers and orients its body so that the early-morning sun heats strips of black-pigmented skin on its dorsal apteria (Hughes 1996).

The net thermal effect of plumage is influenced by the wind. Wind, or windchill, increases the rate of heat loss and compensatory heat production. The thick plumage of the Snowy Owl provides excellent insulation, but the rate of heat loss triples in winds of only 27 kilometers per hour compared with the rate of heat loss in still air (Parmelee 1992). The use of wind-sheltered sites, including holes or burrows for roosting and nesting, can protect birds from such heat loss.

The cooling effects of wind are most pronounced on black feathers, which concentrate solar heat near the surface of the plumage. Black feath-

ers can increase the amount of heat that a bird's body absorbs from the environment when there is no breeze. A light breeze, however, removes the accumulating surface heat and reduces further penetration of the radiant heat. The black plumage of desert ravens increases convective heat loss, as do the black robes and tents of Bedouin tribes in the Sahara.

A Model of Endothermy

The model of endothermy developed by Per Fredrik Scholander and his colleagues (1950) provides a way of understanding the dynamics of temperature regulation. Their model is one of the foundations of avian physiology (Dawson and Whittow 2000; Figure 6–12). This model projects that birds expend the least energy on temperature regulation in the thermoneutral zone—the range in which the amount of oxygen consumed by resting birds does not change with temperature. Most birds do not have to change their rates of heat production to maintain an average body temperature of 40°C in the thermoneutral zone. Instead, birds can control the rates of heat loss by changing feather positions, by varying rates of the return of venous blood flow from the skin, by manipulating blood circulation in their feet, and by changing the exposure of their extremities, all of which require little direct energy expenditure. Temperature regulation by shivering or panting increases metabolism at lower and higher temperatures outside the thermoneutral zone.

The Gambel's Quail—a medium-sized species with a cute dangling topknot—is active during summer days in the seasonally hot and dry

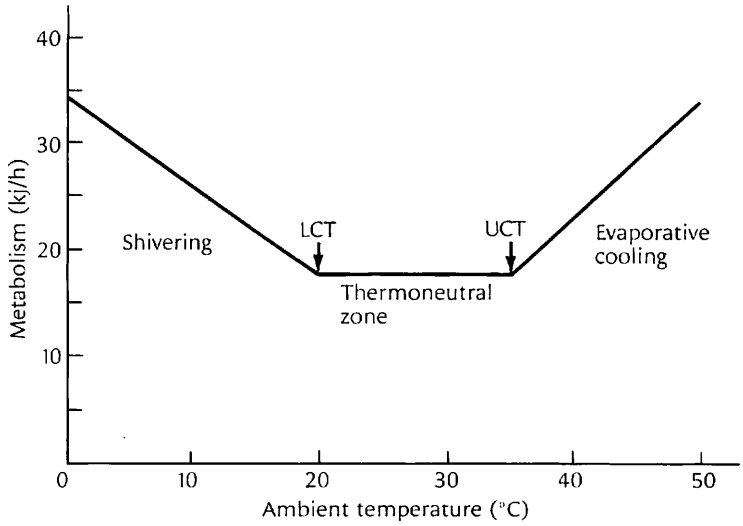


FIGURE 6–12 Scholander's model of endothermy. Metabolism increases below the lower critical temperature (LCT) primarily as a result of heat production due to shivering. Metabolism increases above the upper critical temperature (UCT) due to active loss of heat through panting and evaporative cooling, as well as to the direct effects of higher temperatures on cellular functions. Metabolism is relatively insensitive to changing ambient temperature in the zone of thermoneutrality. [*After Calder and King 1974*]

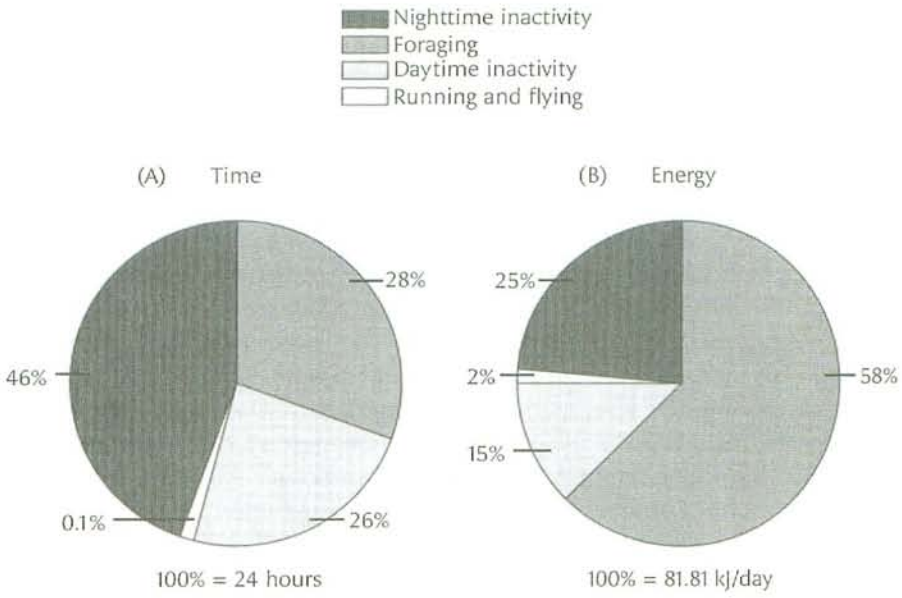


FIGURE 6–13 Time and energy budgets of Gambel's Quail in summer. (A) Fractions (percentages) of the 24-hour day spent foraging, resting, and running and flying. (B) Time budgets are multiplied by metabolic rates appropriate to each activity to estimate total daytime energy expenditures. Note that feeding, a costly activity, makes up a larger part of the energy budget than of the time budget. [*From Goldstein and Nagy 1985*]

Colorado Desert. These quail divide their time each day between foraging (6.2 hours/day) and resting (6.7 hours/day): they sleep or rest overnight (Figure 6–13). They run only to move quickly across hot, sunlit areas to another bush, and they fly short distances only two or three times a day; the time and energy costs of these activities are minor. The costs of thermoregulation also are minor. Nighttime temperatures stay within the zone of thermoneutrality and the quail avoid heat stress during the heat of the day by resting in the shade and reducing their metabolic heat production (Brown et al. 1998).

Responses to Cold Stress

When cold, a bird tenses its muscles and begins to shiver. This response increases oxygen consumption. The temperature at which shivering begins is called the lower critical temperature (LCT). The pectoralis muscles are the major source of heat produced by shivering, supplemented by the leg muscles in some species. Mammals can produce heat by nonshivering thermogenesis (heat production) in a particular kind of fat called brown adipose tissue. Birds probably lack such capability for nonshivering thermogenesis (Saarela et al. 1991).

The temperatures included in the thermoneutral zone of bird species are partly a result of adaptations to the average environmental temperatures in which they live (Weathers 1979). Birds living in colder northern

climates start to shiver at lower air temperatures than do species of warmer southern climates. Snow Buntings, for example, do not shiver until air temperature drops below 10°C (Lyon and Montgomerie 1995); Northern Cardinals start shivering at 18°C (Halkin and Linville 1999). The LCTs of large birds are lower than those of small birds, a pattern seen also in mammals. In the absence of special adaptations, small birds lose heat faster and are thus more sensitive to cold than are large birds: small birds start to shiver at a higher temperature.

Energy constraints govern the distributions and abundances of species (Root 1988). Three species of titmice and chickadees (Paridae), for example, divide local habitats and climates in the western United States (Weathers and Greene 1998; Cooper and Gessamen 2004). The Juniper Titmouse occupies the lowest, hottest, and driest semidesert habitats. The smaller Bridled Titmouse occupies slightly higher, cooler, and moister habitats. The Mountain Chickadee occupies still cooler conifer habitats at higher altitudes. Their physiologies correspond to the temperatures that prevail in their respective habitats. The Juniper Titmouse of the warmest lowland habitats has higher upper critical temperatures, greater heat tolerance, and lower rates of metabolic heat production than those of the other two species of higher elevations. Conversely, the thermal neutral zone of the Mountain Chickadee extends to cooler, lower critical temperatures than those of the other species. The distributions of these and other species of North America are predicted to change with global warming (Box 6–2).

Natural adjustments to seasonal changes in temperature are called acclimatization. Winter-acclimatized American Goldfinches (see Figure 3–4), for example, can maintain normal body temperature for 6 to 8 hours when subjected to extremely cold temperatures of −70°C (Carey et al. 1983). Summer-acclimatized goldfinches, however, cannot maintain normal body temperature for more than 1 hour when exposed to such frigid temperatures. The ability of goldfinches to withstand winter cold stress stems from an upscaling of their metabolism, including increases both in basal metabolic rates and in short-term heat production. Goldfinches

BOX 6–2

GLOBAL WARMING

The geographical distributions of birds are directly related to their temperature tolerances, water requirements, and other physiological constraints. Changes in the Earth's climate, therefore, have long regulated the distributions of birds. Now, the projected pace of global warming will likely subject birds to unprecedented changes in the location of optimal habitats and climate spaces. Models of how climate changes will affect the distributions of North American bird species suggest major reallocations of bird species from state to state (Price and Glick 2002). Painted Buntings and Great-tailed Grackles of the south will replace Bobolinks and Evening Grosbeaks in parts of southern Minnesota. Savannah Sparrows and Sage Thrashers may leave the southwestern states of Arizona and New Mexico. And some states may lose their official state birds, such as the Baltimore Oriole of Maryland.

acclimatize by restructuring the metabolic pathways that mobilize and use energy substrates, especially fatty acids (Dawson et al. 1992; Likenes et al. 2002).

Birds also select microclimates—small places where weather conditions differ from the general climate—that reduce their rate of heat loss. Roosting in holes or protected sites, such as evergreen trees, greatly reduces heat loss, which is important during cold winter nights for small passerine birds. Grouse and ptarmigan burrow into the snow to insulate themselves from cold air temperatures; so do Willow Tits, Gray-headed Chickadees, and Common Redpolls (Korhonen 1981).

Huddling together also reduces heat loss, but sometimes birds go to extremes: about 100 Pygmy Nuthatches roosted together in one pine-tree cavity, so densely huddled that some suffocated (Knorr 1957). On cold days, Inca Doves sit on top of one another between flock feeding forays, forming two- or three-row "pyramids" of as many as 12 birds (Mueller 1992). With feathers fluffed, pyramiding doves face downwind in a sheltered sunny place. In large pyramids, doves exposed on outside positions try for better positions in the top row and cause the whole pyramid to readjust. Huddling is also critical to the life style of Emperor Penguins (Ancel et al. 1997). Males of these largest of all penguins incubate their mates' eggs in total darkness in the dead of the Antarctic winter, enduring frigid air temperatures down to −50°C and winds as high as 180 kilometers per hour. Their LCT is a relatively warm −10°C. By huddling together in a giant side-by-side assemblage, thousands of egg-attentive penguins each cut their rates of energy expenditure and weight loss in half. This reduction buys an extra three weeks of incubation effort and prevents triggering the need to go to sea to feed, abandoning the egg, before the female returns and takes over.

Hypothermia and Torpor

As an energy-saving measure, avian body temperatures fluctuate a few degrees during the day and may drop significantly at night (McKechnie and Lovegrove 2002). The physiological condition in which the body temperature drops below normal is called facultative hypothermia. Many birds, ranging from Black-capped Chickadees to Turkey Vultures can lower their body temperatures by 6°C at night and by even more on extremely cold nights. They become mildly hypothermic.

Some birds lower their actual body temperatures: hummingbirds to just between 8° and 20°C and the Common Poorwill, a desert nightjar, to an extreme 4.3°C (Brigham 1992; Figure 6–14). These birds enter a state of torpor—pronounced hypothermia—in which they are unresponsive to most stimuli and are incapable of normal activity. However, a torpid bird does not abandon control of its body temperature and let it drop to air temperature. Instead, a bird in torpor regulates a lower body temperature, increasing oxygen consumption as needed at low air temperatures (Figure 6–15).

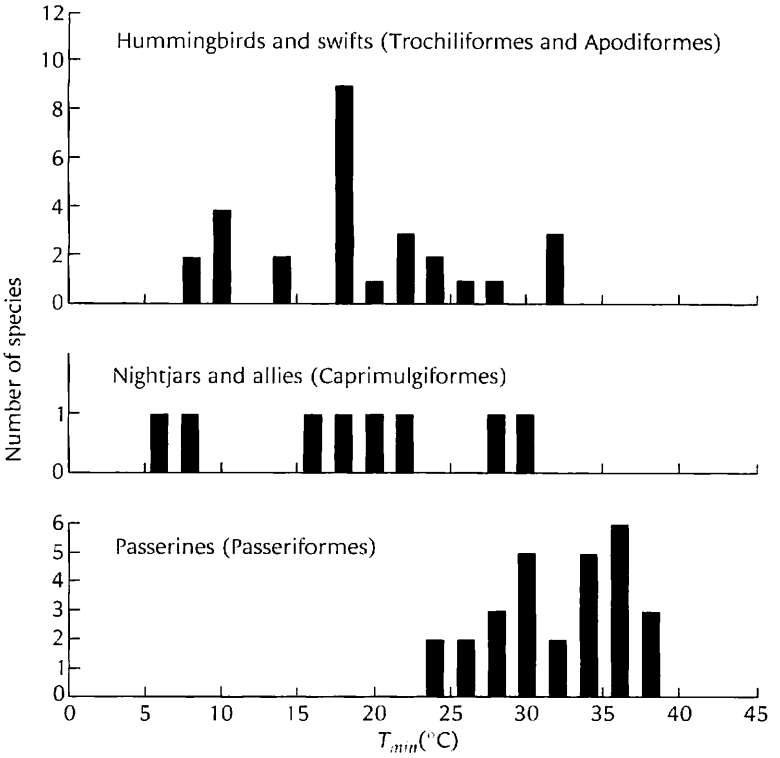


FIGURE 6–14 Minimum body temperatures during hypothermia of 28 species of hummingbirds and swifts, 8 species of nightjars and relatives, and 28 passerines. [*After McKechnie and Lovegrove 2002*]

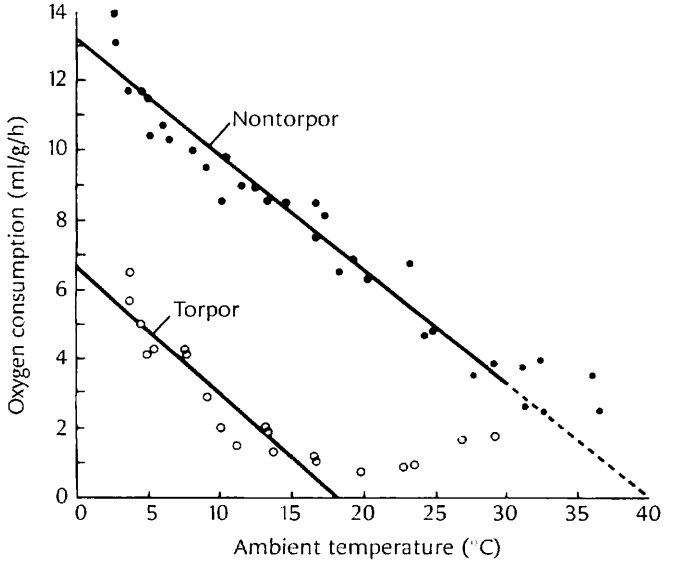


FIGURE 6–15 Metabolism of the Purple-throated Carib, a tropical hummingbird, during torpor and nontorpor. Nontorpid birds increase their metabolism (measured here in terms of oxygen consumption) as temperature decreases below the LCT of about 30°C. Torpid birds regulate their body temperatures to about 17.5°C. [*After Hainsworth and Wolf 1970*]

Torpor is characteristic of bird species in only six families: todies (Todidae); mousebirds (Coliidae); hummingbirds (Trochilidae); swifts (Apodidae), nightjars (Caprimulgidae), and pigeons (Columbidae). Passerine birds typically do not exhibit a capacity for torpor.

Facultative hypothermia saves critical energy supplies. Daily cycles of hypothermia—mild or pronounced—may be tied to internal clocks, but facultative hypothermia is also triggered on a day-to-day basis by food deprivation and low energy stores. Fruit-eating, nectar-feeding, and aerial insect-eating species in the families just named are able to respond to unpredictable food supplies by saving energy through overnight hypothermia or torpor as needed. Hummingbirds save as much as 27 percent of their total daily energy expenditures by allowing their nighttime body temperatures to drop from 20° to 32°C below normal. Beyond saving energy when hungry, hypothermia is used proactively by both hummingbirds and geese to increase the energy that they can allocate to building fat supplies needed for migration (Hiebert 1993; Butler and Woakes 2001).

Warming up is the main challenge of hypothermia, especially torpor. Birds waking from torpor begin to show good muscular coordination at 26° to 27°C but require body temperatures of at least 34° to 35°C for normal activity. A small hummingbird requires about an hour to arouse from torpor at 20°C, but a medium-sized bird such as an American Kestrel requires 12 hours to warm up from the same reduced body temperature.

Full torpor is usually neither practical nor economical for short periods in larger birds. Nightjars and their relatives (Order Caprimulgiformes) are an exception. As a group, the nightjars have low basal metabolic rates, 59 percent lower than those of other birds when corrected for body size (Lane et al. 2004). Low metabolism combined with torpor enables them to exploit an unpredictable food source—temperature-dependent aerial insects at twilight. In addition to the daily use of torpor, the Common Poorwill (55 grams) actually "hibernates" for two to three months during the winter (Csada and Brigham 1992). Its body temperature drops to a (regulated) 4.3°C. This habit was long known to Native Americans; the Hopi people refer to the poorwill as Hölchoko, "the sleeping one." Torpor reduces a poorwill's oxygen consumption by more than 90 percent. Poorwills are capable of spontaneous arousal at low ambient temperatures but require about 7 hours to warm up fully. Poorwills also save energy by using torpor regularly during the summer and spring, especially when faced with cold, wet weather; they even occasionally become torpid during incubation.

Responses to Heat Stress

Birds reduce heat loads through avoidance behaviors; through controlled elevation of body temperature, called hyperthermia; and through active heat loss by means of evaporative cooling.

Reduced activity at midday, seeking shade, bathing, and soaring in cooler air are simple ways to reduce heat loads. More cleverly, domestic pigeons can be trained to turn on cooling fans, especially when thirsty

(Schmidt and Rautenberg 1975). Desert birds generally tend to have low metabolic rates and highly efficient evaporative cooling systems. Poorwills, for example, tolerate severe heat stress when baked by the desert sun by dissipating as much as five times their metabolic heat production.

Controlled hyperthermia has both advantages and risks. In heat-stressed birds, especially dehydrated ones, body temperatures may rise from 4° to 6°C above normal, approaching the near lethal threshold of 46°C. Such controlled hyperthermia reduces the rate of heat gain from the environment by bringing body temperature closer to air temperature. If body temperatures exceed air temperatures, the hyperthermic bird can lose heat without evaporative cooling and save water. The body temperatures of ostriches increase 4.2°C during the daily cycle, a response that saves liters of water per day that would otherwise be lost in evaporative cooling. Controlled hyperthermia during the warm daylight hours also allows for the storage of extra heat needed to save fuel at cooler nighttime temperatures, especially in large birds.

Birds actively lose heat by evaporative cooling and other means above the UCT. Evaporative cooling is a highly effective method of heat loss that can dissipate from 100 to 200 percent of heat production. Evaporative water loss, however, is the major source of water loss to the environment; small birds lose five times as much water in this way compared with their loss of water in feces or urine (Williams and Tieleman 2000). Storks and New World vultures increase heat loss through evaporative cooling from the legs by defecating directly onto their own legs.

The body sizes of nonmigratory birds correspond to geographical gradients in temperature and humidity. Climatic rules, such as Bergmann's Rule—the increase in body size with cooler temperatures—refer to these correlations in a simplistic way (Zink and Remsen 1986). Widespread North American birds, such as the American Robin and the Downy Woodpecker, tend to be smallest in hot, humid climates and largest in cold, dry climates (Figure 6–16). The potential for heat loss by evaporative cooling is lowest in hot, humid climates, which favor small birds with more

BOX 6–3

SELECTION FOR LARGER HOUSE SPARROWS

Geographical differences in body size as well as plumage color can evolve rapidly among populations—within 100 years for House Sparrows introduced to both North America and New Zealand (Lowther and Cink 1992). The body size of House Sparrows is positively correlated with seasonality and annual temperature range in both North America and Europe. Increased fasting ability appears to be the primary advantage of large size in seasonal environments. Conversely, small size minimizes individual maintenance costs in equable and more predictable or aseasonal environments.

Studies of the effects of severe winter weather have documented the survival advantages of larger House Sparrows. Large-sized males, in particular, survived best because they have superior thermoregulation efficiencies and fasting abilities—and greater access to well-protected roost sites (Buttemer 1992).

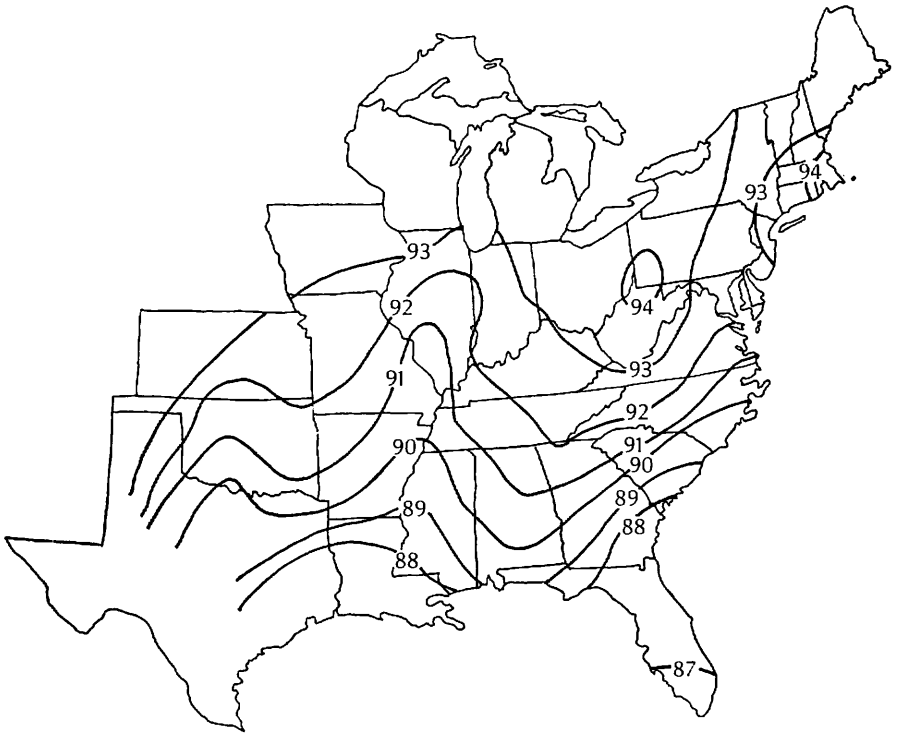


FIGURE 6–16 Size variation in Downy Woodpeckers. Body size (which is directly proportional to wing length) increases to the north, but individual birds in the warm, humid Mississippi Valley and coastal areas are small compared with those at other localities at similar latitudes. Numbers indicate average wing lengths in millimeters. [*From James 1970*]

heat-losing surface area relative to mass. Conversely, cool, dry air favors larger bodies with reduced surface areas that conserve heat (Box 6–3).

Metabolism increases above the UCT because of panting and other efforts that facilitate heat loss. In birds, as in dogs, panting increases evaporative cooling from the upper respiratory tract. Birds typically ventilate faster during heat stress, when body temperatures rise to 41° to 44°C and above. To supplement panting when they are hot, some birds rapidly vibrate the hyoid muscles and bones in their throats. This action, called gular fluttering, increases the rate of evaporative water loss from the mouth lining and upper throat. Many seabirds, both adults and young, regulate body temperature by means of gular fluttering when baked by hot sun shining on their exposed nests. Desert species, including Common Poorwills, achieve more than half of their evaporative cooling in this way.

Evaporative water loss includes loss through the skin as well as in respiration. Birds do not have sweat glands. Instead, they evaporate water directly through the skin, a process called cutaneous water loss—a process that is especially well developed in certain pigeons and doves (Marder et al. 1989). In larks (Alaudidae), cutaneous water loss comprises from 50 to 70 percent of total evaporative water loss at moderate air temperatures. Larks rely increasingly on respiratory water loss for evaporative cooling at

high air temperatures. Desert-adapted Greater Hoopoe-Larks that are acclimatized to high temperatures reduce their cutaneous water loss by changing the lipid composition of the epidermis (Haugen et al. 2003).

When necessary, birds, especially large-footed water birds such as herons and gulls, can lose most of their metabolic heat through their legs and feet (Figure 6–17). Alternatively, when heat conservation is important, they control blood flow to reduce this loss by more than 90 percent. The control of heat loss from the feet is made possible by a network of special blood vessels in the avian leg, which act to conserve or dissipate heat as needed. The arteries and veins intertwine at the base of the legs in such a way that heat carried by arterial blood from the body core can be transferred directly to blood returning in the veins. This so-called countercurrent exchange conserves body heat at low air temperatures. For cooling, the blood can completely bypass the network and go directly into the extremities. An overheated Southern Giant-Petrel can increase by 20-fold the rate of blood flow through its feet.

Blood vessels of the head also enable countercurrent heat exchange there. Most birds maintain the temperature of their brains about 1°C cooler than that of their bodies. Helmeted Guineafowl take this maintenance to an extreme. They have colorful, naked heads with large protrusions, or helmets, and wattles that enhance convective heat loss, as do the wattles of chickens and other fowl. Heat loss from these wattles may be so great that a guineafowl's head cools faster than its body, beyond the ability of

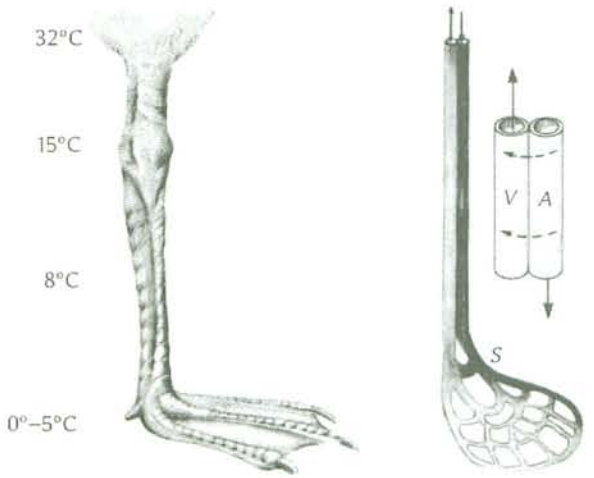


FIGURE 6–17 Gulls regulate the rate of heat loss from their feet by varying the amount of blood shunted from the base of the leg, where the temperature is roughly 32°C, to veins at the base of the foot, where the temperature may be close to 0°C. They can decrease circulation through the foot, where the rate of heat loss is high, by opening a shunt (S) and constricting the blood vessels in the feet, thereby providing a more direct return of the blood. In addition, heat from outgoing arterial blood can be transferred directly to incoming venous blood. Arrows indicate the direction of arterial (A) and venous (V) blood flow and dashed arrows the direction of heat transfer. [*From Ricklefs 1990*]

increased blood flow from the body core to replace lost heat (Crowe and Withers 1979). Unlike those of most birds, the brain temperatures of guineafowl vary as much as 6.5°C without serious consequence.

The heat produced during flight could cause lethal increases in body temperature. Common Pigeons, for example, produce seven times as much heat in flight as they do at rest, and their body temperatures quickly rise from 1° to 2°C. Some birds apparently will not fly at temperatures above 35°C, because of their inability to control hyperthermia. White-necked Ravens, for example, fly only short distances in the heat or fly in the cooler air at high altitudes (Hudson and Bernstein 1981).

Flight itself increases convective heat loss. The airstream compresses the plumage to the skin, and extension of the wings exposes the thinly feathered ventral base of the wing. As a result, the rate of heat loss by flying parakeets increases to 3.1 times the resting value at 20°C and that of Laughing Gulls increases to 5.8 times the resting value.

Feeding and Digestion

Because birds burn energy at high rates, they must feed frequently to refuel themselves. Adaptations for feeding are a conspicuous feature of avian evolution (see Chapter 1). These adaptations include not only the ways in which birds move while feeding and capturing food, but also many specializations of the entire digestive tract, starting with diverse tongue structures, which include the woodpecker's spear tip, the hummingbird's tube tip, and the duck's fringed filter (Figure 6–18). Gizzards range from large, hard seed-crushing structures in fowl and finches to softer bags in fish-eating birds such as the Anhinga to miniscule pouches in the Hoatzin, which digests leaves in specialized cervical and thoracic crops. The digestive tract itself changes size and structure seasonally, especially in relation to migration (Karasov 1996; see Box 10–3).

Several characters distinguish the digestive systems of birds from other those of other vertebrates (Figure 6–19, pages 166–167). The lack of teeth means that the bill and mouth function mainly in food getting. Food processing by the bill is limited to such activities as cracking and shucking seeds or tearing prey into bite-size pieces. Birds have little saliva and few taste buds compared with mammals, which chew and physically process food as the first step and then subject it to chemical processing as the second step. Birds reverse this sequence. They start chemical digestion in the proventriculus, a unique structure that handles food before it undergoes physical digestion in the gizzard. Some birds also regurgitate undigestible parts of their food—bones or seeds, for example—as pellets.

Food passes from the oral cavity to the stomach through the esophagus, a muscular structure lined with lubricating mucous glands. In birds that swallow large prey whole—fish-eating birds, for example—the esophagus expands as needed. No mere passageway, the esophagus is a versatile organ. The esophagus of pigeons produces nutritious fluid, called pigeon milk, for their young. The esophagus of pigeons and many other species can also be inflated for display and sound resonance. Some birds have

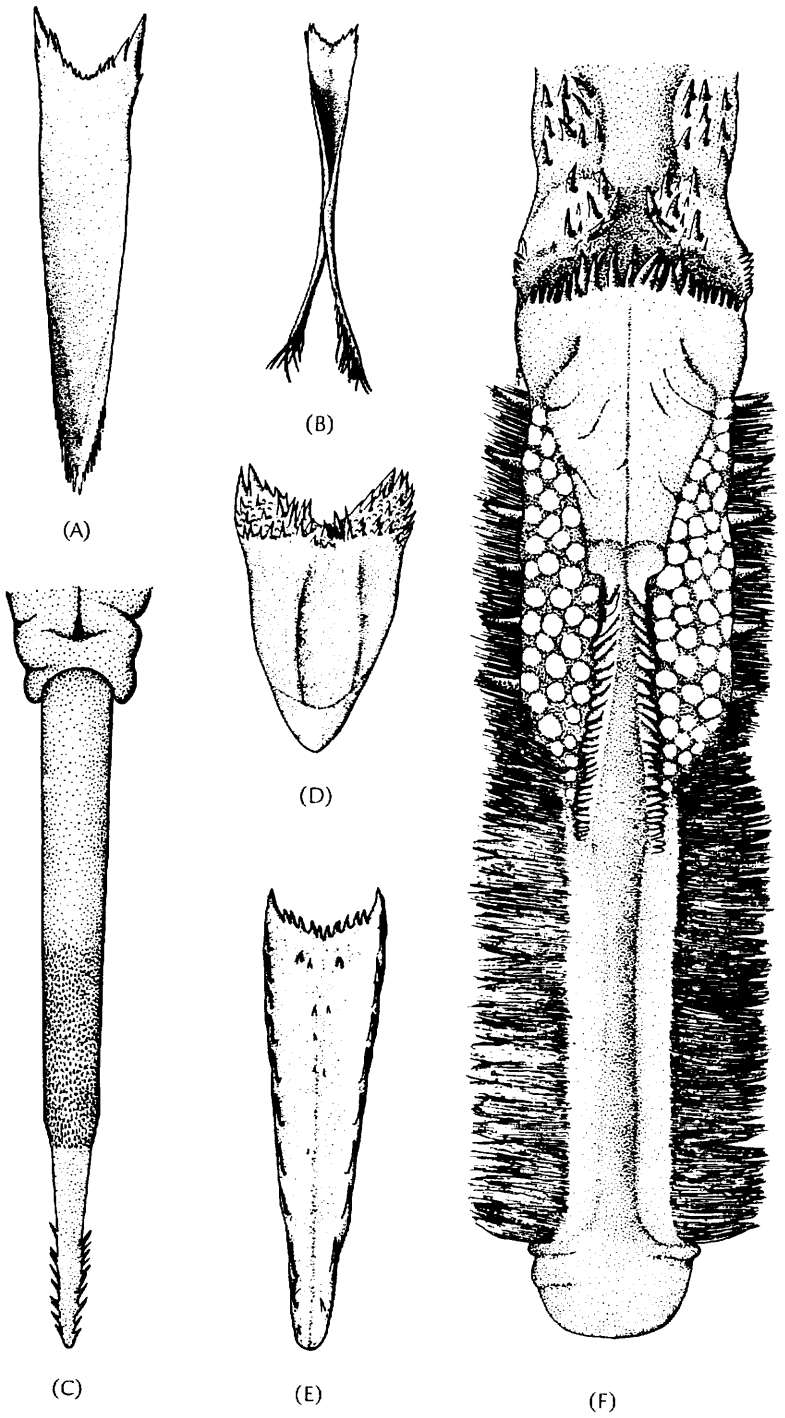


FIGURE 6–18 Bird tongues (dorsal view): (A) generalized passerine tongue with terminal fringes (American Robin); (B) tubular, fringed nectar-feeding tongue (Bananaquit); (C) probing and spearing woodpecker tongue fitted with barbs (White-headed Woodpecker); (D) short, broad tongue of a fruit eater (Diard's Trogon); (E) fish-eater tongue with rear-directed hooks that keep slippery fish from wriggling back to freedom (Sooty Shearwater); (F) food-straining tongue (Northern Shoveler). [*After Gardner 1925*]

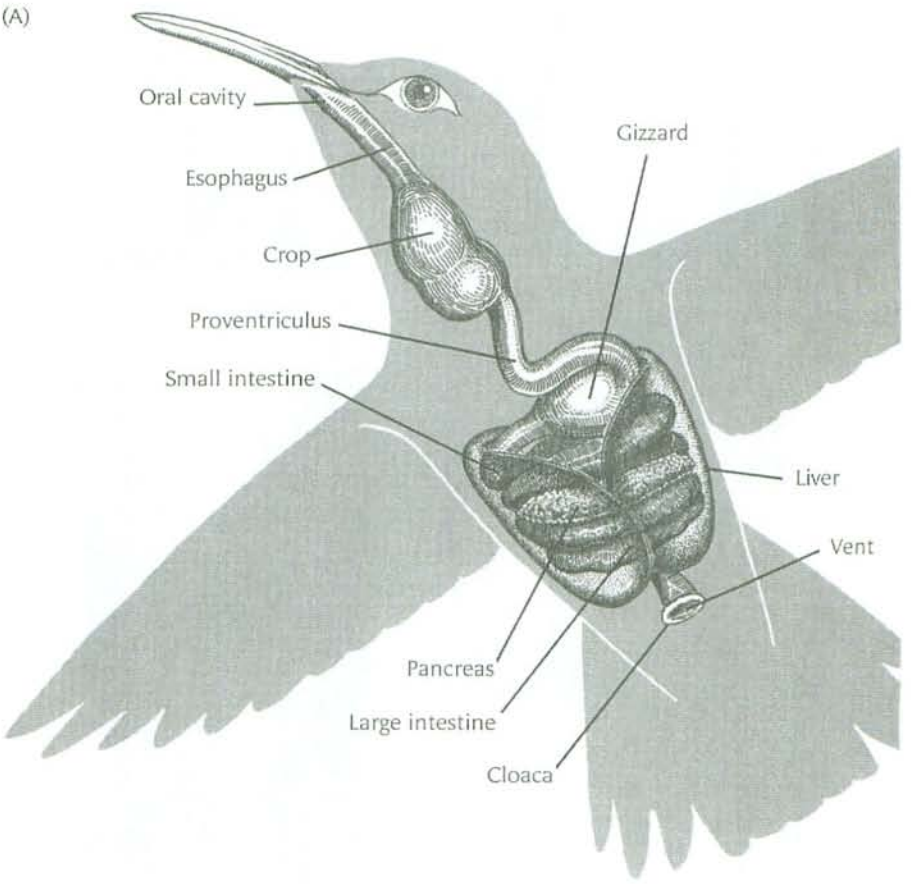


FIGURE 6–19 Bird digestive tracts. (A) The digestive tract of a hummingbird.
(*continued*)

crops, which vary in size and structure (Figure 6–20). The crop—an expanded esophageal section—stores and softens food and regulates its flow through the digestive tract. The chambers of the enlarged crop and esophagus of the Hoatzin, a leaf-eating bird of South America, have evolved into a multichambered, glandular stomach that ferments and digests tough leaves (Grajal 1995).

Most birds have two-chambered stomachs composed of an anterior glandular part, or proventriculus, and a posterior muscular part, or gizzard. Shapes and structures of the stomach differ more than any other internal organ, corresponding to the dietary habits of different species. The proventriculus, a structure not present in reptiles, is most developed in fish-eating birds and raptors. It secretes acidic gastric juices (pH 0.2–1.2) from its glandular walls, thereby creating a favorable chemical environment for digestion. Peptic enzymes in the proventriculus dissolve bones rapidly. The Bearded Vulture can digest a cow vertebra in two days. A shrike can digest a mouse in 3 hours. In addition to the usual functions, a petrel uses its well-developed proventriculus to store oil by-products of

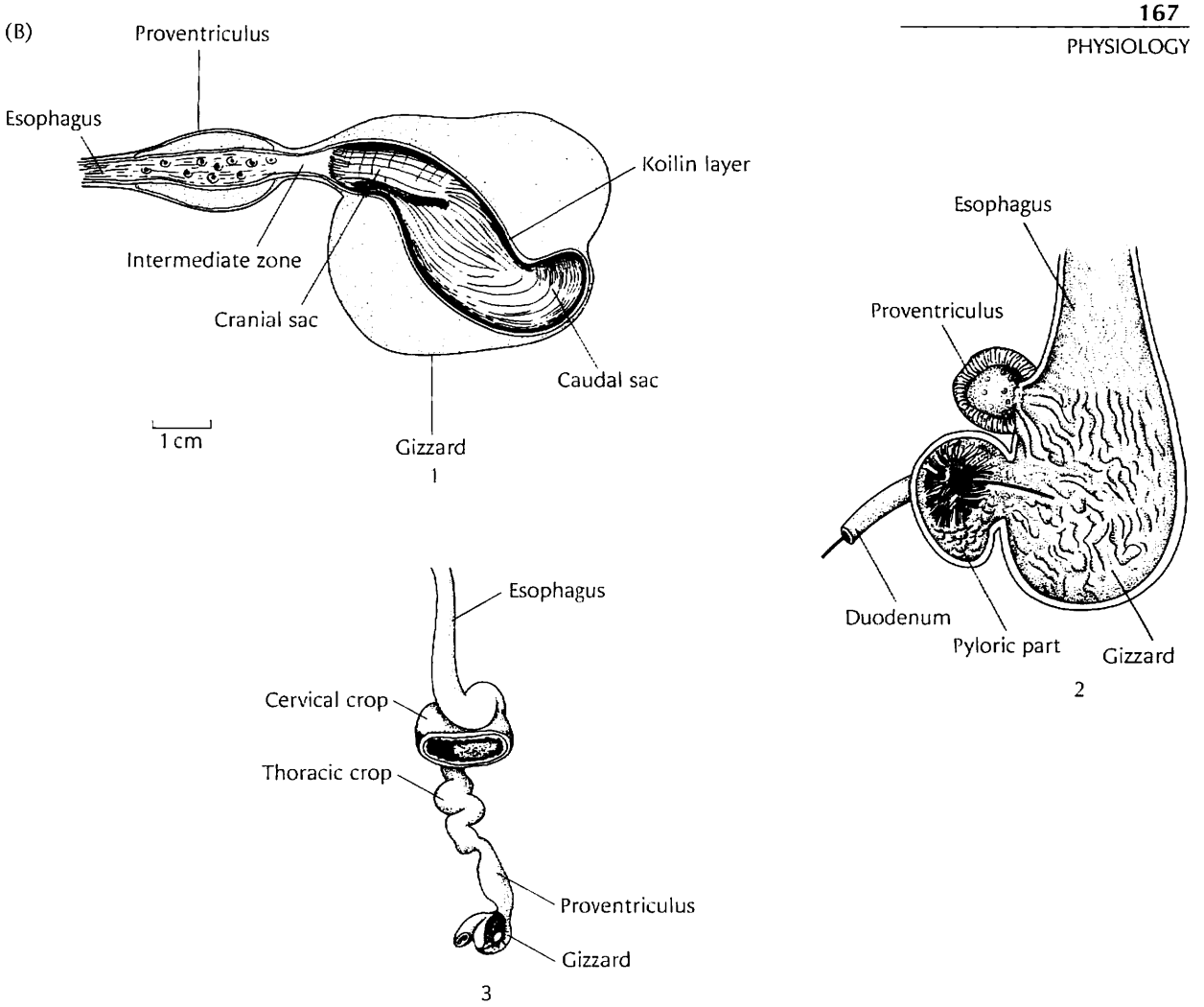


FIGURE 6–19 *(Continued)* (B) Stomachs of (1) domestic chicken; (2) Anhinga; (3) Hoatzin. (All 66 percent of natural size.) [*(A) After Tyrrell and Tyrrell 1985; (B) after McLelland 1975; Garrod 1876; Pernkopf and Lehner 1937*]

digestion, which it regurgitates as food for its young—and sometimes spews at predators and ornithologists.

The length of a bird's intestinal tract averages 8.6 times its body length but varies from 3 times body length in the Common Swift to 20 times body length in the Common Ostrich. The intestine tends to be short in species that feed on fruit, meat, and insects and long in species that feed on seeds, plants, and fish.

Near the terminus of the digestive tract, small side sacs, called ceca, are present in many birds. The ceca (sing. cecum) attach to the posterior end of the large intestine, may be paired or single, and vary from small or absent to prominent in fowl and ostriches. The avian cecum is a multipurpose, vitally important organ (Clench and Mathias 1995). Among their

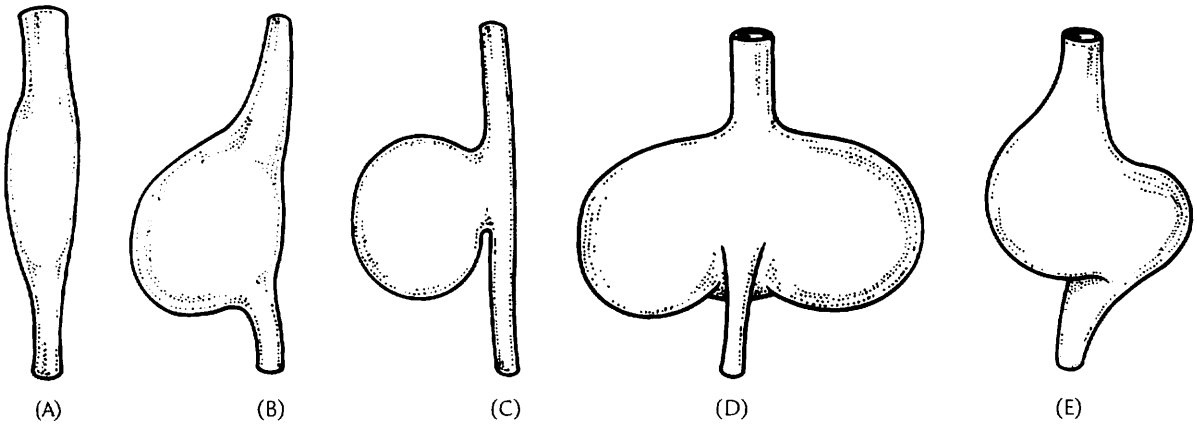


FIGURE 6–20 The avian crop varies greatly in shape from a simple, expanded section of the esophagus, as found in cormorants, ducks, and shorebirds, to a lobed, saclike diverticulum, as found in vultures, fowl, pigeons, parakeets, and certain northern finches, the redpolls: (A) cormorant, (B) vulture, (C) fowl, (D) pigeon, and (E) parakeet. [*From Pernkopf and Lehner 1937*]

many functions, ceca aid digestion, especially of fibrous plant foods. Bacteria in the ceca further digest and ferment partly digested foods into usable compounds absorbed through the cecal walls. In addition, ceca produce antibodies that fight disease organisms, aid the absorption of water, and aid in the metabolism of uric acid into amino acids (Clench 1999).

Linked to the development of flight and high metabolic rates, the digestive systems of birds extract nutrients and energy with high efficiencies from small volumes of rapidly processed food (Place 1991). The passage time of food through the digestive tract—from the esophagus through the glandular stomach and gizzard into the intestine and finally out the cloaca as feces—varies from less than half an hour for fruit and berries ingested by thrushes and the Phainopepla (Figure 6–21) to half a day or more for less easily digested food.

Mammals typically absorb nutrients by active transport into cells that line the intestine. Most birds absorb glucose sugars and amino acids by active transport, but they take up other nutrients passively and nonspecifically into cells along with fluid uptake. The passive absorption of nutrients requires little energy and is directly responsive to concentration, allowing quick uptake of needed energy. But toxins in fruits and seeds also may be absorbed indiscriminately.

Parrots eat seeds and bitter green fruits that are full of toxins that would be distasteful and even lethal to other animals. Parrots of several species, large and small, also gather in large, colorful assemblages to eat dirt, long thought to be grit that aided food processing by the gizzard. It turns out that the dirt is actually clay with minerals that serve as an antidote to toxins. Kaopectate, which consists partly of clay, soothes a person's upset stomach in similar ways (Gilardi et al. 1999). The negatively charged sites

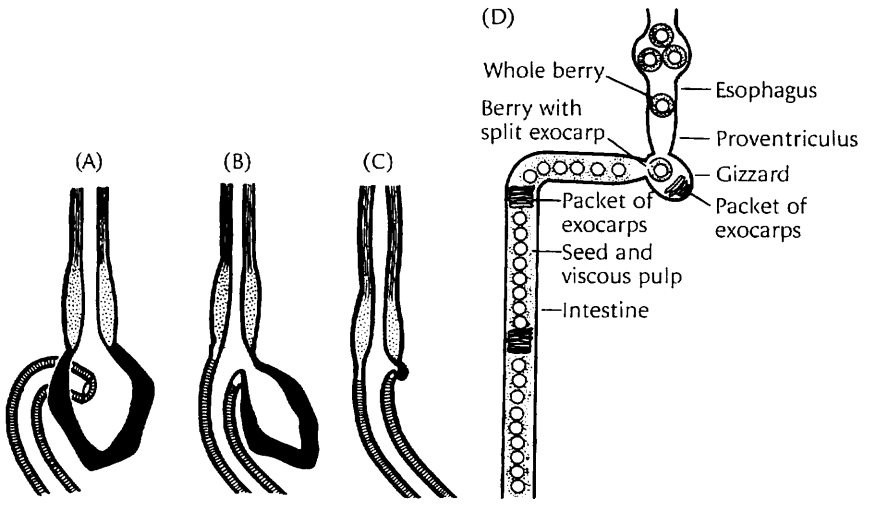


FIGURE 6–21 Specialized stomachs of fruit eaters: (A) unmodified gizzard of a primitive flowerpecker; (B) more specialized stomach of the Black-sided Flowerpecker, which allows fruit to bypass the gizzard and allows insects to enter the gizzard for grinding; (C) rudimentary gizzard of the Violaceous Euphonia; (D) gizzard of the Phainopepla, which can shuck the outer-layer skin (exocarp) from mistletoe berries and then defecate a pack of skins at intervals between the undigested parts of the berries. [*After Desselberger 1931; Walsberg 1975*]

of the clay minerals bind to the positively charged toxin molecules in the acid environment of the stomach. Mammals, including hunter–gatherer humans, eat soil selectively for the same reasons (Diamond 1999).

The assimilation of digested food through the intestinal walls depends on the nature of the food ingested. Raptors assimilate 66 to 88 percent of the energy contained in ingested meat and fish. Herbivores assimilate as much as 60 to 70 percent of the energy contained in the young plants that they ingest but only 30 to 40 percent of the energy in ingested mature foliage. At the low end, Spruce Grouse assimilate only 30 percent of the energy contained in the spruce leaves that they eat (Boag and Schroeder 1992). Assimilation efficiencies and other digestive responses shift with seasonal changes in diet (Levey and Karasov 1989). For example, American Robins show improved assimilation efficiency of lipids coupled to their increased use of lipid-rich berries in the fall (Lepczyk et al. 2000).

Fruits provide "predigested" nutrients in the form of free amino acids rather than proteins and in the form of simple sugars instead of complex carbohydrates (Levey and Martinez del Rio 2001). This "predigestion" allows rapid processing—as little as 20 minutes to pass through the gut—and the ingestion of large quantities within short time spans. Fruits and fruit-eating birds come in two major categories: carbohydrate-rich and lipid-poor versus lipid-rich and carbohydrate-poor.

The digestion of lipids requires longer retention times in the gut than does the digestion of sugars; lipid digestion and sugar digestion also differ in the enzymes required. Corresponding to their digestive physiologies, some birds, such as North American thrushes, favor lipid-rich berries, whereas others, such as Cedar Waxwings, favor sugar-rich berries. The fast passage of berries through the gut means that lots of glucose is still in the semidigested fruit pulp just before evacuation. The Cedar Waxwing appears to be unique among birds in that it absorbs glucose in its rectum through active transport at the same high rate as it was previously absorbed in its intestines.

Like junk food, sugar-rich berries may require supplementary nutrition. Cedar Waxwings, therefore, eat the ripe fruits of *Viburnum opulus* only when protein-rich cottonwood *(Populus deltoides)* catkins are available as a supplementary food source (Witmer 2001). In the laboratory, waxwings lose weight when fed only fruit or only catkins. Together, however, they provide a balanced and healthy diet.

The nutrition requirements of chickens are known in detail (Klasing 1998). Less is known about the degree to which the diets and foraging behaviors of wild birds are directed specifically toward nutrition. Birds are usually assumed to passively obtain adequate nutrition to meet their energy needs in the course of their daily foraging and to rarely suffer malnutrition or nutritional stress. Among the known exceptions, the Willow Ptarmigan, an alpine grouse, prefers heather leaves that are rich in nitrogen and phosphorus (Moss et al. 1972). In the laboratory, White-crowned Sparrows are sensitive to concentrations of certain amino acids—namely, valine and lysine—in synthetic diets; they were adept at selecting diets that satisfied their amino acid requirements (Murphy and King 1989).

Many passerine songbirds cannot digest sucrose—a complex sugar that we humans take for granted—because these songbirds lack the enzyme sucrase, which breaks sucrose into smaller sugars—glucose and fructose—that are amenable to assimilation (Martinez del Rio and Stevens 1989). The ingestion of sucrose at high concentrations can cause sickness and diarrhea, owing to malabsorption. As a result, Common Starlings learn to shun sucrose in laboratory tests (Clark and Mason 1993).

In contrast, hummingbirds feed on sucrose-rich nectar. Hummingbirds assimilate from 95 to 99 percent of the energy in nectar, which consists primarily of sugars and water. Their intestines exhibit 10 times as much sucrase activity as is evident in passerine intestines (Schondube and Martinez del Rio 2004). They also quickly absorb glucose from their fluid meals at the highest levels known among vertebrates. They achieve this record by means of unusually high densities of sites that actively bind sugar and transport it across cell membranes (Karasov et al. 1986). They appear to function normally at the maximum levels and are unable to absorb sugars faster when stressed by cold temperatures or extreme activity (McWhorter and Martinez del Rio 2000).

Waxes, which consist of saturated, long-chain fatty acids, are among the least digestible of all foods. Several groups of birds, however, use wax

as a source of metabolic energy. Seabirds, including petrels and auklets, metabolize the rich wax compounds in the marine crustaceans that they eat (Roby et al. 1986; Place 1991). Waxy foods, together with bile and pancreatic digestive juices, recycle several times from the small intestine back to the churning actions of the gizzard and proventriculus to break the complex fatty acids into smaller, usable elements.

Among the few land-bird species that eat wax are the Yellow-rumped Warblers and the Tree Swallows of North America. They consume large quantities of wax-coated bayberries. Both warbler and swallow are capable of high assimilation efficiencies (80 percent) of bayberry wax (Place and Stiles 1992). Their special gastrointestinal traits include elevated gallbladder and intestinal bile-salt concentrations, slow gastrointestinal transit of dietary lipids, and probably the return of the partly digested food to the gizzard from the small intestine. The ability to use an unusual food source such as bayberry wax allows these birds to occupy northern coastal regions during periods when insects are not available.

Honeyguides are well known for their ability to eat and assimilate pure wax, usually from the honeycombs of bees but occasionally from candles on the altars of Christian missions (Diamond and Place 1988). The Greater Honeyguide of Africa leads animals with a sweet tooth, such as the ratel (honey badger), as well as people, to beehives that it has found. First, the honeyguide solicits attention by approaching closely and giving distinctive churring calls. If it gets its helper's attention, the honeyguide flies a short distance in the direction of the beehive, returning frequently to ensure progress. In this manner, the honeyguide leads its assistant a kilometer or more to the beehive, which it announces with a new set of excited vocalizations. The assistant then opens up the hive, takes the honey, which is prized by many African peoples, and leaves the wax and the bee larvae for the honeyguide.

Energy Balance and Reserves

Whether hungry or temporarily sated, all birds face the challenge of maintaining their energy balances. Energy balance is the dynamic relation between energy intake and energy expenditure. Ideally, intake and expenditure are roughly equal, and so the bird neither gains nor loses much weight. Preceding migration or winter, however, a bird may eat more than it metabolizes each day so that the excess can be stored as fat reserves.

Foraging Time

The amount of time that a bird must feed each day depends on its total energy requirements and its achieved rate of energy intake. Roughly speaking, a bird's foraging time must double when its rate of net energy gain is reduced by half.

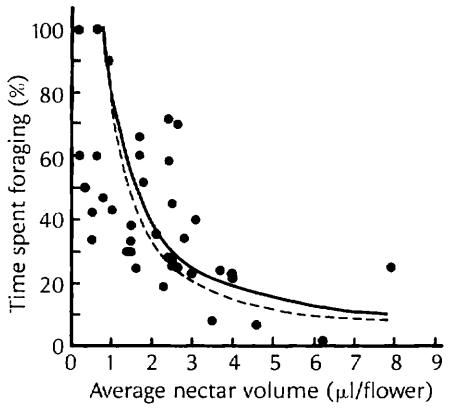


FIGURE 6–22 The amount of time spent feeding by a Golden-winged Sunbird depends on the average amount of nectar that it gets from a flower. The solid line is the predicted relation, assuming that the sunbird visits only as many flowers as it needs to replace total daily expenditures. The dashed line is fitted to the actual field measurements of foraging efforts. [*After Gill and Wolf 1979*]

Sunbirds' daily foraging times, for example, decline with an increase in floral nectar content (Figure 6–22). By providing supplemental food and water, Irene Tieleman and Joe Williams (2002) caused Greater Hoopoe-Larks in the Arabian desert to decrease their foraging time by 13 to 29 percent, resting instead and reducing exposure to the midday heat. Foraging times also vary with seasonal changes in food availability. Small titmice and goldcrests in England may forage 90 percent of the day in winter when food is scarce, their metabolism is high, and days are short (Gibb 1960). Goldcrests in arctic Finland and Norway sometimes suffer high mortality rates in harsh winters because they are unable to balance their energy budgets (Österlöf 1966; Hogstad 1967). At the other end of the spectrum, tropical fruit-eating birds meet their needs in minimum time, less than 10 percent of daylight hours.

If a short foraging time is sufficient for self-maintenance, individual birds can afford to build up energy reserves or undertake energy-expensive activities such as migration, molting, and breeding (see Chapter 9). Low foraging times also allow birds more time to hide from predators, select favorable microclimates, establish dominance and property rights over other individual birds, court potential mates, and rear young. Birds routinely act to increase foraging efficiency and reduce required foraging time.

Fat Reserves and Fasting

Most birds maintain minimal fat (lipid) reserves. Excess mass increases flight costs and reduces agility and the odds of escaping predators. Small, temperate-zone passerines typically have fat reserves of no more than 10 percent of body mass to cover their fasting needs during midwinter. Yellow-vented Bulbuls in tropical Singapore maintain fat reserves of only 5 percent of body weight throughout the year, little more than is

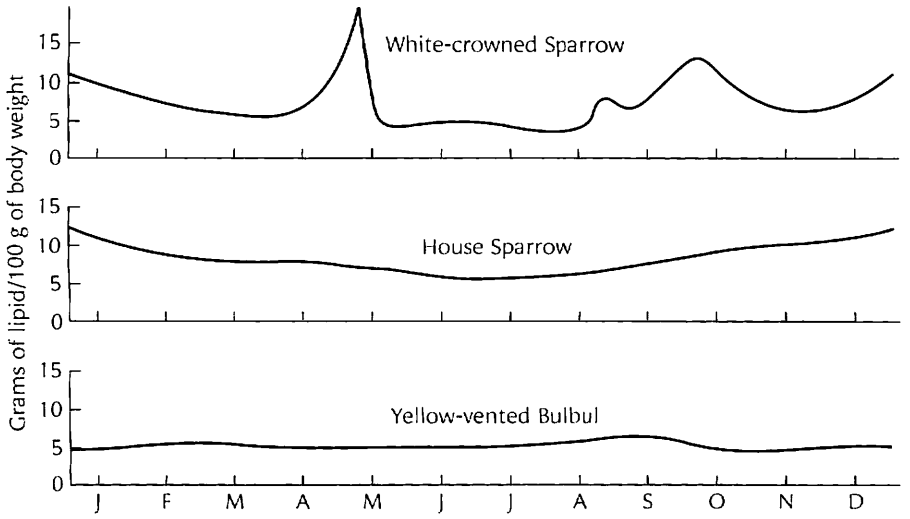


FIGURE 6–23 Annual cycles of fat deposition in a temperate-zone migrant (White-crowned Sparrow), a temperate-zone nonmigrant (House Sparrow), and a tropical nonmigrant (Yellow-vented Bulbul). [*From Blem 2000*]

needed to survive overnight and to begin feeding the next morning (Figure 6–23).

In general, large birds can store more fat and can fast longer than smaller birds can. At moderately low temperatures (1°–9°C), a 10-gram warbler, for example, may not survive a day without food, whereas a 200-gram American Kestrel can survive for five days (Calder 1974). Male Emperor Penguins fast for 90 to 120 frigid days during their incubation vigils of the Antarctic winter and may lose 45 percent of their mass during this period (del Hoyo et al. 1992).

Hoarding food for future use is one way of preparing for food shortages (Vander Wall 1990; Källander and Smith 1990). Groups of Acorn Woodpeckers, for example, build large granaries of acorns for the winter (see Figure 11–3). Meat eaters such as hawks, owls, and shrikes routinely set aside a fraction of their prey for future use. Shrikes impale prey on thorns for later consumption. Crested Tits of Europe obtain as much as 60 percent of their winter food from provisions amassed earlier in the year. These seed caches are more difficult to relocate than other stored foods, such as the acorn granaries of woodpeckers and the impaled prey of shrikes. The recovery of widely dispersed, concealed seed caches requires extraordinary spatial memory, which is processed by an enlarged hippocampal complex of the forebrain (see Chapter 7).

Water Economy

Balancing daily energy expenditures is one side of the physiological coin. The other side, water economy, is equally important, especially in arid environments. The potential for debilitating water loss is a corollary of

the high body temperatures and activity levels of birds, especially during exposure to midday heat. Enhanced evaporative heat loss is essential to prevent heat stress during strenuous activity. For example, evaporative water loss in a desert finch—the California Towhee—quadruples when ambient temperature increases from 30° to 40°C, whereas oxygen use only doubles (Bartholomew and Cade 1963). Water is used and replaced at high rates as a result of high evaporative water losses and the limited capacity of birds for concentrating electrolytes in the urine.

Birds replace lost water from several sources. Water present in food satisfies the fluid needs of many birds, particularly nectar-eating or fruit-eating birds and meat-eating raptors such as Sooty Falcons, which can nest in arid parts of the Sahara where midday shade temperatures exceed 49°C. Likewise, insect-eating birds get most of the water that they need from the body fluids of consumed insects; unlike seed-eating birds, they rarely visit water holes. California Quail, a close relative of the aforementioned Gambel's Quail, and Rock Wrens obtain adequate water by supplementing their diets of seeds with insects.

Metabolic water is produced as a by-product of the oxidation of organic compounds containing hydrogen. Metabolic water supplements ingested water and, in some cases, is all that a bird needs. Because of their

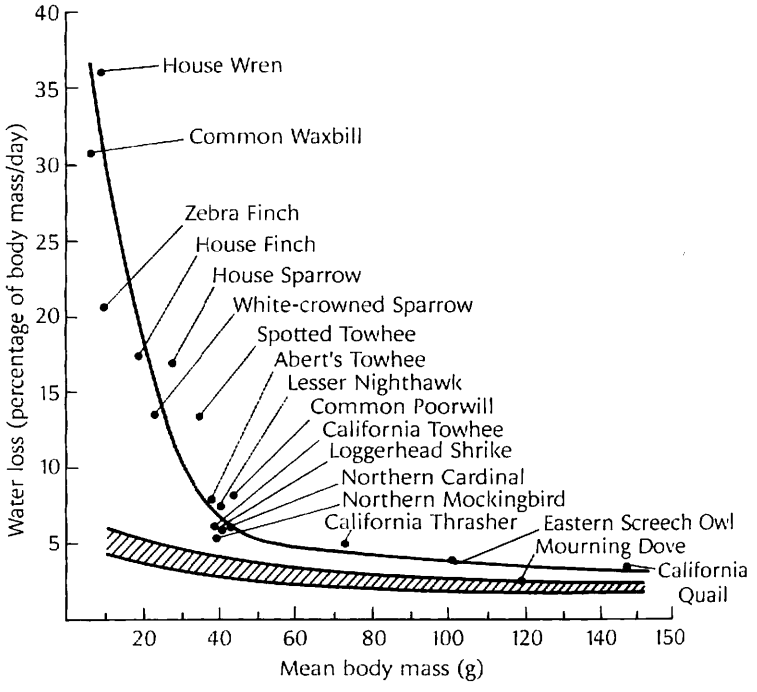


FIGURE 6–24 Evaporative water loss (as percentage of body mass lost per day) at nonstressful ambient temperatures (near 25°C) decreases sharply with increasing size (and therefore reduced surface area relative to mass) of small birds. Metabolic water production, the projected range of which is indicated by the cross-hatching, partly offsets evaporative loss. [*After Bartholomew and Cade 1963*]

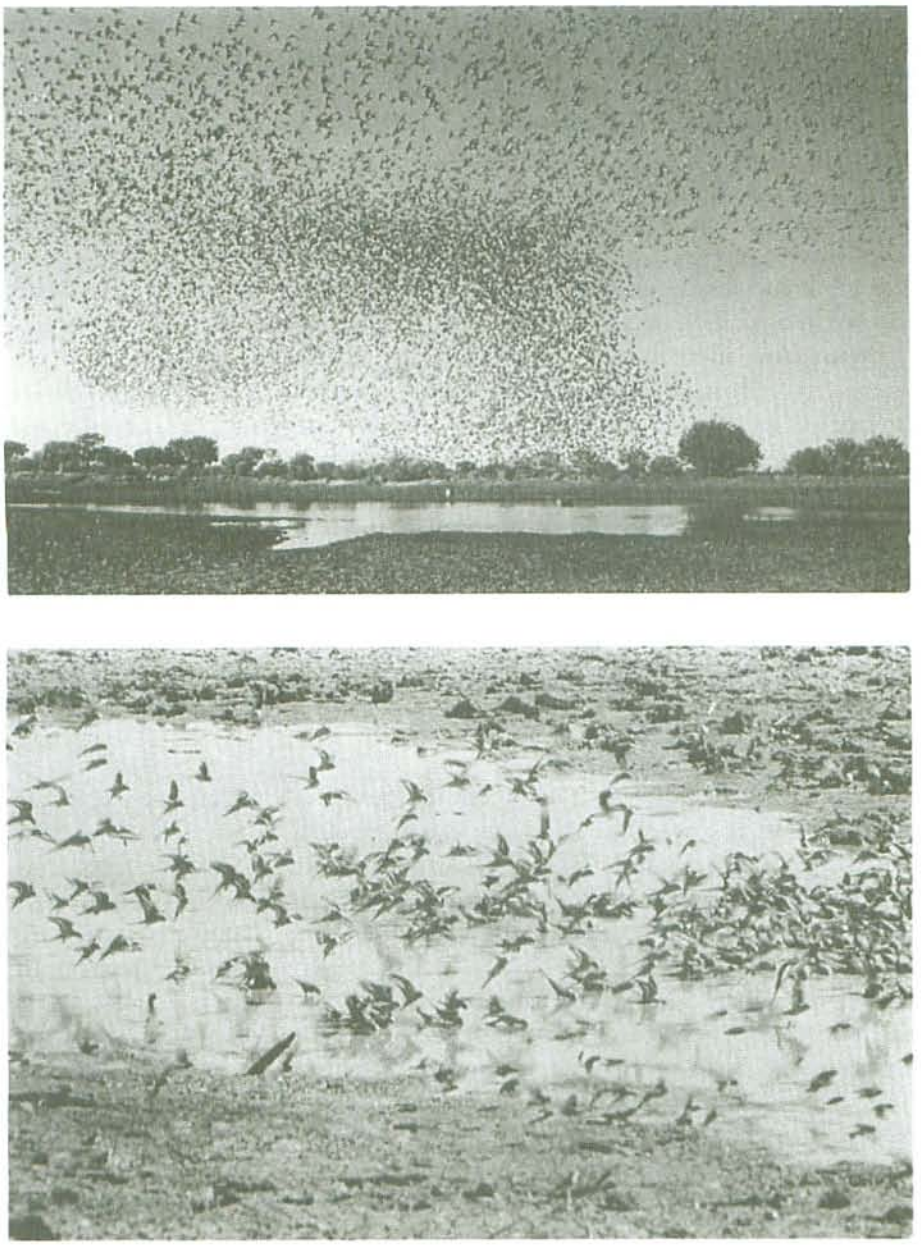


FIGURE 6–25 (*Top*) Huge flocks of birds regularly visit water holes in arid Australia. (*Bottom*) Budgerigars at a water hole. [*Courtesy of C. D. Fisher*]

high metabolism, birds produce more metabolic water in relation to body size than do most vertebrates. The metabolism of 1 gram of fat yields 38.5 kilojoules of energy plus 1.07 grams of water. Metabolic water production increases directly with oxygen consumption and thus with increased metabolism at both colder and higher temperatures. Large birds can replace more of their evaporative water loss with metabolic water than can small birds (Figure 6–24). Certain exceptional seed-eating birds, such as Zebra Finches, can survive, drinking not a drop, on a diet of air-dried seeds containing less than 10 percent water; they supplement this with metabolic water.

Water potentially lost in exhaled air may be conserved by countercurrent cooling in the nasal chambers and respiratory passages. This form of conservation is well established for mammals at low temperatures (Schmidt-Nielsen 1981). Studies of African larks, however, do not support the importance of this form of water conservation in desert birds (Tieleman et al. 1999).

Drinking free water from streams, water holes, dew, raindrops, and even snow is a casual, incidental activity in most mesic habitats—those having a moderate amount of moisture. In deserts, however, daily visits to isolated springs or water holes, where predators wait, may be necessary. Because their diets are limited to dry foods, seed-eating birds experience the greatest need for freestanding water and visit natural water sources in large numbers. Dean Fisher and his colleagues (1972) conducted dawn-to-dusk watches at water holes in the arid regions of western and central Australia. More than half of the 118 species of birds in the area appeared to be independent of surface water. Parrots, however, were not. Their visits to a water hole to drink correlated closely with maximum daily temperatures. Sometimes, they appeared in spectacular numbers (Figure 6–25). One day, during an unusually dry period, Fisher recorded 67,000 bird visits to one water hole.

Excretory Systems

The excretion of water and nitrogenous wastes by birds takes place in the kidneys and the intestines and, in some species, by the action of salt-secreting glands. Avian kidneys—flat structures sited against the fused vertebrae on the dorsal wall of the abdominal cavity—differ in structure and function from those of reptiles or mammals. Urine produced by the kidneys mixes with fecal components in the lower intestine, where additional water can be resorbed as needed.

The most conspicuous physiological adaptation for promoting water economy in birds is the excretion of nitrogenous wastes in the form of uric acid—white crystals that give bird droppings their usual color. This ability is in accord with the reptilian ancestry of birds: uric acid excretion evolved early in the history of archosaur reptiles. The turnover of proteins in the maintenance of body structures produces nitrogenous products that would become toxic if allowed to accumulate. The excretion of nitrogen as urea in aqueous solution, as done by mammals, requires flushing by large quantities of water. Uric acid can be excreted, instead, as a semisolid suspension in which each molecule of uric acid contains twice as much nitrogen as a molecule of urea does. Therefore, birds require from only 0.5 to 1.0 milliliter of water to excrete 370 milliliters of nitrogen as uric acid, whereas mammals require 20 milliliters of water to excrete the same amount of nitrogen as urea. Birds can concentrate uric acid in the cloaca, just before defecation, to amazing levels—as much as 3000 times the acid level in their blood. Kangaroo rats, among the most efficient mammalian water conservationists, can concentrate urea to levels from only 20 to 30 times those in the blood.

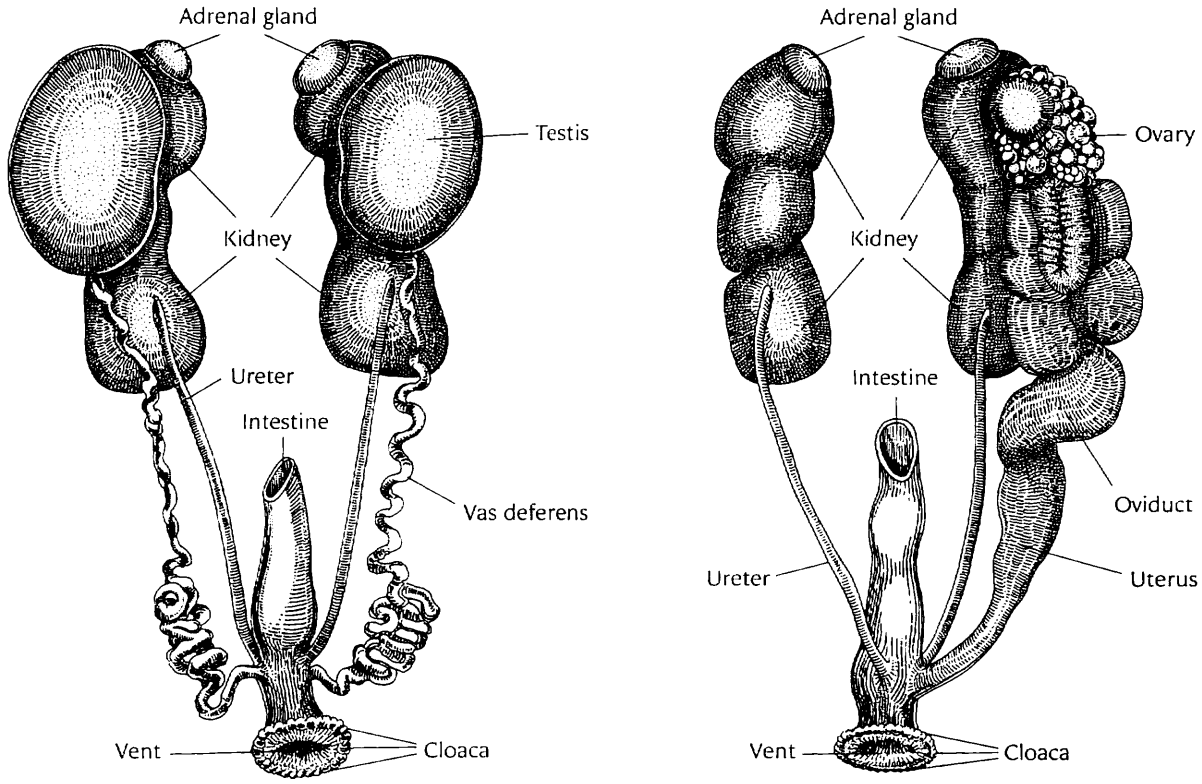


FIGURE 6–26 The urogenital systems of a male hummingbird (*left*) and a female hummingbird (*right*).

Hummingbirds face a different problem: too much water (Beuchat et al. 1990). Among the many physiological records held by hummingbirds is their claim to the highest rates of water flux of any endothermic vertebrate. Their use of nectar as a primary energy source is the reason for this achievement. To get the energy from the sugars in nectar, a hummingbird must also consume substantial volumes of liquid. When daily energy demands are high, the Anna's Hummingbird consumes and excretes liquid about 3.3 times its body mass. Most of this water passes through the body at rates that exceed the highest known urine production by freshwater amphibians. A hummingbird's kidneys are not specialized for unusual levels of water processing; they are essentially the same as a reptile's kidney (Figure 6–26). Rather, hummingbirds lay claim to the highest rates of evaporative water loss among birds. In addition, as already mentioned, their digestive systems selectively absorb sugar and allow much of the ingested water to pass through rapidly without absorption and processing through the kidneys.

Although avian kidneys can concentrate nitrogenous wastes, they usually cannot concentrate salt or electrolytes much above normal blood levels. Mammalian kidneys, especially those of the kangaroo rat, excel at concentrating salts and electrolytes because of their long loops of Henle—structures that help regulate salt levels and when necessary retain water.

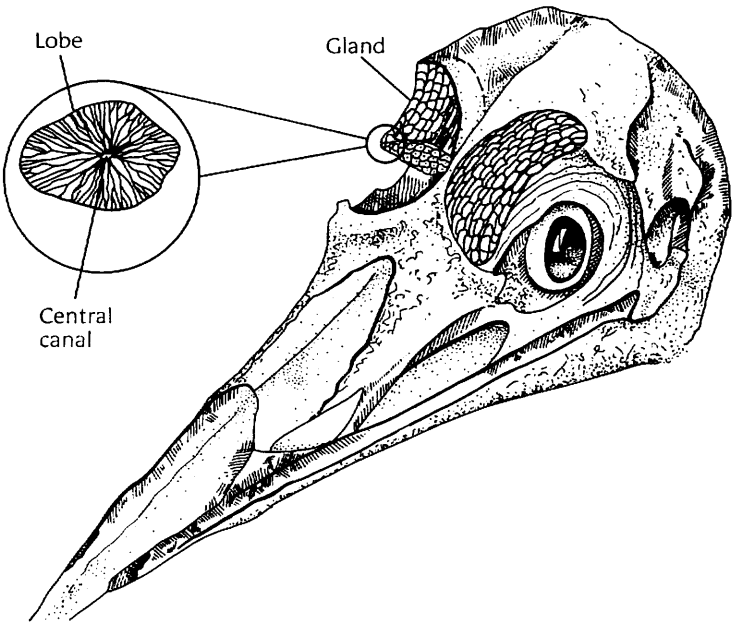


FIGURE 6–27 The salt glands of some marine birds are located on top of the head in shallow depressions above each eye. [*After Schmidt-Nielsen 1983*]

In contrast, the loops of Henle in the avian kidney are short. This anatomical shortcoming presents a problem, particularly for oceanic birds that drink seawater, which is about 3 percent salt. The body fluids of birds are 1 percent salt. The high salt content of their marine foods further increases their need to excrete electrolytes. For this reason, seabirds, as well as other birds with water-conservation problems, rely on extrarenal structures called nasal salt glands (Figure 6–27).

Salt glands are widespread among birds subject to salty diets. Large, conspicuous structures located in special depressions in the skull just above the eyes, salt glands enable seabirds to drink seawater and to unload the newly ingested salt rapidly through concentrated salt solutions. For example, if a gull drank one-tenth of its body weight in seawater, it would excrete 90 percent of the new salt load within 3 hours (Schmidt-Nielsen 1983). These amazing glands produce and excrete salt solutions that are as much as 5 percent salt, more concentrated than seawater.

Salt glands are special infoldings of the cellular lining of the nares. Inside the salt gland are many secretory tubules arranged in lobes. The tubules extract salt from blood in the capillaries of the ophthalamic arteries (which also service the eyes). The tubules then empty directly into a central canal leading to the main duct. Each of the pairs of glands has a main duct that leads to the anterior nasal cavity. The salt concentrate runs out of the nostril and down grooves to the bill tip before dripping off. Some birds, such as storm petrels, eject the fluid forcibly. The activity of the salt gland is stimulated directly by the intake of salt or, sometimes, just by an overload of salt in the blood. These energy-demanding, active-transport

processes in the salt gland may increase the resting metabolic rate by as much as 7 percent (Peaker and Linzell 1975).

Salt glands are largest and best developed in oceanic birds such as albatrosses, which must drink seawater. The size of the gland depends on the number of lobes in it and varies among bird species. Auks and gulls have particularly large glands, with as many as 20 lobes. When individual birds, such as Mallards, drink salt water instead of fresh water, their salt glands increase in size accordingly. Surprisingly, no passerines have salt glands, not even those that live in salt marshes or feed on intertidal invertebrates on the seacoast.

Summary

Birds have high metabolism. Flight and the maintenance of high body temperatures use large amounts of energy. Both the circulatory and the respiratory systems have evolved exceptional capacities for the delivery of fuel and the removal of metabolic products. Water loss linked to high metabolic rates poses difficulties for some birds.

Birds regulate their body temperatures at 40° to 42°C by adjusting plumage insulation, by increasing heat production through shivering when cold, and by evaporative water loss through panting and gular fluttering when hot. The regulation of blood flow through the feet aids heat loss or retention. To save energy, some birds—notably, hummingbirds, swifts, and nightjars—can lower body temperature and become torpid. Birds can also elevate body temperature a few degrees to reduce the need for evaporative water loss and to store body heat for cold nights. Heat produced during flight can be lost quickly with little loss of water. However, birds have little latitude for higher body temperatures: 46°C is lethal.

The digestive tracts of birds are specialized for particular diets and may change with seasonal changes in diet. Assimilation efficiencies range from less than 30 percent for spruce needles by Spruce Grouse to 99 percent for sugars from nectar for hummingbirds. The ceca—small side sacs on the large intestine—aid the digestion of plant foods. Some birds digest waxes, particularly the honeyguides of Africa and seabirds, but most birds cannot. Parrots detoxify bitter fruits and seeds by eating clay minerals.

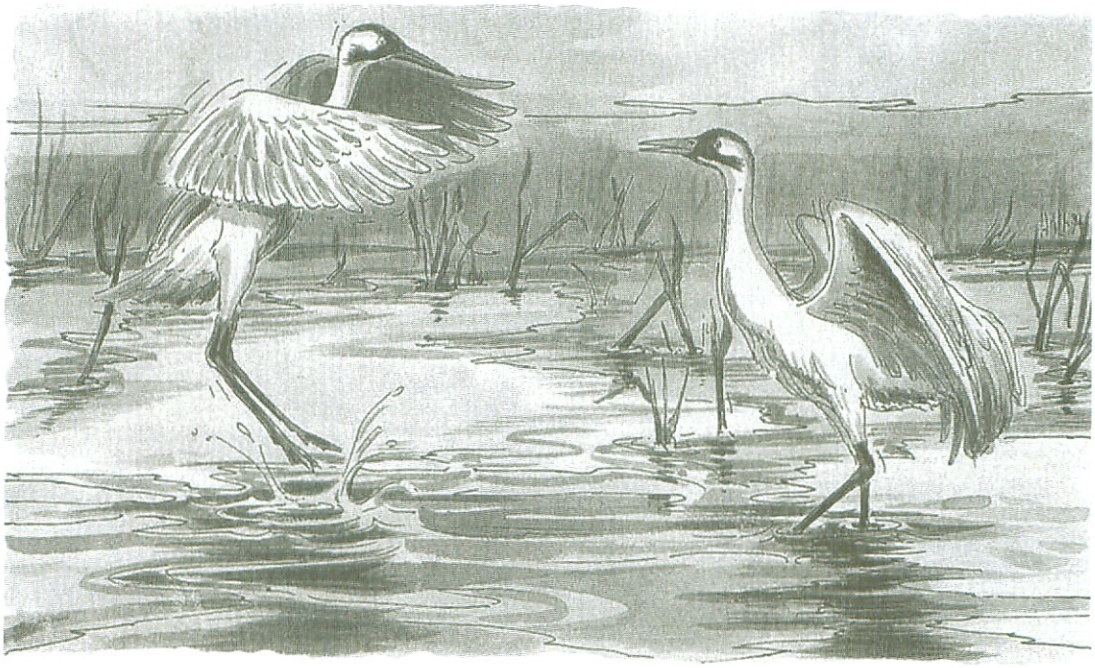
Birds adjust their foraging efforts in relation to food availability and build up reserves or cache foods for use in periods of food shortage or exceptional expenditures of energy.

Birds depend on metabolic water as well as on that ingested in their food or drunk as free water. Some species get all the water that they need from food and metabolic water. Most species require some free water; thus, desert water holes attract huge aggregations of thirsty birds.

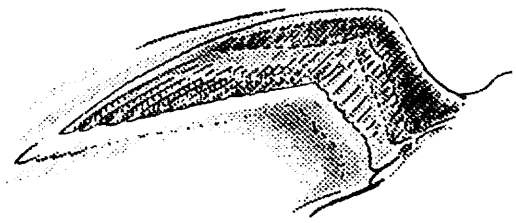
The excretion of nitrogenous wastes as uric acid rather than as urea promotes water economy in birds. Seabirds have well-developed salt glands embedded in their skulls over their eyes. These glands void concentrated salt solutions and thereby enable the birds to drink seawater and to eat prey having high salt content.

PART 3

BEHAVIOR AND COMMUNICATION



CHAPTER 7



Senses, Brains, and Intelligence

If men had wings and bore black feathers, few of them would be clever enough to be crows.

[Reverend Henry Ward Beecher, mid-1800s, in Savage 1995, p. 1]

Ornithologists once assumed that birds perceive the world in the same way as people do. They don't. Their daily sensory experience is substantially different and extends beyond the sensory experience of humans. Their highly developed color vision reaches strongly into the ultraviolet range of the spectrum. Birds navigate by using magnetism, polarized light, and calibrated celestial compasses. They are also sensitive to minuscule shifts in gravity and barometric pressure.

Birds have well-developed brains and are more intelligent than most mammals. Language, tools, and culture are all features of the life of birds. Substantial learning by birds guides the mastery of complex motor tasks, social behavior, and vocalizations. Advanced spatial memory and navigational abilities guide hemispheric migrations as well as the recovery of hidden food. Studies of the avian brain have helped to understand how the central nervous system controls complex behavior and how neural connections restructure themselves.

The sensory world of birds is the initial focus of this chapter, followed by the major features of the avian brain and the scope of avian cognition and intelligence. Advanced behaviors illustrate the abilities of birds to solve, sometimes creatively, the daily and seasonal challenges of gathering food by using their cognitive skills. The concluding sections of this chapter feature the intelligence feats of crows, jays, and their relatives, which challenge those of primates.

Vision

Birds are extremely visual animals. They use their large eyes to search for food and to detect predators at great distances. They also engage in complex, colorful courtship displays, amplified by an exceptional system of color vision. Songbirds and raptors, believed to have the keenest sight of all birds, can resolve details at 2.5 to 3 times the distance that humans can. The American Kestrel, for example, can spot a 2-millimeter insect from the top of an 18-meter-high tree (Fox et al. 1976). Wide-angle vision combined with double centers of high resolution in the retina enable some species to capture a whole scene at a glance, rather than piecing it together as we do. The visual field of the American Woodcock is one extreme of this ability. With eyes located at the midpoint of its head, the American Woodcock can monitor 360 degrees laterally and 180 degrees vertically (Waldvogel 1990).

Avian eyes are large, prominent structures. The Common Starling's eyes account for 15 percent of its head mass. The eyes of eagles and owls are as big as human eyes. The eye of an ostrich is the largest of any land vertebrate (Martin and Katzir 1995). Unlike the uniformly round, rotating eyes of mammals, the eyes of birds vary in shape from round to flat to tubular. They fill the orbits fully but are capable of only limited rotation, mostly toward the bill tip.

Because birds' eyes are generally set on the sides of their heads, birds see better to the side than to the front. Penguins and passerines, for example, examine nearby objects with one eye at a time. The resulting image is relatively flat, because monocular vision does not achieve depth perception with the same accuracy as binocular vision does. To compensate, birds bob their heads quickly, viewing an object with one eye from two different angles in rapid succession (Box 7–1). Some birds, such as swallows, nightjars, hawks, and owls, restrict lateral monocular vision to close objects and use forward binocular vision for distant viewing. Generally, binocular vision is atypical. Among ducks, only the Blue Duck of New

BOX 7–1

HOW ROBINS FIND WORMS

The familiar American Robin runs a few steps, cocks its head, and then suddenly tugs an earthworm out of the soil. Capture rates may be as high as 20 worms hiding in the lawn topsoil in an hour. How does a robin spot an earthworm invisible to human eyes? The cocked-head position could enhance close vision in one eye or it could focus the robin's hearing toward the ground. The results of initial experiments suggested that robins find the worms by sight (Heppner 1965). A more elaborate series of experiments conducted on the campus of Queen's University in Ontario by Bob Montgomerie and Pat Weatherhead (1997) revealed that robins actually detect hidden worms by listening for the slight sounds made by the worms while moving through the soil. After the robin has detected a worm, the actual strike is likely guided visually. Both sound and sight would be aided by the cock of the head.

Zealand can stare forward; other ducks use one eye at a time. Bitterns stare forward with binocular vision while pointing their bills skyward. Quite the opposite are woodcocks, already mentioned. Their huge eyes are set far back on the head, allowing broad rearview binocular vision.

Birds have not two but three eyelids. Supplementing the two normal eyelids is the nictitating membrane, a thin transparent membrane that brushes off and moistens the cornea with each blink. The nictating membrane serves as a pair of goggles for diving birds, complete with a central lens of high refractive index to help see underwater. Among the few exceptions, owls have thick, opaque nictating membranes that protect their eyes and Eurasian Magpies flash a white membrane with bright orange spots when they blink slowly, as in courtship or aggression.

Eye Anatomy

A cross section of the avian eye reveals a small anterior component, which houses the cornea and lens, and a larger posterior component, which is the main body of the eye (Figure 7–1). The two sections are separated by a scleral ring composed of 12 to 15 small bones, called ossicles. Two striated muscles—Crampton's muscle and Brucke's muscle—attach to

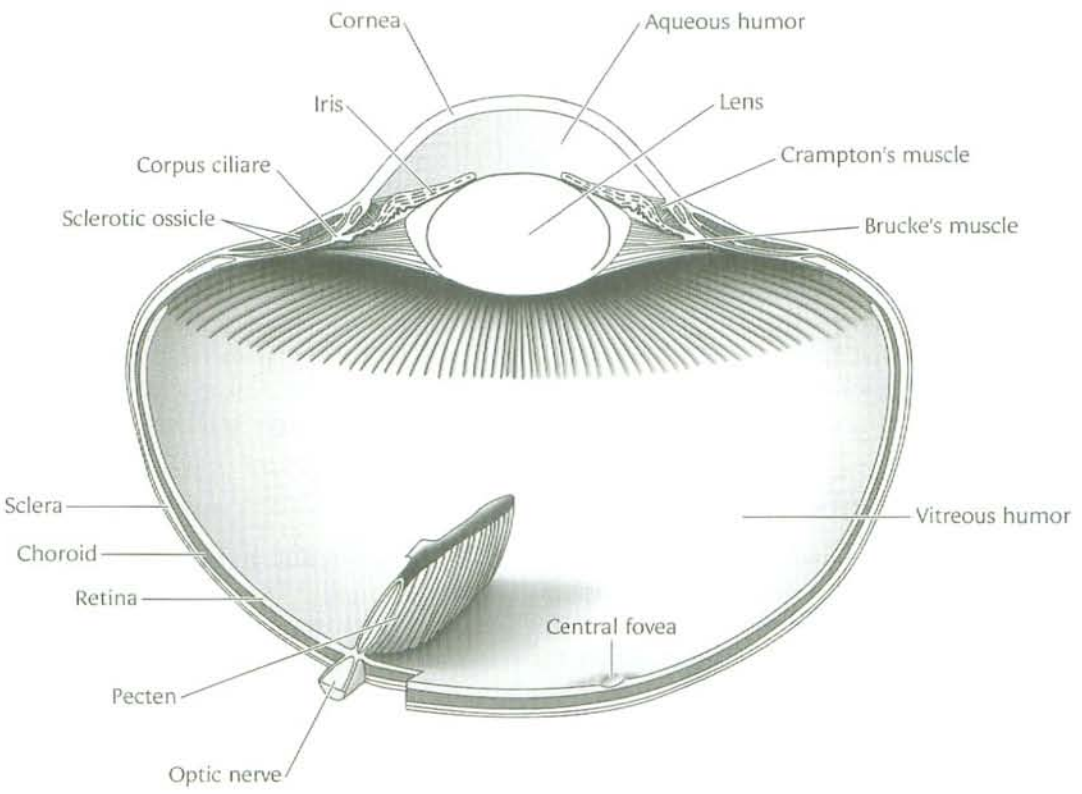


FIGURE 7–1 Cross section of the avian eye. [*After Evans 1996*]

these ossicles and are responsible for focusing on objects. The lens is large and conspicuous. The pecten, a distinctive and intriguing feature of the avian eye, projects from the rear surface of the eye near the optic nerve into the large cavity filled with vitreous humor—the clear substance that fills the eye behind the lens.

Cornea and Lens

In birds, both the cornea and the lens change their curvature while focusing; only the lens does so in mammals. Contraction of Crampton's muscle increases the corneal curvature and thus the cornea's refractive power. A change in the cornea has little effect underwater, however, because the refractive index of the cornea is nearly the same as that of water. As we might expect, diving birds, such as cormorants, have weakly developed Crampton's muscles; to compensate, they have strong Brucke's muscles, which control the shape of the soft, flexible lens. Plunge divers such as kingfishers can even keep a target fish in focus as they dive.

Lens shape varies more among bird species than in other vertebrates. The lenses of parrots, storm petrels, and hoopoes have flat anterior surfaces but strongly convex posterior surfaces. Ducks, owls, and nightjars have lenses that are strongly convex in both front and back, whereas, in passerines and raptors, the convex posterior curvature is noticeably greater than the anterior curvature. The reasons for these differences and their benefits are not yet known.

The pupil opening is round in all birds except the gull-like skimmers. The skimmer pupil constricts into a catlike, vertical slit to protect the retina from bright (polarized) light; it expands to form a rounded shape in dim light (Zusi and Bridge 1981). Iris colors of birds vary from the common deep brown to bright red, white or bright yellow, green (cormorants), or pale blue (gannets) and may aid species recognition. At night, some birds' eyes shine bright red in the beam of a flashlight or automobile headlights. This "eyeshine" is a reflection from the vascular membrane—the tapetum lucidum—which, like a mirror, reflects light back through the retina and helps night birds in particular to see better. Kiwis, thick-knees, the Boat-billed Heron, the flightless Kakapo, many nightjars, owls, and other night birds have this distinctive trait in common.

Retina and Fovea

The highly developed anatomy of the avian retina and its light-receptor cells suggest excellent vision. The large number of cones—the daylight (color) receptors of the retina—enables birds to form sharp images, no matter where light strikes their retina. The number of cones can be as high as 400,000 per square millimeter in House Sparrows and 1 million per square millimeter in the Common Buzzard. In comparison, the human eye has at most 200,000 cones per square millimeter (Walls 1942). Away from the densest concentrations in the foveae, cone concentrations in the human retina drop sharply to only one-tenth of those of birds.

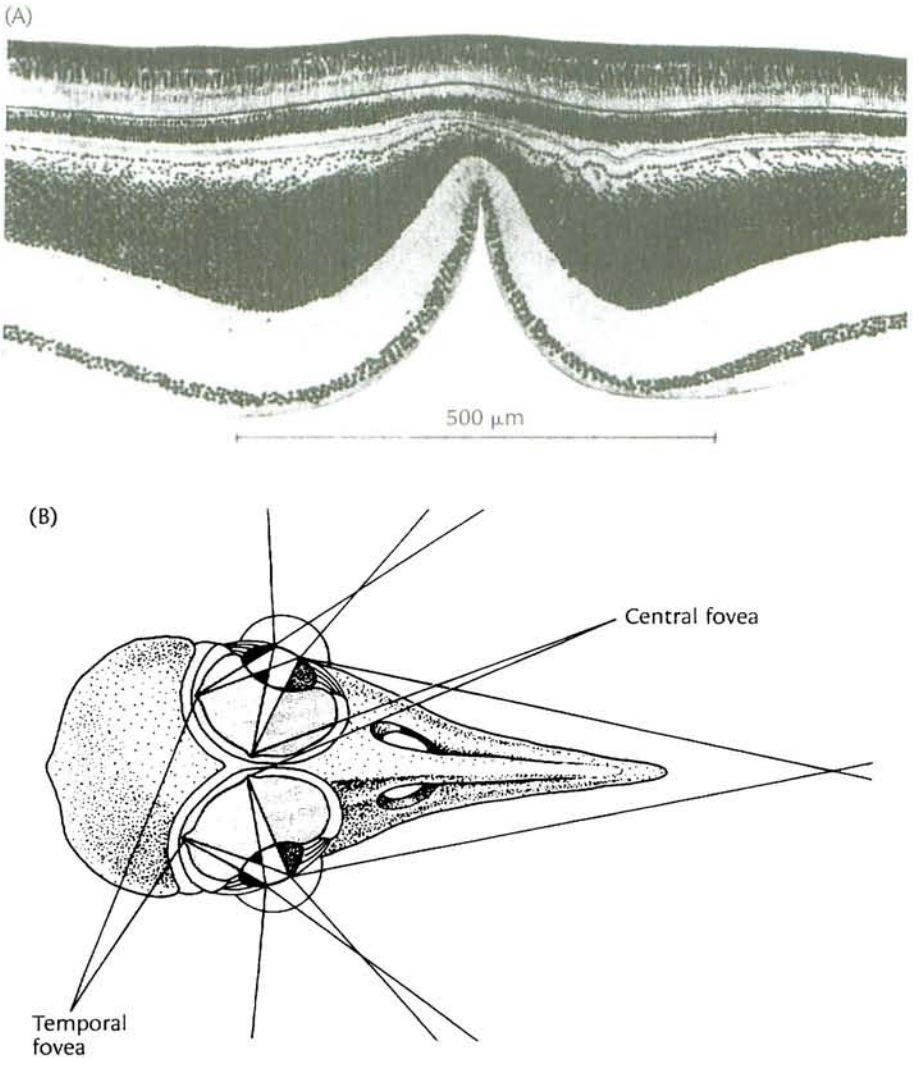


FIGURE 7–2 (A) Cross section of a Least Tern retina, showing the visual-cell layer with rods and cones and the deep central fovea. (B) Some birds, such as raptors, have temporal foveae, which enhance forward binocular vision. [*(A) From Rochon-Duvigneaud 1950; (B) after Wilson 1980*]

Foveae—concave depressions of high cone density (Figure 7–2)—are known to be the sites of greatest visual sharpness in humans. Like humans, most birds have one fovea in each eye, located in the center of the retina near the optic nerve. This central fovea is deeper and more complex in its cell structure in visually acute passerines, woodpeckers, and raptors than it is in pigeons and domestic chickens.

Whether deep foveae enhance avian visual acuity is not clear. They may, however, aid in the detection of the movements of small images. Fast-flying birds that must judge distances and speeds accurately, such as

hawks, eagles, terns, hummingbirds, kingfishers, and swallows, have temporal as well as central foveae. These birds also have forward-directed eyes and, therefore, good binocular vision, which projects images onto the temporal foveae. Images of their peripheral, or lateral, monocular vision fall on the central foveae.

Although cones are most abundant in the foveae, high cone densities are also found in horizontal, ribbonlike strips around the retina in albatrosses, grebes, plovers, and other birds. These ribbons apparently increase a bird's ability to perceive the horizon and work in concert with the semicircular canals of the inner ear to achieve proper body orientation.

The complex avian retinal structure confers a high sensitivity to motion and the ability to detect both rapidly moving objects and slowly moving ones (Waldvogel 1990). The human eye cannot resolve movements faster than 60 cycles per second, or 60 hertz, a measure of what is termed flicker-fusion frequency. Birds have higher thresholds of more than 100 hertz. Thus the 60-hertz oscillation of light in a fluorescent light bulb appears as a steady light to the human eye but as a series of individual flashes to a bird. The same would be true for a television screen: humans see the rapidly scanning signal as a single picture, but birds would see a little spot moving back and forth on the screen as the image refreshes. The visual motion sensitivity of birds serves them well in all aspects of flight, in prey and predator detection, and in potentially seeing navigation stars actually move through their arcs in the night sky.

The Pecten

The pecten, a remarkable feature of the avian eye, is a large, black-pigmented, pleated, and vascularized structure attached to the retina near the optic nerve (see Figure 7–1). Protruding conspicuously into the vitreous humor and, in some birds, almost touching the lens, the large, elaborate avian pecten is unique among vertebrates. In most birds, the pecten has 20 or more accordion-pleated fins (Figure 7–3). Nocturnal birds have fewer folds. The pectens of owls, nightjars, and the Kakapo have only four to eight folds, and the simple, reptilelike pectens of kiwis have no folds at all—probably representative of an evolutionarily degenerate condition (Sillman 1973).

The avian pecten has fascinated scientists for centuries. At least 30 theories have been proposed to explain its existence. Some researchers believe that the pecten participates in the regulation of internal eye temperatures and hydrostatic pressures; others suggest that it reduces glare; still others hypothesize that it might be a sextant for navigation or a dark mirror for indirectly viewing objects near the sun. Primarily, however, the avian pecten serves as a source of nutrition and oxygen for the retina (Güntürkün 2000). Unlike the mammalian retina, the avian retina has no embedded blood vessels. Instead, the vascular supply system is concentrated in the pecten, which interferes less with visual functions than would a complex network of blood vessels.

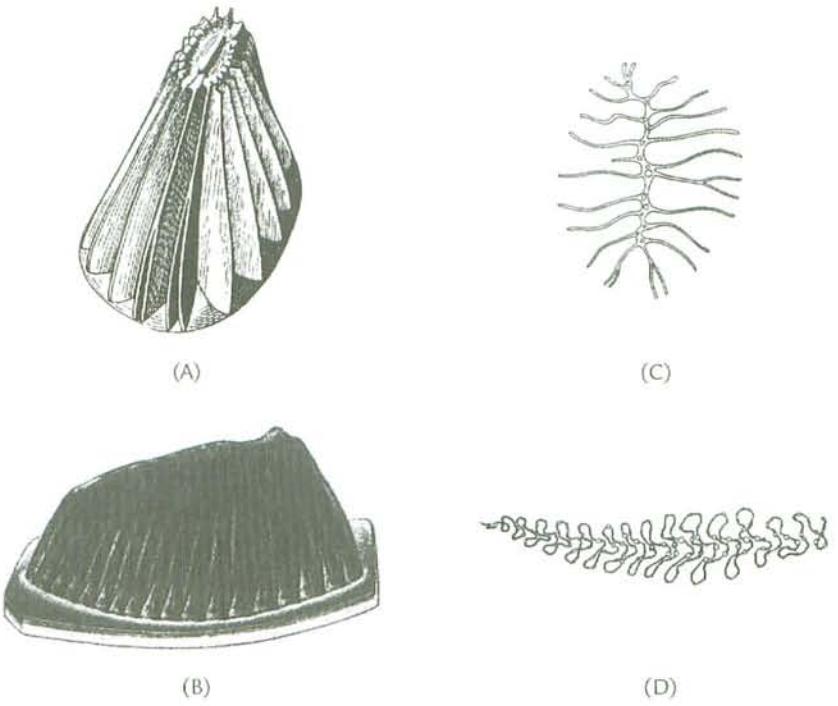


FIGURE 7–3 Structure of the pecten of (A) an ostrich and (B) most modern birds. (C) Basal cross section of the structure of part A, including central web and lateral vanes. (D) Dorsal view of the typical pleated structure of avian pectens. [*After Walls 1942*]

Color Vision

Color vision is based on visual pigments, which convert the electromagnetic energy of light into neural energy. In addition to their visual pigments, the cones of diurnal birds often contain colored oil droplets with carotenoid pigments. The pigments, which range from yellow to red, act as filters against damaging UV light, as they do in the yellowish lenses of the eyes of mammals. They may also enhance the contrast of objects against different backgrounds—yellow for objects seen against the blue sky, and red for objects against green backgrounds, such as fields and trees.

Primitive mammals, including the ancestors of primates, were night creatures that lost the retinal oil droplets associated with sensitive color vision. Once lost, these droplets did not evolve again in placental mammals. Instead, the color vision of humans and other primates re-evolved on a different and more limited basis. Birds retained and enhanced the color vision systems of their ancestors. The richness of avian color perception, therefore, is beyond that of human experience. Very likely, the avian retina—with its high cone densities including visual pigments, near-ultraviolet receptors, and colored oil droplets—is the most capable daylight retina of any animal. The color sensitivities of birds span color combinations from near-ultraviolet to red (Chen and Goldsmith 1986).

Unlike humans, birds are sensitive to light in the near-ultraviolet spectrum. The lenses of the human eye absorb UV light; in birds, the lenses transmit UV light to the retina, where an extra set of cones, lacking in humans, have peak sensitivity in the near-ultraviolet spectrum (Chen et al. 1984). The daily visual experience of birds is thus substantially different from ours: birds do not see the world or themselves as we do, or as we thought they did.

The reality of widespread ultraviolet plumage coloration was introduced in Chapter 4. Differences in ultraviolet intensity in plumage guide the choice of mates, dominance relations, and reproductive success (Bennett et al. 1996; Chapter 12). Here's a selection of some of the roles of UV light in the lives of birds. Common Starlings preferentially feed those nestlings having UV-reflective skin (Jourdie et al. 2004). A thrush, the Redwing of Europe, prefers *Viburnum* berries that reflect UV light to those that do not (Siitari et al. 1999). And Common Kestrels use UV light to find concentrations of a favorite prey—voles, which (unwittingly) illuminate their meadow trails with urine and feces that shine in the ultraviolet (Viitala et al. 1995).

Most diurnal birds operate in a rich color environment that not only includes ultraviolet but is tetrachromatic with four types of cones, as is the color world of some fish and turtles and possibly lobe-finned ancestors of all land vertebrates (Robinson 1994). The tetrachromatic color world of diurnal birds is not only broad in the range of colors detected but offers a qualitative change in color perception and the hues seen. In contrast, the retinas of nocturnal birds such as owls contain mostly rods, which are simple light receptors important in black-and-white (and hence night) vision.

Detection of Magnetic Fields

Birds use magnetic information to navigate both locally and globally. (See Chapter 10 for a detailed discussion of this topic.) They respond to magnetic fields as weak as 50 nanoteslas and to fields as strong as those that prevail on the Earth's surface, roughly 60 microteslas. Exactly how they detect the strength and orientation of the Earth's natural magnetic fields is still unknown (Beason 2005). Likely participants are tiny particles of an iron compound called magnetite, which can be polarized by even a handheld magnet. Such crystals are the basis for the magnetic orientation of bacteria and algae.

Magnetite-like elements are present in the heads of birds, especially in the ophthalmic branch of the cranial (trigeminal) nerve system and the thin (ethmoid) bones at the front of the orbits of the eyes. Adjacent nerve tissues or pressure receptors could detect subtle changes in the position of the magnetite particles. Migratory Bobolinks (see page 300) have magnetite in their ophthalmic nerve cells. When magnetized with different polarities, the Bobolinks will orient in appropriately different directions (Beason et al. 1995).

An entirely different reception mechanism called optical pumping also may take part. The photopigment rhodopsin is theoretically capable of converting both light (electromagnetic energy) and magnetic fields into nerve impulses that are then processed by the central nervous system (Leask 1977). The avian retina does respond to magnetic stimulation. Circular arrays of specialized photoreceptors present in the avian eye could theoretically organize a directional compass that can be calibrated through experience. The relative roles of magnetite and these photoreceptors in navigation are still unknown (though see page 301).

The avian pineal gland also houses magnetite and is responsive to magnetic stimulation. This organ plays a major role in guiding daily rhythms (see Chapter 9), but the role of magnetism in doing so is still a mystery.

Hearing

Sounds provide birds with essential information. From territorial defense and mate choice to navigation, birds depend on their hearing for a wide range of activities.

Ear Structure

The three sections of the avian ear are the external ear, the middle ear, and the inner ear. The external ears of birds are inconspicuous structures located behind and slightly below the eye. They lack the elaborate pinnae, or projecting parts, of mammalian ears. Specialized "auricular" feathers on the external ear protect the hearing organs from air turbulence during flight while permitting sound waves to pass inside. Diving birds, such as auks and penguins, have strong, protective feathers covering the external ear openings. These birds protect their middle and inner ears from pressure damage in deep water by closing the enlarged rear rim of the external ear. The entire muscular rim to which the auricular feathers are attached forms an enlarged, though inconspicuous, ear funnel in some birds, especially passerines, parrots, and raptors. The superb hearing of nocturnal owls is related to their exceptional ear funnels. Large anterior and posterior ear flaps regulate the size of the ear opening and enhance acoustical acuity more than fivefold (Schwartzkopff 1973). In many owls, the external ears and, in some cases, the skull are bilaterally asymmetrical, a condition that aids in the precise location of prey.

In contrast with the three bones in the middle ear of a mammal, the middle ear of a bird has only one bone—the columella, or stapes—which connects the eardrum, or tympanic membrane, to the pressure-sensitive fluid system of the inner ear (Figure 7–4). Located next to the attachment of the columella to the bony cochlea is the flexible round window, which protects the inner ear from pressure damage. The shape of the columella varies with taxon, but most birds have a simple columella similar to that of reptiles (Feduccia 1977).

The external and middle ears funnel sound waves from the environment into the cochlea—the fluid-filled, coiled section of the inner ear

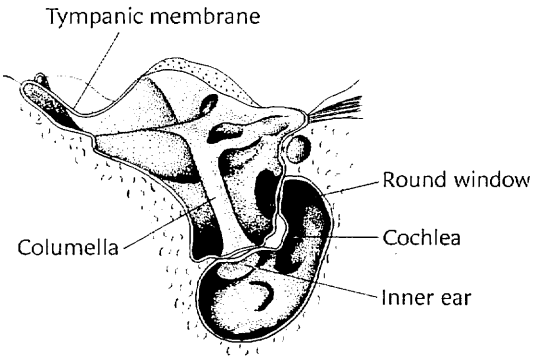


FIGURE 7–4 Middle-ear region of a chicken. A single bone—the columella, or stapes—transmits sound from the eardrum to the fluid-filled cochlea of the inner ear. [*After Pohlman 1921*]

that is the base of the hearing organ. Hair cells in the cochlea monitor vibrations transmitted by the fluid and encode them into a temporal sequence of nerve impulses that register in the acoustical centers of the brain. These hair cells regenerate after damage to restore full hearing ability.

The avian ear is structurally simpler than that of mammals. Compared with those of mammals, avian inner ears have a short basilar membrane, no division between inner and outer hair cells, and a simple system of cochlear nerves. Its acoustical efficiency, however, is the same as that of the mammalian ear.

Acoustical information is processed primarily by auditory nuclei in the hindbrain. The basic plan of the avian auditory central nervous system is the same as that of reptiles, with some derived specializations (Carr 1992). Specialized dark-hunting owls that rely on sound have an extraordinary number of ganglionic cells in the medulla for processing sound and spatial information. The Barn Owl, for example, has about 47,600 ganglionic cells in one half of the medulla; the Carrion Crow has about 13,600; and the Little Owl, which hunts in the early-morning light, has about 11,200 (Winter 1963). Oilbirds, which use sound to navigate in the dark, also have highly developed auditory centers.

Hearing Ability

The substantial amount of experimental data on the hearing abilities of birds supports a surprising conclusion. Most birds do not have extraordinary hearing by standard measures. Humans can hear fainter sounds than most birds at most frequencies. Furthermore, the frequency range of good hearing tends to be wider in mammals than in birds. Some birds, however, can detect low, infrasound frequencies outside the range of human hearing.

The frequencies of sound are measured as cycles per second (hertz) or, for high-frequency sounds, as thousands of cycles per second (kilohertz). Birds hear best at frequencies between 1 and 5 kilohertz. Sensitivity de-

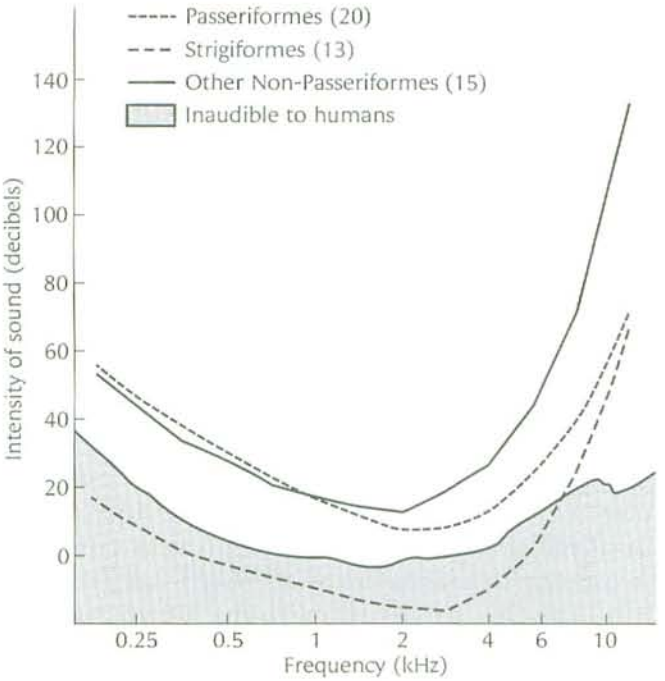


FIGURE 7–5 Median hearing threshold curves of birds. Humans cannot hear sounds in the lower shaded area, but owls can. The higher the required intensity, the poorer is a bird's or a person's hearing. Birds hear well (required intensity less than 40 decibels) over a narrower range of frequencies than do humans. [*After Dooling 1982; Dooling et al. 2000*]

creases rapidly at both lower and higher frequencies. Owls are an exception; they hear better at these frequencies than human do and have greater sensitivity than that of humans to low-frequency sounds (Great Horned Owls) and high-frequency sounds (Barn Owls). Pigeons, chickens, and guineafowl, however, hear very low frequencies (infrasound below 20 Hz) extremely well: pigeons can hear much fainter sounds (50 decibels lower) in the 1 to 10 hertz range than humans can hear. The significance of this ability is not yet understood. Oscine songbirds tend to hear high-frequency sounds better and low-frequency sounds less well than do other birds (Figure 7–5).

Unlike bats and some other mammals, birds do not hear ultrasonic sounds—that is, sounds with frequencies higher than those audible to humans. Birds are sensitive to small changes in the frequency and intensity of sound signals, but not unusually so. Humans detect frequency changes better than birds at all frequencies. Birds can discriminate temporal variations in sound, such as duration of notes, gaps, and rate of amplitude modulation, as can other vertebrates, including humans. Laboratory tests, however, do not support the idea that birds have exceptional powers of temporal resolution, a result that bears directly on the abilities of birds to recognize subtle call variations and on the evolution of vocalizations (see Chapter 8).

Orienting by Sound

Owls can locate prey by sound in complete darkness. The Barn Owl can catch a running mouse in total darkness because it can precisely locate sounds to within 1 degree in both the vertical and the horizontal plane (Payne 1972). The Barn Owl can also determine the direction and speed of a mouse's movement. Humans can locate sounds in the horizontal plane about as well as a Barn Owl but only one-third as well in the vertical plane.

Both owls and humans locate the sources of sounds by means of differences in the intensity and time of arrival of sounds at the two ears. Looking directly at the source equalizes these stimuli. The asymmetrical arrangement of the ears of some owls enhances reception differences and thus the ability to locate prey quickly and accurately. This ability is well developed in the Barn Owl, which locates sounds in the vertical plane by means of its asymmetrical ear openings and the troughs formed by the feathered facial ruff (Figure 7–6). The left ruff faces downward, thereby increasing sensitivity to sounds below the horizontal, and the right ruff faces upward, increasing sensitivity above the horizontal. The owl need

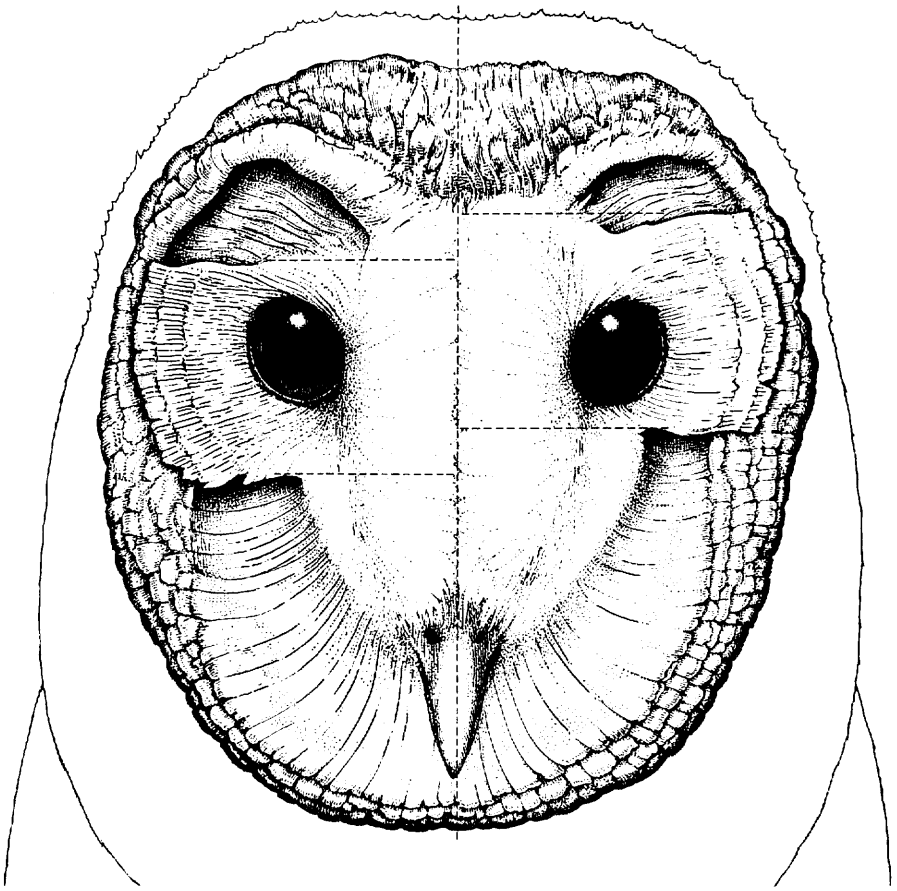


FIGURE 7–6 The heart-shaped face of the Barn Owl is not perfectly symmetrical. The left ear, which is higher than the right ear, is most sensitive to sounds from below the horizontal (an imaginary horizontal plane that is parallel to the ground and passes through the owl's head). Conversely, the lower right ear is most sensitive to sounds from above the horizontal. Enhancing the difference in ear positions are the downward-oriented, feathered ruff on the left side of the face and the upward-oriented ruff on the right side. This asymmetry causes a sound to arrive at each ear at slightly different times, thereby enabling the owl to precisely locate the source of the sound. [*From Knudsen 1981, with permission from Scientific American*]

only tilt its head up or down to equalize input to the two sides and thus to identify the location of a mouse.

A few birds use echolocation, or reflected vocalizations, for navigation. Some swiftlets *(Collocalia)* of Southeast Asia find their way through dark cave corridors by emitting short, probing clicks of 1-millisecond duration at normal frequencies (2–10 kHz); they do not employ ultrasound as bats do (Medway and Pye 1977). Echolocation at these normal hearing frequencies is at best only one-tenth as functional as the ultrasound sonar system of bats. For example, the cave-nesting Oilbird, a fruit-eating nightjar of South America, echolocates with sharp clicks from 15 to 20 milliseconds long over a broad frequency spectrum ranging from 1 to 15 kilohertz (Konishi and Knudsen 1979). It can avoid disks that are 20 millimeters or more in diameter, but it collides with smaller objects.

Mechanoreception

Birds are extremely sensitive to mechanical stimulation through the senses of mechanoreception (Schwartzkopff 1973). Included among these senses are tactile reception, equilibrium (balance), and the detection of barometric pressure. Mechanoreception reaches its highest level in the hearing organ.

Tactile corpuscles, the primary sources of skin sensitivity, also monitor changes in muscle tension, or proprioception. These cells, specialized for tactile response, are found at the ends of sheathed nerve fibers. The ellipsoidal Herbst corpuscle is the largest and most elaborate of the tactile corpuscles. It consists of an outer multilayered sheath and an inner core. The onion-like layers of the outer sheath allow elastic reception and transfer of rapid pressure changes; the inner, cylindrical core is an elaborate sensory nerve fiber (Figure 7–7). Herbst corpuscles are abundant in the

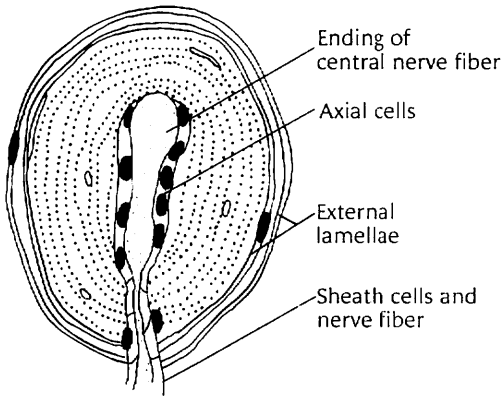


FIGURE 7–7 Herbst corpuscle from the bill of a duck. The most elaborate of avian tactile sensors, it consists of as many as 12 onion-like layers of external lamellae that transfer slight pressure changes to the elaborate nerve ending of the receptor axon in the center. [*After Portmann 1961*]

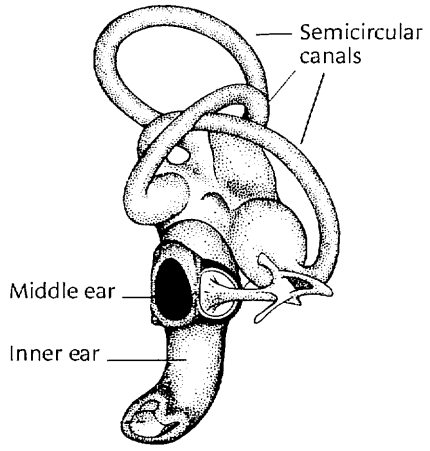


FIGURE 7–8 The semicircular canals, which are the organs of equilibrium, are located next to the apparatus of the middle ear. [*After Pumphrey 1961*]

sensitive bill tips of sandpipers and snipes, which use tactile foraging to find small prey in the mud, and in the tips of woodpecker tongues. They are also concentrated in feather follicles that have sensory functions, especially those of filoplumes and bristles (see Chapter 4). They are numerous in the wing joints of birds, where they help govern wing positions in flight.

The organs of equilibrium—the semicircular canals located in the ears and the associated sets of specialized sensory cells—are among a bird's most important sensory organs because they regulate the balance and spatial orientation so essential to skilled flight. They give birds an excellent sense of balance and body position, enabling them to reorient automatically with respect to gravity, even when blindfolded.

Three semicircular canals, one oriented horizontally and two oriented vertically, connect directly to the cerebrospinal fluid system (Figure 7–8). When the position of a bird's head changes, fluid moves through the canals (Werner 1958). At the bases of the semicircular canals are delicate sets of membranes equipped with sensory hair cells, which detect the movements of small crystals of calcium carbonate, or statoliths, floating in the fluid. Spatial variations in the pressure of the crystals on the hair cells cause different patterns of excitation, which enable the bird to sense the direction of gravity and of linear and circular acceleration.

The size of the semicircular canals is related to flight performance: pigeons, owls, thrushes, ravens, and raptors have larger canals than those of fowl-like birds and ducks. Among fowl-like birds, the size of the semicircular canal increases with the mobility of a species. So does the size of the cerebellum of the avian midbrain, which is responsible for balanced muscular coordination.

Ornithologists have long known that birds sense an approaching winter storm and feed actively to build their energy reserves. Birds also know how to choose altitudes for migration. These abilities suggest sensitivity

to differences in atmospheric or barometric pressure. Homing pigeons are, in fact, extremely sensitive to small changes in air pressure, comparable to differences of only 5 to 10 meters in altitude (Kreithen and Keeton 1974). Sensitivity to atmospheric pressure is believed to be based in a small sense organ, called the paratympanic organ, in the bird middle ear (von Bartheld 1994).

Chemical Senses: Taste and Smell

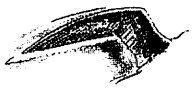
Birds can taste and smell. The few studies of taste acuity in birds suggest only that they may be equally or less sensitive than mammals with respect to some ingredients (Box 7–2). A few taste buds are located on the rear of the avian tongue and on the floor of the pharynx: about 24 in the chicken, 37 in the pigeon, and 62 in Japanese Quail. Avian taste buds are similar in structure to mammalian taste buds but are negligible in number by comparison. Humans, for example, have roughly 10,000 taste buds. The limited number of taste buds of birds, however, guide preferences for basic tastes—sweet, salt, sour, and bitter—as well as such features as lipid and sugar concentration (Mason and Clark 2000).

The avian sense of smell is based in the surface epithelium of the posterior concha of the olfactory cavities (see Chapter 6). Although they have been underestimated in the past, the olfactory abilities of most birds are comparable to those of some mammals (Mason and Clark 2000). Birds use the sense of smell in a variety of activities ranging from finding food to orientation (Box 7–3). Goslings learn to choose and reject food plants by smell at an early age (Würdinger 1979) and Common Starlings select appropriate nest-construction materials by smell (see Chapter 15). In Africa, honeyguides lead animals and people to beehives (see Chapter 6). These relatives of the woodpeckers can find the beehives by their pungent smells. In experiments, honeyguides can find concealed beeswax candles and are attracted by the odor plume of a burning candle.

The small size of the olfactory bulbs in most birds (relative to brain size) fostered the belief that only a few exceptional birds—those with large olfactory bulbs, namely, vultures, kiwis, and petrels—use the sense of smell

BOX 7–2

BIRDS LIKE CHILI PEPPERS



Donald Norman and his colleagues (1992) discovered an ecological link between birds and chili peppers. The active chemical ingredients, called capsaicins, in chili peppers have a familiar, flaming effect on the mammalian oral epithelia and taste buds, mediated by the trigeminal nerve. The normal concentration of these chemicals (1000 ppm) in wild chilies repels rodents but does not make food distasteful to birds. Indeed, birds are attracted to wild capsicum fruits, called bird peppers, because they are high in vitamins, proteins, and lipids. A reasonable hypothesis is that capsaicins protect the pepper seeds from consumption by rodents and allow or even attract birds to eat the fruits and disperse the seeds.

BOX 7–3

NEW ZEALAND KIWIS SNIFF FOR THEIR FOOD

Unlike mammals, birds rarely sniff. Kiwis—those well-known flightless, chicken-sized birds found only in New Zealand—are an exception (see Figure 2–16). Active only at night, kiwis probe their long bills into wet soil to find earthworms, which they locate by sniffing through nostrils located at the bill tip. All other living birds have nostrils at the base of the bill.

A series of classic experiments demonstrated that kiwis rely on their highly developed sense of smell to find food (Wenzel 1968, 1971). Screened tubes containing either fragrant food or just dirt (the control) were buried 3 centimeters deep in a large cage. The captive kiwis quickly found the baited tubes and punctured them to extract the food, but they ignored the control tubes containing only dirt. Parallel laboratory experiments demonstrated increased respiration and brain neural activity with exposure to food odors and conditioned aversion to food containing noxious chemicals.

in their daily activities. Now that view is changing; most birds can probably smell and use odors in their daily routines (Mason and Clark 2000). Even passerine songbirds, which have minimal olfactory-bulb sizes (1.5 mm) and were assumed to lack a sense of smell, can detect certain odors with the same acuities as rats and rabbits (Clark et al. 1992). Simple and critical olfactory functions can be accommodated by very small amounts of olfactory tissue. Among the orders of birds, however, thresholds for odor detection are correlated with the size of the olfactory bulb relative to the size of the cerebrum (Figure 7–9). Olfactory bulbs also tend to be larger in nocturnal birds, which need expanded nonvisual sensory abilities, than in related diurnal taxa (Healy and Guilford 1990).

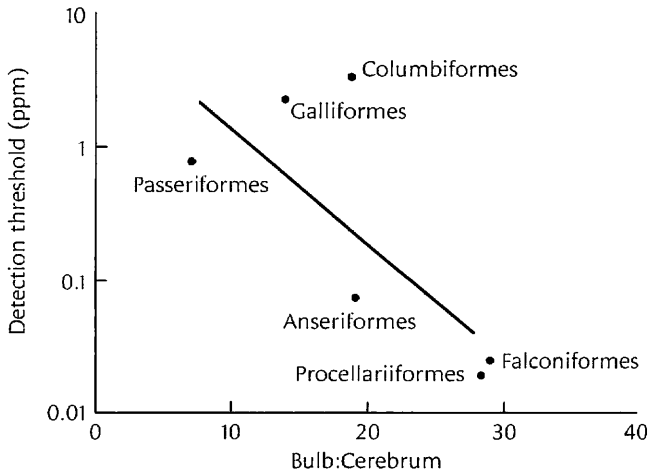


FIGURE 7–9 The relation between olfactory acuity, expressed by the detection threshold for a chemical in parts per million (ppm), and the proportion of brain tissue allocated to the olfactory bulb for six orders of birds. [*From Clark et al. 1992*]

Odors mediate the daily sexual and foraging behaviors of birds. The sexual prowess of male Mallards depends on their ability to smell a female's breeding odors. Experimental cutting of their olfactory nerves inhibits courtship and sexual behavior (Balthazart and Schoffeniels 1979). Female odors apparently come from oil-gland secretions, which change in composition during the breeding season (Box 7–4). Wild flying Turkey Vultures, which find carcasses by smell, are attracted to ethyl mercaptan fumes released into the air to simulate the smell of rotting meat (Stager 1964, 1967; Smith and Paselk 1986). Engineers have used the remarkable olfactory abilities of vultures to locate leaks in long pipelines by pumping such chemicals through them and then spotting where the vultures gather.

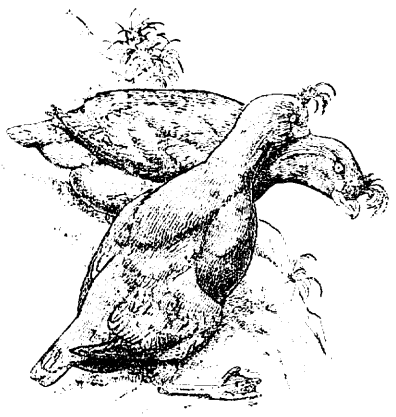
Tube-nosed seabirds (Order Procellariiformes) locate zooplankton on the open seas by smell. Zooplankton, including the krill consumed by whales and penguins, is a primary food of storm petrels and other seabirds. The seabirds home in on the scent of dimethyl sulfide, a compound that is released by phytoplankton in response to being eaten by zooplankton (Nevitt et al. 1995; Nevitt 1999). Leach's Storm Petrels are highly attracted to this scent, which they can detect as far as 12 kilometers from the source (Clark and Shah 1992).

Beyond finding meals of krill, such seabirds also use smell to find their nest burrows and to locate their mates. Leach's Storm Petrels use their well-developed sense of smell to locate their nesting burrows in the dark

BOX 7–4

AUKLETS USE PERFUME

Millions of Crested Auklets nest in crowded colonies on the cliffs of the Aleutian Islands in the North Pacific. Clouds of these small buzzy seabirds commute between their nest burrows and rich ocean feeding grounds. On land, the Crested Auklet flaunts its jaunty crest and bright orange bill and practices a striking courtship display that includes "sniffing" its mate's neck (see illustration). Ornithologists have long noticed the rich odor of tangerines that hangs in the air over colonies of Crested Auklets. This odor turns out to be a key element of their social life (Hagelin et al. 2004). The auklets are attracted to their distinctive citrus-scented odor in preference to other odors. The auklets produce the chemical compounds responsible for the scent, *cis*-4-decenal and octanal, just during the breeding season. They orient specifically to these chemicals in maze experiments. Finally, the neck ruff that is sniffed during their courtship display is highly scented with these chemicals. Social odors, the avian equivalent of perfumes, are a relatively unexplored and possibly widespread channel for communication and sexual selection.



Crested Auklets displaying and sniffing.

conifer forests on islands in the Bay of Fundy (Grubb 1974). They reliably chose scents from their own nests in experimental mazes. The Antarctic Prion of the southern oceans distinguishes the smell of its mate from that of other birds and from its own scent (Bonadonna and Nevitt 2004). This ability enables it to find the right nest when returning from sea to relieve its incubating partner and may also play a role in mate choice and kin recognition.

Bird Brains

Contrary to public "wisdom," birds in general and songbirds in particular have big brains relative to their body mass. Indeed, birds have well-developed brains that are 6 to 11 times as large as those of like-sized reptiles. The brains of most birds and most mammals account for 2 to 9 percent of their total body mass. Parrots, owls, crows, woodpeckers, and hornbills have larger-than-average brains (Ricklefs 2004; Figure 7–10).

The midbrain and forebrain, or telencephalon, in both birds and mammals are conspicuously more highly developed than those of reptiles (Figure 7–11). The optic lobes and the cerebellum dominate the avian midbrain. The two avian optic lobes are huge in relation to the rest of the brain. Together with large eyes, this visual apparatus displaces the rest of the brain from the ventral and lateral parts of the skull, the usual positions in other vertebrates. Balance and coordination during flight require extensive input from sensory receptors throughout the body and in the middle ear; the large size of the cerebellum emphasizes the importance of this input.

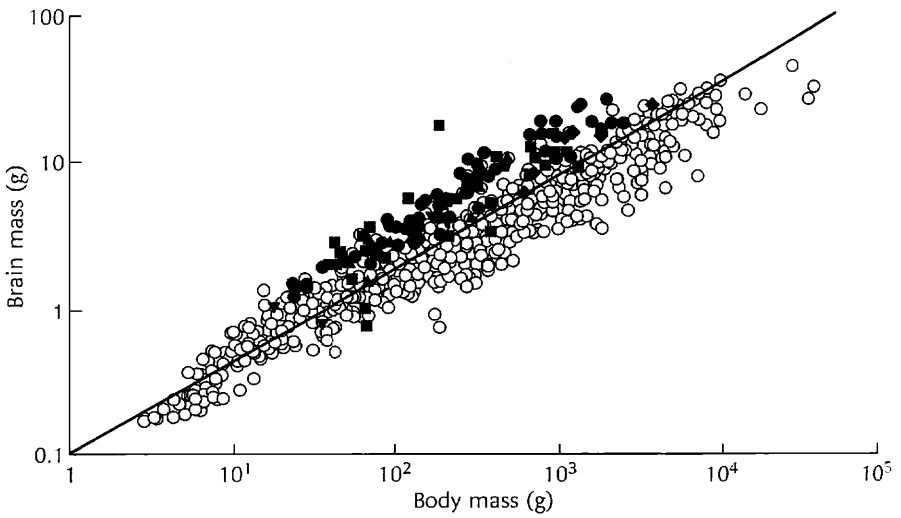


FIGURE 7–10 Relation between brain mass and total body mass in birds, based on data for 837 species. Black circles: Parrots (Psittacidae), owls (Strigidae), crows (Corvidae), woodpeckers (Picidae), and hornbills (Bucerotidae) have relatively large brains. White circles: All other species. [*From Ricklefs 2004*]

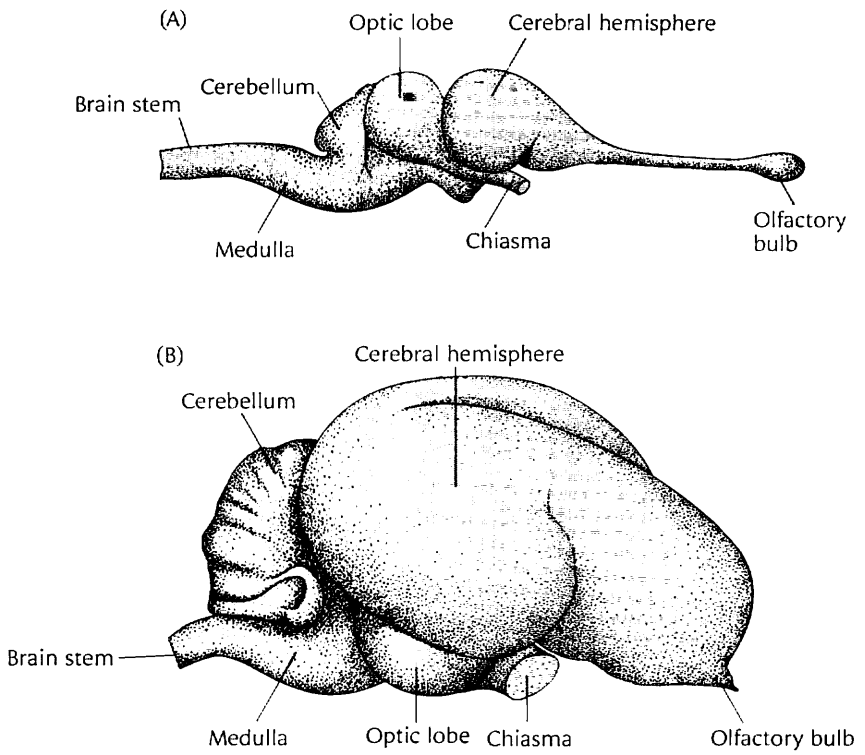


FIGURE 7–11 Left side of the brain of (A) a monitor lizard and (B) a macaw, drawn to the same scale. Note the well-developed cerebral hemisphere and cerebellum in the avian brain. The forebrain is responsible for complex behavioral instincts and instructions, sensory integration, and learned intelligence. It includes the olfactory bulbs and cerebral hemispheres. The midbrain regulates vision, muscular coordination and balance, physiological controls, and the secretion of neurohormones that control seasonal reproduction. It includes the optic lobes and chiasmata and the cerebella. The hindbrain, or medulla, links the spinal cord and peripheral nervous system to the major control centers of the brain. Cranial nerves, except those controlling vision and smell, enter the brain through the medulla.

Peripheral organs receive signals from all the senses—vision, hearing, touch, taste, and smell—and feed them to the brain for processing, integration, and response. Before reaching the main integration centers of the forebrain, sensory signals pass through their respective control centers. Visual information goes to the optic lobes of the midbrain; information on body orientation and localized pressure goes to the cerebellum in the midbrain; acoustical information goes to its related processing centers in the hindbrain; olfactory information goes to the olfactory bulbs and then to the olfactory lobe in the forebrain. [*After Portmann and Stingelin 1961*]

The 100-year-old, classical view of the structure of the avian forebrain represents it as an evolutionary step from primitive vertebrate brains to the superior brain of mammals. In this view, instinctive and reflexive behavioral systems expanded from the primitive basal ganglia in the core striatal region to dominate the avian forebrain (Figure 7–12). The deeply fissured cerebral cortex of the mammalian brain was thought to feature more advanced "pallial domains" that process advanced learning and other cognitive abilities. This view is incorrect and obsolete (Avian Brain

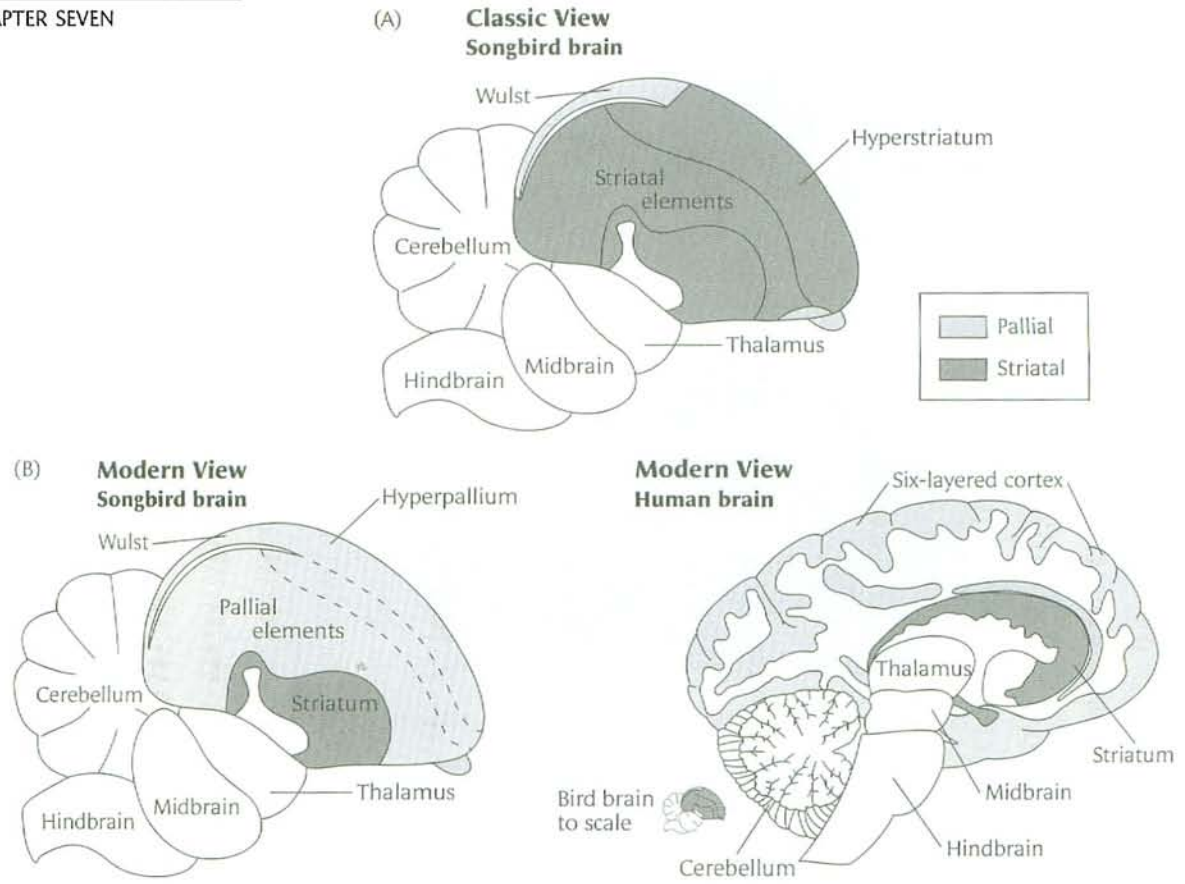


FIGURE 7–12 Classical and modern views of the avian brain. (A) The classical view considered most of the avian forebrain (the cerebrum, or telecephalon) to be an expansion of the primitive striatal elements of the vertebrate brain. These elements are limited in extent in the human forebrain, which is dominated instead by the expanded, highly folded cortex that enabled higher intelligence. (B) The modern view considers most of the avian forebrain to be made of pallial neurons homologous to those in the mammalian cerebrum, constructed differently but still enabling higher cognitive abilities. [*After Avian Brain Nomenclature Consortium 2005*]

Nomenclature Consortium 2005). Specifically, the avian forebrain also is made up largely of pallial domains, though organized differently from the mammalian cortex. The avian pallial domains are responsible for their substantial and even superior cognitive abilities.

In mammals, the cerebral cortex is the principal feature of the forebrain. It overgrows the small corpus striatum and reaches its largest and most deeply fissured state in higher primates such as chimpanzees and humans. In birds, the so-called hyperstriatum has been identified to be the center of learning and intelligence. Under the revised terminology, this section of the avian forebrain is now called the hyperpallium to indicate its cellular homology with the mammalian cerebral cortex. The hyperpallium, however, is unique to birds and is best developed in intelligent

birds such as crows, parrots, and passerines. Domestic chickens, Japanese Quail, and Common Pigeons, which do not perform as well in laboratory intelligence tests, have smaller hyperpallia. Damage to the hyperpallium severely impairs a bird's behavior. The anterior hyperpallium, particularly a bump called the Wulst, may be the seat of higher learning processes in birds. The removal of the Wulst does not impair a bird's normal motor functions or its ability to make simple choices; however, it does destroy the bird's ability to learn complex tasks.

Like primate brains, bird brains exhibit functional lateralization. The left hemisphere is dominant. In general, the left cerebral hemisphere controls complex integration and learning processes and suppresses sexual and attack behavior. The right cerebral hemisphere monitors the environment and selects novel stimuli for further processing, which may entail memory by the left side.

In humans, right-handedness relates to dominance of the left hemisphere of the brain, and weak lateralization can lead to dyslexia and learning challenges in children. Some birds also may be righties or lefties. Crossbills *(Loxia)* are either left-billed or right-billed, and they approach pine cones counterclockwise or clockwise accordingly (Knox 1983). Individual Red-necked Phalaropes spin consistently left or right while feeding (Rubega et al. 2000). Dark-eyed Juncos favor the right eye (which feeds visual information to the dominant left hemisphere) to scan for predators, as predicted (Franklin and Lima 2001). And parrot lovers have known for centuries that captive parrots are either left-footed or right-footed when they hold food. Perhaps the strongest case for true primatelike handedness in birds is that of New Caledonian crows, now well known for their skilled toolmaking (see pages 212–213). Most of these crows use the right eye and left part of the brain to make tools, just as most humans do.

Bird song is normally controlled by the left hemisphere of the forebrain, specifically with learning and innovation in vocal repertoires (Nottebohm 1980). The right cerebral hemisphere assumes control of the functions of the left hemisphere only if the left hemisphere is damaged. The impairment of a young Atlantic Canary's song-control centers in the left hemisphere leads to the formation of an alternative set in the right hemisphere and the acquisition of a new song repertoire. Such functional lateralization of the brain was once thought to be an exclusively human attribute, associated with extraordinary language abilities.

Spatial Memory and the Hippocampus

The hippocampal complex of the avian brain is a primary target of analysis of the relation between brain evolution and social behavior in birds (Sherry 1992; Sherry et al. 1992). Homologous in structure and function to the same structures in mammals, the avian hippocampal complex includes the hippocampus and the associated parahippocampus of the forebrain. The hippocampal complex is a well-delineated, paired anatomical structure that lies adjacent to the midline of the dorsal forebrain. The hippocampi of birds and mammals are functionally equivalent with respect

to controlling certain memory tasks, including spatial orientation and cognitive memory. Spatial memory processed in the hippocampus controls the daily behavior of highly mobile animals, such as birds that accurately revisit feeding places, nests, and remote wintering grounds. For example, lesions in the hippocampi of homing pigeons—a specialized, domesticated breed of Common Pigeons—disrupt their ability to learn a navigational map (Bingman 1988).

The extraordinary spatial memory of seed-caching birds is processed by an enlarged hippocampus (Krebs et al. 1989; Sherry et al. 1989). Mem-

FIGURE 7–13 Clark's Nutcracker, a seed-caching bird with extraordinary spatial memory.

bers of three families of passerine birds—Corvidae (crows, jays, and nutcrackers), Sittidae (nuthatches), and Paridae (titmice and chickadees)—cache thousands of seeds as a means of exploiting temporary food surpluses and providing reserves for future use. These three families have significantly larger hippocampal volumes than do other passerine birds. Experimental studies of chickadees and nutcrackers have demonstrated that spatial memory for seed recovery is indeed based in the hippocampus (Sherry 1989, 1990). Chickadees with experimental lesions to the hippocampus continue to hide seeds in normal fashion but cannot find them again, except by chance.

The spatial memories of seed-caching birds are prodigious. Each autumn, individual titmice may stock more than 50,000 caches of one spruce seed each (Haftorn 1959). They recover seeds as many as 28 days later (Sherry 1989; Hitchcock and Sherry 1990). Crows, jays, and nutcrackers are especially diligent hoarders. The development of spatial memory varies among species in relation to their dependence on cached seeds (Balda et al. 1996). Probably the most able is the Clark's Nutcracker (Figure 7–13), which hides between 22,000 and 33,000 individual pine seeds in more than 2000 unique cache sites to survive the winter and early spring. The ability to accurately find these caches as many as nine months later is evidence of a phenomenal spatial memory.

New Neurons

Research on neural pathways that control song and spatial memory in birds led to a major discovery: the fine structure of the adult brain is dynamic, not static. New connections, called synapses, form in spring when some birds, such as Atlantic Canaries, learn new songs; these connections disintegrate in the fall when the birds stop singing (Alvarez-Buylla and Kim 1998). Chickadees cache seeds in the autumn for use later in the winter. They increase their capacity for remembering where they put the seeds by adding new cells to the hippocampus, which expands in volume by almost 30 percent, and then shrinks in size the following spring when fresh insect food is available (Saldanha et al. 2004). Thus, adult songbirds can form new neurons, replace old ones, and reallocate brain space appropriately to seasonal efforts. This process, called neurogenesis, is now an established fact (Nottebohm 2002).

At least in a few specific circuits, the transient brain cells have limited life spans—in some cases, only several weeks or months. They are culled and replaced on a regular as well as seasonal basis in brain circuits controlling behaviors as varied as singing, food caching, and even social interactions. Such dynamics call for new theories of long-term memory (Nottebohm 2002). One of the advantages proposed is that the replacement of some old neurons by new ones enables the rejuvenation of key brain circuits and continued ability to learn new information or skills. Long-term memory resides in other neurons that are retained.

The study of the replacement of neurons in songbird brains helps to inform medical research concerned with treating damaged brains and spinal

cords. When he tried to isolate the neural growth factor in Zebra Finches, for example, Mark Gurney (1988) found a large protein molecule, which he named neuroleukin. Analysis of the functional structure of neuroleukin led Gurney and his colleagues to the part of the AIDS retrovirus that destroys neurons in the human brain, thereby causing dementia.

Sleep

Sleep evolved as a way of maintaining the neural circuitry of the brain; 1 hour of sleep stabilizes the brain synapses of a hibernating arctic ground squirrel for as long as 4 hours (Kavanau 1996). Without sleep, the synapses are less reactive, leading among other things to short-term loss of memory. Most vertebrates sleep in one way or another; sleepless bullfrogs, sea turtles, alligators, and some fishes are the exception. The evolution of the large brains and advanced endothermic metabolisms of birds and mammals has been accompanied by complex sleep patterns. Birds exhibit three stages of sleep: slow-wave sleep, or SWF; intermediate sleep; and rapid-eye-movement sleep, or REM (as in mammals).

Slow-wave sleeping requires the use of only one side of the brain at a time, a primary feature of bird sleep (Kavanau 1996; Rattenborg et al. 1999). This so-called unihemispheric sleep has been observed in 29 bird species belonging to 13 orders. Birds typically close their eyes when they sleep, but just one eye at a time for unihemispheric sleep. Unihemispheric sleep enables continued vigilance. Thus, an apparently sleeping duck watches for predators with one eye open and sleeps with the other eye closed. Mallard ducks on the edge of a group engage in unihemispheric sleep more regularly than their flock mates in more secure, central positions.

REM sleep takes place with both eyes closed. Very short and frequent bouts of REM sleep are a feature of sleep in birds (Ayala-Guerrero et al. 2003). Quick bouts of REM sleep combined with (one-eyed) unihemispheric sleep enable birds such as Sooty Terns and swifts to sleep on the wing.

Electroencephalograms of brain activity while sleeping suggest that birds dream. In one study, Zebra Finches were shown to practice new song patterns in their dreams (Dave and Margoliash 2000; Spinney 2003).

Cognition and Intelligence

Behavior in its broadest sense mediates a bird's relations to the environment, both social and ecological. Central to daily behavior are the acquisition and processing of information from the environment, or cognition (Ricklefs 2004). More formally defined, cognition "includes perception, learning, memory, and decision making, in short, all ways in which animals take in information about the world through the senses, process, retain, and decide to act on it" (Shettleworth 2001). Of greatest interest are flexible and novel behaviors that solve problems adaptively or with apparent intelligence. Complex social interactions and creative foraging behavior

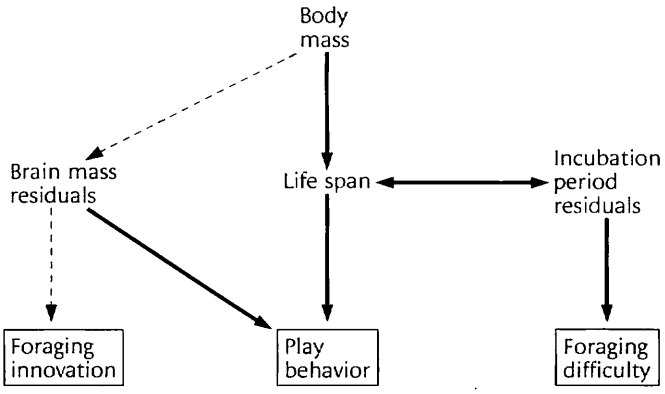


FIGURE 7–14 Connections between life-history variables and indicators of cognitive functions. Dashed arrows indicate weak correlations. [*From Ricklefs 2004*]

are evident in many bird species. For example, they routinely assess the relative abundance and economic values of alternative foods to make foraging decisions. Superior cognitive abilities are evident in crows and jays, which can remember what happened not only where, but also when (see page 211).

Bird species vary greatly in their cognition skills, in ways that affect an individual bird's survival and reproduction. The benefits and costs of cognition are tied to the evolution of life-history traits that characterize species and major groups of birds (Ricklefs 2004). Larger brain sizes, for example, require longer incubation periods to mature, as well as greater investment of metabolic and cellular resources. Foraging skills, cooperative breeding, parental care, long life span, and play behavior are correlates of the brain sizes and cognitive abilities of birds (Figure 7–14). Our understanding of the sophisticated cognitive abilities of birds increases every year, as will be apparent in each of the subsequent chapters of this book. As a prelude, here are some highlights of avian cognition and intelligence.

Birds master complex problems in the laboratory, outperforming many mammals in advanced learning experiments (Kamil 1985, 1988). Crows and magpies do especially well in laboratory experiments that test higher faculties. In one such experiment, the Krushinsky problem, the bird looks through a slit in a wall at two food dishes, one empty and one full, that move out of sight in opposite directions (Figure 7–15). The bird must then decide which way to go around the intervening wall to get to the dish that contains food. Cats, rabbits, and chickens do poorly in this test, but dogs and crows solve the problem immediately.

Learning to count is a formidable problem for most mammals. Monkeys require a long training ordeal of 21,000 trials to learn to distinguish between sound series with two or three different tones; rats never learn to make this distinction. Birds, however, more easily master complex counting problems (Davis and Perusse 1988). Ravens and parakeets, for example, can learn to count to seven and can learn to identify a box

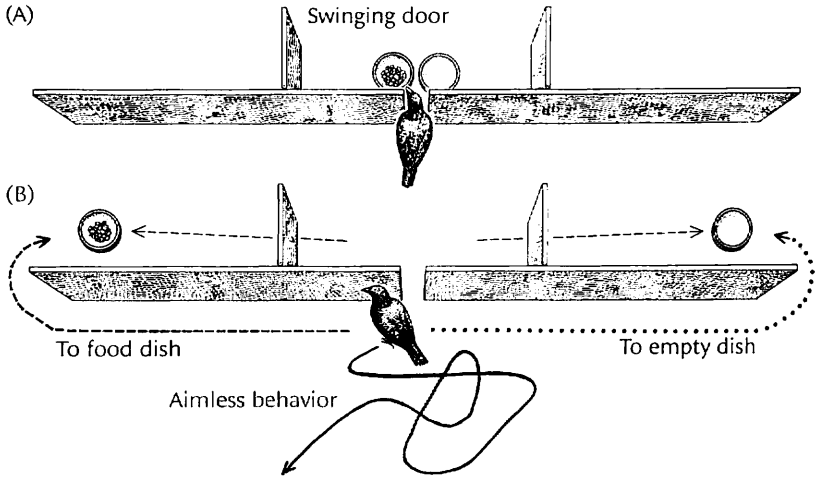


FIGURE 7–15 Crows and dogs performed best in the Krushinsky problem experiment, in which food dishes, (A) viewed by the subject through a slit in a wall, move out of sight behind swinging doors. (B) The subject must then choose to proceed left or right to find the food dish. [*From Stettner and Matyniak 1968, with permission from Scientific American*]

containing food by counting the number of small objects in front of it (Koehler 1951). Female coots can count their own eggs in a nest, ignoring eggs laid by other females, and decide how many more to add (Lyon 2003; see also Chapter 13).

One of the most advanced forms of learning, insight learning—that is, learning by the observation and imitation of others—may be routine among birds. Blue Jays, for example, learn the difference between edible and inedible butterflies by watching the feeding behavior of jays in another cage (Brower et al. 1970). The spread of the milk bottle feeding habit among English titmice, described on page 210, is attributed to learning by imitation. Novel tool use, such as throwing stones at ostrich eggs by Egyptian Vultures, also probably spreads through imitation of individual innovative birds.

Parrots are capable of complex reasoning and communication (Box 7–5). Common Pigeons, amazingly, can converse without any assistance from humans (Epstein et al. 1980). In this experiment, modeled after the demonstration of communication through symbols by chimpanzees, two pigeons named Jack and Jill learned to ask about different colors coded by symbols and to find them. In the ultimate conversation, Jack asked Jill "What was a hidden color?" by using a symbol. Jill peeked at the color and told Jack which color it was by depressing a key with the symbol for that color. Jack responded by pecking the "Thank you" key, which rewarded Jill with food. The conversation continued for other colors and their symbols. The transmission of novel behavioral traits from one individual bird to another, a kind of culture, can thus be important in the evolution of behavior in birds.

Many years ago, pioneering behavioral psychologist B. F. Skinner (1960) declared that a pigeon is capable of performances that can be

BOX 7–5

CONVERSATIONS WITH A PARROT EXPLORE AVIAN INTELLIGENCE

A Gray Parrot named Alex has been a source of deep insights into the intellectual abilities of some birds (see illustration). Irene Pepperberg (2000) first taught Alex a vocabulary of English vocalizations to identify, request, refuse, or comment on more than 80 objects of different colors, shapes, and materials. Alex's comprehension of categories and labels was illustrated by his performance in a series of trials. Alex was presented with an array of objects—purple truck, yellow key, green wood, orange paper, gray peg wood, and red box—and was then asked, "What object is green?" Alex replied, "Wood." He responded with an accuracy of 81 percent over 48 such trials. The ability for two-way communication between Irene and Alex increased, enabling increasingly complex tests of Alex's abilities. He could provide additional information about an object that was uniquely defined by the conjunction of two other categories. For example, to the question "What color is the three-corner [shape] key [object]?" Alex would answer, "Yellow."

In general, birds quickly learn to recognize the odd object, not only in a set of familiar objects but also in sets of unfamiliar objects; monkeys master this task with difficulty. Alex went a step further; he learned to report on the absence or presence of similarity and difference between two objects (Pepperberg 1988). When asked either "What's same?" or "What's different?" he responded, "None," if the two objects were, respectively, totally dissimilar or identical. The required concepts of nonexistence or absence are related to advanced cognitive (and linguistic) abilities to deal with discrepancies between the expected and the actual state of affairs.

Alex, an African Gray Parrot that has changed our understanding of avian intelligence, and his companion, Irene Pepperberg, discuss the different objects between them. [*Courtesy of I. Pepperberg*]

equaled by electronic equipment only of vastly greater weight and size. In particular, the pigeon is especially good at responding to patterns and those classes of patterns called "concepts." These conclusions followed years of experiments training pigeons to be homing devices for a model air-to-ground missile during World War II (Wasserman 1995). The pigeons were trained to follow specific targets or classes of targets on land and at sea. Some exercises required a majority decision of the members of a team of three pigeons. These early experiments have been extended by generations of other experiments. We now know that pigeons can memorize as many as 725 different visual patterns, separate human-made from natural objects, discriminate different styles (cubistic versus impressionistic) of painting, communicate by using visual symbols, and even "lie" (Avian Brain Nomenclature Consortium 2005, p. 156).

Smart Feeding

Food gathering requires sophisticated hunting skills and even innovative practices. Innovation increases with forebrain size across a variety of bird species (Lefebvre et al. 2001). Forty years ago, a few Great Tits in the British Isles learned to rip open milk bottle caps to drink the cream. Apparently, it was a novel application of normal bark-tearing behavior (Morse 1980). The skill passed rapidly to other titmice, forcing milk companies to replace the cardboard caps with sturdier aluminum ones. The tits learned to open the aluminum caps, too. Darwin's finches of the Galápagos Islands are renowned for their novel feeding efforts. In one extraordinary example, the Small Ground Finch and Large Cactus Finch learned to push aside sizable stones with their feet by first bracing their heads against a large rock for leverage; in one case, a 27-gram finch moved a 378-gram stone in this manner (DeBenedictis 1966).

Birds tend to choose food of high energetic profit. A classic example is that of White Wagtails, which prefer medium-sized flies, even though large flies with greater energy content are more common (Davies 1977). Medium-sized flies yield comparatively more energy per second of foraging time because large flies take too long to subdue and swallow relative to their higher energy content (Figure 7–16).

Many birds, from gulls to raptors, drop hard-shelled prey from the air to crack them open. Crows *(Corvus)* break open hard-shelled food items in a variety of clever ways. On the coast of British Columbia, Canada, Northwestern Crows eat whelks, a kind of marine snail (Zach 1979). To eat them, a crow must fly up high and drop them repeatedly onto rocks

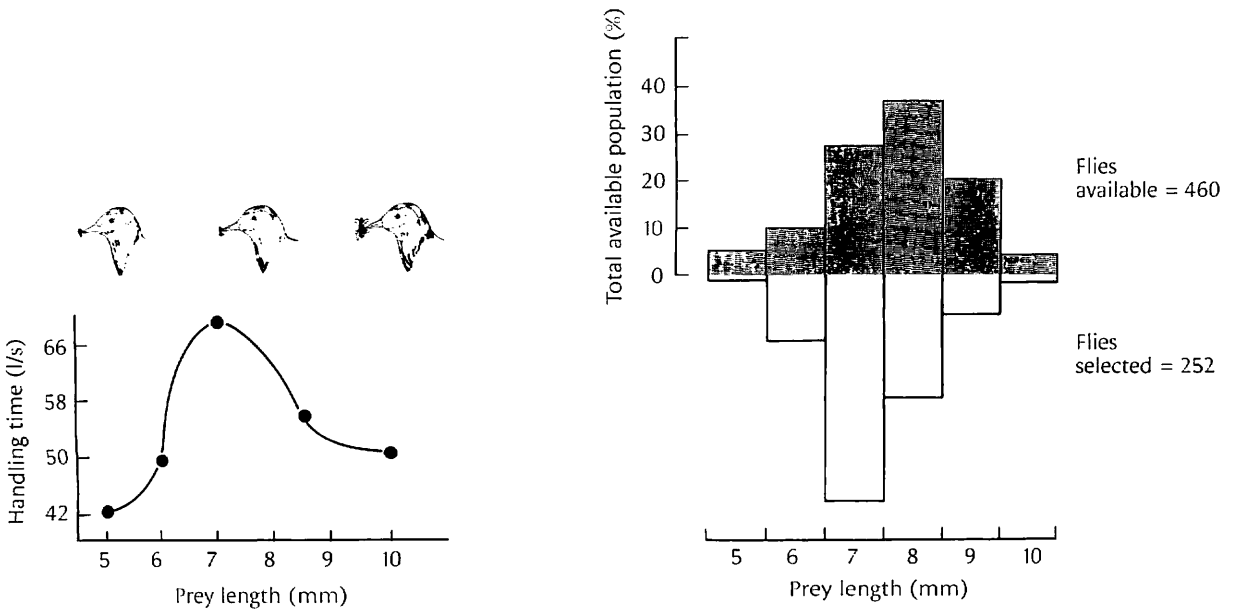


FIGURE 7–16 White Wagtails select medium-sized flies (7 mm) that yield the most energy per second of handling time. [*After Krebs 1978*]

until they break; 20 drops per whelk is not unusual. On the basis of size only, the crows select whelks that supply about 8.5 kilojoules of energy, a yield that exceeds the high foraging costs of 2.3 kilojoules per whelk. Crows include factors other than simple energetics in their foraging. In California, American Crows crack walnuts by dropping them (Switzer and Cristol 1999; Cristol and Switzer 1999). The height from which they choose to drop a nut depends on how hard the surface is below, how many times they have already dropped it (and thus the probability of some cracks already), and the prospect of losses to other crows, which increases with the height of the drop and thus the diminished ability of the dropper to get to it first.

In Japan, Carrion Crows learned a new trick: they now use cars as big tools to crack their walnuts. Since 1990, newly urbanized crows have learned to wait for a red traffic light, then place the nuts on the crosswalk in front of stopped cars, and return on the next red light to pick up meat from the crushed nuts (Attenborough 1998).

Birds also use time adaptively when they harvest renewable resources by returning regularly to productive foraging sites, such as backyard bird feeders. Hummingbirds, for example, repeatedly return to flowers to harvest nectar produced by the flowers since their last visit. Some hummingbirds cycle among widely scattered flowers, just as fur trappers check their circuit of widely scattered traps, called a trapline. In one field study, traplining hummingbirds of the rain forest learned to time their returns to coincide with the interval of experimental refill, a form of operant conditioning (Gill 1988). Marked birds also learned to wait longer if they could get more nectar by doing so. Counteracting the advantages of waiting, however, was the prospect of losing the nectar to a competitor. When that happened, the hummingbirds returned frequently to harvest small amounts of nectar, keeping flowers almost empty and unattractive to competing birds.

Western Scrub Jays apply the concepts of past, present, and future in ways similar to what is called "episodic memory" or "memory time travel" in humans. They remember where and when they hid what kinds of food (Clayton and Dickinson 1998; Jeffrey and O'Keefe 1998; Clayton et al. 2003). The jays also adjust their efforts to future needs and future conditions. Briefly, in a series of elegant experiments, the jays hid two types of food—perishable insects and nonperishable nuts—for later recovery and eating. They quickly learned to recover the insects before they spoiled. If too much time had elapsed, causing likely decay, they switched to their hidden nuts without checking on the status of the hidden insects. When known thieving colleagues were allowed to watch a jay hide its food, the jay would move the food to a new site at its first private opportunity.

Innovation and the Use of Tools

Some birds use tools in feeding and some, when faced with dramatic changes in resources, have developed innovative behaviors. Many anecdotes describe the seemingly deliberate use of bait, including pieces of

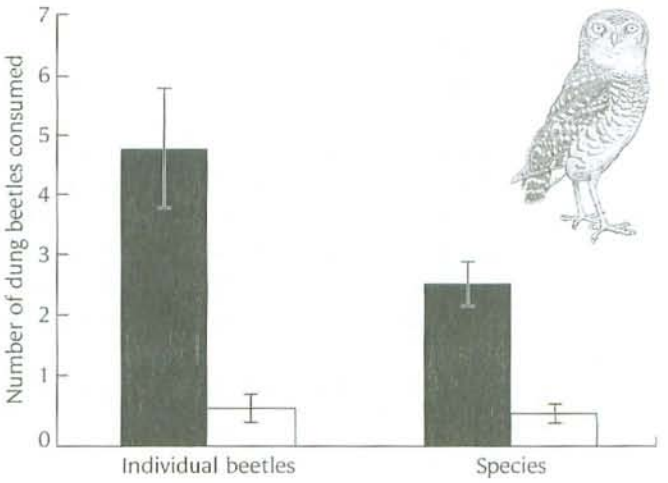


FIGURE 7–17 Number of dung beetles eaten by Burrowing Owls in the presence (black) and the absence (white) of cow dung positioned at their burrows. [*From Levey et al. 2004*]

paper used by feeding herons to attract fish. Similarly, Burrowing Owls use mammal dung to attract one of their main prey, dung beetles. Burrowing Owls routinely gather dung and place it around the entrance to their nest burrows as bait. By experimentally adding and removing dung from the burrows, Doug Levey and his colleagues (2004) found that owls consumed ten times as many dung beetles and six times as many dung-beetle species when dung was present than when it was absent (Figure 7–17).

Like chimpanzees, the long well known Woodpecker Finch of the Galápagos pries grubs from crevices with a stick or a cactus spine held in its bill. Other instances of probing and prying have since been recorded, but the making of tools by New Caledonian Crows is the premier example of advanced toolmaking by birds (Hunt 1996; Hunt and Gray 2003; Figure 7–18). These crows "craft" a variety of hooked tools by first selecting the raw material, then trimming it, and finally sculpting it into a hook. In the laboratory, one female crow named Betty figured out how to make the hooks that she needed to get food from inside a tube by crafting them from metal wire. Beyond her use of a novel material, Betty also chose, from a large assortment of wires in a toolbox, the wire of the correct length and diameter to make a functional tool (Weir et al. 2002).

New Caledonian Crows craft a second kind of tool from the leaves of a screw pine *(Pandanus)* by alternating angled cuts with horizontal rips to create a serrated edge. They use the tools for extracting insect prey from crevices. The fundamentals required—standardization, discrete tool types with deliberate sculpting, and the creation of hooks—are not known in any free-living nonhuman organisms. Further, the design of the leaf tools has diversified with the passage of time throughout the is-

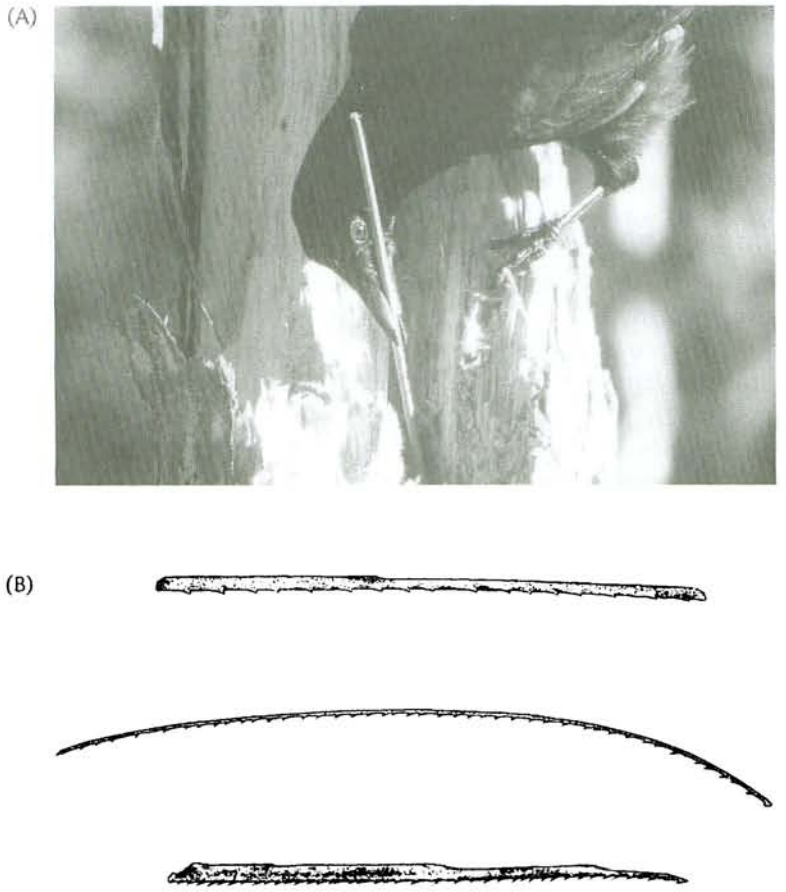


FIGURE 7–18 (A) New Caledonian Crow probing for insect food with the use of a self-fashioned tool. (B) Selection of tools crafted by New Caledonian Crows. [*Courtesy of G. Hunt*]

land of New Caledonia. The crow has developed the cultural capacity to evolve its tools in ways that resemble the feats of the early ancestors of modern humans.

The sophisticated behaviors of crows and jays suggest levels of complex cognition and intelligence that rival those of the great apes (Emery and Clayton 2004). Crows and chimpanzees are both large-brained and highly social animals that perform comparable feats of tool manufacture, mental time travel, and social cognition. The still fresh and sometimes controversial evidence suggests that such complex, advanced cognitive abilities evolved several times in unrelated species having different brain structures. Yet their skills depend on the same four basic elements: causal reasoning, flexibility, imagination, and prospection. Whether in the construction of tools from novel materials, the caching of food strategically for the future, or communicating novel information, the amazing abilities of birds and apes match their exceptional brain development.

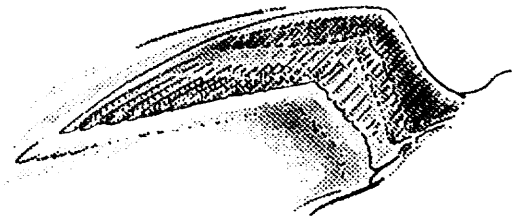
Summary

Birds have a full repertoire of well-developed senses. Large eyes and well-developed optic lobes of the brain provide excellent vision, including an ability to follow small moving objects. Birds may also have the most highly developed color vision, including ultraviolet vision, of any vertebrate. The hearing of birds as a group is good but not extraordinary. Birds are sensitive to slight differences in barometric pressure and to magnetism. The senses of smell, taste, and touch are also better developed in birds than was once thought.

The evolution of the avian brain has taken a different course from that of the mammalian brain but has achieved advanced cognitive processing and intelligence. The hyperpallium layer of the forebrain is the center of intelligence in birds. The hippocampus houses spatial memory and other functions. The dominant left hemisphere of the avian brain controls right-sided and left-sided behaviors, including the learning of songs. The seed-caching behaviors of crows and jays include prodigious spatial memories as well as the ability to remember what kinds of food were hidden where and when, with planning for the future. Neurons are added and lost programmatically in some circuits of the brains of adult birds, a discovery of import to human medicine and one that is advancing new theories of long-term memory.

Birds exhibit greater intelligence than most people think and was understood historically by scientists. Birds have large and well-developed brains, and they outperform mammals in many laboratory problem-solving experiments. Experiments on two-way verbal communication with a Gray Parrot have revealed advanced abstracting and conceptual abilities. Pigeons communicate by using symbols, and crows, which craft tools for feeding, match chimpanzees in key features of social intelligence.

CHAPTER 8



Vocalizations

Birds have the greatest sound-producing capabilities of all vertebrates, and their vocal repertoires are among the richest and most varied in the animal kingdom.

[Marler and Hamilton 1966]

Rich vocabularies of elaborate sounds connect birds over long distances and through dense cover. The vocalizations of many birds, such as nightjars or tyrant flycatchers, are more distinct to humans than are their cryptic plumage colors. Their key message—the species identity of the sender—pervades both the visual and the vocal displays of all birds, oscine songbirds and nonpasserine alike. Birds respond readily to playback of tape-recorded vocalizations, as they do to one another's sounds. Using this technique, we can draw out and view secretive species, census populations of birds such as owls and rails, and assess whether well-separated populations can recognize one another.

This chapter begins with the physical characteristics of bird vocalizations and examines how the syrinx and the brain interact to produce these sounds. Then follows the process of how songbirds learn their songs, including the development of specific neural pathways in the brain and the resulting formation of regional dialects or "accents" within a species. Vocal repertoires and displays are central to reproductive success and subject to sexual selection, just as are plumage ornaments and visual displays. The final section of this chapter explores the roles of song repertoires and vocal displays in species recognition, the choice of superior mates, and the maintenance of pair bonds.

Physical Attributes

Bird vocalizations range from the short clicks of swifts, to the quavering whistles of the tropical, partridgelike tinamous, to the long, tinkling

BOX 8–1

A VOCABULARY FOR SOUNDS AND VOCALIZATIONS

Discussions of bird vocalizations require a small, specialized working vocabulary of terms from music and from the scientific study of sounds (acoustical physics).

Amplitude Loudness, or maximum energy content, of a sound.

Fundamental tone See **Harmonic.**

Frequency Number of complete cycles per unit time completed by an oscillating sound waveform; usually expressed in hertz or kilohertz.

Glissando A blending of one tone into the next in a scalelike passage.

Harmonic A tone in the series of overtones produced by a fundamental tone. The frequencies of the tones in a harmonic series are consecutive multiples of the frequency of the fundamental tone.

Hertz (Hz) Unit of frequency equal to one cycle per second.

Modulation Defining the form of a sound (technically, the carrier wave) by variation of either frequency or amplitude.

Oscillograph Device that records oscillations as a continuous graph, called an oscillogram, of corresponding variations in an electric current, as would be generated by a tape recording of a sound.

Overtone See **Harmonic.**

Pitch Relative position of a tone in a scale, as determined by its frequency.

Resonance The intensification and prolongation of sound, especially of a musical tone, produced by sympathetic vibration.

Sinusoidal waveform Simple, pulsed cycles of energy that describe a regularly rising and falling sine curve, defined by the equation $y = \sin x$.

Sonogram Visual display of the frequency content of a sound distributed in relation to time.

Tone A sound of distinct pitch and quality; in music, the interval of a major second.

melodies of wrens, to the seemingly endless imitations of other birds by mockingbirds and lyrebirds. They range in pitch from deep infrasounds to high pitches inaudible to older human ears. Some bird species are virtually silent; others are garrulous. At one extreme, Mute Swans, Turkey Vultures, and Greater Rheas merely hiss and grunt occasionally. At the other extreme are the seemingly unlimited vocabularies of mynas, parrots, mockingbirds, and skylarks.

The modulations of frequency (pitch) and amplitude (energy, or loudness) within bird songs are unique among animal sounds (Box 8–1). Simple tones, such as the notes of a White-throated Sparrow, contain little modulation, whereas the variable songs of a Song Sparrow and the brief notes of a Tree Swallow contain complex, rapid modulations. Even short phrases within songs may include rapid modulations. The brief "glug glug glee" song of the Brown-headed Cowbird spans a four-octave interval from 700 to 11,000 hertz, the greatest frequency range in a single bird song. In one 4-millisecond fraction of the "glee," the signal rises continuously from 5 to 8 kilohertz, an amazingly rapid glissando (Figure 8–1).

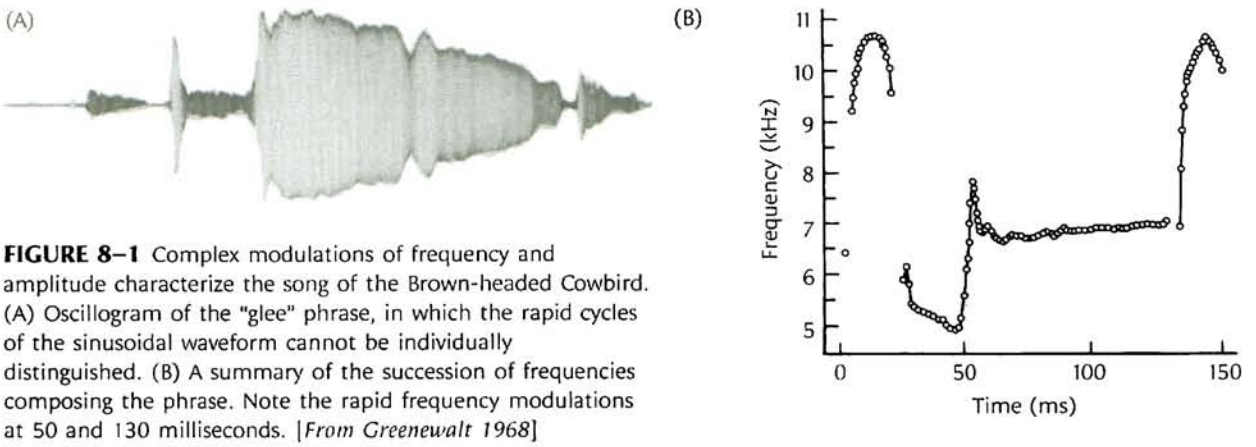


FIGURE 8–1 Complex modulations of frequency and amplitude characterize the song of the Brown-headed Cowbird. (A) Oscillogram of the "glee" phrase, in which the rapid cycles of the sinusoidal waveform cannot be individually distinguished. (B) A summary of the succession of frequencies composing the phrase. Note the rapid frequency modulations at 50 and 130 milliseconds. [*From Greenewalt 1968*]

Females select males on the basis of their abilities to perform such vocal gymnastics.

A traditional distinction exists between "songs" and "calls." The term song refers primarily to the loud, often long, vocal displays of territorial male birds. Specific, repeated patterns are often pleasing to the human ear. The primary components of a bird song are syllables, phrases, and trills (Figure 8–2). The term call connotes a short and simple vocalization, usually given by either sex. Various calls include distress calls, flight calls, warning calls, feeding calls, nest calls, and flock calls. There is, however, no real dichotomy between songs and calls in their acoustical structure,

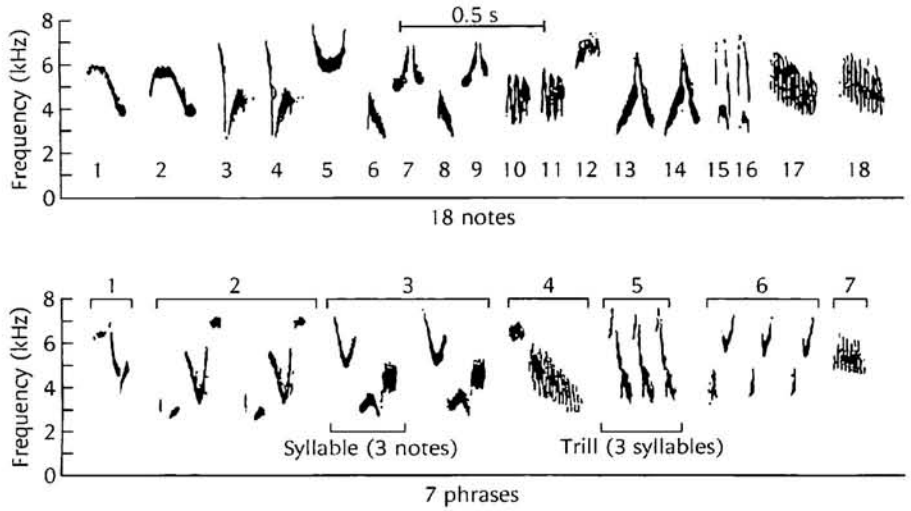


FIGURE 8–2 Components of a bird song, as illustrated by two songs (upper and lower) of buntings (*Passerina*). Syllables are the principal basic units. They may appear as a single continuous trace on a sonogram or as a set of two or more different notes that occur together and are separated from other such groups of notes. Phrases are groups of repeated syllables. Trills are rapid repetitions of three or more (simple-note) syllables. [*From Baker 2001*]

delivery, physiology, development, function, and taxonomy, all of which have served as criteria for different definitions of "song" in birds (Spector 1994; Baker 2001). Despite the lack of a single accepted definition, we continue to use the term song because it is so entrenched and because we lack better alternatives.

A fundamental dichotomy, unlinked to the perception of songs versus calls, defines the acoustical structure of bird vocalizations: whistled songs versus harmonic songs (Greenewalt 1968). Whistled songs consist of nearly pure (lacking harmonics) sinusoidal waveforms—the higher the pitch, the more frequent are the oscillations of the sound waves. Both the basso profundo (80–90 Hz) of a Spruce Grouse and the high, thin notes (9000 Hz) of a Blackpoll Warbler are, technically speaking, whistled songs (Figure 8–3).

Harmonic songs employ overtones with frequencies that are multiples of the fundamental frequency. The number of harmonics and their relative

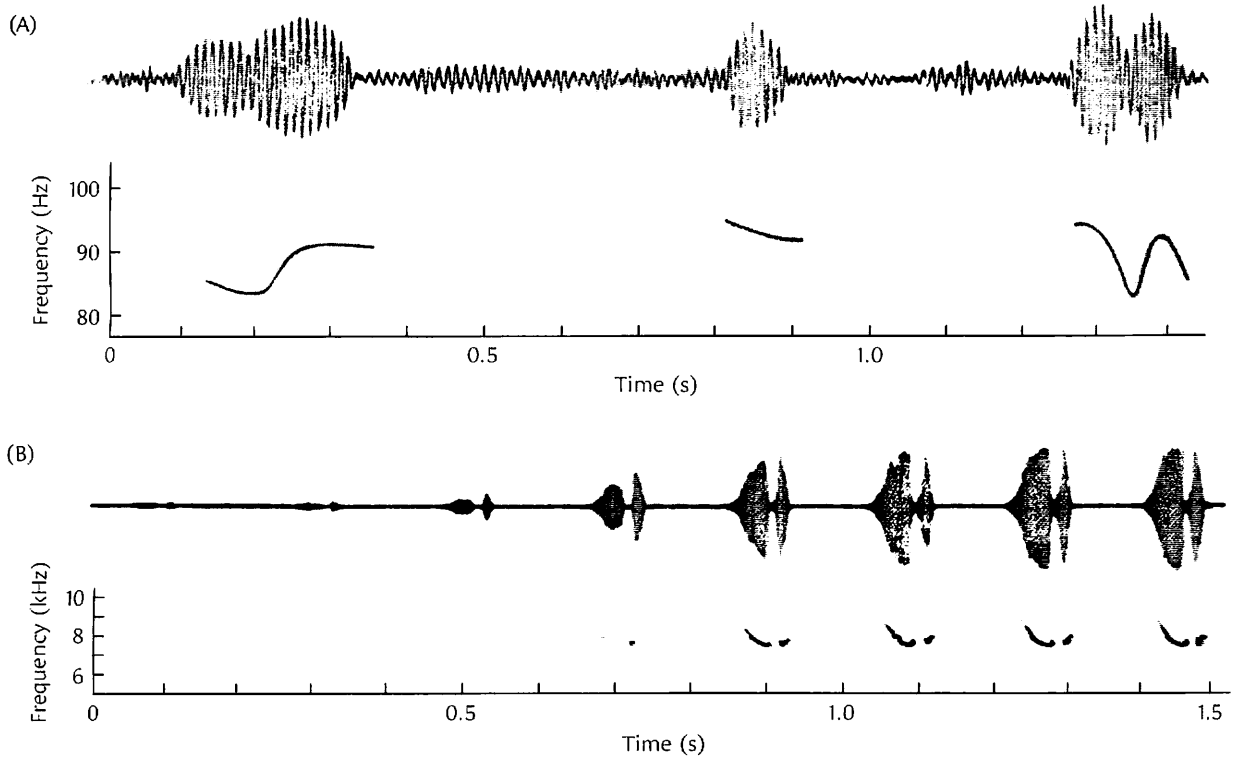


FIGURE 8–3 Paired oscillograms and sonograms of (A) the bass notes (90 cycles per second = 90 Hz) of the whistled song of a Spruce Grouse and (B) the high, thin notes (9 kilocycles per second = 9 kHz) of the whistled song of a Blackpoll Warbler. The oscillograms (upper graphical records) display patterns of amplitude modulation as the vertical deflection (above and below the midpoint) of the sinusoidal waveform; frequency is calculated from the number of complete cycles per second. The sonograms (lower records) display the distribution of energy (1 kilocycle per second = 1 kHz) in a song with respect to time. [*From Greenewalt 1968*]

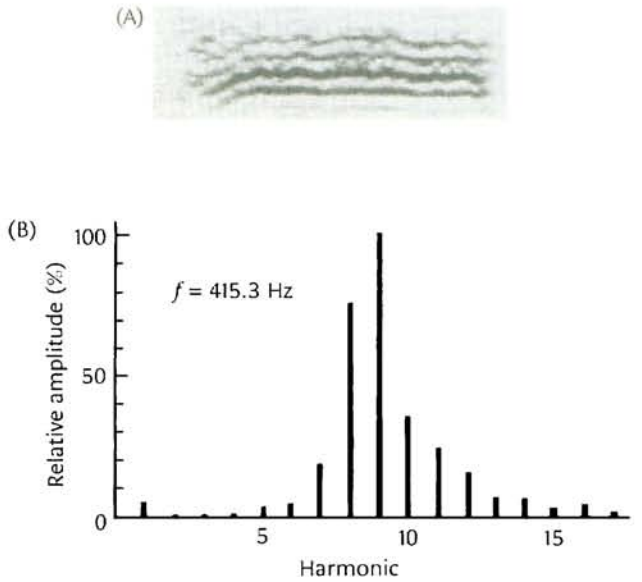


FIGURE 8–4 The *dee-dee-dee-dee* scold call of a Black-capped Chickadee consists of a series of harmonic phrases. (A) Sonogram of one "dee" phrase. Chickadees increase the number of these phrases in relation to the threat of predation (see Box 8–2). (B) Relative amplitudes of the tones of the harmonic series; the fundamental frequency, *f*, is 415.3 hertz. Numbers on the abscissa represent the frequencies of the harmonics as multiples of the fundamental ($1 = f$ at 415.3 Hz). The loudest tone is assigned an amplitude of 100 percent, and the amplitudes of the other tones are calculated relative to that value. [*From Greenewalt 1968*]

amplitudes determine the timbre, or general tonal quality, of the notes of bird songs (and musical instruments). One dominant harmonic has more energy, or greater amplitude, than do the others in the spectrum. Qualities such as clarity, brilliance, and shrillness, as well as nasal and hornlike tones, are due to various combinations of harmonics and their emphases (Figure 8–4). For example, the distinctive sounds of a clarinet and a Hermit Thrush result from an emphasis on the odd-numbered (3, 5, 7, etc.) harmonics (Marler 1969).

Bird song has much in common with human music and speech, having similar sounds, tones, and tempos. Furthermore, bird song is produced by a series of rapid and complex motor activities, much like those controlling the tongue of a person speaking or the fingers of a skilled violinist playing an intricate passage (Marler 1981; Suthers et al. 1999). Some of the pure high-pitched whistles of birds are quite like the notes from a human-made flute. Models of the avian vocal system, however, reveal a unique configuration of acoustical elements: the avian vocal system is a new instrument (Smyth and Smith 2002).

The physical structure of a sound affects the ease with which a listener—predator or neighbor—can locate its source. The calls that birds use to locate or attract one another, for example, are made up of short notes with broad frequency ranges that enrich the information about direction

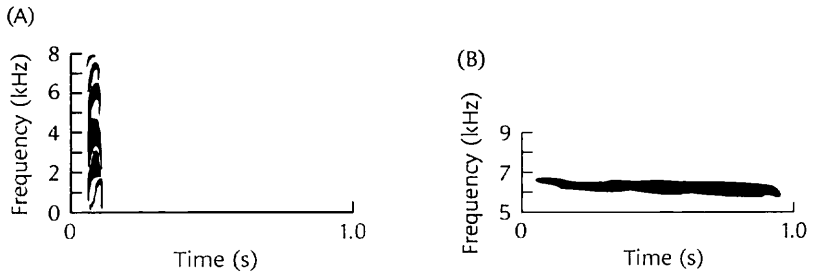


FIGURE 8–5 Sonograms of two vocalizations of a Eurasian Blackbird. (A) The call used when mobbing an owl is of short duration and has a broad frequency range; its source is easy to locate, and it attracts other birds to the site. (B) The alarm call, used when a hawk flies over, is of long duration and has a narrow frequency range; its source is difficult to locate, and thus this call does not reveal the blackbird's location to the hawk. [*After Marler 1969*]

and distance. In contrast, alarm calls are faint, thin (narrow frequency range), high-pitched calls of long duration that conceal the sender's whereabouts (Figure 8–5).

The physical structure of a particular sound also determines the distance that it will travel and how much distortion that it will sustain before reaching the listener. Interference, absorption, and scattering of the sound waves by vegetation, the ground, and the air progressively distort a sound. Low-frequency sounds, such as the calls of grouse, bustards, cuckoos, doves, and large owls, are the most effective for long-distance communication; they are less subject to attenuation and interference than are high-frequency sounds. Reverberations in forests mask the fine temporal structure of bird songs. Forest-dwelling birds, therefore, tend to produce simple sounds. Conversely, broadband songs rich in temporal structure (with complex frequency modulations) are advantageous in open habitats because simple, sustained tones tend to be distorted by strong temperature gradients and air turbulence. Thus, the complex buzzy songs of open-field birds, such as Grasshopper Sparrows, contrast with the simpler clear whistles of forest birds, such as Rose-breasted Grosbeaks.

Birds adjust their singing behavior in relation to their sound environment. Even hummingbirds sing louder in the presence of increased background noise, such as that of a nearby creek (Pytte et al. 2003). Urban noise, in particular, now affects the ability of birds to communicate with one another. Just as we humans have a hard time hearing birds singing at a distance because of the intense background noise of traffic, and so forth, so do birds. Low-frequency sounds prevail in urban noise. To communicate more effectively in an urban environment, male Great Tits in Leiden, Holland, now sing at higher frequencies above the background noise than do male Great Tits in quieter places (Slabbekoorn and Peet 2003).

Some birds can hear low-frequency noises called infrasounds that are below the range of human hearing (see page 192). Elephants and some whales talk to other members of their species over long distances by us-

ing infrasounds below 20 hertz. Birds are not known to do so, with one recently discovered exception. Cassowaries—large flightless, solitary birds of the dense rainforests of New Guinea—produce low, pulsed booms of infrasound as low as 23 to 32 hertz that are felt as strange vibrations by humans (Mack and Jones 2003). These low-frequency sounds are ideal for communication between cassowaries over long distances through thick forests, just as they are for elephants that keep track of one another in the dense forests of West Africa. Exactly how a cassowary produces the low, booming notes is not known, but, if you were lucky enough to see one sing in the infrasound, here is what you would see:

> Prior to booming it made several gulping motions, possibly inflating internal air sacs. It then opened its bill wide, raised its body upward, inhaling deeply, then threw its head down between its legs and began booming. . . . The entire bird vibrated visibly during the booming. The colorful, wrinkled, naked skin at the back of the lower neck inflated tightly during vocalization, roughly doubling the apparent width of the neck. [Mack and Jones 2003, p. 1066]

Vocabularies and Communication

Most birds have from 5 to 14 distinct vocalizations of varied acoustical structures and overlapping functions. The Chaffinch of Europe, the subject of pioneering studies of bird song, renders 12 adult sounds, 7 of which are used only in the breeding season—6 by the male and 1 by the female (Table 8–1). The functions of these calls include proclamation of territorial ownership, attraction of mates, broadcast of personal characteristics (species, age, sex, competence), warning of potential dangers, and maintenance of social contact. Most birds also have calls that are used only occasionally for special purposes. Alarm calls, which signal danger and advise escape flight, can even tell flock mates which predator is threatening (Box 8–2). Precopulatory trills and postcopulatory grunts integral to mating ceremonies are heard at no other time.

Among different species of songbirds, the repertoires of territorial songs alone vary from the single song type of the White-throated Sparrow and the two distinct territorial songs of many species of North American wood warblers to the hundreds of songs used by some wrens and mockingbirds. Among wrens, Canyon Wrens have but three simple songs per individual bird, whereas individual Sedge Wrens and Marsh Wrens have more than 100 songs (Kroodsma 1999). Even though Winter Wrens in Oregon have a relatively small repertoire of roughly 30 songs per individual bird, the songs are extraordinary. Lasting a full 8 seconds, their songs are composed of organized sets of syllables, each consisting of 50 notes selected from a pool of 100 (Kroodsma 1980).

In addition to species identity, bird vocalizations also communicate individual identity and sex, with implications for social status, pair bonds,

TABLE 8–1 Repertoire of the Chaffinch

Vocalization	Transcription	Context
Flight call	tupe or tsup	Flight or flight preparation
Social call	chink or spink	Seeking companion of unknown whereabouts
Injury call	seeee	Injured in flight
Aggressive call	zzzzzz or zh-zh-zh	Fighting (captive males only)
Alarm calls	tew	Danger, used especially by young birds
	seee	Escaping a real threat, just after copulation (breeding males only)
	huit	Moderate danger or after real danger (breeding males only)
Courtship calls	kseep	Active courtship (breeding males only)
	tchirp	Ambivalence toward approach and copulation with female (breeding males only)
	seep	Ready for copulation (females only)
Subsong		Practice of real song
Song		Territoriality, identification, and courtship; average is two or three per male, as many as six

From Marler 1956.

and family relationships. Details of song pitch, phrase structure, syntax, and composition serve as individual signatures that enable birds to identify offspring, parents, mates, and neighbors. White-throated Sparrows, for example, use variations in pitch to this end. Ovenbirds use variations in the structure of the phrase that can be verbalized as "tea-cher," and Indigo Buntings use groups of repeated syllables as individual signatures. Discrimination of individual vocalizations enables mates to recognize each other. Colonial seabirds—penguins in particular—use unique vocalizations to distinguish their partners from the hordes of potentially antagonistic neighbors (Jouventin and Aubin 2002). Individual vocal differences also enable birds to distinguish neighbors from strangers and to respond accordingly. Territorial males concentrate their defense efforts against strangers and accommodate neighbors as long as they stay where they belong, in their own territories.

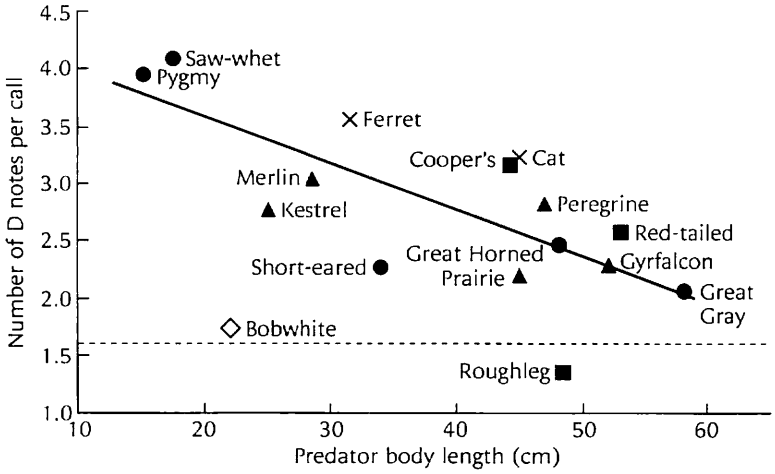
Sound Production by the Syrinx

The scientific literature on bird vocalizations began almost 400 years ago with the observation by Ulyssis Aldrovandus that ducks and chickens called even after their heads were chopped off: the source of the vocalizations was apparently located in the body and not the head. The source of avian

BOX 8–2

CHICKADEES TELL FLOCK MATES WHICH PREDATOR IS LURKING

When alarmed, Black-capped Chickadees typically start to scold with their familiar *chick-a-dee dee dee* call. In fact, one of the best ways to find an owl is to seek what a chickadee is scolding. Recent studies of the scolding behavior of these chickadees in Montana revealed that chickadees rank predators according to their size and potential threat (Templeton et al. 2005). A chickadee tells its flock mates which type of predator that it has spotted and the degree of threat posed by the predator. The chickadee increases the number of "dee" syllables as the potential threat increases. Small owls (with short wings) are more likely than big owls to catch a chickadee; so small owls elicit the most dees.



Chickadees react to predator body size and potential threat by increasing the average number of "dee" syllables. Big predators that pose minimal threat elicit only two dees; little owls elicit four dees. Different symbols indicate each taxonomic group of raptors: circle, owl; triangle, falcon; square, buteo hawk; ×, mammal. [*From Templeton et al. 2005*]

vocal abilities is, in fact, a unique organ—the syrinx—that operates with nearly 100 percent physical efficiency to create loud, complex sounds and can produce two independent songs simultaneously.

The avian larynx is located at the top of the trachea at the back of the oral cavity, but, unlike the mammalian larynx, does not house vocal cords. It serves only to open and close the glottis and thereby keep food and water out of the respiratory tract. All songs and calls come instead from the syrinx, a complex organ located in the body cavity at the junction of the trachea and the two primary bronchi (Figure 8–6A). The efficiency of sound production by the syrinx is extraordinary; nearly 100 percent of the air passing through it is used to make sound, compared with only 2 percent in the human larynx.

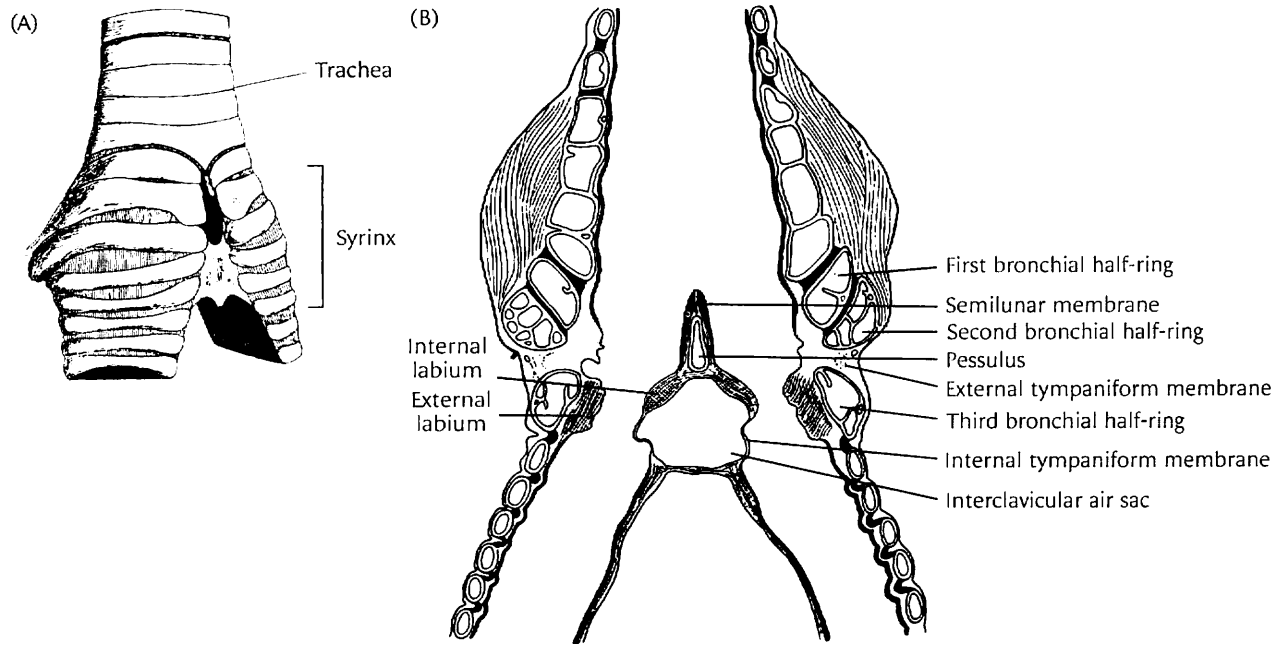


FIGURE 8–6 (A) Bird vocalizations originate from the syrinx, an elaboration of the junction of the base of the trachea and the two bronchi. The syrinx is made of tracheal tissues (Neotropical woodcreepers, antbirds), bronchial tissues (cuckoos, nightjars, owls), or both tracheal and bronchial tissues (most birds). (B) The main elements of the syrinx are its vibrating tympaniform membranes, the muscles that control tension in these membranes, and the supporting cartilage. [*After Häcker 1900*]

Sound is caused by the vibration of the air column as air passes through the syringeal passageway. Projections called the internal labium and the external labium constrict these narrow passageways (Figure 8–6B). On each side of the syrinx itself is a thin, glass-clear membrane—the internal tympaniform membrane. Surrounding the syrinx is a single interclavicular air sac. Pressure in the interclavicular air sac pushes the thin tympaniform membranes of the syrinx into the bronchial air space. A needle puncture of the interclavicular air sac prevents buildup of the pressures needed to move the tympaniform membranes, thereby rendering a bird voiceless. Recent work indicates that vibrations of the labia, not the tympaniform membranes, determine the basic characteristics of the sounds produced in the syrinx (Suthers and Margoliash 2002). The opposite sides of the syrinx can produce different songs simultaneously (Box 8–3).

Specific muscles, logically called syringeal muscles, control syrinx action during song production. Species that lack functional syringeal muscles, such as ratites, storks, and New World vultures, can only grunt, hiss, or make similar noises. Most nonpasserine birds have two pairs of narrow muscles on the sides of the trachea above the syrinx; these muscles are called extrinsic muscles because they originate outside the syrinx. Oscine songbirds have more elaborate musculature—as many as six pairs of in-

trinsic syringeal muscles in addition to the extrinsic muscles (Figure 8–7). The intrinsic syringeal muscles originate within the syrinx and insert onto the bronchial rings, the internal and external tympaniform membranes, and the syringeal cartilage. Despite the help of elaborate syringeal muscles, the songs of oscines are not predictably more complex than those of birds with simpler syringeal muscle arrangements.

The syrinx is a complex organ, but the production of vocalizations is even more so. Intricately coordinated are the vocal centers and neural pathways of the brain (see page 227), the thoracic and abdominal respiratory muscles, the diameter and length of the trachea, the mouth and bill, and the opposite sides of the syrinx itself. Vibrations of the syringeal membranes, especially the labia, combined with filtering of the source by the vocal tract explain all types of avian vocalizations (Baker 2001). The tone and pitch of a sound depends on the precise tensions of the labia and their vibrations (Suthers et al. 1999).

For many years, the central nervous system was assumed to control most of the intricate details of bird song. However, intrinsic mechanical properties of the syrinx combined with regulation of airflow by the respiratory muscles also contribute strongly to the structure of bird songs (Goller 1998; Fee et al. 1998). Contractions of thoracic and abdominal

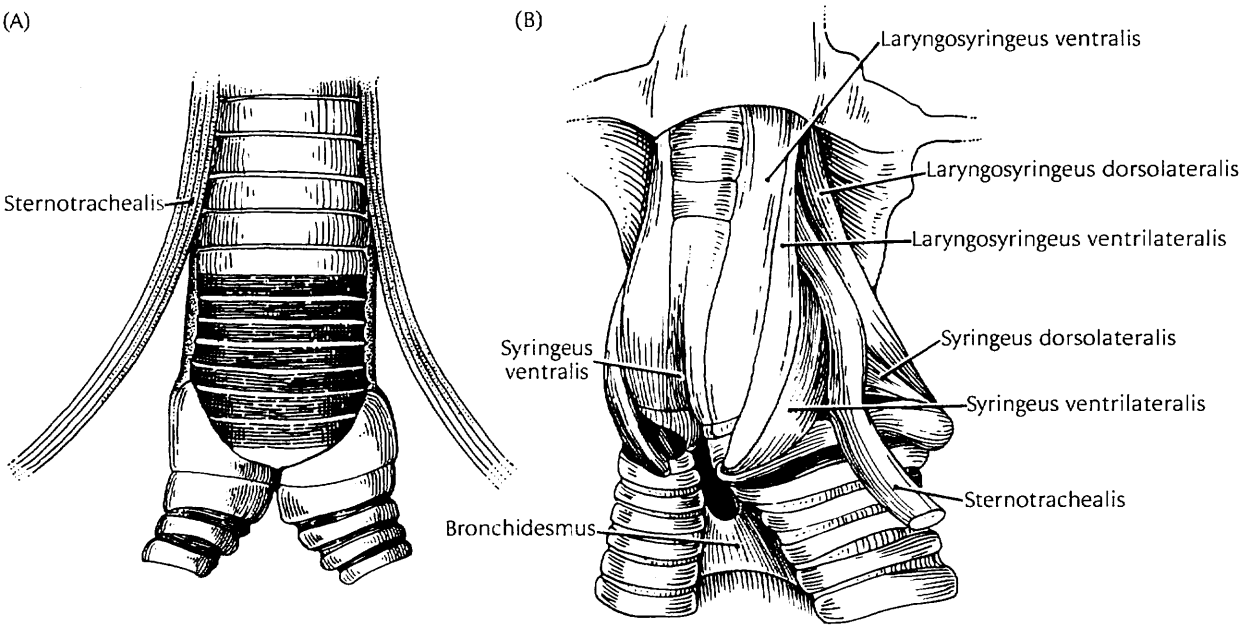
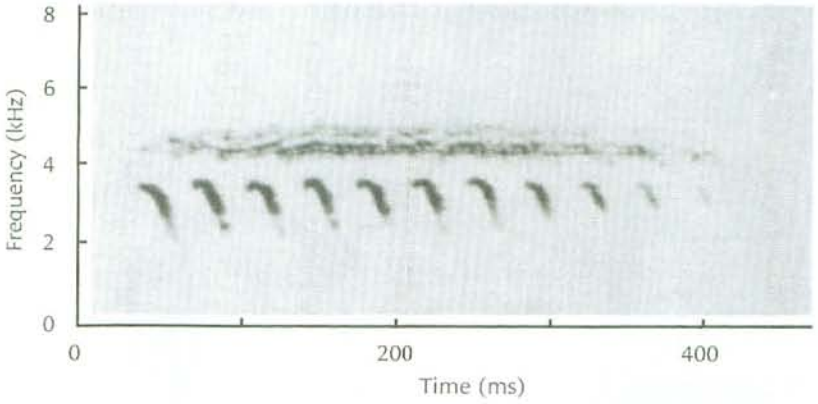


FIGURE 8–7 Simple and complex syringeal musculature. (A) The simple tracheal syrinx of the Chestnut-belted Gnateater, a suboscine passerine bird of South America; note the single pair of extrinsic syringeal muscles. (B) The elaborate tracheobronchial syrinx of the Little Spiderhunter of Southeast Asia, with six pairs of intrinsic syringeal muscles. The bronchidesmus is a wide band of tissue that ties the two bronchi together. [*After Van Tyne and Berger 1976*]

BOX 8–3

BIRDS HAVE TWO INDEPENDENT VOICES

The syrinx consists of two halves that are controlled separately and can produce different, complex songs alternatively or simultaneously (see Suthers et al. 1999; see also Figure 8–6). In addition to having different frequency content, the notes produced by the dual voices can be modulated independently of one another. The two sources can also be coupled to produce a single, complex sound (Nowicki and Capranica 1986). First discovered in an analysis of the song of a Brown Thrasher, the phenomenon of two independent voices has since been reported for many diverse birds, including grebes, bitterns, ducks, sandpipers, bellbirds (Cotingidae), and songbirds (Miller 1977). One side of the syrinx produces most of the songs of some species, such as the canary. Specifically the left side has larger muscles and produces 90 percent of the songs. In other species, such as the thrasher, the two sides contribute equally to song production. The left and right sides switch to produce successive notes of the complex song of the Brown-headed Cowbird. In Northern Cardinals, the left side of the syrinx produces fundamental frequencies below 3.5 kilohertz, whereas the right side produces fundamental frequencies above 4.0 kilohertz.



The Wood Thrush can sing a duet by itself, by using two separate voices. Shown here is a sonogram of the final double phrase of the song. One voice sings a continuous series of complex, modulated phrase elements while the other voice sings a steady trill at a lower frequency. [*From Greenewalt 1968*]

muscles force air from the main air sacs through the bronchi to the syrinx. Rapid-fire control of airflow by the respiratory system determines the temporal pattern of a vocalization. Syllables of expired air are spaced by short pauses of inspiration. Birds with long, sustained songs such as the Common Grasshopper Warbler breathe and sing simultaneously by using shallow "minibreaths" (Brackenbury 1982). Fast series of syllables can result from fast pulses of expiration without breaks for inspiration. For example, rapid vibrations of the abdominal muscles (as many as 50 cycles per second) produce the trilled whistles of young chicks (Phillips and Youngren 1981).

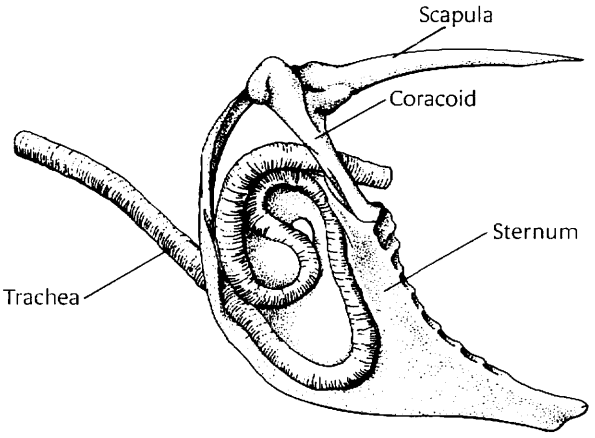


FIGURE 8–8 A crane's elongated trachea is coiled inside the sternum. [*After Grassé 1950*]

Sounds produced by the syrinx can be filtered and modified by changes in the length and diameter of the trachea (Nowicki 1987). The loud, rich, resonating, trumpetlike calls of swans, cranes, some curassows, and guineafowl are due in part to an unusually long trachea that is coiled in the body cavity or in the bony sternum itself (Figure 8–8). Whether the trachea modulates sounds produced by the syrinx was once in dispute.

Critical experiments with the use of a helium atmosphere then proved that it did. Bird song, like human speech, is the result of rapid, coordinated output of two or more motor systems acting in concert (Nowicki 1987). The clever experiments were based on the fact that sound travels faster in a helium atmosphere than in a normal nitrogen-based atmosphere, with predictable effects on frequency and harmonic structure. (Recall your own high-pitched voice after having inhaled helium from a balloon.) The helium experiments revealed that a bird's vocal tract filters the harmonic spectrum produced by the syrinx and concentrates the energy at particular frequencies. Furthermore, a bird actively controls the filtering process by varying tracheal length, by constricting the larynx, and by flaring or closing its throat and its beak. The rapid beak and throat movements of singing birds help to produce and purify the tones of their complex songs by suppressing low-frequency harmonics (Suthers et al. 1999).

Roles of the Central Nervous System

The neural pathways of the brain that control song memory and production are now mapped in detail. Bird song is controlled through two primary pathways that connect key parts (nuclei) of the brain and, in turn, the syrinx (Figure 8–9).

One pathway—the main descending motor pathway—regulates song production. Stimulation of the motor neurons in this pathway contracts

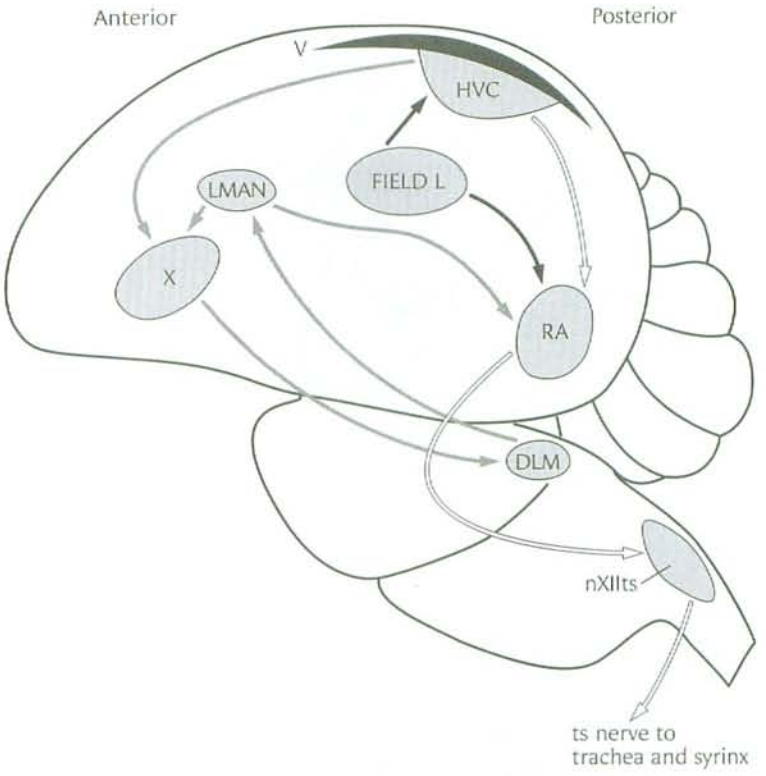


FIGURE 8–9 A sagittal section through the brain of a songbird, showing the two main pathways that affect song production and development. The main descending motor pathway (white arrows) controls song production. The anterior forebrain pathway (gray arrows) controls song learning and recognition. [*After Nottebohm et al. 1990; see also Brenowitz and Kroodsma 1999*]

The descending motor pathway transmits nerve impulses from the high vocal center (HVC) of the hyperpallium layer of the forebrain to the robust archopallial (RA) and intercollicular nuclei, then to the tracheosyringeal motor (hypoglossal) neurons (nXIIts) in the hindbrain, and, finally, through the tracheosyringeal motor neurons to the syringeal muscles that control the syrinx. A variety of calls, some recognizable and some abnormal, can be evoked by electrical stimulation of the RA nuclei. Destruction of the HVC nuclei renders a songbird mute.

The anterior forebrain pathway connects the HVC to area X, which plays a critical role in the crystallization of male song, with feedback loops to the auditory centers of the forebrain (LMAN) and midbrain (DLM) as well as the motor pathway through the RA nuclei. Field L is the auditory region of the forebrain. It projects (black arrows) to the HVC and the RA nuclei.

the syringeal muscles that control the tensions and the dimensions of the vocal tract.

The other pathway—the anterior forebrain pathway—plays a central role in song recognition and song learning in oscine passerines. The anterior forebrain pathway unites the song motor-control centers with the auditory centers in the forebrain and midbrain. It may also play a secondary role in the actual control of song production (Kao et al. 2005). One discrete nucleus, LMAN (see Figure 8–9), in this pathway appears to con-

trol the learning of songs by the young Zebra Finch, a small cage bird commonly used for such research. Lesions made in this nucleus in a young bird permanently impair its song-learning abilities (Bottjer et al. 1984). However, lesions made later in adult birds do not affect the maintenance of song patterns.

Functional lateralization of the brain was once thought to be an exclusively human attribute, associated with extraordinary language abilities. Bird brains, as well as the syrinx, also are lateralized (see page 203). The left hemisphere of the forebrain controls bird song—specifically, learning and innovation in vocal repertoires. The right cerebral hemisphere assumes control of the functions of the left hemisphere only if the left hemisphere is damaged. The impairment of a young Atlantic Canary's song-control centers in the left hemisphere leads to the formation of an alternative set in the right hemisphere and the acquisition of a new song repertoire.

The amount of brain space that controls song is flexible. In particular, the development of brain tissue controlling song increases with the size of individual song repertoires (Brenowitz and Kroodsma 1999). Male canaries with large repertoires have larger song-control nuclei than do male canaries with small song repertoires. Populations of Marsh Wrens that differ in song-repertoire size also differ in the amount of brain space allocated to the high vocal song-control center (Brenowitz et al. 1994). Marsh Wrens in California learn three times as many songs as do Marsh Wrens in New York and have 40 percent larger volumes of the song-control nuclei. This difference in brain space and song-learning ability appears to be genetically controlled and related to the competition among males for mates—competition that is more intense in the West than in the East.

The song nuclei also wax and wane in size with the season in response to changes in the levels of the sex hormones that control them. The male hormone testosterone increases the length and branching complexity of dendrites, or receptor branches, of some neurons in the song centers (Alvarez-Buyalla et al. 1990). Experimental exposure to the sex hormone estradiol at an early age enlarges the sizes of the nuclei of the song centers and, in adult birds, increases their sensitivity to the sex hormones that stimulate singing during the breeding season (Gurney and Konishi 1980).

Learning to Sing

Only birds and a few mammals—whales, humans, and some bats—have the ability to learn songs or language. Among birds, learning guides vocal development in three known groups: oscine songbirds, parrots, and hummingbirds. The vocalizations of other birds—chickens and doves, for example, as well as flycatchers and other suboscine passerines—are inherited. When these birds are raised in acoustical isolation or are deafened before they hear their fellow birds sing, they nonetheless sing normal songs as adults. In contrast, songbirds listen to the songs of other individual birds and practice them in a series of well-documented stages

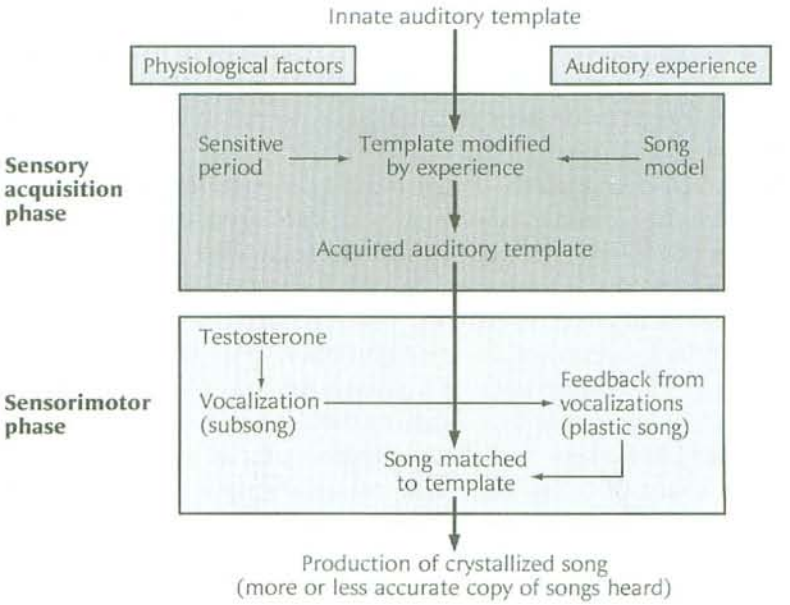


FIGURE 8–10 Stages of song acquisition by an oscine songbird. In the initial sensory acquisition phase, auditory experiences with external models or tutors refine the innate template during a physiologically based sensitive period. In the second, sensorimotor phase, practice and feedback mold initial subsong elements into plastic song, which is then refined into crystallized song by matching components to the template produced in the first phase. [*Courtesy of Susan Volman; after Slater 1989*]

of song development (Box 8–4, page 232). The stages can be grouped into two phases: (1) the sensory acquisition phase in which hearing song models is paramount and (2) the sensorimotor phase in which practice is paramount (Figure 8–10).

The early development of bird song provides one of the best working models of how a complex, learned motor skill develops (Brenowitz and Kroodsma 1999). Specifically, neurobiologists can track how specific parts of the brain's song system participate in the process of song development. Zebra Finches provide one example. Corresponding to the timing and detailed structure of normal song outputs of a male Zebra Finch are bursts of electrical activity in the neurons of one song-control center technically named the nucleus robustus of the arcopallium, or RA for short (see Figure 8–9). Similar patterns of electrical activity take place when the Zebra Finch is sleeping and apparently singing in its dreams. The details of the RA electrical activity while dreaming shift in the direction of the patterns linked to "improved" songs when awake. Sleeping Zebra Finches seem to practice songs in their dreams for future performances (Chi and Margoliash 2001).

Some virtuoso birds, such as Northern Mockingbirds (Figure 8–11), add new vocalizations to their repertoires throughout their lives. These "open-ended" learners often mimic other species' songs (see page 237). At the other extreme are "age-limited" learners, which acquire their songs

FIGURE 8–11 Northern Mockingbird.

mainly during a restricted critical learning, or sensitive, period at early age. Age-limited species differ in the timing and duration of their critical learning periods. For example, White-crowned Sparrows memorize song phrases that they hear when they are from 10 to 50 days old, whereas Chaffinches are receptive to song models for 10 to 12 months into the first breeding season, at which time first-year males have a chance to learn songs from more experienced males. Termination of the critical learning period of the Chaffinch corresponds to the rise of its testosterone level in the spring.

Isolation from the model songs of adults during the critical learning period permanently handicaps a young bird's future singing ability; it will never develop a normal song. Although individual birds isolated at an early age still sing, their songs are less complex, have fewer notes per syllable, and have less frequency modulation than normal songs. Nevertheless, the innate songs of isolated birds may resemble the normal songs of their species in the form, rhythm, and rough tonal quality of syllables.

During the second stage of song development—the silent period— the young bird stores syllables that it memorized during the critical learning period. Swamp Sparrows store memorized song syllables for 240 days (Marler and Peters 1981). When this period has elapsed, young sparrows start practicing by listening to themselves and matching some of their vocalizations to previously memorized syllables. Thus, the initial, sensitive perceptual phase of song learning is well separated from the later motor phase by a period of silence.

BOX 8–4

BIRDS WITH FIXED REPERTOIRES LEARN SONGS IN FOUR STAGES

Observations of the development of the singing behavior of hand-reared baby birds, as well as experiments on it, have revealed four key periods that influence adult songs.

1. Critical learning period The early period during which information is stored for use in later stages of learning. In most species, the critical learning stage lasts less than a year—sometimes much less.

2. Silent period The long period (as long as eight months) in which syllables learned during the early critical learning period are stored without practice or rehearsal.

3. Subsong period This practice period is analogous to infant babbling. It apparently bridges the gap between the perceptual and sensorimotor stages of vocal learning. The subsong period is a period of practice without communication; perhaps subsong is a form of vocal play. (See text for a discussion of subsong.)

4. Song crystallization The next practice period during which the young bird transforms plastic song into real song by selecting a few syllables from its unstructured repertoire, perfecting them, and then organizing them into correct patterns and timing. (See text for a discussion of plastic song.)

The practice stages begin with subsong—a long, soft, unstructured series of syllables and ill-formed sounds. Distinctly formed sounds begin to emerge, some of them recognizable as syllables heard during the sensitive period. Within a month or so, depending on the species, subsong develops into the first attempts to produce mature song. This so-called plastic song contains only rudiments of the final structure. In a matter of weeks, during what is called "song crystallization," the young bird transforms plastic song into final form. Not all syllables learned or practiced are included in the final performance. In their final songs, young male Swamp Sparrows use only one-fourth of the syllables that they learned and practiced in the earlier phases of song development (Marler and Peters 1982b).

Auditory feedback is essential for song development in these species. No oscine songbird produces a normal song if it has been deafened before song crystallization begins. In the deaf bird, recognizable structural entities seldom appear and, when they do, they deteriorate quickly. Frequency modulation of syllables also is poor in deaf birds; they do not repeat sounds accurately. Experimental deafening of male White-crowned Sparrows during their silent period (70–100 days of age) erases their original song memory or interferes with a necessary matching process. Songs of such males do not differ from those of males that have been deafened before they hear model songs. Deafening after song is crystallized, however, has little effect.

A young bird must select appropriate song models with precision from a rich sound environment. Song learning is mediated and constrained by inherited sensory templates—neural filters that pass only particular sounds with species-typical features.

The filters screen out irrelevant sounds, such as those made by insects, frogs, waterfalls, and trains, and respond to appropriate song models. Even more exacting, the hearts of young Song Sparrows actually beat faster the first time that they hear the song of their species, but not when they hear the song of another kind of sparrow.

Comparisons of song development in Swamp Sparrows and Song Sparrows illustrate this aspect of song learning. A Swamp Sparrow's song is a repetitious trill of a single syllable, whereas a Song Sparrow's song uses a pattern of several complex syllables. To discover how the young of these species learn their own songs, despite the fact that they grow up hearing both songs, Peter Marler and Susan Peters (1989) isolated nestling sparrows and then exposed them to taped songs during the critical learning period. Syllable structure is the key to song learning for young Song Sparrows, whereas temporal pattern is the key for young Swamp Sparrows. Swamp Sparrows do not learn the Song Sparrow song, because they

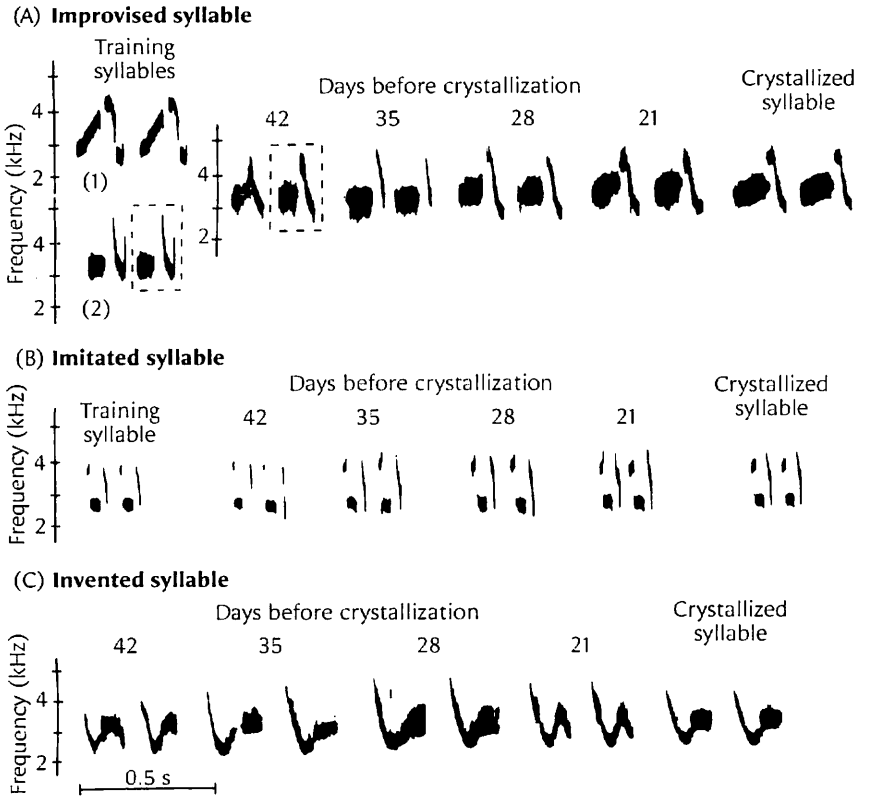


FIGURE 8–12 Development of three Swamp Sparrow song syllables by means of (A) improvisation, (B) imitation, and (C) invention. Improvisation entailed changing training syllable A2 to a new syllable by combining the second note of training syllable A1 with the first note of syllable A2. The invented syllable was unlike any training syllable but proceeded through the same developmental stages as those of the improvised and imitated syllables to a final crystallized form. [*From Marler and Peters 1982a*]

cannot learn its syllables. Song Sparrows do not learn the Swamp Sparrow song, because they cannot learn its temporal pattern.

Learning and imitation are not the only elements of song acquisition. Individuality is important, too. Young birds transform and improvise as they develop individual signatures in their songs. They systematically transform memorized themes or mix syllables from several models into unique themes. A single song of the Swamp Sparrow, for example, may contain invented, improvised, and imitated elements (Figure 8–12). However, the creative sparrow rarely breaks up a series of notes that constitute a syllable. The syllable itself may be a natural perceptual unit, designed to map readily onto a template of acceptable patterns of sound production (Marler 1981; Baptista 1999).

We don't know exactly how this template works or even where it resides in the song system of the brain. Studies of how young White-crowned Sparrows assemble their songs in the proper sequence, however, have been sources of an important insight (Rose et al. 2004; Margoliash 2004). The process of song development in White-crowned Sparrows is one of the best known, in part because this species produces song dialects that differ strikingly among local populations in California (see next section). Like other age-limited species, the fledgling White-crowned Sparrow memorizes songs when it is between 20 and 70 days old. The basic song of all populations consists of an initial whistle followed by four or five distinct phrases (Figure 8–13). Phrase-sequence information, it turns out, is a key part of the template for song development. Young sparrows assemble a complete song when tutored with just pairs of phrases—that is, without ever hearing a full normal song. When they hear the phrase pairs AB, BC, CD, and DE in that order, they construct a final song rendered correctly as A-BCDE, where A is the standard initial whistle. Conversely, if they hear the phrase pairs BA, CB, DC, ED in that order, their final song inverts to EDCB-A.

The Common Nightingale of Europe is renowned for its vocal virtuosity and its long solo singing bouts often late at night. Each male has roughly 200 distinct and discrete song types. It sings them in long continuous strings of successively different songs (Todt and Hultsch 1999). Which sequence packages it sings depend on social context—for example, daytime group singing versus nighttime solo singing—and which other males countersing. They learn most of their songs from 15 to 90 days of age. Individual songs are the unit of learning, which the young nightingale assembles early on as packages that are probably limited in length to constraints of its short-term memory. Interactions between males are defined by exchanges of appropriate packages. Similarly, sentences of human language are constrained by short-term memory to interactive packages of reasonable length.

Most of the classical studies of song learning by young birds explored responses to recorded song by birds raised in isolation. One study revealed that White-crowned Sparrows learned their songs better from other White-crowned Sparrows—that is, live tutors—than from tapes (Baptista and Petrinovich 1984). Through field studies, young birds were then dis-

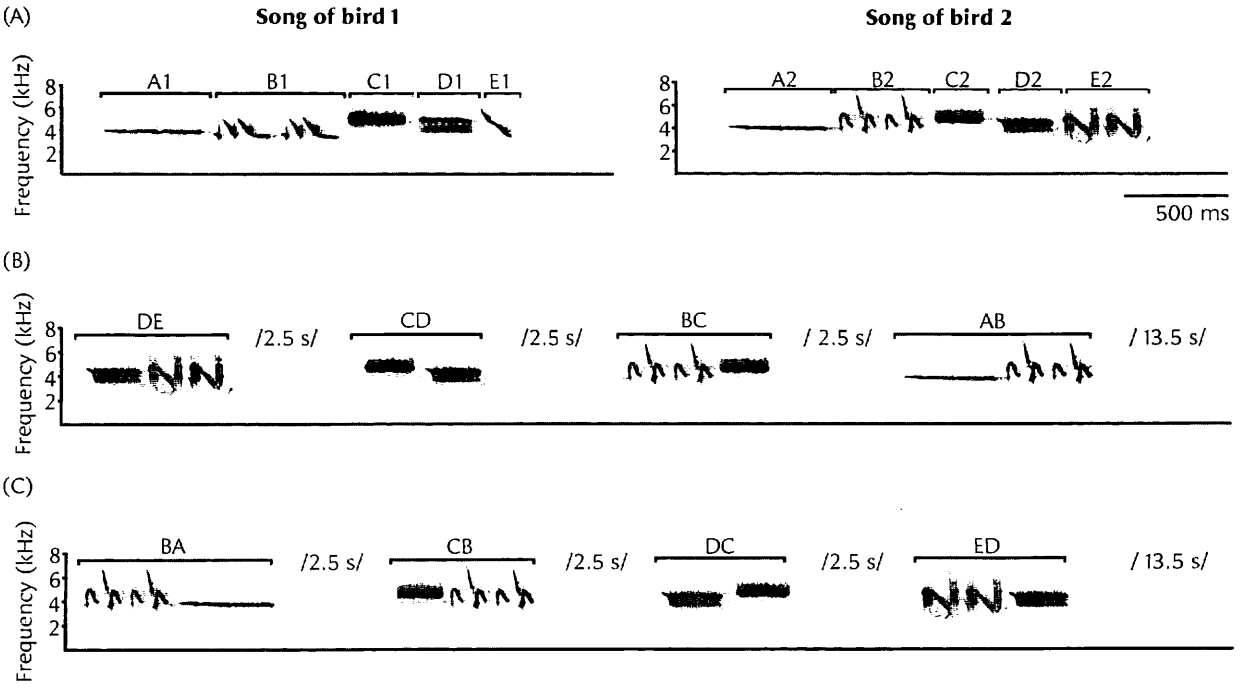


FIGURE 8–13 Sound spectrograms of (A) the full songs of two White-crowned Sparrow and (B and C) the tutor models of syllable combinations. In these experiments, the young sparrows assembled a full song from only the paired syllable combinations used for tutoring. Note the long introductory whistle designed by A1 or A2. [*From Rose et al. 2004, with permission from Nature*]

covered to prefer to learn songs shared by several male tutors. The process of song acquisition by young, free-living Song Sparrows, for example, follows three main rules: (1) sample the repertoires of at least three or four adult neighbor tutors, (2) preserve the identity of the song tutor and its song type, and (3) learn with priority the song types shared among tutors (Beecher 1999). These rules lead naturally to the formation of local song dialects.

Dialects

Bird songs can vary within a species from one hilltop to the next or from one region of the country to another. Copying the vocalizations of parents or neighbors leads naturally to regional dialects—local variations in syllable structure or delivery patterns, quite like the local accents of humans. Carolina Wrens in Ohio, for example, sing faster than those in Florida. Bewick's Wrens in California, Arizona, and Colorado each have distinct song patterns (Figure 8–14). The local dialects of the handsome White-crowned Sparrow on the central California coast are restricted to areas of only a few square kilometers. Dialects may be stable and long-lived.

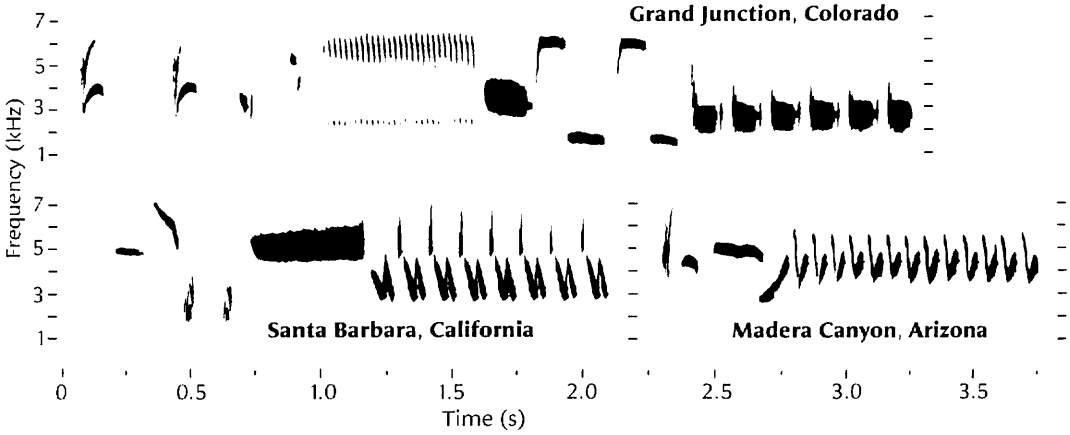


FIGURE 8–14 Song dialects: Bewick's Wrens sing strikingly different songs in Colorado, California, and Arizona. [*From Kroodsma 1982*]

The song themes in one well-known dialect of White-crowned Sparrows in California, the Berkeley dialect, have persisted for at least 60 years (Payne 1999).

Patterns of geographical song variation may simply reflect recent history. New song traditions arise when young birds colonize new areas and start a local culture of song forms. More interesting, perhaps, is the choice of song models and tutors that define local themes. Most notably, song dialects arise when young males imitate their older neighbors as a way of increasing their personal success. In southern Africa, young males of the promiscuous and brood-parasitic Village Indigobird increase their chances of attracting females by mimicking the song details of the dominant males that do most of the mating in a local area (Payne et al. 2000). In southern Michigan, first-year male Indigo Buntings copy the song of an established neighbor and thereby increase their chances of holding a territory and pairing with a female (Payne 1999). The details of the songs that define a neighborhood of Indigo Buntings undergo steady change or evolution through improvisation and as a result of the immigration of young birds with new songs. Songs that are matched by yearling males persist in the population three times as long as a male bunting does. The half-life expectancy of a copied song over a 15-year period was 4.23 years compared with 1.33 years for the average individual male bunting (Payne 1999).

The changing song traditions of birds are a form of cultural evolution, inasmuch as they are traits passed from one population or generation to the next by learning, with parallels to human language and other cultural traits (Lynch 1999). Cultural traits, including bird songs, can be passed vertically from parents to offspring, horizontally between unrelated individual birds or populations of the same generation, or obliquely, between unrelated individual birds of successive generations. All three modes of transmission are found for songbirds. Oblique transmission, as is the case

from unrelated neighbor to yearling Indigo Buntings, may be the most common mode in songbirds.

If song traits were linked to specific genes, then song dialects could cause local populations to diverge in other traits and perhaps even to speciate. There is no such (vertical) transmission of song traits from father to son in Indigo Buntings and thus no coevolution of song and genes. But song learning and transmission are vertical for the Medium Ground Finch, a species of Darwin's finches found in the Galápagos Islands (Grant and Grant 1995). Young males learn their single, structurally simple song from their fathers. They pass it in turn to their sons as a strictly cultural trait that drives species recognition and mate choice. Females are faithful to the songs of their species. On rare occasions, a male may mistakenly learn the very different song of the Cactus Finch, in which case it will be picked as a mate by a female Cactus Finch and produce hybrid offspring. The rare mistakes document the importance of song in mate choice and definition of the species.

Vocal Mimicry

Roughly 20 percent of the passerine songbirds worldwide practice vocal mimicry. Many of these birds are open-ended learners. They enlarge their repertoires by imitating the calls of other species. The most renowned vocal mimics include the Northern Mockingbird, Common Starling, Marsh Warbler, Australian lyrebirds, bowerbirds, scrubbirds, and African robin-chats. Some of these species imitate human-made sounds. In Australia, a variety of species now imitate cell phones, and the versatile lyrebirds imitate the buzz of a chain saw, the roar of a motorcycle, and even the clicks of a camera.

Male Northern Mockingbirds have repertoires that can exceed 150 songs, which both change from year to year and increase in number with age (Derrickson and Breitwisch 1992). Mockingbirds enhance their repertoires by imitating other birds, the calls of frogs and insects, and car alarms. One Northern Mockingbird can imitate dozens of different species, broadcasting in sequence the songs of the American Robin, Blue Jay, Northern Cardinal, and a variety of other common species of the eastern United States. In Texas, mockingbirds broadcast the calls of Bell's Vireos, Great-tailed Grackles, and Dickcissels, among others. Some mockingbirds imitate species found hundreds of kilometers away. For example, Jim Tucker of Austin, Texas, was surprised one morning to hear a mockingbird imitate a Green Jay, a species that is found only in the Rio Grande valley 500 kilometers to the south. Was this song learned directly from a Green Jay in the Rio Grande valley or was it passed northward through a series of mockingbird generations?

Migratory species may have international repertoires. Marsh Warblers, among Europe's most versatile vocal mimics, spend much of the year in Africa. Although they imitate some European species, most of the songs broadcast by Marsh Warblers are those of African birds heard during

migration and on the wintering grounds (Dowsett-Lemaire 1979). Territorial male Marsh Warblers may thus inform potential mates where they spend the winter. It could be to a female's advantage to pair with males adapted for wintering in the same part of Africa as she does and thus to produce young with similar tendencies.

Songs and Mates

Song repertoires enhance a male's attractiveness to females and his ability to compete with neighboring or rival males. Winning vocal duels is one route to local dominance (Box 8–5). Territorial songs signal to potential rivals that the resident male is prepared to protect his exclusive use of that space and any associated females. When a territorial male Great Tit, for example, is removed from its territory, another male will take over within 10 daylight hours unless territorial song is broadcast from loudspeakers on the territory (Krebs 1977). When a song is broadcast, rival males take three times as long (30 daylight hours) to exploit the vacancy.

Inseparably coupled to the contests between males is advertisement to unmated females. Female attraction to territorial male song, as well as the use of this song to assay male quality, is the first step toward courtship and pair formation. Females sometimes respond directly to male song with either precopulatory trills or copulatory postures. Female Song Sparrows and Swamp Sparrows whose sex drives have been experimentally enhanced by the hormone estradiol will respond more strongly to songs of their own species than to alien songs. They discriminate between the two by recognizing distinctive syllable structures and patterns of syllable delivery (Searcy and Marler 1981).

Regular vocal communication increases the coherence of social groups and strengthens the pair bond between mates. Birds vary in the loudness

BOX 8–5

BOTH BIRD VOCALISTS AND HUMAN FIDDLERS HAVE TECHNICAL DUELS

Large song repertoires provide ammunition for vocal duels among competing males. Marsh Wrens, for example, duel vocally for control of quality territories, which attract multiple females. Increased competition for limited marsh habitat in the western United States favored larger repertoires and related brain space. Using their large repertoires of songs that can be arranged in complex, varied sequences, neighboring males try to match one another's sequences or take the initiative in a duel (Kroodsma 1979). Leadership in the duels, which draws on both singing skill and repertoire size, promotes social dominance and increased reproductive success. Such avian vocal duels parallel guitar or banjo duels (as in the movie *Deliverance*) or dominance contests among human fiddlers to demonstrate technical mastery of their musical instrument. How well a fiddler plays and embellishes the traditional tune "Orange Blossom Special" quickly establishes his or her rank among the masters.

of their songs and calls and in the vocalizations that they use, depending on who else is present: the so-called audience effect. Zebra Finches are quite sophisticated in this respect, and other species of birds may be as well. The male Zebra Finch pays attention to the mating status of other pairs in its group or flock and adjusts its singing behavior toward its mate accordingly. Specifically, a male Zebra Finch distinguishes its mate's "distance" call from those of other flock mates and responds quickly and strongly to it when in the presence of other mated pairs, but not in the presence of unpaired finches (Vignal et al. 2004). Mate attentiveness and "guarding" is heightened in a reproductive social environment.

Some birds recognize one another and maintain their pair bond with distinctive vocal duets. Vocal duets are bouts of overlapping and precisely synchronized sounds by members of a mated pair or extended family group. To the human ear, the duet sounds like the song of a single bird. The thrushlike Rufous Hornero, the national bird of Argentina, duets with a strong rhythm in which the female punctuates the male's primary beat with one of her own (Laje and Mindlin 2003; see also Ball 2003). One female note to each three male notes is a common rhythm, but some pairs use different rhythms. As the male increases its song tempo, the female rapidly switches the counterrhythm of its perfectly synchronized notes in predictable sequences that would be impossible for a human musician.

At least 222 species in 44 families are known to sing duets (Farabaugh 1982). Most of them are tropical birds such as the Tropical Boubou, an African shrike that defends a year-round territory (Box 8–6). Their duets function both in maintenance of the pair bond and in joint defense of territorial space against encroaching neighbors. They even have a special loud and longer victory duet that they deliver after a protagonist slinks off in defeat (Grafe and Bitz 2004).

Can female birds really use the songs of males to assess the quality of their potential mates, choosing older, more experienced mates and thus increasing their own social or reproductive potential? The answer to this question depends, first, on whether better males have signature song features and, second, on whether females actually chose better males on the basis of those features. The evidence for both is increasing. For example, the elaborate songs of male Brown-headed Cowbirds vary in their potency, defined by how readily estradiol-treated females solicit copulation (West and King 1980; West et al. 1981). Male cowbirds, even those hand-raised in isolation, are capable of singing high-potency songs, but only the top-ranked dominant members of a group actually do so. If a subordinate dares to use potent vocalizations while displaying, it invites attack by the dominant male. As a result, subordinate males deliberately downgrade their vocalizations and wait for an opportunity to sing their best songs without risk. In addition, differences in these male songs distinguish regional dialects in the western United States. A female cowbird distinctly prefers the high-potency songs of a male singing in her home dialect (Freeberg et al. 2001).

Long songs and vigorous singing are preferred by the females of many species studied to date (Nowicki and Searcy 2005). They can also be valid

BOX 8–6

BUSH SHRIKES DUET WITH PRECISION

Each pair of Tropical Boubous, a kind of African bush shrike, develops a unique set of duetting patterns, which they use to keep track of each other in dense vegetation, to synchronize their reproductive cycles, and to maintain their territorial integrity (Thorpe and North 1966). Either member of the pair can initiate the duet. The respective note contributions are so well synchronized that few people realize that two birds, not one, are singing. A pair of Tropical Boubous increases the complexity of its duet patterns as the density of shrikes and, perhaps, the need for distinction increase.

Duetting bush shrikes respond to cues—preceding notes—in only a fraction of a second and with astonishing precision (Thorpe 1963). These reaction times can be measured quite accurately in the duets of the Black-headed Gonolek, a bush shrike with a simpler duet than that of the Tropical Boubou. The female gonolek responds to the male's lead "youck" with a sneezelike hiss. The average response time of one female was only 144 milliseconds, with a standard deviation of 12.6 milliseconds. Another female responded in 425 milliseconds, with a standard deviation of 4.9 milliseconds. These values (12.6 and 4.9 ms) are exceedingly low. Human auditory reaction times, not nearly as precise, have a standard deviation of 20 milliseconds.

Tropical Boubou, an African bird well known for its precision duets.

indicators of male quality. Female House Finches prefer long songs delivered at fast rates, which indicate a male's energy reserves (Nolan and Hill 2004). In another study, female Common Starlings preferred males with the strongest immune systems, which would be valuable to pass on to her offspring (Duffy and Ball 2002). How do they assess the immunocompetence of males without checking blood chemistry with laboratory equipment? Simple solution: males with the strongest immune systems are also the best singers, preferred by females because they deliver the longest songs and sing most frequently.

Female songbirds tend to prefer males with larger and more varied song repertoires; in turn, those males have greater reproductive success. Do large song repertoires somehow reveal superior male qualities? They do, in a way that brings us back full circle to the process of song learning by young birds. Recall that the size of the song nuclei in the brain correlates with repertoire size. The size of the song nuclei is subject to the allocation of energy and neural tissue invested in them during the development of the nestling bird. When stressed, for example, by food deprivation during periods of food shortage, poor parental care, or laboratory manipulation, baby birds invest less into the growth of song nuclei. The smaller nuclei handicap both the accuracy and the quantity of song learning in subsequent weeks. In elegant experiments, Steve Nowicki and his colleagues at Duke University demonstrated that female Song Sparrows chose the superior songs and repertoires not damaged by early developmental stresses (Nowicki et al. 2002). Many other studies now support the so-called deprivation hypothesis of female preferences for song quality as a valid indicator of male quality (Nowicki and Searcy 2005).

In conclusion, oscine songbirds certainly, and probably birds generally, exhibit striking flexibility and advanced social uses of vocal behavior (Brenowitz and Kroodsma 1999). The neurons that compose their song-control systems change dynamically during development and with the season. The process of song acquisition itself varies from hard-wired, innate control to age-limited learning to open-ended learning. This process leads to local dialects and the adjustments of song features to local habitats and major environments. Also dynamic in real time are levels of song activity, the use of specific vocalizations, relationships to different individual birds, and habituation. Advanced and flexible communication is central to individual success not just during the breeding season but throughout the annual cycle.

Summary

Birds use vocalizations to mediate social interaction over long distances, at night, and in dense cover. The physical characteristics of vocalizations affect their information content and the effectiveness of their transmission through the environment.

The vocal virtuosity of birds springs from the structure of the syrinx, a sound-producing organ located at the junction of the two bronchi at the base of the trachea. Sound results from the vibration of a thin membrane, the tension and position of which are controlled by syringeal muscles and air pressure in the interclavicular air sac. Many birds can stimulate the two sides of the syrinx independently and can thus sing two songs simultaneously. The vocal tract, particularly the trachea, filters the sounds produced by the syrinx and can add resonant qualities to the calls of cranes, swans, and some birds-of-paradise, which have long, coiled tracheas.

The vocal repertoires of birds are among the richest in the animal kingdom. The loud broadcasts of territorial birds, which are among the most familiar vocal displays, convey information about the identity, location, and motivation of the singer, including ownership of territorial space. More varied song repertoires help to attract females and foster superiority in vocal duels between competing males. Included in the acoustical structure of songs are features used by birds for both species and individual recognition. Precise duets used by mated pairs also serve as distinctive vocal signatures. Vocal mimicry is one way in which some species increase the size of their vocal repertoires.

Avian vocalizations may be inherited, learned, or invented. Learning guides vocalization development in songbirds, parrots, and hummingbirds. Four stages of song learning are evident: an early critical learning period, a long silent period, and two practice periods, which include subsong production and song crystallization. Guiding this process are inherited templates of song characteristics. The templates screen out irrelevant sounds.

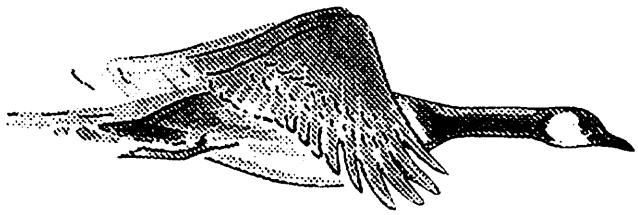
The formation of song dialects in local cultures is a possible consequence of the process of song learning. Dialects may be due to accidents of history and cultural change, may be used to enhance the reproductive success of young males, and may foster the evolution of local genetic differences among bird populations.

Song repertoires enhance a male's attractiveness to females and his ability to compete with neighboring or rival males and are thus subject to elaboration through sexual selection. The size of a song repertoire, the length of songs, the frequency of singing, and the quality of learned songs all help females to select superior males as mates.

PART 4

BEHAVIOR AND THE ENVIRONMENT

CHAPTER 9



The Annual Cycles of Birds

One swallow does not make a summer, but one skein of geese, cleaving the murk of a March thaw, is the spring.

[Leopold 1966, p. 19]

Birds face seasons of stress and seasons of opportunity that correspond to predictable calendar changes in day length, climate, and resources, especially food. The primary seasons are usually related to changes in temperature in the temperate zones and to changes in rainfall in the Tropics. Just to survive, much less to breed and otherwise function appropriately at different times of their year, an individual bird must change its appearance, its physiology, and its behavior. It must transition smoothly from one life-history stage to another, with advance notice and preparation so as to time each stage appropriately to the next set of environmental conditions (Jacobs and Wingfield 2000). Environmental and social cues activate internal endocrine management systems that orchestrate the sequencing of life-history stages, with contingencies for the unpredictable.

Each year, an adult bird invests time and energy above and beyond that required for daily survival into three main efforts: reproduction, molt, and, in some cases, migration. The conflicting demands of these efforts combine with seasonal resources and opportunities to define a bird's annual cycle (Figure 9–1). Tight scheduling, tradeoffs, and compromises are often required. Natural selection will favor those individual birds that schedule well and optimize the balance of their seasonal efforts.

This chapter first describes the basic components of avian annual cycles and then proceeds to the physiological clocks, called circadian rhythms, that control the avian annual calendars by synchronizing a bird's internal state with its seasonal environment. The photoperiod—the length of daylight—is an essential environmental cue for the clocks. It triggers activity in the brain and then the pituitary gland that leads to a cascade of hormonal controls of physiology and behavior. Then we more closely examine the timing, costs, and tradeoffs related to breeding, molt, and

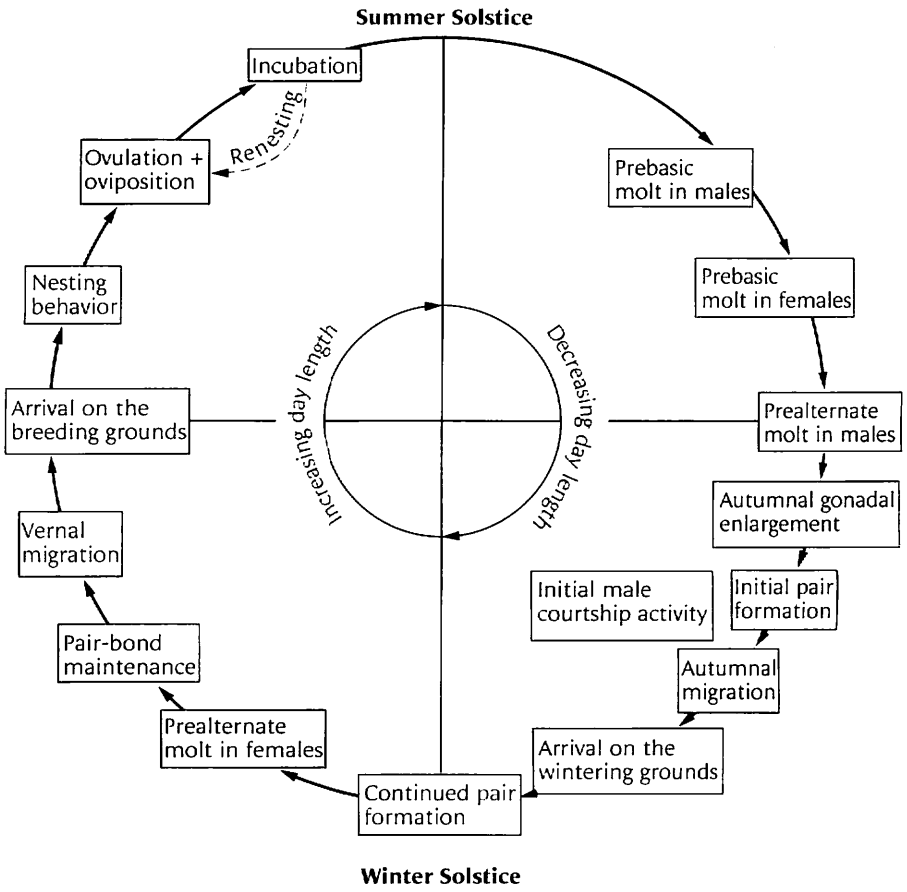


FIGURE 9–1 Annual cycle of the Mallard. Most individual birds attempt to breed when they are one year old. The terms prealternate molt and prebasic molt correspond to the prenuptial molt and postnuptial molt of Dwight's (1900) system of molt and plumage nomenclature (see Chapter 4). [*From Bluhm 1988*]

migration, including how birds handle stress. The chapter concludes with the effects of global warming on the annual cycles of birds.

Basic Annual Cycles

The simplest type of annual cycle and the typical year of permanent residents—birds that live in the same place year-round—present three main sequential tasks: breed, molt, and survive until the next breeding season. Consider, for example, the simple life of the Common Pigeon (Figure 9–2). The pigeons cycle between two life-cycle stages. As long as they have ample food and a mate, they nest until the young fledge (or until the mate is lost). Then they transition to the alternative, nonbreeding stage and remain in that stage until they have a mate in breeding condition and adequate food is available to initiate nesting.

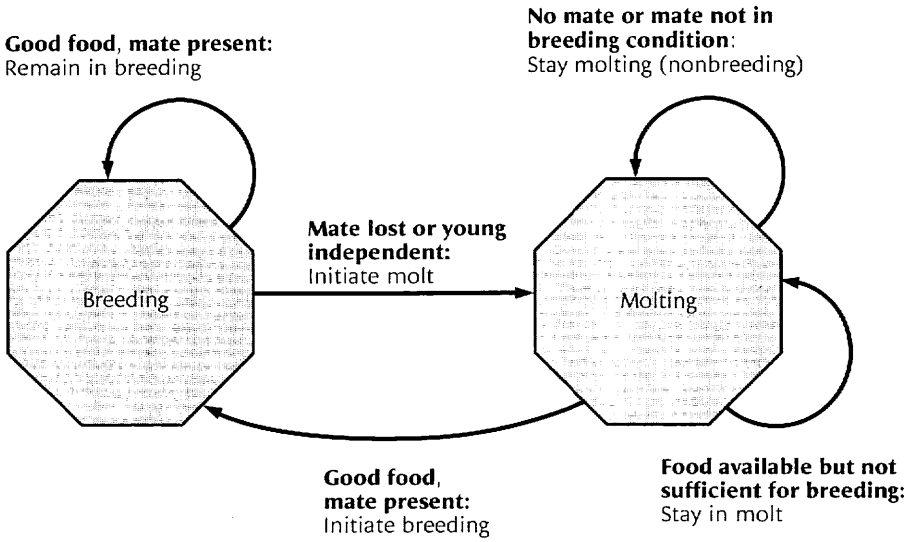


FIGURE 9–2 Simple life cycle of the Common Pigeon, which alternates between a breeding stage and a nonbreeding, or molting, stage. Arrows indicate conditions (boldface type) for remaining in one stage or switching to the other. Each condition is followed by a response to the change in environmental cues. [*After Jacobs and Wingfield 2000*]

The annual cycles of forest birds in equatorial Borneo also are simple ones. The temperature and day length stay the same all year. Small birds start to nest when the heavy rains begin in December (Fogden 1972). Adults start to molt shortly after the young have left the nest in May and continue molting until the beginning of the two-month "dry" season, when food starts to become scarce. When heavy rains resume and food supplies increase, gonads increase in size and the cycle repeats itself (Figure 9–3).

Similar cycles of reproduction and molt are typical of permanent residents of northern temperate localities, including Song Sparrows in Ohio, Black-capped Chickadees in Wisconsin, and Common Chaffinches in

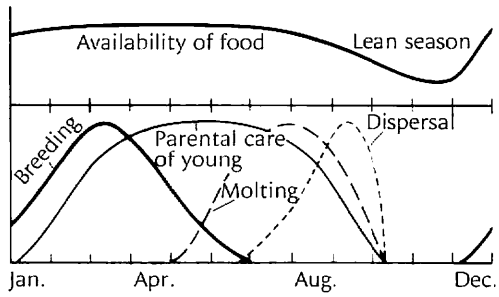


FIGURE 9–3 Birds have well-defined breeding and molting seasons, which coincide with the months of greatest food availability, even in the equatorial rain forests of Borneo. [*After Fogden 1972*]

Britain. After the quiescent winter months, sex hormones flow, gonads increase in size, and males proclaim their territories with conspicuous songs and, sometimes, brutal fights. Pair bonds are established or reaffirmed and mating takes place. Young hatch in May and June and generally reach independence by late July. Molt follows in August and September. At this time, young birds leave their natal territories, and families aggregate into well-organized flocks for the winter. Social competition for territories, food, and mates—all resources essential for reproduction next spring—may start in the autumn.

Migration adds a complicating challenge to the annual cycle. Major changes in physiology, body composition, and behavior take place (see Chapter 10). After they breed and molt, migratory birds generally gather in flocks and eat tremendous amounts of food, fueling themselves for their trips. To fuel their marathon flights, many species double their body mass with large stores of fat as fuel. As the date for departure approaches, they become restless after dark and then leave on a major trip to a distant wintering ground. Migratory preparations are repeated the following spring for the return north, where the cycle of reproduction, molt, and preparation for migration repeats. Many temperate-zone birds, especially those that migrate, molt twice a year, once after breeding and again in late winter or early spring.

Annual Cycles of the White-crowned Sparrow

The annual cycles of White-crowned Sparrows, including their physiological controls, have been studied in depth (Chilton et al. 1996). The White-crowned Sparrow breeds throughout northern Canada and from southern Alaska to central California (Figure 9–4).

The annual cycle of White-crowned Sparrows can be diagrammed as a series of specific stages activated by environmental cues (Figure 9–5). The stages are activated by internal (usually hormonal) responses that, in turn, trigger the transition to the next stage in the sequence.

Populations on the Pacific Coast differ in the extent of their annual migrations and in other aspects of their annual cycles. Those that breed in Alaska and in northwestern Canada (subspecies *gambelii*) are long-distance migrants that winter primarily in California, where they mix with winter flocks of the local nonmigratory White-crowned Sparrows (subspecies *nuttalli*). Members of another population (subspecies *pugetensis*), which breed on the coasts of Washington, Oregon, and British Columbia, also mix with *nuttalli* flocks in California during the winter.

White-crowned Sparrows from northern localities nest later in the spring than those from southern localities. The southern resident *nuttalli* come into breeding condition first, then the *pugetensis*, and, finally, the *gambelii* of the far north. Differences in the timing of the enlargement of the gonads and breeding activities characterize not only the three subspecies but also the geographical gradients of populations within each subspecies.

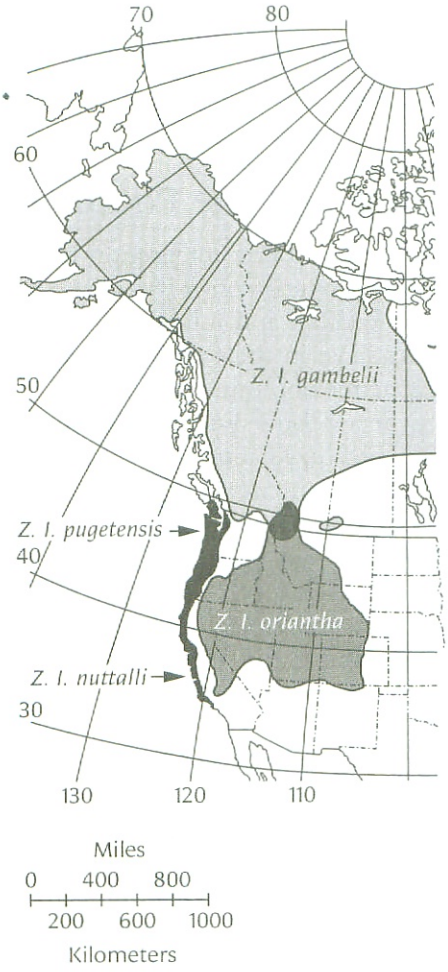


FIGURE 9–4 Breeding ranges of four western subspecies of White-crowned Sparrows, *Zonotrichia leucophrys*. The most northern races, *Z. l. gambelii* and *Z. l. pugetensis*, migrate to central California, where they winter with resident *Z. l. nuttalli*. The Rocky Mountain race, *Z. l. oriantha*, migrates south to Arizona and Mexico. [*From Cortopassi and Mewaldt 1965*]

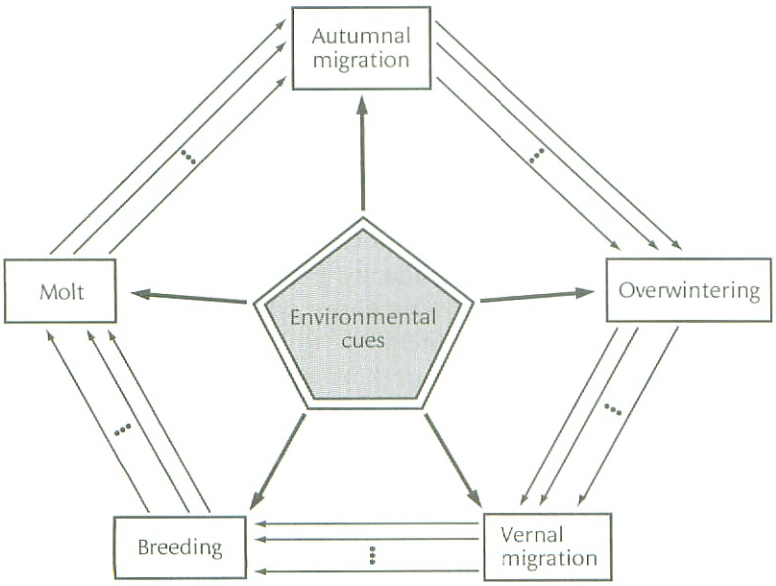


FIGURE 9–5 Annual life cycle of a migratory population of the White-crowned Sparrow (subspecies *gambelii*). Each seasonal stage (squares) is triggered by environmental cues (large arrows) and by the physiological changes of a preceding stage (thin arrows). [*After Jacobs and Wingfield 2000*]

Finally, some, but not all, of these White-crowned Sparrows molt in the spring before breeding. This extra "prenuptial" molt is known as the prealternate molt (see Chapter 4).

Circadian Rhythms and the Photoperiod

The annual cycle requires an orderly integration of behavior and physiology. A network of physiological controls regulate the schedules of reproduction, molt, sleep, feeding, and migration.

All plants and animals have in their cells biological clocks that release the hormones that regulate metabolism, reproduction, and behavior. Birds are no exception. Neuroendocrine systems synchronize cellular rhythms so that an entire bird is organized internally and appropriately synchronized with its periodic environment. In addition to regulating the daily activity and cycles of body temperature, these internal clocks measure day length itself and calibrate the sun compass by which birds navigate (see Chapter 10). They govern migratory restlessness, premigratory fattening, and egg laying. Some biological clocks, called circadian rhythms, match the daily 24-hour cycle of the Earth's rotation on its axis. Others, called circannual cycles, synchronize to the annual cycle of the Earth's revolution around the sun.

The triangle-shaped pineal gland, which is located on top of the brain, houses the biological clock in birds (Gwinner and Hau 2000; Sassone-Corsi 1998). Most diurnal birds have a well-developed pineal gland. This gland includes photosensitive cells, each having gene-based pacemakers that direct the rhythmic production of melatonin, the chemical that regulates daily rhythms in concert with daily light–dark cycles. Experimental removal of the pineal gland in House Sparrows causes normal 24-hour cycles to disappear. The pineal melatonin rhythm interacts with photosensitive cells of the hypothalamus of the lower midbrain and the retina of the eye, both of which also secrete some melatonin.

Circadian rhythms are a basic adaptation of cellular organisms to the 24-hour light–dark cycle of the planet (Farner 1980a). Twilight triggers a switch in physiology from diurnal to nocturnal systems. Every individual bird has an intrinsic rhythm approximately 23 hours in length in which body temperature, rate of metabolism, and level of alertness fluctuate in predictable ways. Because they are not exactly 24 hours in length, these internal cycles tend to depart gradually from real time, starting slightly earlier each day, unless they are somehow synchronized or entrained by external cues called *Zeitgebers*—literally, "time givers."

When Common Chaffinches are kept in constant dim light, their endogenous rhythms of activity and metabolic rate function in a period of about 23 hours and therefore drift about 1 hour per day (Figure 9–6). White-crowned Sparrows have a regular cycle of activity and sleep that is just under 24 hours long when they are kept in a dimly lit experimental cage. Natural, external light–dark cycles then synchronize the endogenous rhythm with the 24-hour cycle.

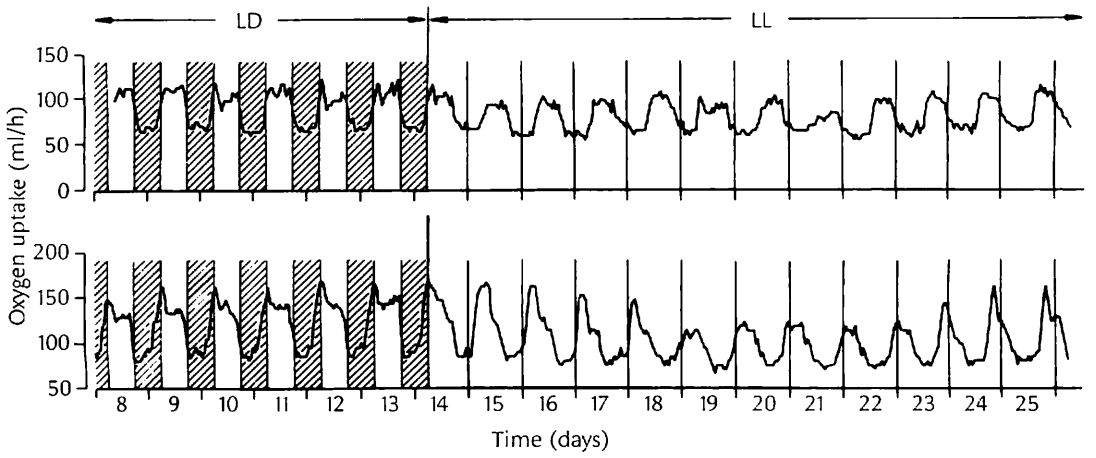


FIGURE 9–6 Common Chaffinches kept in a dimly lit environment have a daily activity cycle (measured here in milliliters of oxygen taken up per hour) of just under 24 hours. This experiment demonstrates that, under constant dim illumination (LL), the cycle drifts 1 hour of clock time unless it is synchronized by an external stimulus such as regular 24-hour light–dark cycles (LD). [*After Aschoff 1980*]

Endogenous rhythms control the annual cycles as well as the daily cycles of some birds. Self-sustaining circannual rhythms have a period of approximately one year. When captive Common Starlings, Garden Warblers, and Eurasian Blackcaps are kept in a constant daily environment of 12 hours of light and 12 hours of dark, they continue to come into breeding condition and molt in a predictable annual cycle (Figure 9–7).

The photoperiodic control system couples two kinds of information. Clock information from the internal circadian cycle enables the bird to measure day length by using time windows of photosensitivity. Environmental-light information stimulates neural receptors to translate day-length information into behavior. This two-part system allows birds to respond at the optimal time for reproduction, to synchronize reproductive function in mating pairs, and to terminate reproductive function—three fundamental requirements for control of the annual reproductive cycle.

Day length, or photoperiod, plays a key role in the control system that synchronizes the physiologies of individual birds with their environment. William Rowan (1929) pioneered research on the photoperiodic control of avian gonadal cycles. He showed that increases in photoperiod of only 5 to 10 minutes per day cause the testes of Dark-eyed Juncos to increase in size, an effect that was reversible and repeatable as many as three times between autumn and spring (Figure 9–8). The phenomenon of the photoperiodic control of gonad cycles has since been recognized in more than 60 north temperate bird species.

Molt and preparations for migration also are triggered by changes in day length and can be experimentally manipulated. Stephen Emlen (1969), for example, accelerated the annual cycle of Indigo Buntings, inducing

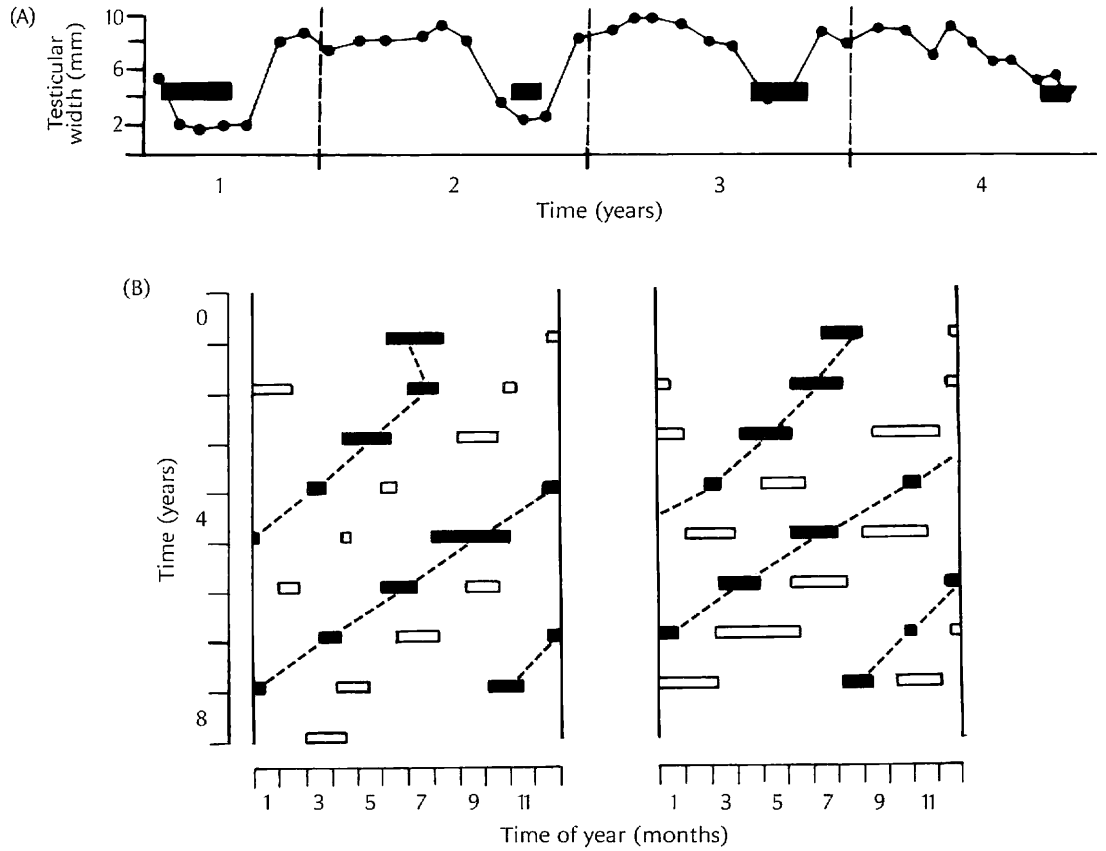


FIGURE 9–7 Circannual rhythms under constant photoperiodic conditions. (A) Rhythms of testicular width (curves) and molt (bars) in a Common Starling. The undamped oscillations in testes size and the intervals between successive molts deviate irregularly from a 12-month cycle. (B) Rhythms of summer molt (solid bars) and winter molt (open bars) in a Garden Warbler (*left*) and in a Eurasian Blackcap (*right*), both maintained in captivity for 8 years. Both molts occur progressively earlier each year because the birds have an internal rhythm with a mean period of about 10 months. [*After Gwinner 1977 and Berthold 1978*]

an extra molt into the year by suddenly increasing the length of the photoperiods to which captive birds were exposed.

The circadian rhythms include a limited period of photosensitivity each day. During this period, external light stimulates receptors in the brain, which in turn trigger a series of physiological reactions. As day length increases, so does the chance that there will be daylight during the photosensitive period (Figure 9–9). Not only does the chance of overlap, or coincidence, increase with day length, but the duration of the period of overlap also increases. The amount of overlap enables birds to measure day length. The "external coincidence" model was originally developed for plants, and we now have evidence of this model for many species of birds.

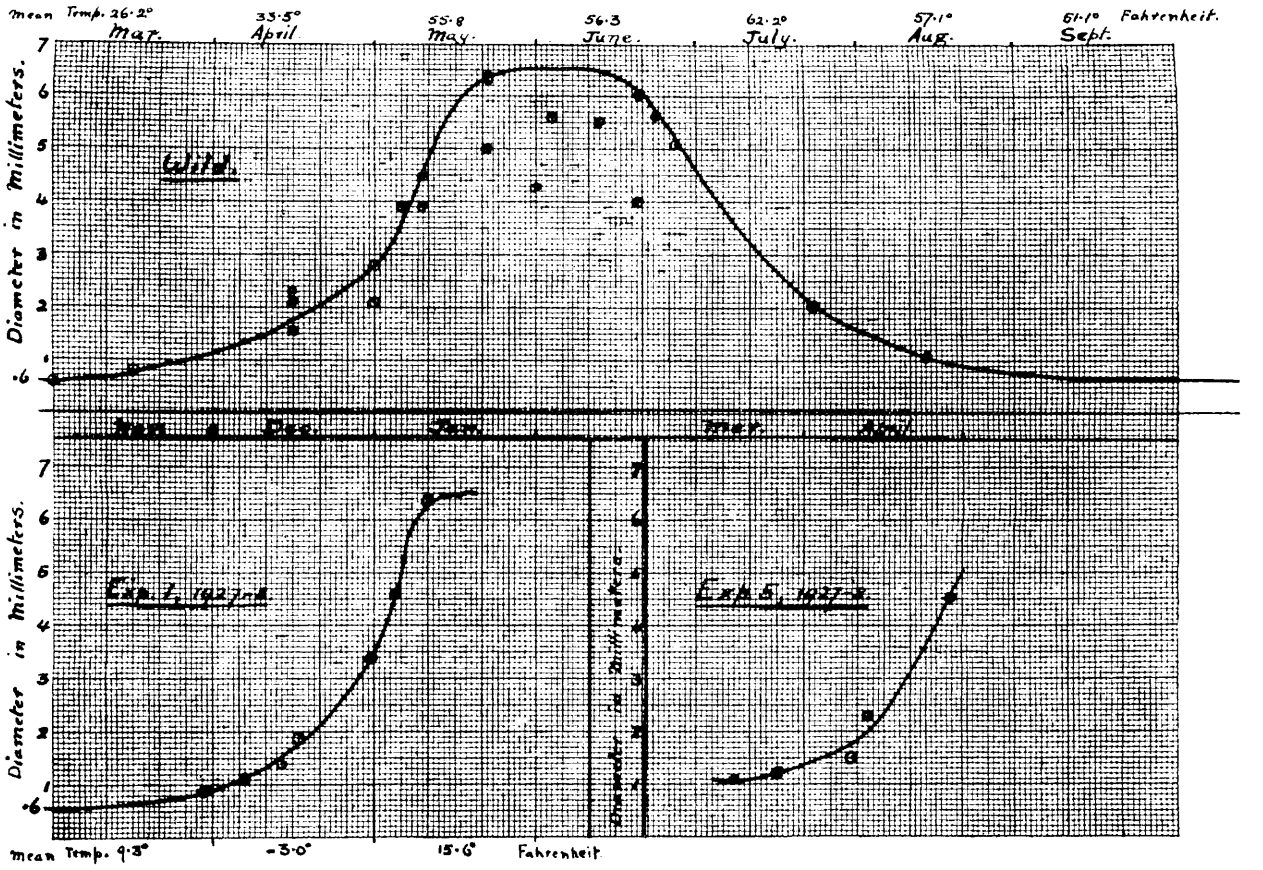


FIGURE 9–8 In the pioneer study of annual cycle control by photoperiod, William K. Rowan demonstrated that longer day lengths cause the testes of captive Dark-eyed Juncos to increase prematurely to full size in January (*lower left*) and again in April (*lower right*), instead of in May and June, as in wild juncos (*upper graph*). Mean temperature is the average air temperature in that month. [*From Rowan 1929*]

Birds monitor day length through special receptors in the hypothalamus of the brain as well as those in the pineal gland and retina. Longer day lengths induce gonad development and migratory behavior even in sightless birds. The light receptors of the White-crowned Sparrow, for example, lie in the ventromedial hypothalamus of the lower midbrain (Figure 9–10). The receptors are structurally unspecialized elements that are sensitive to extremely low light intensities such as those that directly penetrate brain tissues. Pinpoint illumination of the hypothalamic receptors by a single, thin light-conducting optical fiber induces both testicular growth and migratory behavior (Yokoyama and Farner 1978).

After stimulation of the photoreceptors, neurosecretory cells in the hypothalamus induce the release of neurohormones from the median eminence, the neural part of the pituitary (see Figure 9–10). The released neurohormones then induce the anterior pituitary gland to produce the hormones (see Table 9–1) that directly affect the activity of the gonads

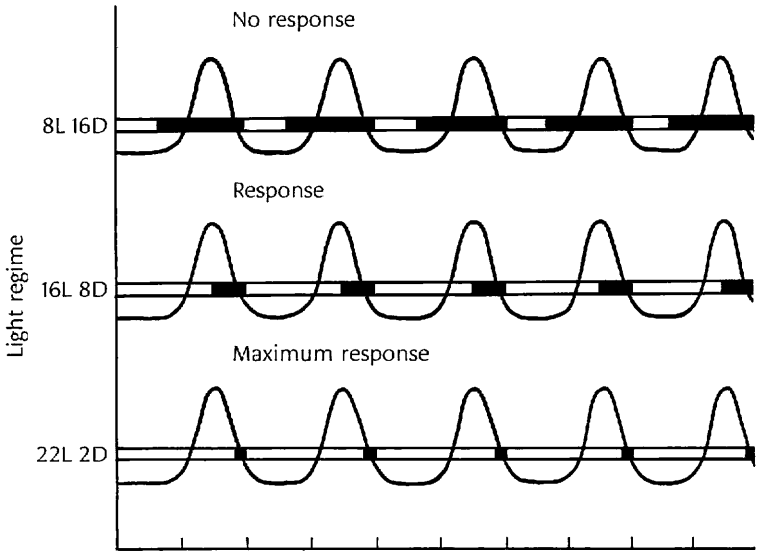


FIGURE 9–9 The external coincidence model suggests that day length is measured by the increased amount of time that daylight periods (open bars) coincide with the photosensitive phase of the circadian rhythm (oscillation peaks). Abbreviations: L, number of hours of light; D, number of hours of dark. Response was measured in terms of gonadal enlargement, which was greatest for a 22-hour light–2-hour dark cycle. [*From Farner 1980a*]

themselves. Thus, a series of neural and physiological events translate increasing day length into sexual activity.

The annual cycle of the White-crowned Sparrow outlined earlier illustrates the translation of seasonal changes in day length into appropriate behaviors. Increasing photoperiods during late winter and early spring

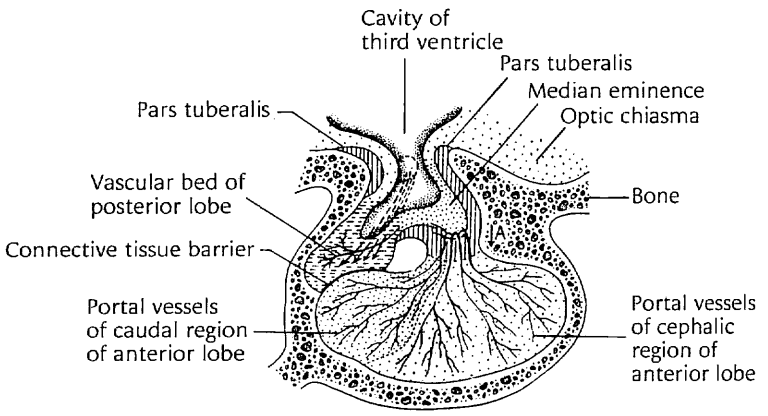


FIGURE 9–10 Avian pituitary gland and adjacent structures. Daylight stimulates special photoreceptors in the tuberal region (pars tuberalis) of the lower hypothalamus of the midbrain. Neurohormones are released in the median eminence and carried to the anterior pituitary gland through the hypophyseal portal blood vessels. They stimulate gonadal hormone production and, as a result, gonadal activity. [*From Höhn 1961*]

trigger events in the annual cycle. The longer days of early spring stimulate gonad development and then the spring (prealternate) molt and migration. Warmer temperatures, rainfall, and the springtime display behavior of other sparrows stimulate the final stages of gonad development on the breeding ground and, as a result, the increased secretion of sexual hormones. After the birds breed, the shortened days of late summer trigger the main (prebasic) molt.

The increasing day lengths of the spring also schedule, in advance, the fall light-insensitive, or photorefractory, period of the testis. After photoperiodic regulation of the annual cycle evolved, some additional safeguards and corrections were essential. Photorefractory physiology is one of them. The gonadal cycle normally concludes with a rapid collapse and reabsorption of gonadal tissue. Then follows the photorefractory period, during which long days do not induce gonadal regrowth. The photorefractory physiology of adults seems to be an adaptation for scheduling molt and migratory preparations during the favorable conditions of late summer by discontinuing reproductive activity while days are still long (Farner 1980b).

Finally, the very short days of early winter inhibit gonad growth and restore sensitivity to long photoperiods by terminating the refractory period. The cycle begins anew as day lengths increase in January. Short winter days are essential to the control of the annual cycle: the testes will not grow in response to the long days of spring unless a bird has experienced a prior period of short day lengths. Thus, White-crowned Sparrows stay in nonbreeding condition for several years when experimentally exposed only to long photoperiods.

Master Hormones

Much of the annual cycle, including specific behaviors in reproduction, molt, and migration, is directly controlled by hormones. Hormone production is headquartered in the lower midbrain, where the hypothalamus connects to the adjacent pituitary gland, directing it to release master hormones that direct the activities of specific organs (Table 9–1).

The Pituitary Gland

As instructed by the hypothalamus, the pituitary gland releases two master hormones that directly control gonadal development and function and that indirectly control many other aspects of the annual cycle. One of them—luteinizing hormone (LH)—stimulates the production of the male hormone testosterone by Leydig cells in the testes. In the female, it induces the ovulation of mature egg follicles as well as the production of the sex hormones progesterone and testosterone. The other master hormone—follicle-stimulating hormone (FSH)—stimulates sperm production in the testes of male birds and the initial development of egg follicles in female birds. Research on male birds has shown that increasing day lengths

TABLE 9–1 Principal hormones that govern the annual cycles of birds

Hormone	Abbreviation	Source	Role(s)
Adrenocorticotropic hormone	ACTH	Adrenal gland	Stress management Suppresses release of gonadal hormones Reduces resistance to disease (immunocompetence) Migratory restlessness
Estrogens			Progesterone release by pituitary gland Egg production in oviduct Secondary sexual morphology and brain function
Follicle-stimulating hormone	FSH	Pituitary gland	Sperm production by testes Egg-follicle development in ovary
Glucagon	None	Pancreas	Metabolism in liver and muscles Release of fatty acids to blood plasma Fasting
Growth hormone	GH	Pituitary gland	Normal posthatching growth Fat metabolism and synthesis Stimulates immune system
Luteinizing hormone	LH	Pituitary gland	Increases production of progesterone and testosterone Induces ovulation
Luteinizing hormone releasing hormone	LHRH	Hypothalamus	Production of LH and FSH by pituitary gland
Melatonin	None	Pineal gland	Circadian rhythm of cells throughout body
		Retina	Photoreception and neural transmission
		Gastrointestinal tract	Food utilization
Progesterone	None	Ovary	Induces ovulation
Prolactin	None	Pituitary gland	Production of crop milk in pigeons Incubation behavior and broodiness Photorefractoriness of testes
Thyroxine	T4	Thyroid gland	Metabolism and thermogenesis Growth and development Onset and pace of molt
Testosterone	None	Testis, ovary	Development of testes Secondary sexual morphology and brain function Ovulation in females

cause the hypothalamus to release luteinizing hormone releasing hormone (LHRH). As its mouthful of a name suggests, LHRH stimulates the pituitary gland to increase LH as well as FSH secretion. Pulses of plasma LH then travel throughout the bird's body and stimulate gonadal activity and a host of reproductive behaviors.

In addition to their role in reproductive behavior, endocrine hormones affect the timing and course of molt. The thyroid hormone thyroxine plays a primary role in the onset and pace of molt (Jenni-Eiermann et al. 2002). Its effects, however, are subject to the presence of the gonadal hormones—particularly the sex steroid hormones such as testosterone, which inhibit molt by suppressing the secretion of thyroid hormones (Hahn et al. 1992). Experimental injections of gonadal hormones into molting birds slow or even stop molt. As a result, nonbreeding and reproductively unsuccessful birds with lower amounts of gonadal hormones begin to molt earlier than successful breeders.

Other hormonal changes take place at the end of the breeding season. In addition to the gonadal hormones, thyroxin, glucagon, corticosterone, and growth hormone all play major roles at different times in the annual cycle. They are central to depositing and using fat as fuel for migration (Tsipoura et al. 1999; Hintz 2000). Among other effects, they stimulate ravenous feeding and fat deposition through the cascade of hormonal controls that starts at the hypothalamus–pituitary headquarters.

Managing Seasonal Stress

Central to seasonal adjustments and the interplay among hormones is the need for birds to manage daily and seasonal stresses. Regular measurements of the amount of the hormone corticosterone in tiny samples of blood plasma from living birds allow ornithologists to monitor the patterns of stress that birds experience at different times of year. Corticosteroid hormones are produced by the adrenal glands and are thus also called "adrenaline." Corticosterones mediate tradeoffs between individual survival and breeding success.

Corticosterone increases rapidly in response to acute stress events such as escaping from a predator, fighting for a territory, or being hungry. A rapid rise in corticosterone—the stress response—redirects a bird's behavior and physiology toward basic survival efforts such as looking for food and increasing the rate of food intake (Wingfield et al. 1995). Corticosterone levels stay high until the bird has offset the energetic challenge, perhaps by mobilizing energy reserves or escaping the source of stress. The return to normal baseline levels as soon as possible is important because continued elevation of corticosterones due to sustained or chronic stress suppresses other activities, such as reproduction. Among the effects, high levels of corticosterone suppress the release of gonadal hormones and reduce resistance to disease (immunocompetence). Thus, breeding activities, including parental care particularly, are not compatible with high levels of corticosterone in most vertebrate animals (Wingfield 2003). Increases in corticosterone during spring storms, for example, cause birds to stop breeding. Experimental treatments with corticosterone reduce territorial behavior and rates of feeding young.

Because of the potentially severe costs, acute stress responses affect many aspects of a bird's annual cycle, including habitat preferences and breeding behavior. Some birds, however, live in difficult, high-stress

environments that would seem to promote debilitating, high levels of corticosterone. Examples include desert birds, such as the Cactus Wren and Curve-billed Thrasher, which endure intense heat and aridity during the summer (Wingfield et al. 1992). At another extreme, species that breed in the Arctic, such as White-crowned Sparrows and American Tree Sparrows, face severe time and energy constraints imposed by the short summers and unpredictable weather (Holberton and Wingfield 2003). Do such birds avoid the tradeoff costs by moderating their corticosterone responses? They seem to do so. The desert-adapted wrens and thrashers suppress the classical adrenocortical response to stress during the hot summer season but reactivate it during the winter. Similarly, the Arctic-nesting sparrows exhibit low responses to stress throughout the season, though males are more sensitive to stress before the young hatch. Then they settle down to the unchanging low levels of their mellow mates. The mechanisms of this modulation are unknown.

Breeding Seasons

Guiding the evolution of the controls of seasonal behavior cycles have been such factors as the timing of adequate food supplies for both parents and their young, the availability of nest sites, the locations of favorable climates, and areas or times of low predation risk. These so-called ultimate factors tune the control systems to the best times for reproduction. However, they provide no guarantee against the vagaries of particular years. Drought or parasites may cause widespread nesting failure in some years. Birds, of course, cannot predict such disasters before starting to nest, but they can make last-minute adjustments.

Proximate factors are the external conditions that actually induce reproduction. Temperature is probably the most important modifier of annual gonadal cycles (Box 9–1). The correct habitat, new vegetation or abundant food, ritualized displays of aggression among neighbors, and social stimulation in general all help to consummate the final stages of gonad enlargement and ovarian development. The annual cycle of Pinyon Jays in New Mexico, for example, is closely tied to the availability of the seeds of the pinyon pine, one of their primary foods. Just the sight of green pine cones is sufficient to trigger gonadal enlargement and timely breeding by these jays (Ligon 1974). Similarly, Red Crossbills in the Rocky Mountains will nest in January and February, surrounded by snow, if conifer seeds, their primary food, are abundant.

Tropical nesting seasons last longer than those in the temperate zones. Favorable tropical climates permit nesting for 6 to 10 months, or even, in some cases, throughout the year. Although some individual birds can be found breeding in most months in the Tropics, nesting activity for most birds in lowland Costa Rica, for example, reaches a peak at the end of the dry season and early in the rainy season. Kingfishers are an exception, preferring to breed during the dry season when streams run shallow

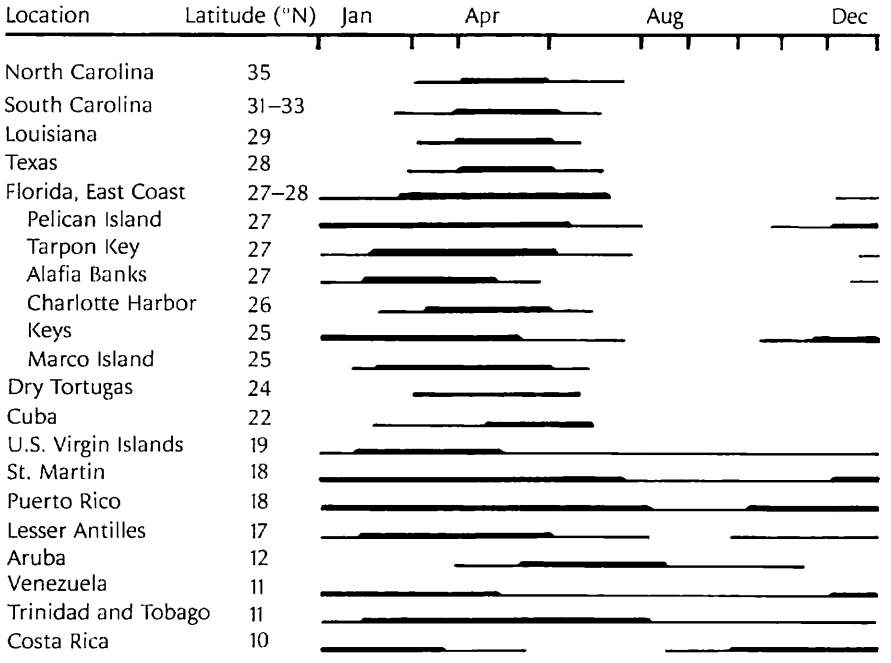


FIGURE 9–11 The time and length of the breeding season (line) of the eastern race of the Brown Pelican vary geographically as shown by the date that eggs are laid. The thicker part of the lines indicates the probable presence of eggs. [*After Schreiber 1980a*]

and clear, making fish easier to capture. Hummingbirds, too, nest at the beginning of the dry season when flowers begin to bloom.

Nesting seasons at temperate latitudes usually last from three to four months or less. In the high Arctic, where only a month or so is suitable for breeding, birds must start nesting immediately after arrival, and sometimes they gain a few days head start by reusing old nests.

Local populations of a species respond to local conditions. Nesting by Brown Pelicans, for example, is strongly seasonal at northern sites but is prolonged at tropical sites (Schreiber 1980a). Low water temperatures, which depress food supplies, appear to delay the onset of nesting at all sites. After food availability, the hurricane season is the second most important factor controlling the onset of nesting in these pelicans (this observation holds true for tropical seabirds in general). Pelicans nest irregularly throughout the year in the Caribbean and northern South America, more predictably after the hurricane season during the winter and spring in Florida, and from March to June in Louisiana and the Carolinas (Figure 9–11).

Timing of Migration

Precise arrival and departure dates are an impressive feature of migration. Every year, after their transequatorial migration, Short-tailed Shearwaters

BOX 9–1

PRECISELY WHEN DO AMERICAN ROBINS NEST?

The American Robin is among the most widespread and familiar species of North American birds. Like many other species that must await the arrival of warm spring climates, robins nest progressively later at more northern and western (mountain) locations. Frances James and Hank Shugart (1974) developed a model that used climatic variables to predict when robins would nest in a particular region. Using dates for the nestling period in 8544 nests on file with the Cornell Laboratory of Ornithology's Nest-Record Card Program, they showed that, in the East, an average robin nested three days later for each degree of increasing latitude and at progressively cooler temperatures as spring progressed northward.

Combinations of temperature and humidity were the best predictors of the nestling period. Robins typically had nests with young in late April and early May when the relative humidity was about 50 percent and the temperatures were between 45° and 65°F. These environments define either directly or indirectly the environments that allow successful nesting. The robins nested later at localities with higher or lower relative humidities. The model also showed that certain localities where robins do not breed, such as San Diego, California, and El Paso, Texas, fall outside the species-defined climate space.

arrive at their breeding colonies off southern Australia within a week of the same date. The traditional return of American Cliff Swallows the week of March 19 to the San Juan Capistrano mission in California has become a symbol of the arrival of spring itself.

Internal rhythms that are linked to other aspects of the annual cycle guide the timing of migration. Caged migratory passerines predictably become restless just before the time at which they would migrate in the wild. This phenomenon—called migratory restlessness, or *Zugunruhe*—has been familiar to bird fanciers for at least 200 years. Typically, a captive bird wakes shortly after dark and then jumps or flutters in the cage until at least midnight. Because the amount of activity is easily measured, it lends itself to experimental study of both the physiology of migration and orientation behavior. Nonmigratory birds do not exhibit *Zugunruhe* behavior. Adrenocortical hormones are known to act in concert with prolactin in stimulating this behavior in White-crowned Sparrows. More generally, however, our knowledge of the endocrine controls of the many different facets of migratory behavior of birds is poor (Wingfield et al. 1990).

We now know that increasing day length in winter stimulates early spring restlessness, hyperphagia (eating to excess), fat deposition, and weight increases in many migratory birds. Extending Rowan's findings about the photoperiodic control of the annual cycle (see page 251), Albert Wolfson showed, in another classical study, that Dark-eyed Juncos from migratory populations respond to increasing day length by adding fat stores, whereas sedentary juncos do not (Wolfson 1942). The spring fat deposition and migratory activity of White-crowned Sparrows are un-

der the direct control of increasing day length, mediated by an internal clock. The average date of onset of springtime premigratory fat deposits in captive White-crowned Sparrows has been shown to remain virtually constant for a period of eight years (King 1972).

The timing of preparations for fall migration is indirectly set by the spring activities. The normal fall sequence of photorefractory testes, prebasic molt, and preparations for migration in White-crowned Sparrows, for example, depends on prior exposure to long photoperiods, but the pace is proximately influenced by shortening days (Farner and Lewis 1971). Rowan suggested some causal relations between gonadal cycles and migration, but the available evidence now indicates that sex hormones do not directly regulate migration (Wingfield et al. 1990). In one set of pioneering experiments, for example, castration did not prevent male Golden-crowned Sparrows from becoming restless and putting on their premigratory fat deposits at the appropriate time of the year (Morton and Mewaldt 1962).

The timing of migration relates first to internal physiological rhythms, but extrinsic weather factors also play a role, primarily one of fine tuning. Northward movements of migrants in the spring correlate with the warming of the higher latitudes. Both the American Robin and the Canada Goose move north in the eastern United States, just behind the main spring thaw, along a front of regions that have a mean daily temperature of 2°C. A line connecting these points is called the 2°C isotherm. Willow Warblers in Europe move north with the 9°C isotherm.

Daily weather conditions and favorable winds, in particular, also influence departure times. In spring, major northward movements in the United States coincide with a depression (lowering of barometric pressure) toward the southwest, followed by a strong flow of warm southern winds from the Gulf of Mexico toward the northeast. The sizes of migration waves relate directly to the intensity of the depression and the strength of the favorable winds (Bagg et al. 1950). The value of favorable winds is clearly seen in records of arrivals of northbound migrants at Baton Rouge, Louisiana (Gauthreaux 1971). Migrants from Central America usually reach Louisiana in midafternoon after crossing the Gulf of Mexico; but, when they have strong southern tailwinds, they arrive several hours earlier, in the late morning. On rainy days with adverse winds, they arrive later in the evening, and they do not arrive at all on days when there are cold fronts or east winds.

Fall migration departures also are stimulated by favorable weather conditions. Good flights of large numbers of raptors at Hawk Mountain, Pennsylvania, and of land birds at the tips of peninsulas such as Cape May, New Jersey, are the result of strong northwest winds due to a barometric depression moving east from the Great Lakes region. Departures from the New England coast are related to favorable tailwinds (Richardson 1978), and peak flights south across the Gulf of Mexico in early October coincide with improved flight conditions to the north (Buskirk 1980).

Exactly how migrants forecast weather conditions is a mystery, but birds are sensitive to changes in barometric pressure and feed more intensely

as storms approach and barometers fall. Wind directions aloft, however, are not easily judged from the ground. Meteorologists track weather fronts by monitoring infrasound with a special system of microphones. Pigeons, too, seem to be sensitive to infrasound and may use this source of information in some way.

Scheduling High-Cost Efforts

The correspondence between breeding season and food availability is central in defining the annual energy budgets of birds. Birds can assume the costs of reproduction, molt, or migration only after they have first met the costs of self-maintenance, their highest priority. Basic social interactions to obtain food or a roost site are their second-highest priority. Some seasons, such as a north temperate winter, permit only self-maintenance for most species, whereas others accommodate additional activities. Reproduction and molt must be scheduled during the months when a bird's requirements for self-maintenance are lowest or when extra food is available. Usually, the costs of only one extra activity can be accommodated. The energetic costs of reproduction and molt favor the segregation of these stages in the annual cycle.

Reproduction

Peak reproductive activities increase total daily energy expenditures by as much as 50 percent. Daytime activity costs may actually double or even triple, but overnight costs remain relatively constant. At the beginning of the breeding season, courtship, territoriality, and nest building demand significant effort. Only minor amounts of productive energy are channeled into the growth of the gonadal tissues themselves, but subsequent egg formation and egg laying by females impose new demands on energy and nutrition (see Chapter 14). The large clutches of the big, richly provisioned eggs of waterfowl are especially expensive to produce. They may temporarily double a female's total daily energy requirement. Large waterfowl, such as the Snow Goose and the Canada Goose, therefore, can rely on their substantial body stores of nutrients and energy to produce their large eggs; smaller ducks must feed to supplement their endogenous reserves (Bluhm 1988). Incubation also can create an energy shortage because it limits the amount of time during which a bird can forage for its own maintenance. The parents then face another surge of demands on their time and energy when the hatched chicks require food and brooding.

Molt

Molt is a costly effort that typically follows breeding in the warmest months of the year and precedes migration. But a bird strategically adjusts the timing and sometimes the pace of its molt.

The complete molt is a major undertaking. The bird sheds and then regenerates thousands of feathers, roughly from 25 to 40 percent of its lean dry mass (i.e., excluding fat and water content). Molt draws significantly on protein and energy reserves to synthesize feather structure and to offset the costs of poorer insulation and flight efficiency. Thomas Bancroft and Glen Woolfenden (1982) estimated that adult Blue Jays and Florida Scrub Jays must increase daily metabolism from 15 to 16 percent during peak periods of feather production. Reduced insulation while molting requires increased heat production, doubling the cost of molt in Brown-headed Cowbirds at low temperatures (Lustick 1970). Molting during the warm summer months can thus be advantageous.

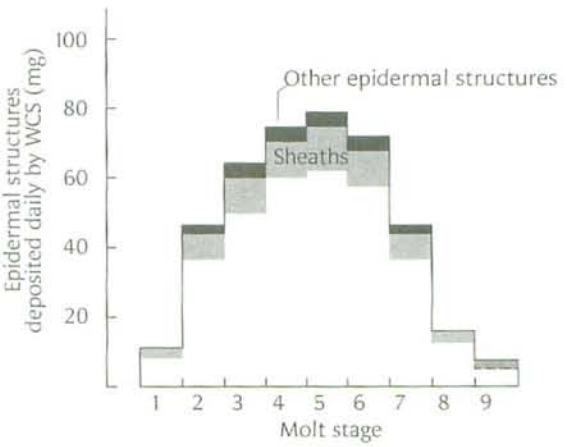
Molt is also a period of intense physiological change (Murphy and King 1992; Box 9–2). Accompanying the replacement of worn feathers is the synthesis of keratin by the skin, increased amino acid metabolism, and increased cardiovascular activity to supply blood to the growing feathers. The long list of changes also includes the shunting of water to

BOX 9–2

MOLT BY WHITE-CROWNED SPARROWS REQUIRES ENERGY AND SPECIAL NUTRITION

Mary Murphy and Jim King (1992) deciphered the costs—in both energy and nutrition—of the rapid fall (prebasic) molt in the *gambelii* subspecies of the White-crowned Sparrow. The complete molt of this sparrow lasts about 54 days, with peak feather production and energy costs from day 18 to day 36 (see illustration). The actual energy costs of molt total 605 kilojoules to 876 kilojoules, with daily investments that are proportional to the molt intensity. The daily energy costs of peak molt (58 percent of basal metabolic rate) are higher than those associated with reproduction.

Obtaining adequate nutrition for the molt is probably not a major problem for sparrows in the wild. Muscle tissues can be broken down as needed to provide most of the amino acids required. Keratin synthesis, however, requires disproportionately high proportions of sulfur-containing amino acids, especially cysteine. To have cysteine available in amounts sufficient to continue feather growth overnight when the sparrows fast, they store extra reserves in the liver during the day, feeding selectively on foods containing such amino acids if needed; the stored cysteine is liberated for use at night.



Plumage, sheaths, and other epidermal structures deposited daily in the 54-day prebasic molt period of the White-crowned Sparrow (WCS). Each of the nine molt stages lasts 6 days. [*From Murphy and King 1992*]

the developing feathers, changes in bone metabolism and calcium distribution, and an increased need for iron for red blood cell production. Together, these and other metabolic changes impose substantial hidden costs beyond the conversion of amino acids into feather proteins. Only about 7 percent of the energy used by molting birds is incorporated into the feathers themselves.

Few species breed and molt at the same time. They mostly are species that live in productive, tropical environments with minimal seasonal variation. There, prolonged molts apparently minimize daily costs in the absence of strong seasonal constraints. From 3 to 4 percent of the African birds examined by Robert Payne (1969) were molting while breeding. From 8 to 10 percent of the Costa Rican birds examined by Mercedes Foster (1975) bore signs of both molt and reproductive activity.

Exceptions to the rule are instructive. Some female hornbills molt while imprisoned in sealed nest cavities to incubate eggs and brood young. Their energy requirements for self-maintenance are minimal; as a result, the added costs of molt can be accommodated. Additionally, the flight feathers are not essential during this sedentary period. The high temperatures that build up inside the nest cavity may favor loss of feathers and reduced insulation. In contrast, male hornbills, which feed the incubating females, wait to molt until their families leave the nest.

Tropical birds molt more predictably than they breed, because reproduction may be tied to irregular periods of rain or may require several renesting attempts due to high rates of nest loss to predators. To give breeding priority, some birds interrupt their molts. Desert birds such as Darwin's finches of the Galápagos and the Zebra Finch of Australia stop the regular seasonal molt to nest whenever the unpredictable rains begin. They resume the interrupted molt after nesting is completed.

Tropical terns such as the Angel Tern on Christmas Island turn the molt on and off to breed whenever possible (Ashmole 1968; Figure 9–12). This delicate seabird has no pigment in its flight feathers, which consequently wear easily and must be replaced more often than those of most other terns. Wave after wave of molt is initiated in the flight feathers. The innermost primaries often begin to molt again before the outermost primaries are replaced in the preceding molt. As many as three successive molts may be in progress simultaneously. When an Angel Tern starts to nest (it simply lays an egg precariously on a bare branch), the molt stops suddenly, no matter which feathers may be missing—the molting equivalent of musical chairs. After the tern has finished nesting, molt resumes as if there had been no interruption in the complicated pattern of feather replacement.

Birds adjust the pace of molt in relation to the time available (Box 9–3, pages 266–267). Gulls and sandpipers that breed in the high Arctic, where the reproductive season is short, start molting before they finish breeding to be ready for migration. The Dunlin, for example, begins to molt its primaries just before incubation and then finishes from four to five weeks later. The northernmost *(pugetensis)* populations of the White-

FIGURE 9–12 The Angel Tern molts almost continuously to replace its worn, unpigmented feathers, but it interrupts the molt upon laying an egg. [*Courtesy of Ralph W. Schreiber*]

crowned Sparrow complete their molt speedily in 47 days, just over half of the time (83 days) that it takes their slow-molting southern *(nuttalli)* relatives. Renesting White-crowned Sparrows molt so fast at high latitudes that they become almost flightless for a short time. Peregrine Falcons and American Golden Plovers, as well as many other shorebirds, begin their molts on their Arctic breeding ground but are unable to complete the process in time to leave for the south. They stop the molt of their flight feathers just before migration and then resume it for several more months after reaching their wintering grounds.

Nonannual Cycles

Not all birds follow a 12-month cycle. The Rufous-collared Sparrow ranges from Mexico to Chile. Near the equator in Colombia, this sparrow breeds and undergoes a complete molt twice a year (Miller 1962). These cycles correspond to the two dry seasons each year.

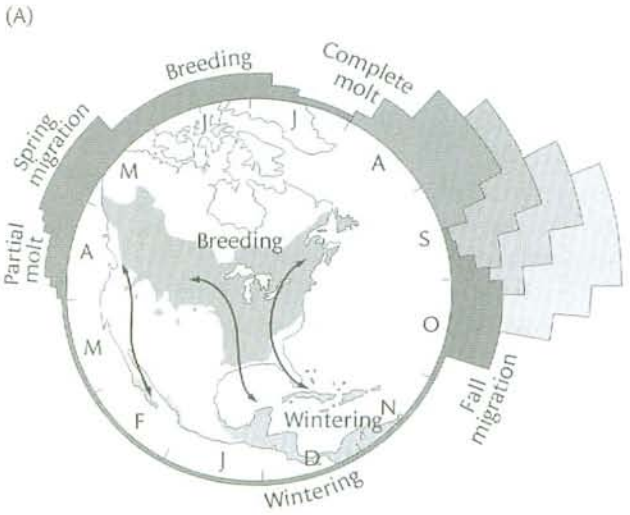
Year-round availability of adequate food fosters double breeding seasons among tropical bird species. The Sooty Terns of Christmas Island breed every 6 months, although the individual birds that breed twice in the same year are those that failed in the first breeding season. Successful birds wait from 8 to 9 months before breeding the following year (Ashmole 1963a). In another example of double breeding seasons, two temporally separated populations of Band-rumped Storm Petrels of the Galápagos

BOX 9–3

LATE MOLTS IN THE AMERICAN REDSTART INCUR COSTS

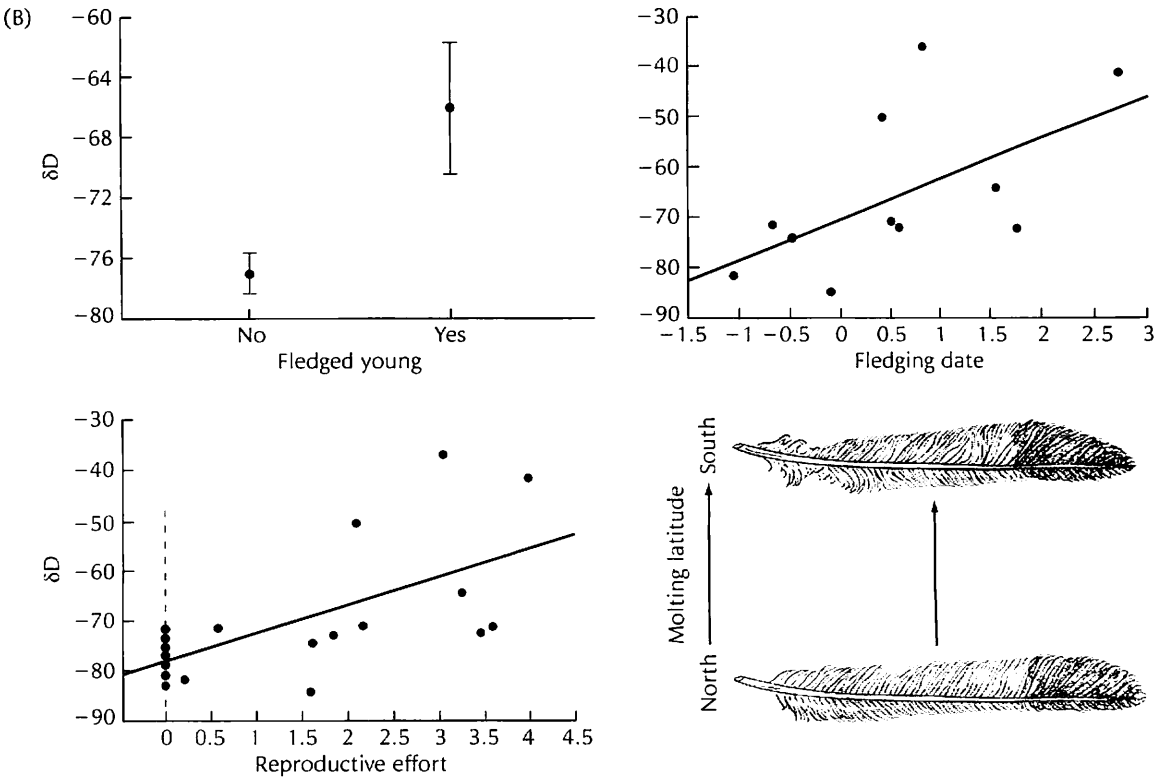
The American Redstart is a common, brightly colored wood warbler that breeds in the young forests of eastern North America. Each fall, redstarts migrate to their wintering grounds in Central America and in the Caribbean. Male redstarts are bright red orange and black in color. The most brightly colored males achieve the best reproductive success. They garner quality nesting territories, nest earlier, and fledge more young sooner (see illustration). But the increased energy investment in reproduction incurs a significant cost, specifically tied to whether they can complete their main (prebasic) molt before they migrate.

New feathers carry a chemical signature (in the form of a stable hydrogen isotope) of the latitude where they grew. Using these signatures, Ryan Norris and his colleagues (2004) discovered that some males, including those that failed to fledge any young, completed their molts on the breeding grounds in Ontario, cleanly segregating



Annual cycle and tradeoffs of molt versus reproduction in the male American Redstart. (A) This wood warbler breeds in the northern forests of North America and migrates to wintering grounds in western Mexico, Central America, and the Caribbean. The overlap of molt and migration increases projected energy costs, indicated by the heights of the bars. Later molts that overlap more with fall migration end up being paler in color (shown as lightest gray), which reduces breeding success the following year.

reproduction, molt, and migration. Other males could not finish in Ontario, because they continued to care for young too late in the summer. As a result, they continued to molt while migrating and completed their molts at more southern latitudes, with an important consequence. Their new feathers were less intensely colored with orange carotenoid pigments. They would pay for this dulling with lower breeding success the following spring back in Ontario. Molting while migrating also potentially undermines their ability to fly across the Gulf of Mexico and to get to the wintering grounds quickly to secure the best winter territories, which in turn will handicap them again in the spring migration race back to the breeding grounds (Marra et al. 1998).



(B) Relation of molting latitude in degrees (δD) to reproduction. *(Upper left)* Males that fledged young (yes) molted at latitudes south of the breeding grounds, whereas those that did not fledge young (no) molted on the breeding grounds. *(Upper right)* Males that fledged young later in the summer (dates standardized by year) also molted at southern latitudes, as did males that scored higher on an index of total reproductive effort *(lower left)*. *(Lower right)* New feathers grown on the breeding grounds were bright orange on black. Those grown south of the breeding grounds were yellow on black. [*(A) After Hill 2004; (B) after Norris et al. 2004*]

FIGURE 9–13 Sooty Terns on Ascension Island do not have a regular 12-month breeding cycle; instead, they breed approximately every 9.6 months and, consequently, in different months in successive years. [*R. L. Pitman/VIREO*]

Islands share alternate use of the same nesting burrows (Harris 1969). Good nest sites may be limited for this species.

In only a few cases is the breeding cycle independent of calendar year. Unlike the Sooty Terns on Christmas Island, the Sooty Terns on Ascension Island in the tropical Atlantic nest every 9.6 months, in different months in successive years. Successful nesting is possible at any time of the year, and so ample food must be available every month (Ashmole 1965; Figure 9–13). The Brown Booby on Ascension Island nests at 8-month intervals, and the White-tailed Tropicbird nests at 10-month intervals if successful and renests in 5 months if not. Successful Audubon's Shearwaters and Swallow-tailed Gulls on the Galápagos Islands nest at 9-month intervals.

A few very large birds cannot fit their extended reproductive efforts into a single year and hence may skip a year between nestings. Frigatebirds, Crowned Eagles, Griffon Vultures, and Wandering Albatrosses nest once every two years. King Penguins take 2 months to incubate their eggs and from 10 to 13 months to raise their nestlings, and then they molt. As a result, they breed only twice every three years (del Hoyo et al. 1992; see also Weimerskirch et al. 1992).

Climate Change

Major changes in global climates, whether yearly or long term, affect the annual cycles of birds. Year-to-year changes cause bird populations to fluctuate, often dramatically (see Chapter 18). Periodic climate cycles cause populations to have good years followed by bad ones. The El Niño Southern Oscillation in 1982 and 1983, for example, severely disrupted nesting by Christmas Island seabirds (Schreiber and Schreiber 1984). El Niño was known historically as the periodic warm-water disruption of cold upwelling off the coasts of Ecuador and Peru; it destroys the anchovy fishing industry and causes severe crashes in the local seabird populations. Now we understand that it is not just a local phenomenon. The entire equatorial Pacific Ocean changes in concert with atmospheric changes that influence global climates. The sudden changes in ocean currents and temperatures and associated flooding rains from August 1982 to July 1983 caused wholesale reproductive failure, severe adult mortality, and the disappearance of the entire seabird community on Christmas Island. With the return of normal oceanic and atmospheric conditions, representatives of all seabird species returned to nest again. This event revealed to ornithologists for the first time the sensitivity of tropical bird populations to unpredictable, anomalous global climate changes.

Global warming is now fact. Surface temperatures of the Earth increased by 0.6°C in the past century. Experts predict average temperatures to increase by 1.4° to 5.8°C by the end of the twenty-first century, with significant rises in sea levels. No one really knows what the full effect of this trend will be on wildlife, but habitats will change with the predicted changes in rainfall, storm patterns, sea levels, and temperature. Many new extinctions are likely, especially on mountaintops and in the polar regions. More immediate are the short-term effects. Roughly 80 percent of the 1400 species of North American plants and animals have changed their flowering times, distributions, migration dates, or behavior in some way (Root et al. 2003; Figure 9–14). Birds, butterflies, and alpine herbs of North America and Europe have shifted their distributions northward by an average of 3.8 miles (6.3 km) per decade (Parmesan and Yohe 2003). British birds alone have expanded their distributions an average of 18.9 km northward in the past 20 years (Thomas and Lennon 1999). British birds also lay their eggs earlier in a significant 25-year trend that corresponds to changes in temperature or rainfall (Crick and Sparks 1999).

At least two species of North American birds nest earlier in response to global warming. Arizona populations of the Mexican Jay now lay their first clutch 10 days earlier than they did in 1971 (Brown et al. 1999). This significant trend corresponds to a local increase in monthly minimum temperatures, not a maximum monthly temperature. More broadly, climate change has affected the breeding date of Tree Swallows throughout North America (Dunn and Winkler 1999). Egg-laying dates in this species advanced by as many as 9 days from 1959 to 1991, correlated with increasing surface air temperatures in the spring (Figure 9–15). For both the jays and the swallows, warmer temperatures can affect food availability and

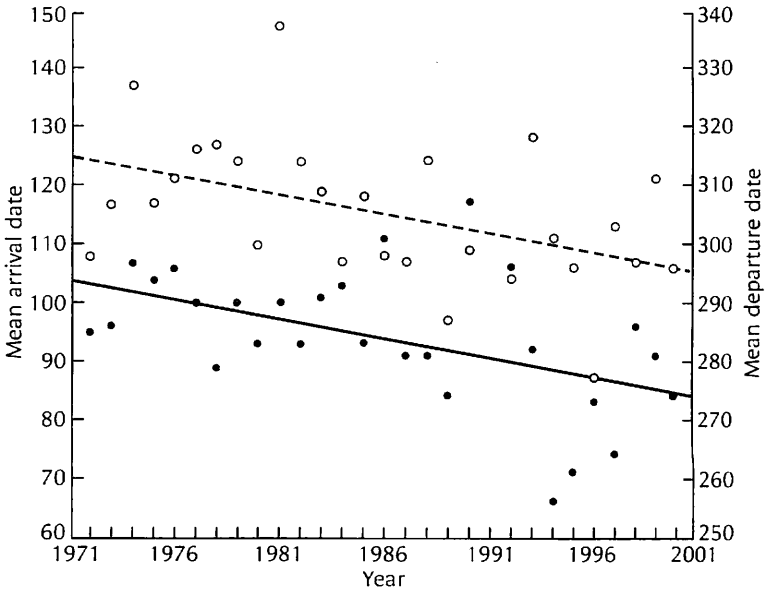


FIGURE 9–14 Trend of earlier arrival dates (black circles, solid regression line) of migrant Common House Martins in Oxfordshire, England, from 1971 to 2000. Earlier departure dates (white circles, dashed regression line) paralleled the arrival dates, and so length of time in Britain stayed the same. The earlier migrations of this species correspond to warming temperature trends in their wintering grounds in Africa. [*After Cotton 2003*]

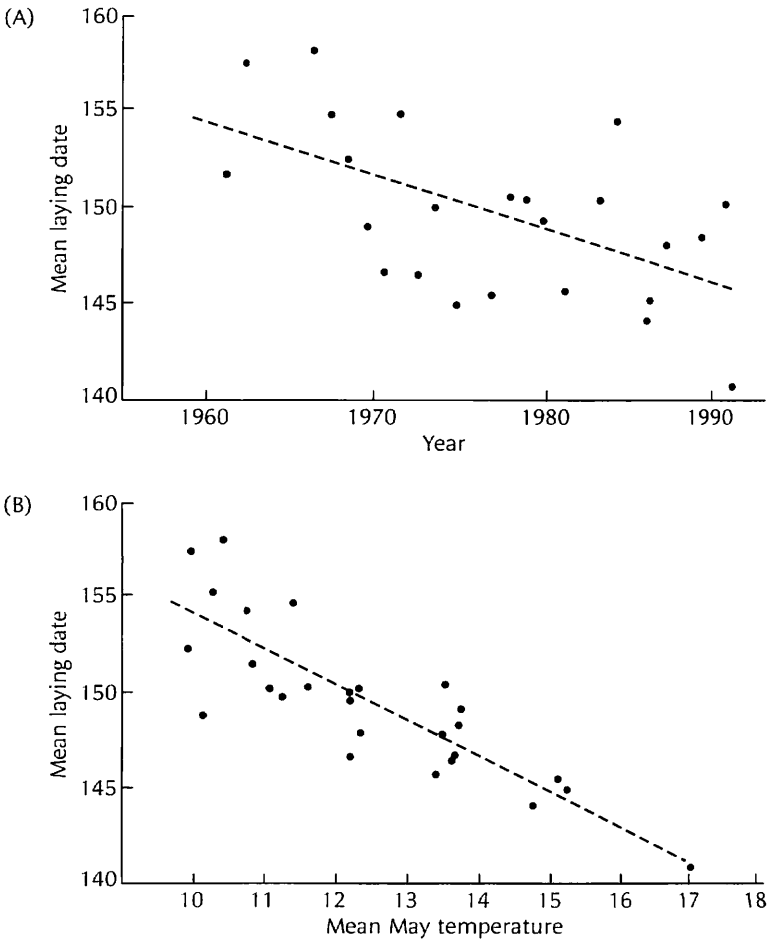


FIGURE 9–15 Tree Swallow egg-laying dates in relation to global warming. (A) The average (mean) laying date was progressively earlier from 1959 to 1991. Mean laying date is graphed here in Julian days, which count from 1 to 365 as the year progresses. (B) Earlier mean laying dates (Julian days again) correlated significantly with warmer average May temperatures. [*After Dunn and Winkler 1999*]

other proximate factors that trigger nesting activity. The cause-and-effect relations, however, are not necessarily straightforward. Less food may actually be available to feed young because insects respond differently to warmer temperatures than birds do (Vissler et al. 1998).

Summary

Birds face seasonal cycles of stress and opportunity. Physiological cycles, guided by internal cellular clocks, prepare a bird for each season. In general, seasonal changes in day length, or photoperiod, control gonadal activity and therefore reproductive efforts by directly stimulating receptors in the midbrain and, in turn, the secretion of gonadal hormones by the pituitary gland. A set of master hormones control different features of the annual cycle. Birds must regulate their responses to acute stress because corticosteroid hormones from the adrenal gland suppress the release of gonadal hormones and reduce immunocompetence.

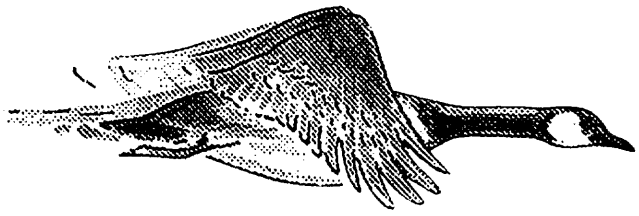
The simplest annual cycles proceed from breeding to molting to surviving seasons of reduced food availability to breeding again. Seasonal migrations and extra molts complicate the annual cycles of many birds. A few, mostly tropical, birds have 6-month cycles, breeding twice a year. Others have 9- or 10-month cycles, thus breeding in different months each year.

Ultimate factors such as food supplies, nest sites, climate, and predator risk determine the evolution of breeding seasons in birds. Proximate factors such as temperature, rainfall, and green vegetation adjust the actual onset of reproduction to local conditions. Warm spring and summer months constitute the main breeding season in temperate zones. Rainfall usually defines tropical breeding seasons.

Birds generally do not breed and molt at the same time but undertake these efforts, which require substantial energy, in different months. In some exceptional cases, molt and breeding do take place simultaneously; for example, female hornbills, confined to the nest and fed by the males, can afford to molt, and some sandpipers must molt and nest to accommodate the short Arctic summer. Opportunistic breeders, such as the Angel Tern of tropical oceans, interrupt molt while they nest. American Redstarts that delay molt to invest more into reproduction, and molt during migration, lose the bright orange luster that provides advantages in breeding opportunities the following year.

Major changes in global climates affect the annual cycles of birds. Short-term responses to global warming are now well documented, including earlier nesting and changes in arrival dates.

CHAPTER 10



Migration and Navigation

Bird migration is the world's only true unifying natural phenomenon, stitching the continents together in a way that even the great weather systems fail to do. [Weidensaul 1999]

Ancient records of the seasonal appearances and disappearances of birds perplexed early naturalists, who were not certain whether birds migrated or hibernated. Aristotle understood that cranes moved seasonally from the steppes of Asia Minor (then Scythia) to the marshes of the Nile, but he believed that swallows, larks, and turtle doves hibernated. Later anecdotes about swallows that were found frozen in marshes and that flew off after being thawed fueled this misconception.

Another legend, which persisted for five centuries until the 1600s, concerned the Barnacle Goose of northern Europe. Its high Arctic breeding grounds were unknown in medieval times, and the birds appeared mysteriously each winter, arising, it was said, directly from the goose-shaped barnacles *(Lepas)* that rode ashore on driftwood (Lockwood 1984).

We now know that, every fall, an estimated 5 billion land birds of 187 species leave Europe and Asia for Africa (Moreau 1972). A similar number of birds of more than 200 species leave North America for Central and South America. Millions of raptors as well as water birds such as American White Pelicans fly past a single migration hot spot in Veracruz, Mexico, on peak days.

Unlike dormancy and hibernation, the means by which many animals live through severe seasons, migration allows year-round activity. The advantage of migration is that birds can exploit seasonal feeding opportunities while living in favorable climates throughout the year. The costs of migration as well as its requirements, however, are potentially great.

This chapter first presents the main patterns of bird migration and a selection of the extraordinary feats that some birds achieve. Then follow the costs and benefits of migration, the tradeoffs that change through natural selection. Long-distance migration requires physiological endurance

and large fuel supplies. Direct extensions of the physiological and ecological controls integrate the timing of migration with other aspects of the annual cycles of birds. The last major section of this chapter examines the cues that birds use to navigate to their destinations thousands of miles away and how young birds acquire the skills needed for their first migratory flights.

Migration

Patterns

Migration is a major part of the annual cycle of many birds (see Chapter 9). Photoperiod, gonad cycles, and hormones guide the preparations for migration and migratory behavior itself. Proximate factors, such as weather and food availability, trigger day-to-day departures and stops to refuel.

Migration is tied to predictable, seasonal opportunities. It is different from nomadic wandering or irruptions tied to unpredictable, aseasonal opportunities. Scattered pine-seed crops or insect infestations attract opportunistic feeding by nomadic species such as Red Crossbills, which breed wherever food is abundant. In the tropics, fruit-eating and nectar-feeding birds wander locally in search of their unpredictable sources of food, but this type of behavior is distinct from the predictable cyclic behavior of migration.

Migration is a seasonal cycle of departures and returns. Seasonal cycles of climate or insect abundance generate corresponding cycles of breeding, flocking, and migratory relocation. To take advantage of predictably favorable conditions, birds undertake both local and long-distance movements. On a local scale, tropical hummingbirds migrate up and *down* mountain slopes. On a global scale, the well-known Arctic Terns leave their nesting colonies in the far northern Atlantic and Arctic Oceans (70°N latitude) for the waters of Antarctica more than 12,000 kilometers away. More common are migrations to closer wintering grounds. Many species of wood warblers that breed in the northern United States and southern Canada spend the winter in Central America and in the West Indies.

Migration routes and patterns are almost as varied as the migrants themselves. The routes trace the histories of populations, their abilities to cross large barriers, the positions of topographical barriers, and the relative locations of summering and wintering grounds. Extensive marking and recovery programs in the past 50 years have mapped the general migration routes for hundreds of species (Figure 10–1). New technologies including satellite tracking, weather radar, and feather chemistry now allow real-time tracking of migrant birds on a global scale and are sources of insight into the global structure of populations (Webster et al. 2002; Figure 10–2).

Radar Ornithology

On peak occasions in spring and fall, millions of migrant birds course through the night sky; the general public is largely unaware of this phe-

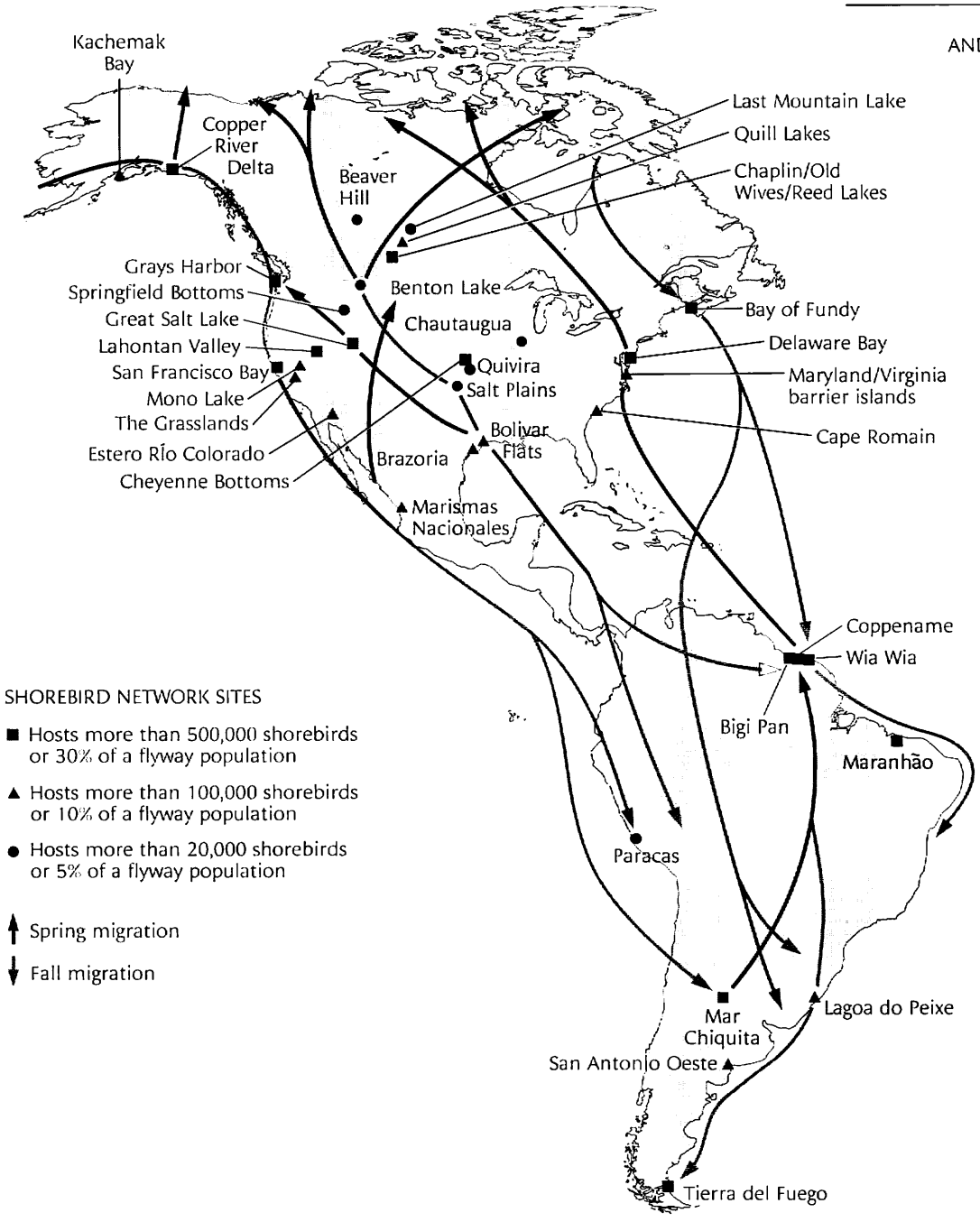


FIGURE 10–1 Major migration routes of shorebirds and their stopover sites in the Western Hemisphere Shorebird Reserve Network. [*After Corven 1998*]

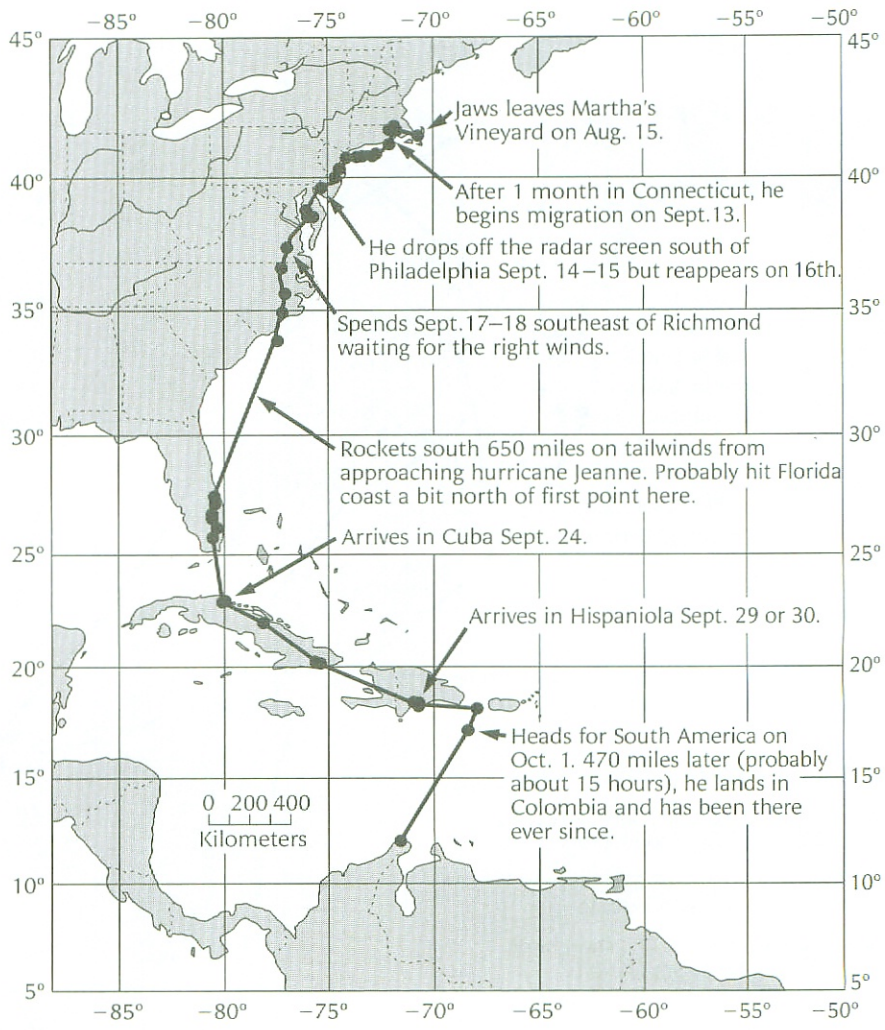


FIGURE 10–2 Satellite tracking map of the first fall migration of a young Osprey named Jaws, which was fledged on Martha's Vineyard in the summer of 2004. He moved south in September, reaching Florida September 21–24 as shown. From there, he flew to the north coast of Cuba, moved overland to its eastern end by September 28, crossed to eastern Hispaniola, and then, from the waters off western Puerto Rico, flew straight down to Colombia where he wintered successfully. [*Courtesy of R.O. Bierregaard*]

nomenon. In the 1960s, George Lowery and Robert Newman at Louisiana State University pioneered the quantitative study of nocturnal migration by counting the birds silhouetted briefly as they crossed in front of the full moon. Now we use radar.

We all follow the weather reflected through Doppler radar images. Doppler radar also reflects from flying birds, which radar operators initially called "angels." Radar reveals the huge dimension of migratory movements. Sid Gauthreaux and his students at Clemson University have pioneered the study of bird migration through Doppler radar (Gauthreaux

et al. 2003). The weather images can be filtered out, leaving just bird images. Some of these images are massive clouds that span hundreds of square miles and include millions of birds (Figure 10–3). Doppler radar studies through the years have documented when birds travel en masse in relation to continental weather patterns. They also document the decline of migrants on the Gulf Coast in fall migration (Box 10–1).

Experts on the interpretation of Doppler radar images can identify warblers, ducks, or shorebirds by their distinctive airspeeds and patterns of movement. Radar images, however, do not allow us to identify exactly what species of birds are flying through the night skies. But there is another way to do so. Nocturnal migrants call regularly, enabling expert ears to identify them by their notes (Farnsworth 2005).

In an elaborate exercise to monitor migration by night, named BirdCast, bird-sound experts from the Cornell Laboratory of Ornithology teamed up with radar experts from Clemson University and citizen scientists recruited by the National Audubon Society (http://www.birdsource.org/birdcast/index.html). Supplementing the radar images were

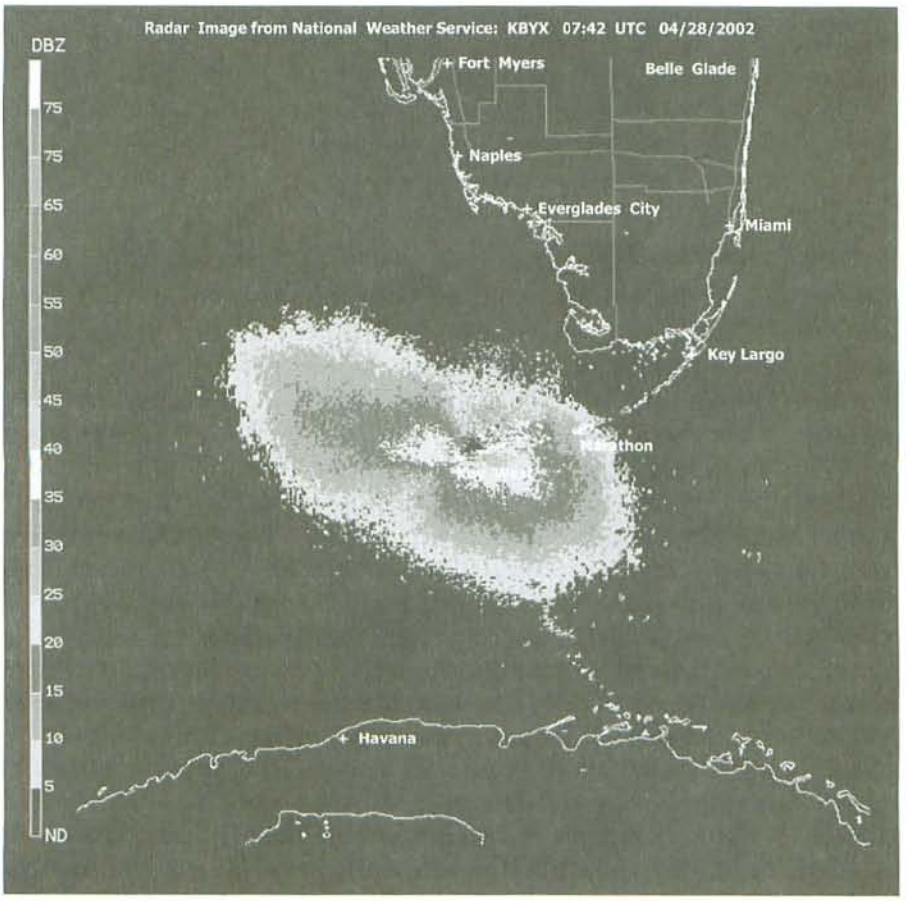


FIGURE 10–3 Doppler radar image of cloud of migrating birds over Key West, Florida, after crossing the Gulf of Mexico. [*NOAA/Photo Researchers*]

BOX 10–1

RADAR RECORDS DOCUMENT THE DECLINE OF MIGRANT BIRDS

Radar is a powerful tool for tracking birds in flight. Military radars can track and identify single birds (by using flap rates, e.g.) and assess their flight speeds, altitudes, and compass orientation. Weather surveillance radar stations also provide continuous monitoring of migration activity (Gauthreaux 1992). Migrating birds show up on the radar screen as small targets that move at predictable speeds. Flocks of migrants can be distinguished from single birds, and the intensity of migration each night can be quantified. Records from a battery of weather radar stations along the Gulf Coast monitor the arrival of trans-Gulf migrants from Central America. A comparison of these records for the spring seasons of 1965 through 1967 and 1987 through 1989 indicates a 50 percent decline in migratory activity on days with favorable weather.

microphones placed on rooftops. The microphones recorded the calls of the migrants, storing them on a computer in the volunteers' study below; the recordings were then uploaded to Cornell for analysis and identification the next day. The frequency of call notes aligned with the radar-measured volumes of birds passing overhead. And, each morning, volunteer birders censused the new arrivals in their backyards. The different data sets meshed well with one another.

Feather Chemistry

The Black-throated Blue Warbler is a widespread Neotropical migrant that winters in the Caribbean and breeds in the cool forests of the Appalachian Mountains, New England, and eastern Canada. Its southernmost populations have been declining for the past 30 years, whereas northern populations are doing well. Conservation initiatives required knowing exactly where warblers from particular breeding locales wintered so that both parts of the annual cycle could be addressed (Rubenstein et al. 2002). But efforts to track individual warblers to their winter territories by using bands and satellite radios failed. So a group of ornithologists turned to their feather chemistry. The ratio of carbon 13 to carbon 12 in plants and animals increases with latitude. This local chemical signature is deposited in new feathers from food eaten while a bird is molting.

Analysis of the carbon ratios in the feathers of more than 700 Black-throated Blue Warblers from throughout their breeding range and from Puerto Rico, Jamaica, Cuba, and Hispaniola in the Caribbean revealed that warblers from the southern Appalachians (from Georgia to West Virginia) winter on the easterly islands of Hispaniola and Puerto Rico. Warblers from northern populations winter in Cuba and Jamaica. The severe deforestation of the island of Hispaniola is likely responsible for the decline in the Appalachian breeding populations and will be the focus of new conservation initiatives.

Routes

The main migration routes of North American land birds are oriented north–south, partly because wintering ranges of most species lie south of breeding ranges and partly because the coasts, major mountain ranges (Appalachian Mountains, Rocky Mountains, and the Sierra Nevada), and major river valleys (Mississippi) trend north–south. In Europe and Asia, birds migrate east–west in accordance with the east–west orientation of the Alps, the Mediterranean Sea and the North Sea coasts, and the great deserts of the Middle East.

Circular or loop routes are features of the migrations of some long-distance migrants. Sooty Shearwaters circle the Pacific Ocean northward from breeding islands in New Zealand, up the west (Asia) longitudes, and then return south along the western shores of North America. Arctic shorebirds stage in eastern Canada and then migrate across the western Atlantic, some nonstop, to South American wintering grounds, returning north the next spring through Latin America and the Great Plains. In the southern oceans, Shy Albatrosses circumnavigate the Antarctic continent in as little as 46 days (Croxall et al. 2005). To call attention to the plight of the world's albatrosses, BirdLife International joined the world's largest bookmaker, Ladbrokes, to track the 10,000-kilometer race of 18 young albatrosses from Australia to South Africa. They were released on April 27, 2004, wearing satellite transmitters. Celebrities throughout the world sponsored the birds and placed bets on which individual bird would reach South Africa first. The winner, Aphrodite, was first detected in South Africa waters on July 13.

In general, birds of the Southern Hemisphere do not migrate as far north as Northern Hemisphere birds migrate south. In South America, the Kelp Goose and Buff-necked Ibis nest at the southern reaches of the continent and then migrate north to central Chile and Argentina for the southern winter. A variety of South American flycatchers and swallows, called austral migrants, migrate seasonally from temperate-zone South America to the tropics of Brazil (Jahn et al. 2004). The annual cycles of birds in Africa and Australia also feature austral migration systems.

Migration routes sometimes trace the recent distributional histories of birds; individual birds that colonize new areas tend to retrace the population's historical expansion routes. Pectoral Sandpipers colonized Siberia from Alaska. Instead of migrating south through the Orient, as do most Siberian shorebirds, these "Siberian" Pectoral Sandpipers fly back to Alaska and then south with the rest of their species to South America. Conversely, Arctic Warblers and Northern Wheatears, species that have spread eastward into Alaska from Asia, return to Siberia before migrating south.

Migrants fly at times of the day and at heights where travel is least costly, safest, and most rapid. Some birds, therefore, migrate by day and others by night, and still others, such as waterfowl and shorebirds, at both

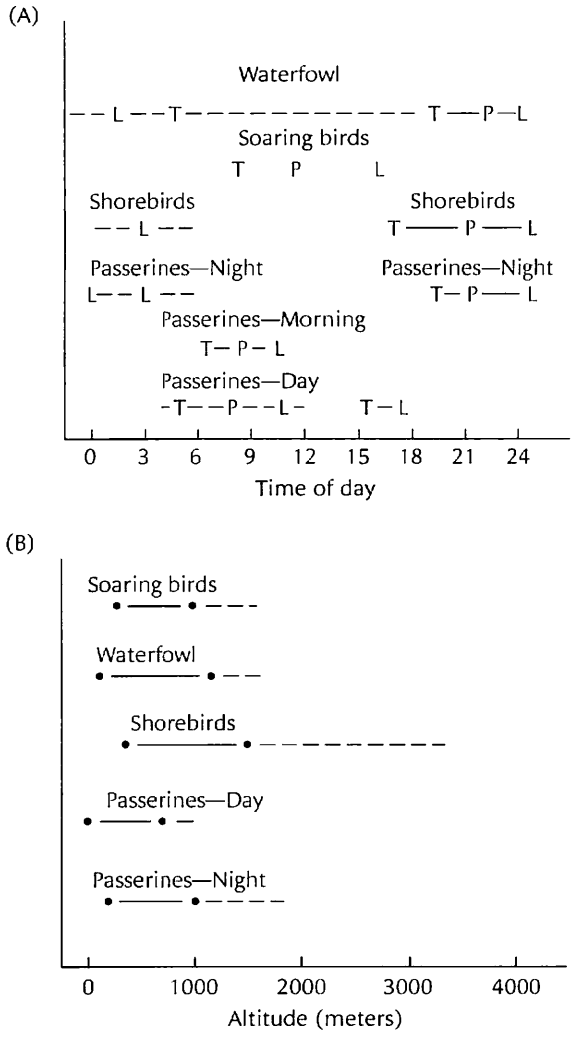


FIGURE 10–4 Times of day and altitudes of migration. Each solid line represents the normal time of migration including takeoff (T), peak migration (P), and landing (L). Dashed lines indicate the data range. Behaviors of diurnal (day) and nocturnal (night) passerine migrants are shown separately. Some nocturnal passerines fly again shortly after dawn (morning). [*From Kerlinger and Moore 1989*]

times (Figure 10–4). Diurnal and nocturnal flights offer different advantages (Kerlinger and Moore 1989). Hawks migrate during daylight hours when they can take advantage of warm rising air currents. Swifts and swallows, which feed on the wing, also migrate by day. Many small land birds, including most flycatchers, thrushes, and wood warblers, as well as rails and woodcocks, depart shortly after sunset and migrate by night. Predation by hawks and gulls is less likely at night, and these migrants can then refuel by day. Cooler and more humid night air also favors heat loss and water retention. Most important, more stable night atmospheres with weaker horizontal winds and less turbulent vertical motion create favorable flight conditions.

Most birds migrate at fairly low altitudes. Night-migrating passerines usually fly at altitudes below 700 to 800 meters, although they climb to more than 3000 meters, sometimes to as high as 7000 meters, to escape turbulent air in the boundary layer near the Earth's surface or to ride good tailwinds (Kerlinger and Moore 1989). Waterfowl have set some of the record altitudes—for example, almost 9000 meters high for the Bar-headed Goose seen flying over Mt. Everest. At the top of the list, however, is the record of a Rüppell's Vulture that was sucked into a jet engine at 12,000 meters over the Ivory Coast, Africa. Migrating shorebirds typically fly higher than do songbirds, often at altitudes of 2000 to 4000 meters, and sometimes much higher. With some exceptions, migration over water takes place at higher altitudes than over land, at usually more than 1000 meters.

Feats

Long-distance migratory flights are extraordinary feats (Box 10–2). The migrations of Arctic shorebirds regularly exceed 13,000 kilometers one way from the high Arctic to distant South America or the South Pacific. Red Knots, for example, fly from Baffin Island above the Arctic Circle to Tierra del Fuego with selective stopovers. The Bar-tailed Godwit

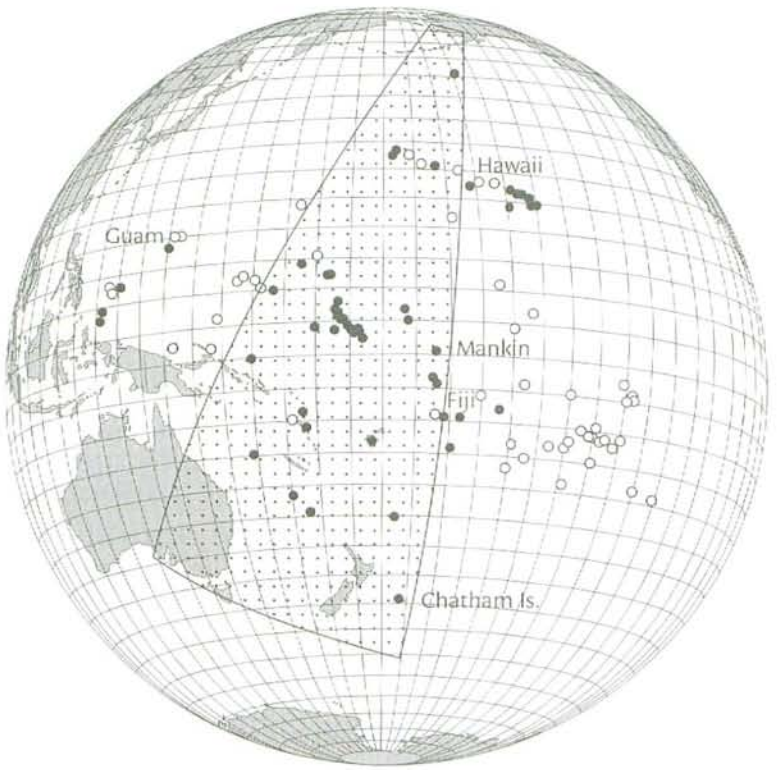


FIGURE 10–5 Bar-tailed Godwits cross the open Pacific Ocean on their fall migration from Alaska to New Zealand. Black circles are sites reporting godwits; white circles are sites at which no godwits were reported. [*From Gill et al. 2005*]

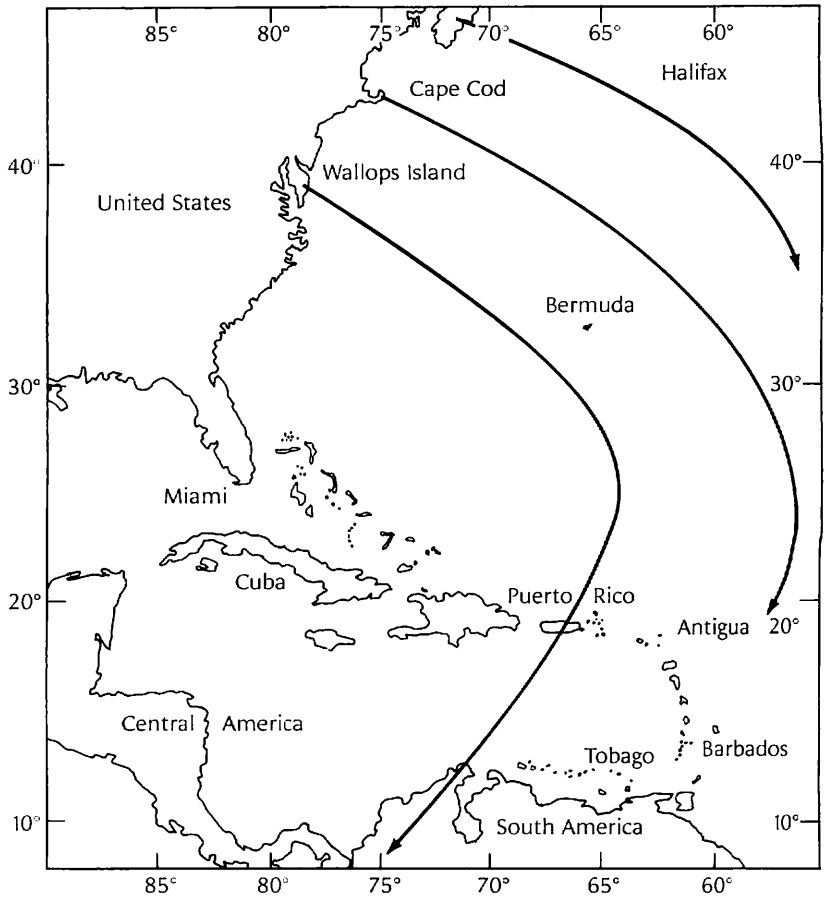


FIGURE 10–6 Millions of fall migrants such as Blackpoll Warblers fly directly from northeastern North America to northeastern South America. This 86-hour marathon flight takes them southeast past Bermuda to the trade winds, which assist them on a southwesterly course to the Lesser Antilles and the coast of South America. [*After Williams and Williams 1978, with permission from Scientific American*]

undertakes one of the longest known migrations. Members of one population *(baueri)* fly nonstop 11,000 kilometers across the Pacific from Alaska to New Zealand and eastern Australia (Gill et al. 2005; Figure 10–5). These migrants and others cross thousands of kilometers of open ocean or inhospitable terrain without stopping, thereby stretching their fuel reserves and physical abilities to the limit. Dangerous as nonstop crossings may be, they are often the only way to reach a destination or they may be preferable to longer, safer routes because of shorter total flight time.

Every fall, vast numbers of migrants leave coastal New England and Canada, heading southeast over the Atlantic Ocean (Figure 10–6). The capacity for such flights by larger, faster shorebirds such as the American Golden Plover has been known for many years. Radar studies now reveal similar efforts by millions of small land birds. As many as 12 million birds pass over Cape Cod in one night, embarking on a nonstop journey of 80 to 90 hours. Wave after wave of the migrants, such as the Blackpoll

BOX 10–2

A MIGRATING THRUSH OUTPERFORMS ORNITHOLOGISTS

William Cochran and his coworkers (1967) captured a migrating Gray-cheeked Thrush in central Illinois one afternoon and attached a tiny radio transmitter to it. At dusk, the thrush took off on the next leg of its journey, followed by the ornithologists in a small plane. A severe thunderstorm and shortage of fuel forced their plane down that night, but the thrush flew on. After refueling, the Cochran group took off again and, remarkably, relocated the thrush in the vast night sky by dead reckoning. The thrush landed at dawn in Wisconsin after flying 650 kilometers on a firm compass bearing *all night*—without refueling.

Warbler, pass Bermuda. Farther on, they encounter strong trade winds from the northeast. The migrants then fly with the wind southwest toward the northern coast of South America.

Tim and Janet Williams (1978) put this feat in perspective: "The trip . . . requires a degree of exertion not matched by any other vertebrate. For a man, the metabolic equivalent would be to run 4-minute miles for 80 hours. . . . If a Blackpoll Warbler burned gasoline for fuel instead of its reserves of body fat, it could boast of getting 720,000 miles to the gallon!"

Evidence of the strenuous nature of the trip can be seen in the exhausted condition of birds that stop at Curaçao, short of their destination, when flight conditions have been poor. Little more than feathered skeletons, they have depleted their fat reserves, metabolized much of their protein, and drained the remnants of their precious body water (Voous 1957).

Eurasian migrants also face Herculean challenges (Moreau 1972; Lövei 1989). Each fall, many of them fly 1100 kilometers directly across the Mediterranean and then, almost immediately thereafter, 1600 formidable kilometers nonstop across the Sahara desert (Moreau 1961). They are vulnerable to diurnal predators such as Eleonora's Falcon, which breeds in the fall so that it can feed its nestlings on migrants trying to cross the Mediterranean.

Why Birds Migrate

Why birds migrate as they do is a long-standing and still challenging question (Wallace 1874; Gauthreaux 1982). The benefits of migration offset its risks and costs for many species. Many species that migrate to high northern latitudes are tropical birds that temporarily exploit the favorable opportunities of the long days and abundant insects of high-latitude summers. Attractive nesting opportunities invite migration to temperate latitudes. The large expanses of northern temperate-zone habitats facilitate dispersed, low-density breeding. Reduced predation of nests may be one result of low densities, breeding opportunities for yearlings another. Several years' wait for a breeding space is often the case in the Tropics. Such factors, contributing to reproductive success in one season and survival during another, are incentives to migrate.

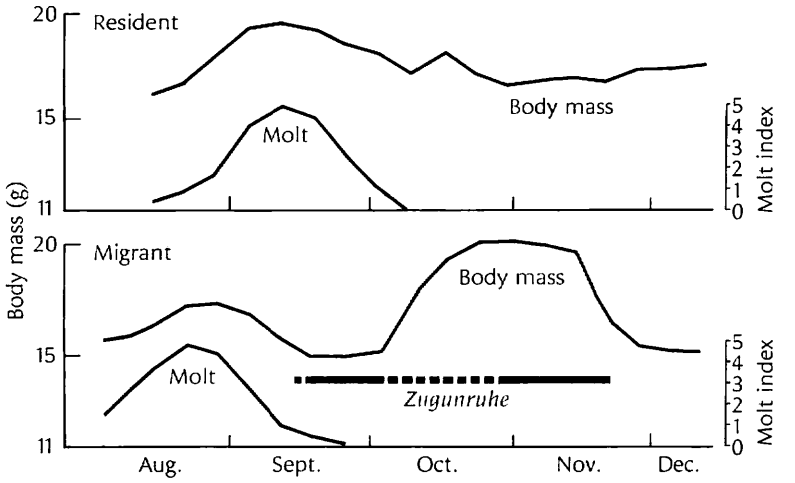


FIGURE 10–7 Body mass (in grams), molt, and *Zugunruhe* behavior (migratory restlessness) of a young resident (*top*) and a young migratory European Robin in the laboratory (*bottom*). Breeding experiments revealed a genetically based polymorphism for migratory behavior, including early molt, premigratory fattening, and migratory restlessness in the two forms of this species. A molt index of 1 indicates the beginning or the end of the molt. A molt index of 5 indicates a heavy molt that includes most of the feather coat. [*After Biebach 1983*]

Consider also the energetic benefits for Red Knots that spend the winter in West Africa compared with those that stay in England. Red Knots that fly all the way to West Africa use at least 40 percent less energy each winter day compared with those that winter in Britain (Piersma 1994a; Wiersma and Piersma 1994). Substantial energy is required to offset the cold winter temperatures, higher wind speeds, and reduced sunshine in Britain. Knots wintering there sustain energy expenditures of four to five times resting rate, which is at the upper limit possible for warm-blooded animals and equivalent to the physical effort of cyclists in the Tour de France. Using another analogy, Theunis Piersma suggests that a knot wintering in Britain would drain the power from a car battery in a day, whereas the battery would last a week in tropical Africa. Further, the costs of migration to West Africa from Siberia are relatively modest because they make good use of tailwinds. Flying to West Africa is a good investment of time and energy.

In regard to local populations of the European Robin, unpredictable winter conditions favor a mixture of migrant birds and resident or nonmigrant birds. Mild winters favor residents; severe winters favor migrants (Figure 10–7). Resident birds make up about one-fifth of the robin population in southwestern Germany. They remain within 5 kilometers of their breeding territories, do not put on large reserves of premigratory fat, and do not exhibit sustained migratory restlessness in the laboratory. In contrast, migrant birds fatten in the fall, exhibit intense migratory restlessness, and travel an average of 1000 kilometers to their winter habitats. Parents pass their heritable migratory behavior to their offspring.

Sex and Age Differences

As their solutions to different tradeoffs, the sexes and age classes of fully migratory species move different distances, called differential migration (Cristol et al. 1999). At least 53 species, and possibly three times that number of species, of diverse taxonomic groups and habits are differential migrants. Typically, females migrate farther than males and young migrate farther than adults. The classes of birds that migrate farthest are usually smaller in body size, subordinate in social behavior, and later arriving on the breeding grounds.

The classic study of differential migration focused on Dark-eyed Juncos, which migrate south from Canada and the northern United States to wintering grounds throughout the eastern United States (Ketterson and Nolan 1983). Adult females migrate farthest to the southernmost states, young males stay farthest north in Indiana and Ohio, and adult males and young females settle at intermediate latitudes. Greater mortality among the young of both sexes, compared with adults, selects for their shorter migrations. Males that get back to the breeding grounds first to establish a territory tend to win, and so they stay farther north than females. Young males, especially, must hurry back to succeed in the competition for breeding territories. Adult females migrate farther south to regions of lower junco densities and the greatest probability of overwinter survival (Figure 10–8).

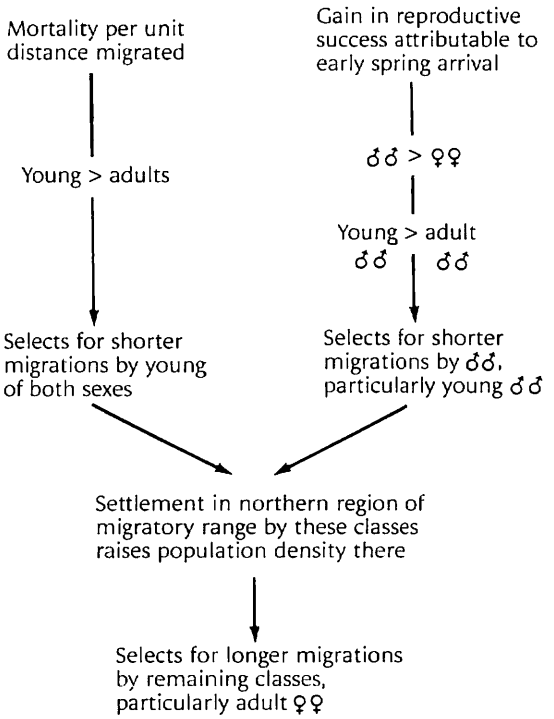


FIGURE 10–8 Model of the evolution of differential migration by age and sex in Dark-eyed Juncos. The probability of death on migration increases with distance traveled and is greater for inexperienced young juncos on their first trip than for adults. Therefore, young birds tend to migrate less far than adults. Early returns to breeding grounds favor males over females and young males over adults, which favors males that winter farther north. Adult females migrate farthest south, where densities of wintering juncos are lower than in the north [*After Ketterson and Nolan 1983*]

Population Differences

Migration is a package of complex behaviors that have separate genetic controls (Zink 2002). *Zugunruhe* behavior (nocturnal restlessness, see page 260), hyperphagia, and navigation systems are each independent systems with deep evolutionary roots (Berthold 1999). Despite those roots, however, migration is a labile and facultative behavior. It has evolved and has been lost repeatedly in different species and lineages of birds. Within species—Fox Sparrows, White-crowned Sparrows, and Common Ringed Plovers (Figure 10–9) to name a few—some populations migrate, whereas others do not. In other species, such as the Red Knot, some migratory populations travel farther than others do. Then species such as the European Robin mix migratory and nonmigratory birds in the same population.

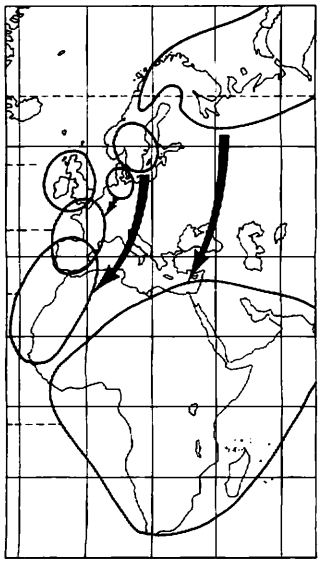


FIGURE 10–9 Populations of the Common Ringed Plover maintain distinct wintering and breeding ranges. The populations that breed farthest north winter farthest south. The Common Ringed Plovers of Britain do not migrate at all. [*After Dorst 1962*]

Within a species, increasingly sedentary populations can competitively replace migratory populations, or vice versa, in a few generations (Bell 2000). The composition of migratory compared with nonmigratory birds and their offspring in populations such as those of the European Robin can shift quickly in relation to natural selection. House Finches introduced from sedentary western populations into the eastern United States in the 1950s quickly became migratory (Able and Belthoff 1998). Conversely, migratory Fieldfares colonized Greenland from Europe and became nonmigratory. Several Palearctic species that migrated to southern Africa for the winter—the European Bee-eater and Black Stork, for example—established resident breeding populations there. Similarly, Barn Swallows wintering in Argentina during the austral (southern) spring and summer stayed to nest there (Martinez 1983).

The Eurasian Blackcap, a familiar songbird of Europe, has added Britain to its list of wintering grounds in the past 50 years. Instead of migrating southwest to the Mediterranean, the Eurasian Blackcap's historical wintering grounds, increasing numbers of Eurasian Blackcaps that nest in Germany and Austria migrate each year northwest to winter in England and Ireland (Berthold et al. 1992). The offspring that winter in England exhibit an innate orientation to the northwest, which suggests a rapid evolutionary change in the genetic program that controls their migratory behavior.

The shift by some Eurasian Blackcaps to new wintering grounds has benefits, including a shorter migration (Bearhop et al. 2005). In combination with faster changes in day length that stimulate the warblers to migrate earlier, shorter migration times lead to earlier returns to the breeding grounds and capture of the best-quality territories. One result is that a female Eurasian Blackcap from England lays one more egg than does a female that winters in Spain, which, in turn, fuels an increase in the new wintering population. Both males and females from England arrive early with another important result. They pair assortatively with each other, not randomly with those that winter in other places. Assortative pairing potentially leads to the evolution of a genetically distinct population and, in time, a new species.

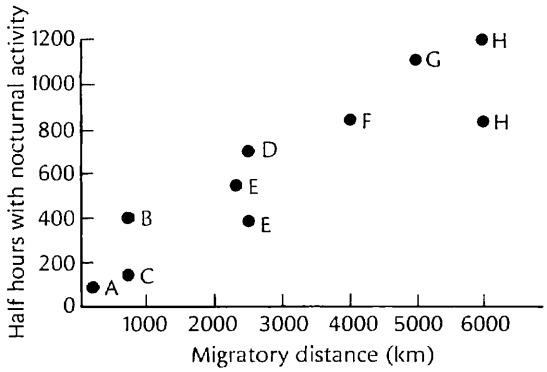


FIGURE 10–10 The lengths of time of nocturnal restlessness in the laboratory correlate with the migration distances covered by eight species of European warblers: (A) Marmora's Warbler; (B) Dartford Warbler; (C) Sardinian Warbler; (D) Eurasian Blackcap; (E) Common Chiffchaff; (F) Subalpine Warbler; (G) Garden Warbler; (H) Willow Warbler. Results for Willow Warblers and Common Chiffchaffs tested under different conditions are shown separately. [*After Gwinner 1977*]

Endogenous Controls

Not only are migratory preparations and migration itself linked directly to endogenous circannual rhythms (see Chapter 9), but the duration and pace of migration are linked to these rhythms as well. The length of *Zugunruhe* activity in the laboratory relates directly to the distances migrated by these warblers to their respective winter ranges (Figure 10–10). The Willow Warbler normally takes from three to four months to migrate from Europe to southern Africa: this warbler's intense migratory restlessness in the laboratory lasts more than four months. The Common Chiffchaff takes only one to two months to migrate from southern Europe to northern Africa; intense migratory restlessness in the laboratory lasts 60 days.

Populations of the Eurasian Blackcap differ from one another in the seasonal course and magnitude of *Zugunruhe*. The differences correspond directly to the normal migration distance of each population. Evidence of direct genetic control of their directional migrations comes from the study of hybrids. Hybrids between the migratory German population and the nonmigratory African population hybrids exhibit intermediate *Zugunruhe* activity (Figure 10–11).

Hand-reared, caged migrants not only exhibit well-defined orientation behavior but also change their compass direction in ways that correspond to their natural migration routes. Garden Warblers change direction in the course of their fall migration from southwest initially to south–southeast from Spain to southern Africa. Devoid of cues other than magnetism, the orientation of migratory restlessness in the laboratory shows a corresponding shift. Restless, caged Garden Warblers orient southwest in August and September and then shift their heading to south–southeast

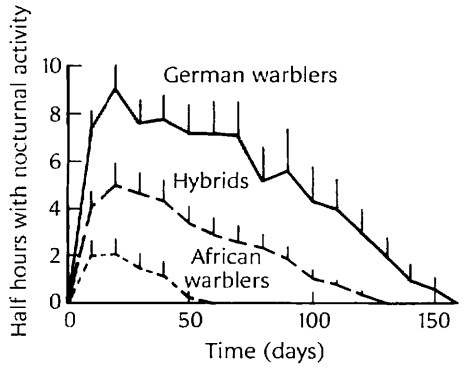


FIGURE 10–11 Eurasian Blackcaps from migratory populations in Germany show intense and prolonged migratory restlessness, whereas birds from a nonmigratory population in Africa show little migratory restlessness. Hand-raised hybrids of these forms have intermediate migratory behavior. [*After Berthold and Querner 1981*]

from October to December (Gwinner 1977). Such internal programs, however, cannot guide migrants precisely to their final winter residences. External forces including food availability, climate, and competitive interactions come into play at various stages of the journey and may be the dominant factors, especially in short-distance migration.

Fat, Fuel, and Flight Ranges

Preparations for a major migratory flight can be intense and transforming (Box 10–3, page 292). Migrants fatten rapidly just before migration by consuming enormous quantities of energy-rich food. Blackpoll Warblers nearly double their weight, from an average of 11 grams to an average of 21 grams. Ruby-throated Hummingbirds, which cross from 500 to 600 miles of open water in the Gulf of Mexico, also nearly double their normal weight of 3 grams to make this trip.

Fat yields two times as much energy and water per gram metabolized as does either carbohydrate or protein (Table 10–1). Fat is stored in adipose tissues under the skin, in the muscles, and in the body cavity. For example, White-crowned Sparrows deposit subcutaneous fat initially at 15 separate sites. With continued deposition, the fat stores spread laterally and coalesce into a continuous layer between the skin and muscles (Figure 10–12). Some fat is also stored in most muscles and in internal

TABLE 10–1 Fuels for migration

Fuel	Energy yield (kJ)	Metabolic water (g)
Fat	38.9	1.07
Carbohydrate	17.6	0.55
Protein	17.2	0.41

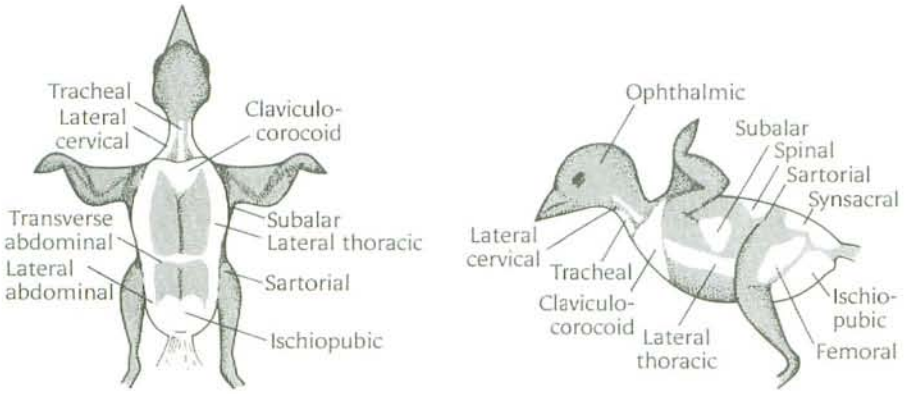


FIGURE 10–12 Principal sites of subcutaneous fat deposition in the White-crowned Sparrow. [*After King and Farner 1965*]

organs. Unlike the human heart, the avian heart does not accumulate much fat, even when the migrant reaches peak obesity.

Adipose tissue does not consist simply of large, inert globs of fat. Instead, it supports a dynamic system for the synthesis, storage, and release of lipids (George and Berger 1966). The enzyme lipase breaks down fat into free fatty acids and glycerol for transport to sites of use. Lipase activity, which is a good index of the capacity of muscles for fat metabolism, increases in relation to migratory activity.

Migrants store fat in proportion to their requirements. Fat makes up 3 to 5 percent of the normal mass of small nonmigrating birds. They depend on larger midwinter fat reserves of 15 percent to survive unpredictable periods of inclement weather. Long-range and intercontinental migrants—shorebirds, for example—build up fat deposits that account for 30 to 47 percent of their total weight, mainly in preparation for long, nonstop flights (Berthold 1975).

How far migrants can fly nonstop depends both on their fat reserves and on how quickly they use their fuel. David Hussell and his associates at Long Point Observatory on the north shore of Lake Ontario captured and weighed nocturnal migrants arriving at various times of the night after flying north across Lake Erie (Hussell and Lambert 1980). These data suggest average weight losses of 0.9 percent of body weight per hour of flight, 0.2 gram per hour for the Ovenbird (Figure 10–13). Weight losses of about 1 percent project to expenditures of about 418 joules of energy per gram of body weight per hour of flight. Blackpoll Warblers were more fuel efficient than most other migrants; they lost weight at 0.6 percent per hour of flight, or expended 250 joules of energy per gram per hour of migration.

Estimates of energy expenditure allow us to project total flight range. Small birds that expend 418 joules per gram per hour during migratory flight and that have fat reserves of 40 percent of total live weight can fly about 100 hours and cover about 2500 kilometers. At that rate, they should be able to cross the most extensive barriers with energy to spare, unless

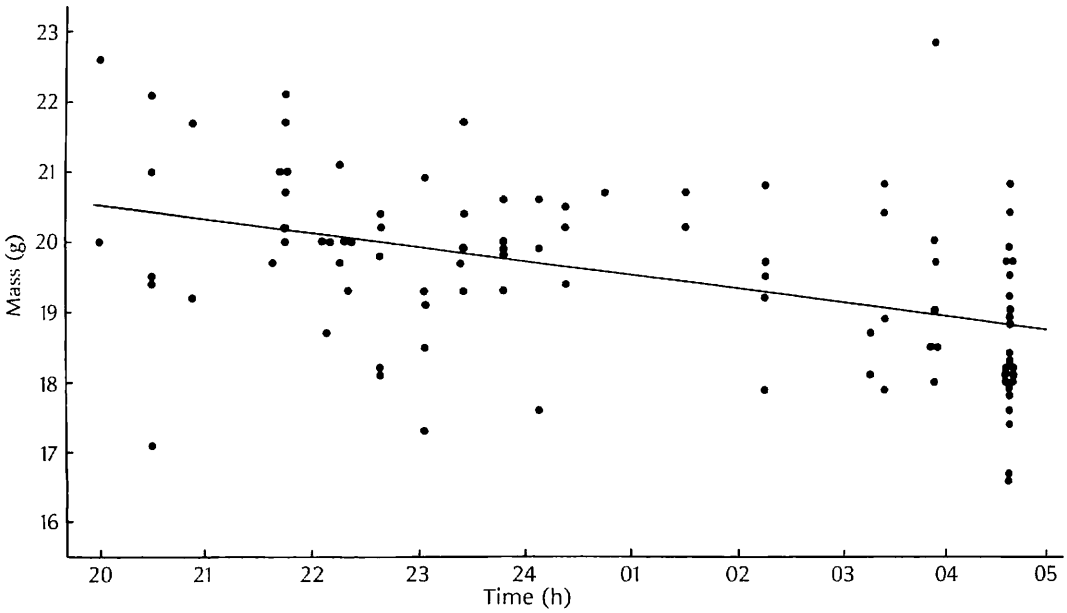


FIGURE 10–13 Ovenbirds, weighed on arrival at Long Point Observatory on the north shore of Lake Ontario, decreased in mass by an average of 0.2 gram per hour as the night proceeded. Assuming that those that arrived later had flown longer than those that arrived earlier, one can use such data to estimate the energy costs of migratory flights. [*After Hussell 1969*]

they encounter strong headwinds. Migrant shorebirds such as the Dunlin have estimated flight-range potentials of 3000 to 4000 kilometers.

Ornithologists had long wondered how such a tiny bird as the Ruby-throated Hummingbird could carry enough fuel to cross the Gulf of Mexico. Some doubted that hummingbirds crossed at all, suggesting, instead, that they took a less direct route overland to Central America. Others proposed that hummingbirds hitched rides on the backs of larger migrants. Laboratory measurements suggested that a hummingbird in flight consumes fat at the rate of 9.18 watts. If the hummingbird carried 2 grams of fat, and flew at a velocity of 40 kilometers per hour, it should be capable of flying more than 1000 kilometers nonstop in about 26 hours, more than enough to cross the Gulf of Mexico (Lasiewski 1962).

Long-distance migrants may need more fuel than is available in their fat deposits. They then turn to stores of protein in their muscles and organs and consume those stores in flight (Battley et al. 2000). Great Knots, medium-sized shorebirds, fly 5400 kilometers from Australia to stopover sites in China. In addition to having used most of their fat, arrivals had used and reduced the size of seven organs while in transit. Only the brain and lungs seemed to be exempt from use as fuel.

Measurements of the flight costs of a related species, the Red Knot, revealed additional costs of long-distance migration. In addition to stored fat, Red Knots use the protein in the pectoral muscles as an energy supply for migratory flight. They draw on this source of energy, and reduce

the size of the flight muscles, at a deliberate pace that parallels the overall loss of total body mass but that still maintains optimal flight performance (Lindström et al. 2000).

Some, perhaps most, birds throttle back and coast with tailwinds, thereby saving energy and potentially increasing their flight range. The land birds that fly to South America pick up the trade winds as they enter the tropical Caribbean region. They backtrack to land on their first night at sea if wind conditions seem unfavorable for intercontinental flight (Richardson 1978).

Headwinds are a different story. Migratory passages across deserts or across major bodies of water may be followed by local groundings, or "fallouts," of thousands of exhausted birds, especially when they encounter strong headwinds. Legendary are the spectacular fallouts on the coasts of Louisiana and Texas of Neotropical migrants after they have flown across the Gulf of Mexico. These fallouts take place in April when bad weather and opposing winds force the northbound migrants to land on the first available land, with high mortality. Victor Emanuel, who grew up in Houston, Texas, and has probably witnessed as many fallouts as anyone, describes his experience when the entire trans-Gulf migration was grounded in late April 1960:

> There were trees decorated with tanagers, orioles, and grosbeaks. Trees dripped with warblers of many species—ten or more varieties in one tree. Birds were everywhere. In the trees, in the bushes, on fenceposts, on fence wires, around houses, and most remarkably, in the grass. Sometimes a hundred orioles and buntings would fly up from the grass and perch in dead stalks. What impressed and delighted me most was seeing warblers in the grass, and even hopping on the ground! Here were these tiny birds, the "butterflies of the bird world," not hidden amid the foliage of tall trees but literally at my feet. I've seen twenty or more Bay-breasteds, a dozen Blackburnians, and many others on the ground. In such a situation, you can approach warblers quite closely and enjoy every detail of their brilliant plumage. [Emanuel 1993, p. 1]

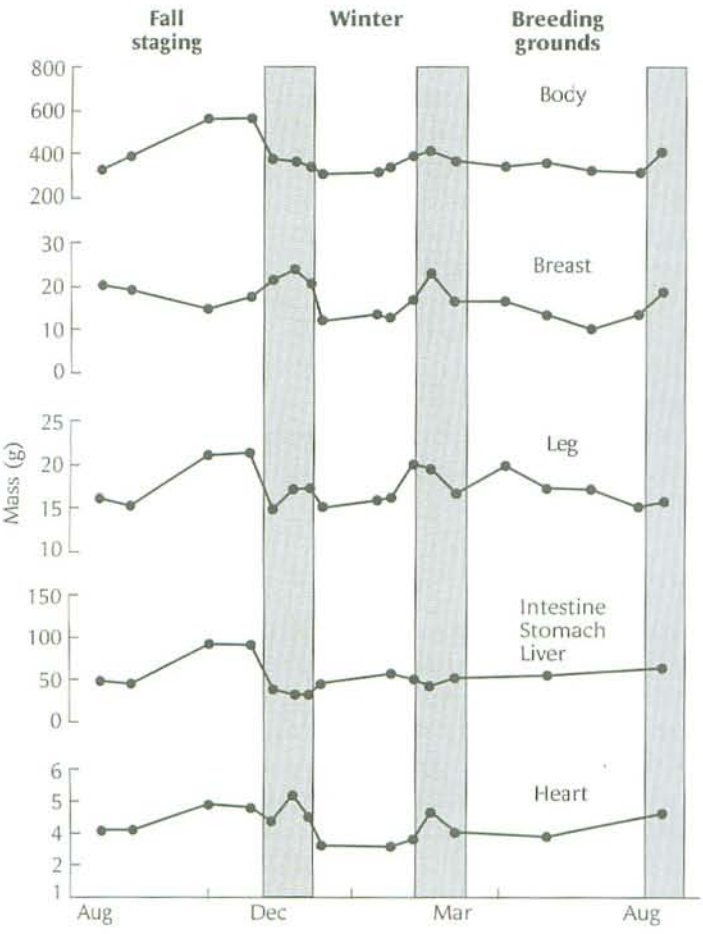
Refueling at Stopover Sites

Regular refueling usually accompanies migrations. Songbirds typically fly several hundred kilometers and then pause for one to three days of rest and refueling (Winker et al. 1992a, 1992b). Some songbirds press on for several nights in succession until their reserves are nearly exhausted. Beyond their expenditures of energy in the air, they also need energy to find food at a stopover site. The stopover ground costs of thrushes migrating north in the spring in the United States, due to cold weather and foraging efforts, were greater than their flight costs (Wikelski et al. 2003). High-quality stopover sites with plenty of food—avian service stations, or McDonald's for birds—are critical to successful migrations.

BOX 10–3

THE BLACK-NECKED GREBE REORGANIZES ITS WHOLE BODY

Beyond just adding fat for the trip ahead, long distance migrants also reorganize the organs of their bodies. Studies of Black-necked Grebes staging for migration on Mono Lake in California revealed this phenomenon (Jehl 1997; Cullen et al. 1999). They quickly more than double their weight from about 260 grams to more than 600 grams, mostly with added fat (see illlustration). To process the large quantities of food (brine shrimp) that they need for this change, they almost double the size of the organs of their digestive tracts. Conversely, their pectoral flight muscles shrink by half, rendering the grebes flightless even before they drop their flight feathers in the major molt of the year. Then the grebes fast for two to three weeks before leaving on migration. They lose weight, shrink their digestive systems to one-third of their former mass, reduce their leg muscles, increase the size of their hearts, and double the mass of their pectoral flight muscles back to their former size. They trade locomotory organs and muscles for digestive organs to build fat deposits; then they trade digestive organs for the muscle and heart power needed for the migration itself. The endocrine and physiological controls of this cycle of body reorganization remain unknown.



Changes in body mass and in the size of organ systems of Black-necked Grebes over the annual cycle. Shaded areas indicate periods of migration. Breast and leg mass determined for one side of body. [*From Cullen et al. 1999*]

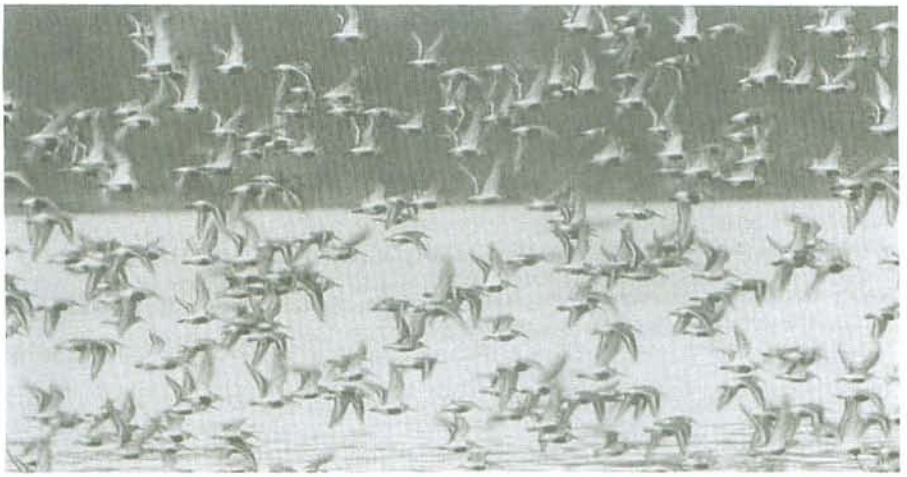


FIGURE 10–14 Millions of shorebirds gather at key staging areas such as the Copper River Delta in Alaska to refuel for the next (in this case, final) leg of their migration to northern breeding grounds. [*Courtesy of D. Norton*]

From three to four refueling stopovers are a strategic aspect of the extraordinary migrations of most Arctic shorebirds, which fly from the Arctic tundra of North America to the southern tip of South America, and back, as many as 30,000 kilometers round trip. The aforementioned nonstop flights of the Bar-tailed Godwits from Alaska to New Zealand are exceptional. Migrating shorebirds congregate by the millions at key staging areas. For example, from 5 million to 20 million shorebirds pass through the Copper River Delta every spring, including almost the entire Pacific Coast populations of two species, Western Sandpipers and Dunlins (Figure 10–14). They time their movements to coincide with the appearance of abundant food at these sites, where they build up fat reserves required for the next leg of their journey.

Good stopover sites can be few and far between. Bar-tailed Godwits require good mud flats with soft sediments and lots of worms and small mollusks. For them, spring migration from West Africa to Siberia requires a series of 1000-kilometer flights, first to estuaries in Mauritania on the edge of the Sahara, then to Morocco, then all the way to the coast of France, and then to the Wadden Sea on the north coast of Europe, followed by a final 4500-kilometer nonstop flight to their final destination in Arctic Siberia (Piersma 1994a). At Wadden Sea, their final refueling station, they undergo a cycle of organ changes quite like that of the Black-necked Grebes (see Box 10–3) (Landys-Ciannelli et al. 2003). The lean dry mass of the digestive-tract organs (stomach, liver, kidneys, and intestines) increases rapidly in the early stages of refueling and then shrinks before departure. Flight muscles increase steadily in lean dry mass, peaking at departure.

Red Knots also require food-rich stopover sites on their seasonal trips to and from the Arctic. One population travels from breeding grounds

on Ellesmere Island in the high Arctic across the ice caps of Greenland to refuel in Iceland before moving on to different wintering grounds in Europe and West Africa and then back again in the spring. Like grebes and godwits, the knots adjust organ allocations (Piersma et al. 1999). In the Western Hemisphere, Red Knots cycle 30,000 kilometers between breeding in the high Arctic to wintering in extreme southern South America—namely, Tierra del Fuego.

The shores of Delaware Bay in the eastern United States are a key stopover place on the Red Knots' northward migration. Here, in late May, they fatten rapidly on horseshoe crab eggs to fuel the final leg of the flight to the Arctic. Spring tides and warming water temperatures stimulate horseshoe crabs to emerge from the ocean depths, to mate, and to lay their nutritious eggs in the beach sand. The sheer abundance of tiny greenish crab eggs attracts thousands of gulls and shorebirds to feast and fatten up in a true spectacle. By consuming an estimated 1000 grams of crab eggs, the average knot adds 54 grams of fuel and nutrients (Castro and Myers 1993). Rough calculations suggest that, at their peak numbers in the 1990s, 95,530 knots stopping at Delaware Bay in the spring would have consumed 226.1 metric tons of horseshoe crab eggs and would have gained 5.2 metric tons of fat (Harrington 2001).

The birds compete with local fishermen, who exploit the horseshoe crabs for conch-fishing bait and for fertilizer. Consequently, more and more of the knots fail to adequately refuel on Delaware Bay, underscoring the vital importance of stopovers. From 1997 to 2002, a larger proportion of knots failed each year to attain a mass of 180 to 200 grams, the critical size required to complete the journey and breed successfully. Reduced nutrient storage and organ shrinkage increased mortality, especially for late-arriving adults, and lowered reproduction. As a result, adult survival dropped 37 percent. Young birds in wintering flocks dropped 47 percent. This population is in serious trouble: it declined precipitously from 51,000 birds to 27,000 in the period from 2000 to 2002 (Baker et al. 2004).

Conservation of Staging Areas

International alliances for the conservation of shorebirds are directed toward the protection of critical staging areas such as Delaware Bay. One of these alliances, the Western Hemisphere Shorebird Reserve Network (WHSRN), was formed in 1985 to address shorebird-conservation problems. Many species of shorebirds were declining in numbers, apparently as a result of habitat loss. WHSRN, a voluntary collaboration of private and government organizations, gives international recognition to critical shorebird habitats and promotes their cooperative management and protection. The shorebirds serve as a symbol for uniting countries in a global effort to maintain the Earth's biodiversity. Using data from private and government sources, the network protects 58 (as of August 2003) of the globally most important stopover sites in North and South America (see Figure 10–1). These reserves contain 4 million acres of

wetlands on which the continued existence of 30 million shorebirds depends.

A worldwide network of Important Bird Areas (IBAs) targeted by BirdLife International and its partners now helps to protect birds in more than 120 countries. Many IBAs are important stopover sites for a variety of migratory species. The stewardship of such sites will be essential to continue the natural connections among ecosystems through the hemispheric migrations of birds (see Chapter 21).

Navigation

In addition to the physical feats, migration requires precise navigation between breeding territories and wintering stations. On hemispheric scales, individual birds return to a particular tree in Canada after wintering in South America or migrate annually between particular sites in Europe and Africa. In one of the earliest experiments, an Eastern Phoebe, wearing a silver thread placed on its leg by John James Audubon in 1803, returned the next spring to Audubon's house in Mill Grove, Pennsylvania, after wintering somewhere in the southern United States. Conversely, banded Northern Waterthrushes, which breed in the northern bogs of Canada, returned predictably every year to the exact same wintering sites in Venezuela (Schwartz 1964).

The choice and maintenance of a compass direction are only part of the challenge of navigation. If a bird is to reach a goal, such as a loft in regard to homing pigeons, it must also know its own position relative to its goal.

The homing feats of displaced birds testify to their navigational abilities. Homing pigeons return to their lofts by flying as much as 800 kilometers per day from unfamiliar places. Ancient Egyptians and Romans developed these messengers by enhancing the natural orientation abilities of feral Common Pigeons. Both shearwaters and sparrows can return to a home site after having been transported thousands of miles away. A Manx Shearwater returned to its nest burrow in Wales only 12.5 days after having been released in Boston (Mazzeo 1953). White-crowned Sparrows that were shipped to Baton Rouge, Louisiana, returned the following winter to their wintering grounds in San Jose, California, where they were recaptured. They returned to California again after a second displacement to Laurel, Maryland (Mewaldt 1964; Figure 10–15).

Avian orientation systems include a toolkit of complementary and interactive compass senses, including landmarks, the positions of the sun by day and the stars by night, the topology of the Earth's magnetic fields, and odors in the atmosphere, as well as the position of the setting sun and its bands of polarized light in the evening. Next, we review each of these compass systems, including the history of their discovery, which illustrates the way in which ornithologists build a detailed understanding of complex bird behaviors. How birds themselves build and calibrate the whole toolkit is the final section of this chapter.

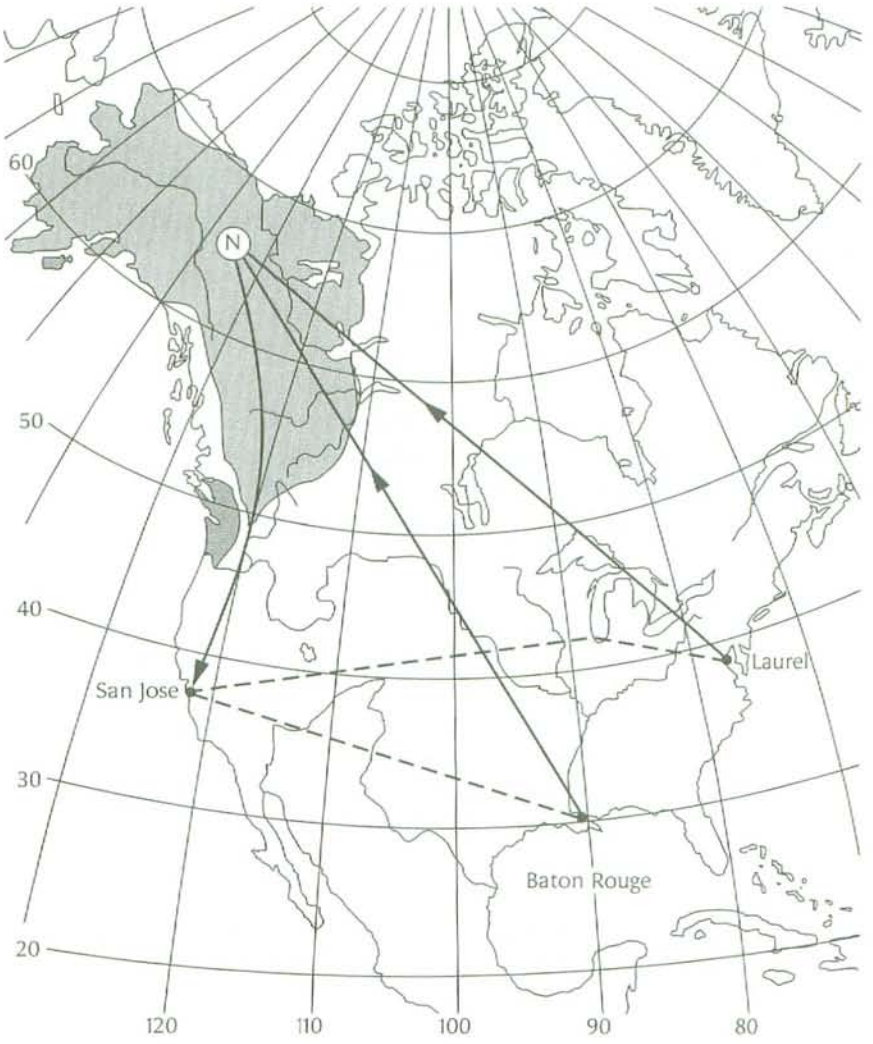


FIGURE 10–15 White-crowned Sparrows returned to their wintering grounds in San Jose, California, after having been carried by aircraft (dashed lines) to Baton Rouge, Louisiana, and to Laurel, Maryland. These marked sparrows apparently spent the intervening summers on their nesting grounds in Alaska. The solid lines show their probable flight paths. [*After Mewaldt 1964*]

Visual Landmarks

First and foremost, birds rely on visual landmarks for both local travel and long-distance migration. Pigeons routinely follow highways, railways, and rivers, even if not the most direct route home (Pilcher 2004). Both diurnal and nocturnal migrants, especially waterfowl, follow watercourses and coastlines but are reluctant to cross large, open bodies of water unless the winds are favorable. As a result, great numbers concentrate where restricted corridors function as funnels. The Strait of Gibraltar and the Bosporus at Istanbul are major funneling points for Eurasian migrants that detour around the Mediterranean Sea. The coasts of Central America fun-

nel thousands of migrating raptors—Broad-winged Hawks, Swainson's Hawks, and Turkey Vultures—over Panama City. Crowds of bird watchers gather to view the spectacle of migrants funneled to the tips of peninsulas such as Point Pelee, Ontario, and Cape May, New Jersey.

Naïve young birds cannot use visual landmarks to guide them on their first migrations across new landscapes. Underlying the experienced use of visual landmarks are more sophisticated navigational compasses. Birds start their orientation with cues other than landmarks and senses other than sight.

In a now classic early experiment, well-trained homing pigeons were fitted with frosted contact lenses that eliminated image formation beyond 3 meters (Schlichte 1973). These severely myopic birds flew "blind" for more than 170 kilometers directly back to their lofts. When they reached the vicinity of their lofts, they hovered and then landed like helicopters. Not all such pigeons performed perfectly, some crashed and some missed the loft altogether, but many oriented well without being able to see landmarks. Orientation by birds is based on a framework of navigational compasses that include the sun, the stars, and the Earth's magnetic fields.

The Sun Compass

Scientists long suspected that birds navigated by the sun, but proof of this ability awaited experiments conducted with starlings and homing pigeons in the 1950s. In Germany, Gustav Kramer (1950, 1951) studied the orientation of *Zugunruhe* in Common Starlings. The birds were housed in circular cages and placed in a large pavilion with windows through which they could see the sun, including its change of position as the day progressed. As long as they could see the sun, they focused their attention toward the northeast, the correct direction for spring migration. On overcast days, however, the starlings showed no directional tendency (Figure 10–16).

At about the same time, in Britain, Geoffrey Matthews (1951) released homing pigeons from unfamiliar sites away from the loft under a variety of weather conditions. The pigeons flew directly home when they could see the sun, but they fared poorly under overcast skies. Matthews discovered a key feature of this orientation behavior: not only could the pigeons use the sun for directional information, but they also compensated for its changing position as the day progressed, as if they could "tell the time."

Testing the so-called Sun-Arc hypothesis, Gustav Kramer and his colleagues demonstrated that birds, indeed, compensate for the apparent motion of the sun (Kramer 1952). They trained starlings (and some other birds) to feed from the northwest cup of a series of cups placed around the perimeter of a circular cage. The birds reliably chose the correct cup when they could see the sun. However, when trained to accept a stationary light bulb as a substitute for the sun, they fed from cups increasingly farther to their left as they compensated for the expected hourly change in the position of the "sun."

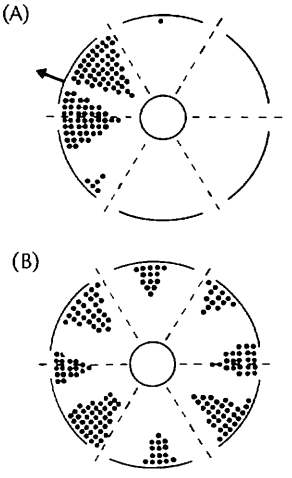


FIGURE 10–16 Common Starlings use the sun to orient in a circular cage. (A) As long as they could see the position of the sun in the sky, they oriented their restless spring migratory behavior toward the northeast. (B) On overcast days when they could not see the sun, they showed no directional orientation. Each dot represents 10 seconds of fluttering activity. [*From Kramer 1951 and Emlen 1975a*]

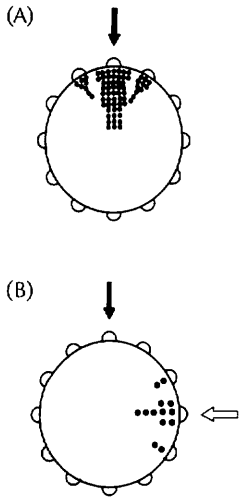


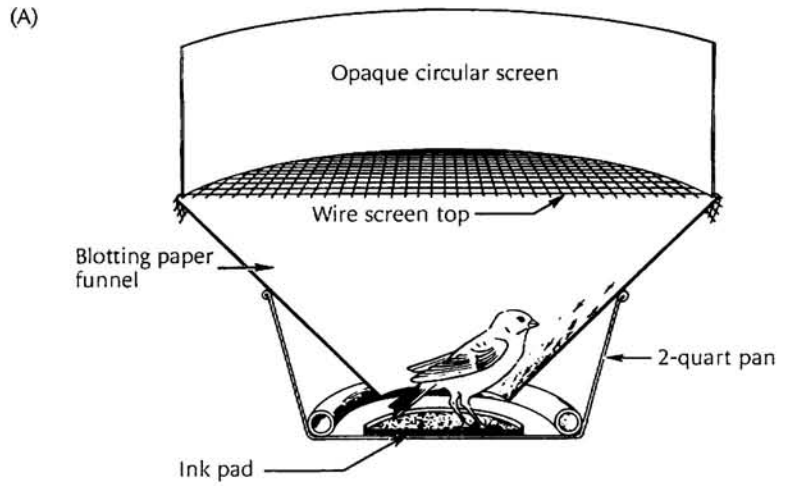
FIGURE 10–17 When the internal clock of a Common Starling is set 6 hours behind natural time (by changing the schedule of light and dark), it misreads the sun's position and looks for food 90 degrees (white arrow) from the correct location (black arrows). (A) Behavior during training, showing correct orientation; (B) behavior after the 6-hour clock shift in internal schedule. Each dot shows an attempt to find food. [*After Hoffman 1954 and Emlen 1975a*]

The next step in the study of a time-compensated solar compass was to trick a bird into misreading the sun's position by changing the bird's internal clock. Konrad Hoffman (1954) kept Common Starlings on a 12-hour-dark and 12-hour-light cycle that was 6 hours out of phase with natural daylight (the lights went on at 1200 instead of 0600). Accustomed to this schedule, the starlings predictably misread the sun's position in the sky. The clock-shifted starlings interpreted the midday position of the sun to be its dawn position. Their "east" was really south, and so they looked for food at a position 90 degrees clockwise from the correct bearing (Figure 10–17). This result is standard: 6-hour clock-shift experiments with many other birds, including homing pigeons, produce a 90-degree disorientation and confirm the widespread use by birds of time-compensated solar cues.

The Star Compass

Land birds and waterfowl maintain their direction when they migrate at night by using the stars as a source of directional information. Franz and Eleanore Sauer (Sauer 1958) first demonstrated the ability of migrating passerine birds to use the stars for navigation in experiments with hand-reared Garden Warblers. The warblers were kept in circular experimental cages in a planetarium. When ready to migrate, they became restless and hopped and tried to fly or hop in their migratory direction. The Sauers watched the birds through the glass bottom of their cage. The warblers oriented north in the "spring" and south in the "fall" under the simulated night skies of the planetarium. When the Sauers turned off the "stars," the warblers became disoriented. When the Sauers rotated the north–south axis of the planetarium sky 180 degrees, the warblers also reversed their compass headings.

Stephen Emlen (1967a) duplicated the Sauers' results with a North American migrant, the Indigo Bunting (Figure 10–18). These buntings oriented north when a spring night sky was simulated in a planetarium and south when a winter night sky was simulated. Like the warblers, the buntings became disoriented when the planetarium sky was turned off and reversed their orientation when the axis of the sky was reversed (Figure 10–19). Then Emlen (1967b) tried to identify the stars that buntings use for orientation by systematically blocking out various constellations. He assumed, logically, that the buntings orient by the North Star, the one obvious, fixed point in the night sky, but they did not. Instead, they used the constellations that were within 35 degrees of the North Star. Moreover, the buntings were familiar with most of the major constellations in the Northern Hemisphere, including the Big Dipper, the Little Dipper, Draco, Cepheus, and Cassiopeia; if one of these constellations was blocked from view, the buntings used the others. Such redundancy is useful when sections of the sky are overcast; it also allows the birds to be flexible in their choice of guideposts in the complex, ever-changing night sky. The axis of rotation of the night sky is a key compass for many nocturnal migrants (Able and Able 1996).



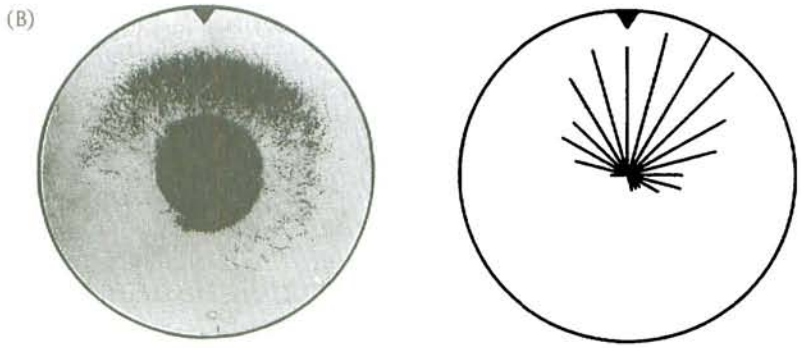


FIGURE 10–18 (A) The Indigo Bunting migrates at night between its summer range in the eastern United States and its winter range in Central America. Buntings in a state of migratory restlessness orient by the stars at night, even when confined to a funnel-like cage placed under a planetarium sky. (B) Inky footprints record the orientation direction; the lengths of line vectors measure the intensity of ink left in each 15-degree sector. [*After Emlen and Emlen 1966*]

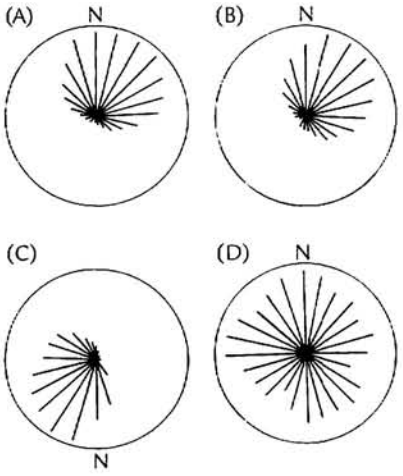


FIGURE 10–19 Line vectors, such as the ones described in Figure 10–18, show how Indigo Buntings use the stars to orient north in the spring. They do so under (A) natural night skies and (B) simulated night skies in a planetarium. (C) When the planetarium stars are shifted so that the North Star, N, is at true south, the birds reverse their orientation. (D) When the stars are turned off and the planetarium is diffusely illuminated, the buntings do not orient. [*After Emlen 1975b*]

A bird's hormonal physiology is easy to change by changing day length, or photoperiod (see Chapter 9). Simulating the seasons by increasing or decreasing day lengths can bring caged birds into breeding condition, can cause them to molt more often than is natural, and can cause them to accumulate premigratory fat at the wrong time of the year. Using unnatural photoperiod regimes, Emlen (1969) manipulated the seasonal physiology of two groups of Indigo Buntings. He induced readiness for northward spring migration in one group and readiness for southward fall migration in the other group. Exposed to the same planetarium sky, buntings in the two groups oriented north and south, respectively. These results showed that migratory orientation is under physiological control, at least in some birds.

Geomagnetism

The geomagnetic fields of the Earth provide a map of horizontal space, just as gravity and barometric pressures give information about vertical space. The intensity and dip angle—or inclination of the magnetic field—change with latitude in ways that provide reliable, omnipresent information about geographical orientation and position.

Ornithologists were slow to accept the hypothesis that birds might use the Earth's magnetic field for orientation. An early report that magnets disrupted a pigeon's homing ability (Yeagley 1947) was discredited, largely because the results could not be repeated. Then Frederick Merkel and Wolfgang Wiltschko (1965) showed that captive European Robins could orient in experimental solid steel cages without celestial cues. In addition, the robin reversed its orientation when the Wiltchkos (1988) reversed the magnetic field imposed on the steel cage.

Years later William Keeton (1971, 1972) showed that free-flying homing pigeons wearing bar magnets often did not orient properly on cloudy days, whereas control pigeons wearing brass bars usually did (Figure 10–20). Failures to repeat Yeagley's earlier experiments were due in part, Keeton revealed, to the use of the solar compass in preference to the magnetic compass on sunny days. Finally, in experiments that swayed the skeptical, Charles Walcott and Robert Green (1974) fitted homing pigeons with electric caps (containing Helmholtz coils) that produced a magnetic field through the birds's heads. Under overcast skies, reversing the field's direction by reversing the electric current caused free-flying pigeons to change their heading (Figure 10–21).

We now understand that many migrating bird species navigate by using the Earth's magnetic fields. Bobolinks rely on their magnetic compasses to undertake extraordinary long-distance migrations annually from North America across the equator to wintering grounds in the pampas grasslands of Argentina and back. One nine-year-old female Bobolink flew the equivalent of 4.5 times around the Earth (at the equator) on this annual 20,000-kilometer round trip (Martin and Gavin 1995). Bobolinks and other birds use two sensory systems to navigate by using geomagnetic information (Beason 2005). One system is a direction-finding magnetic

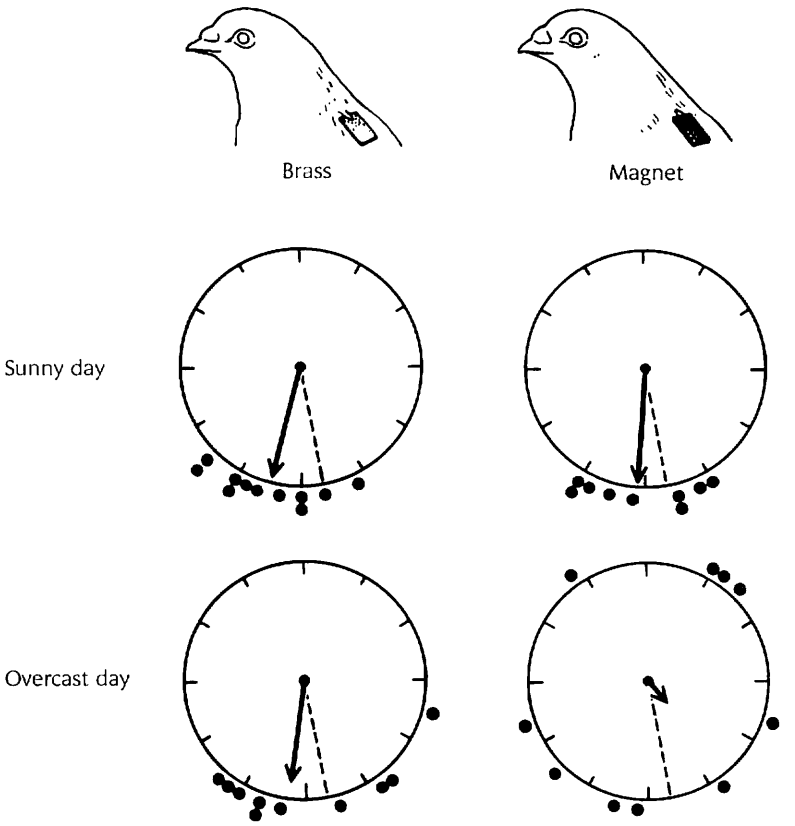
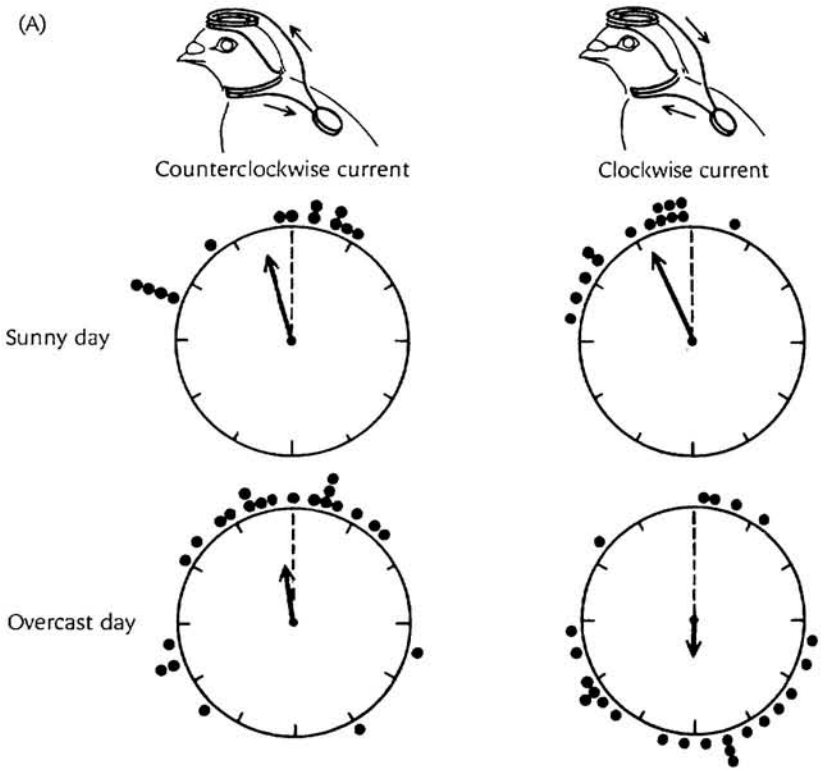


FIGURE 10–20 A bar magnet interferes with a homing pigeon's ability to return to its loft on overcast days. On sunny days, pigeons wearing magnets and control pigeons wearing brass bars both adopt accurate home bearings at unfamiliar release sites. On overcast days when they cannot orient by the sun (their preferred cue), the pigeons wearing magnets become disoriented. The control group, however, orients by means of the Earth's magnetic information. Vectors (arrows) show mean direction and consistency of orientation among individual birds: long vectors show consistent orientation, and the short vector shows variable orientation. Dots represent bearings recorded for each pigeon tested. The dashed line represents the correct orientation. [*From Keeton 1974*]

compass based on photopigments in the eye. This magnetic compass responds to the "poleward" or "equatorward" angles of inclination of a magnetic field, not to its "north–south" polarity.

The other system, a map location system, is based on magnetite (iron oxide) receptors in the ophthalmic branch of the trigeminal nerve. The magnetite-based system enables a bird to determine its location relative to goal. The magnetite receptors (both single domain and superparamagnetic) are sensitive to very small changes in the intensity or topography of the Earth's magnetic fields.

As noted, two different systems determine direction and position respectively. The sensitivity of these systems to extremely weak magnetic fields is one reason why some early experiments succeeded and others did



(B)

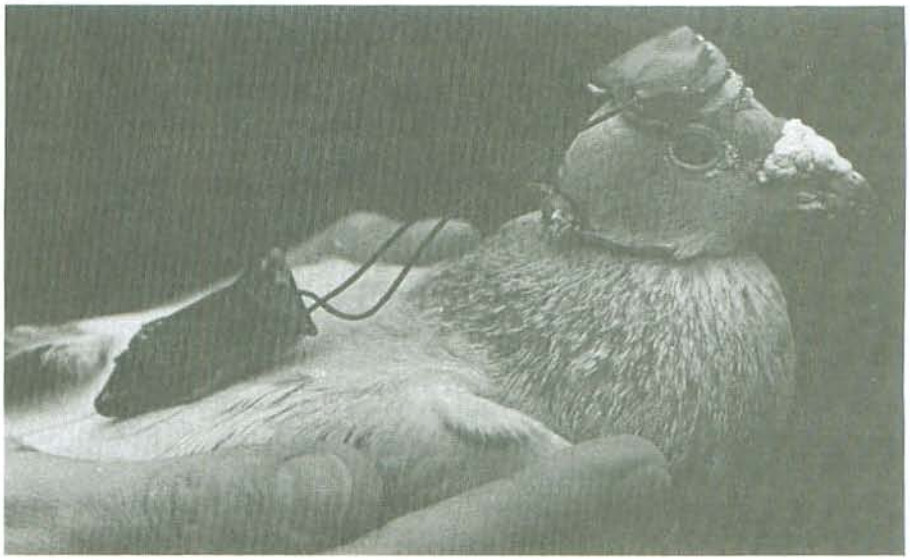


FIGURE 10–21 (A) By attaching Helmholtz coils to the heads of homing pigeons, Charles Walcott and Robert Green generated artificial magnetic fields by allowing an electric current to flow through the coils. The reversal of electric current, which reversed the magnetic field, caused the pigeons to reverse their orientation direction on overcast days. Vectors are portrayed as in Figure 10–20. (B) A homing pigeon equipped with Helmholtz coils. [*(A) After Walcott and Green 1974 and Keeton 1974; (B) courtesy of C. Walcott*]

not. Natural fluctuations in the Earth's magnetic field, such as those caused by sunspots and hills of iron ore, even disrupt the orientation of passerine birds migrating at night.

Odors and Twilight Cues

Supplementing the principal features of a bird's toolkit for navigation are cues as subtle as chemical odors in the prevailing winds, polarized light in the atmosphere, and sunset itself.

Navigation by smell once seemed improbable, but it is now clear that pigeons at least obtain information about their location from trace gases in the atmosphere (Gagliardo et al. 2001; Wallraff 2004). Maps of compounds such as volatile hydrocarbons are reliable sources of information and are even resistant to disruption by wind, at least in urban environments. Early experience with local smells is important: a young pigeon does not orient well after fledging if its nest was screened from prevailing winds and the odors carried by them.

The sky at dawn and dusk also is full of directional information (Helbig 1990; Able and Able 1993). The direction of the setting sun establishes a primary direction (west). In addition, the rays of the setting sun include a band of strongly polarized light that runs (north–south) perpendicularly to the sun's daily arc. Migratory songbirds use both of these sources of information to define their departure directions after dark. Experiments with freely migrating birds show that they also recalibrate their magnetic compasses each evening by using the setting sun. William Cochran and his colleagues (2004) tricked Gray-cheeked and Swainson's thrushes by exposing them to false magnetic fields (80 degrees off to the east) at sunset and then released them with radio transmitters. They flew in the wrong direction on the first night but recalibrated to the correct heading the following night.

Learning and Calibration

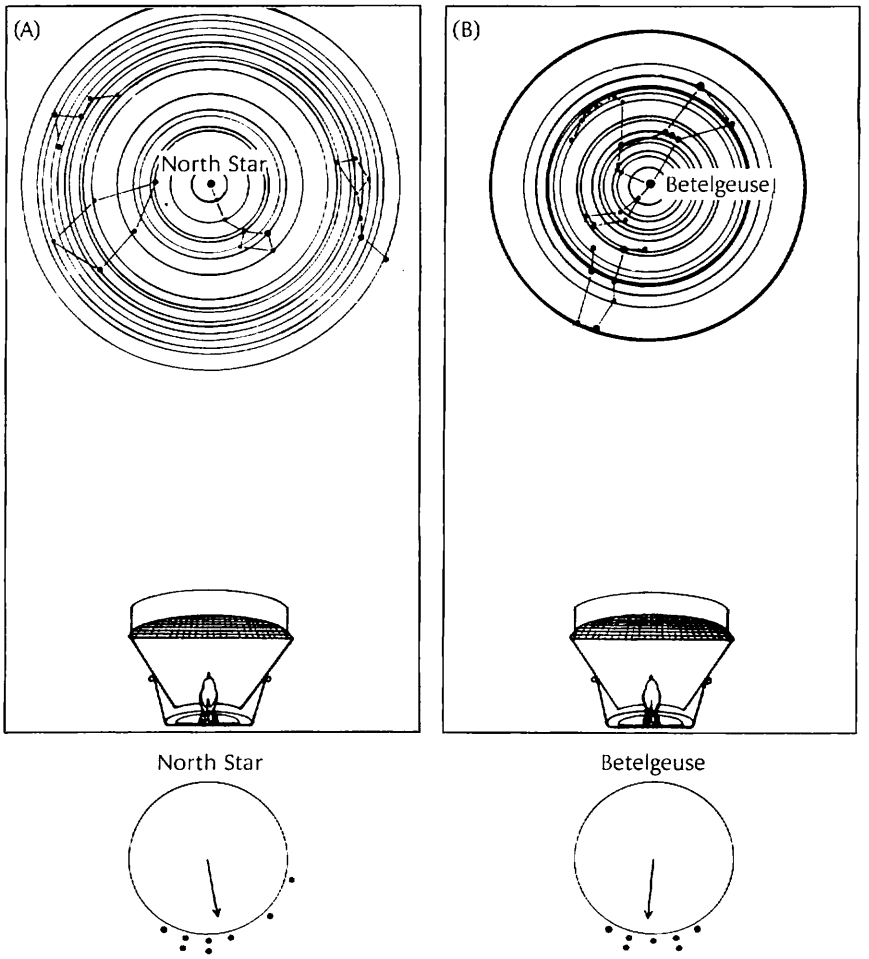
The navigational abilities of birds are partly innate and partly learned, with the result that inexperienced young migrant birds become lost more often than experienced adults. The rare visitors that excite birders, for example, are often lost immature birds (De Sante 1983).

Global navigation is a direct extension of the natural homing abilities of birds. The process of learning how to navigate globally starts early with a young bird's first explorations and, in some cases, adult leadership. Young cranes and geese undertake their first migrations with their parents in the lead. They learn the route and stopover locations from this experience. In an amazing chapter of the program to rebuild viable populations of the endangered Whooping Crane, William Lishman and his partner Joseph Duff taught young hand-reared cranes (without parents) to follow them in an ultralight plane, colored black and white like an adult crane (http://www.bringbackthecranes.org/). Step by step, they are establishing a new population that will migrate from the Necedah National Wildlife Refuge in central Wisconsin to Florida's Gulf Coast and back each year.

BOX 10–4

BABY BUNTINGS LEARN THE NIGHT SKY

Baby Indigo Buntings, hand-reared without seeing the stars, cannot orient when they are first exposed to the night sky. In fact, they must see the sky regularly during the first month of life to be able to choose their migratory direction. The axis of rotation of the night sky, which centers on the North Star, establishes their north–south frame of reference (Emlen 1970; see illustration). They then learn the constellations associated with this axis. If the axis of rotation of a planetarium sky is switched from the North Star to Betelgeuse, the brightest star in the constellation Orion in the southern sky, the baby buntings orient south in line with the new axis of rotation.



(A) Early visual experience of the natural night sky entrains an Indigo Bunting's use of the stars for orientation. (B) Buntings raised under a modified night sky that rotated around Betelgeuse instead of the North Star adopted Betelgeuse as the pole star and consistently oriented from it. Each dot represents the direction selected by one young bunting. The vectors (arrows) show the general direction of orientation. [*After Emlen 1975b*]

Aside from visual cues, the magnetic compass serves as the initial and primary basis for orientation by some young birds (Box 10–4). A young pigeon's ability to use magnetic-compass information develops first, before its ability use a solar compass. On their first flight, young homing pigeons calibrate the general direction of their outbound journey based on magnetic-field information. Reversal of this direction on the return flight establishes the "home direction" that expands to full sensitivity to the polarity and declination lines of the Earth's magnetic field. Proof of these steps comes from experiments that interfere with the exposure to natural magnetic fields. A young pigeon does not establish a home direction if it is transported in a distorted magnetic field from its nest on its first trip or if it is made to carry a magnet on its maiden flight.

After a home direction has been established through route reversal and use of the magnetic compass, however, a young pigeon adds other clues to its navigation toolbox. The addition of learned compasses, such as the solar compass, then builds the bird's integrated orientation system (Wiltschko and Wiltschko 1988). Exposure to the sun for less than 1 hour activates its solar compass. The young bird then calibrates it by reference to the magnetic compass. Refinements, including compensation for the sun's daily movement through the sky, follow with experience (Wiltschko et al. 1983).

The development of the navigation toolkit in migratory species, such as the Savannah Sparrow, follows a different sequence from that in pigeons (Able and Able 1995, 1996; Figure 10–22). Pigeons navigate locally; so they do not usually experience major changes in the angles (declination) of the magnetic field. Long-distance migrants encounter major changes in declination, extremely so for those species, such as Bobolinks, that cross the equator to winter in the southern hemisphere. In addition, they use celestial information, especially star configurations, as guidance systems. Rather than starting with a well-calibrated magnetic compass and adding other systems to it, as does the pigeon, Savannah Sparrows and other nocturnal migrants first establish their celestial compasses.

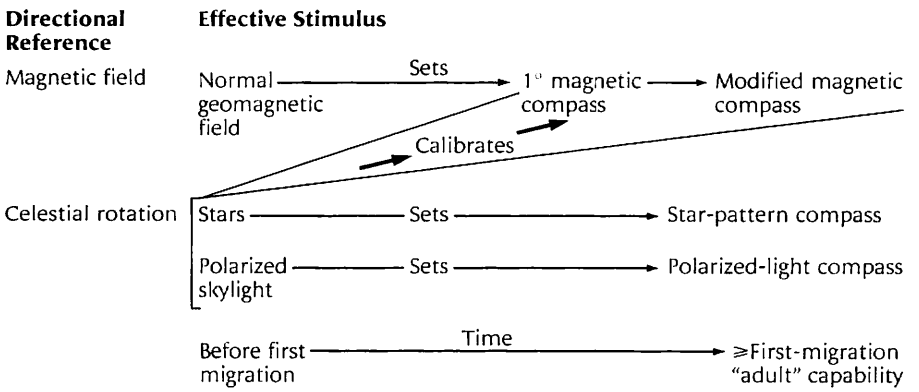


FIGURE 10–22 Development of navigation systems in the Savannah Sparrow. [*From Able and Able 1996*]

The axis of rotation of the stars in the night sky has primacy, supplemented by twilight cues, such as polarized light. These cues are of primary importance for the initial calibration of their magnetic compasses. The sparrows, as well as some thrushes (Cochran et al. 2004), also recalibrate and fine-tune their magnetic compasses regularly as adults at different locations in the course of the annual cycle.

Summary

Billions of birds migrate every fall and spring to exploit seasonal feeding and nesting opportunities. Corresponding in part to the topography of the continents, major migration routes orient north–south in North America and east–west in Europe. The migratory routes of some birds retrace the history of the expansion of the range of their species.

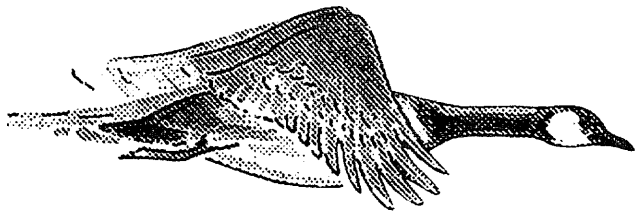
Why some populations migrate and others of the same species are sedentary is an age-old and unresolved question. The migratory habit may appear in newly established populations of nonmigratory species or, in contrast, may be lost by colonizing populations of migratory species. Tradeoffs between the costs and the benefits of migration determine how far individual birds migrate. Wintering shorebirds distribute themselves widely in relation to the food availability in coastal wetlands, with apparently no extra cost to migrating long distances to achieve energy savings.

The flights of many long-distance migrants require extraordinary physical endurance. Nonstop three- to four-day journeys across the open ocean or desert regions are fueled by reserves of fat. Small land birds have a maximum flight range of about 2500 kilometers, and shorebirds can fly from 3000 to 4000 kilometers. Regular refueling stops, however, are typical of most migrants. Shorebirds, for example, gather in vast numbers at critical en route staging areas such as the Copper River Delta in Alaska. Many birds migrate at night, when flight conditions are more favorable and predators are few.

The conservation of declining migrant species presents special challenges because they face widespread loss of suitable habitats on their wintering grounds in Central America and the Caribbean, on their breeding grounds in North America, and at critical stopover sites along their migration corridors.

Birds use different sources of information to navigate while migrating, while commuting between nest sites and feeding grounds, and while flying home after having been displaced by curious ornithologists. Birds often prefer one source if it is available and use the others when necessary. In addition to using visual landmarks such as landscapes and buildings, migrants use the sun by day and the stars by night. Birds also use olfactory cues and the Earth's magnetic field. In addition, an innate magnetic compass that includes both direction and duration serves as the platform for the development of advanced navigation abilities. Nocturnal migrants calibrate their magnetic compasses to local field conditions by using the axis of rotation of the night sky and bands of polarized light at sunset.

CHAPTER 11



Social Behavior

Social vertebrates, and particularly birds, are excellent subjects for generating and testing darwinian hypotheses about living with relatives. [Emlen 1995a, p. 8098]

Birds are both predators and prey. Their needs for food and for protection—the most pressing requirements of any living creature—determine where and how they live. These needs also determine whether they are social or asocial, cooperative or competitive. Sometimes, an individual bird should go it alone; at other times, there is safety in numbers. Ultimately, birds must share limited space. Whether breeding or not, birds space themselves at regular intervals over large territories, congregate in large numbers, or cluster together in small groups. At one extreme, Montane Solitary Eagles live in pairs on exclusive expanses of tropical forest in the mountains of South America. At the other extreme, hundreds of Sociable Weavers occupy gigantic communal nests in the Kalahari Desert in southern Africa.

Birds establish and protect their spatial relations; aggressive assertions of status or rights to resources are normal parts of avian social life. Social behaviors of individual birds—territoriality, flocking, dominance displacements—vary flexibly in relation to the mix of costs and benefits. Territorial birds, in particular, assert personal control over food supplies and mates but rarely achieve exclusive rights.

This chapter provides an overview of the major features of the social behavior of birds, including the costs and benefits of territoriality, social status, flocking behaviors, and coloniality. The first four sections of this chapter emphasize nonbreeding social behavior. The final section examines the advantages and disadvantages of colonial nesting and communal roosting. The next two chapters (Chapter 12, on mates, and Chapter 13, on breeding systems) explore the social behavior of breeding birds. Their sexual relations often do not match their overt social relations.

Individual Space

Spacing patterns depend on the scale of one's perspective. When birds fly in flocks, the distances between individual birds within a flock may be small but the distances between different flocks may be large. That said, most birds maintain a small individual space around themselves wherever they go. Swallows, for example, space themselves at regular intervals on a telephone wire (Figure 11–1). Sparrows and sandpipers feeding in large flocks also maintain small distances between one another; their individual spaces reduce hostile interactions. Certain highly social species overcome the usual tendency to stay apart. They huddle together, sometimes in large groups, to stay warm while roosting overnight (see page 158).

The tendency of individual birds to space themselves promotes uniform dispersion patterns. If birds landed on a field at random, some sites in the field would remain empty and others would receive several birds in succession, resulting in random patterns of association. Individual birds close to one another would move apart and fill the unoccupied spaces. Such regular, or uniform, dispersion patterns are typical of birds that occupy uniform habitats. Killdeers residing in large fields, Sanderlings feeding on the beach, American Robins nesting in suburbia, and American Kestrels wintering along roadsides space themselves in a regular manner.

Individual distances vary not only among species but also among individual members of the same species. Individual Barn Swallows differ innately in their sociality, as measured by the distances of their nests from those of their nearest neighbors and by the size of the colony that they join. These individual tendencies have a genetic basis that can be demonstrated by raising the young in nests of other parents and then tracking the social behavior of the young birds after they fledge (Moller 2002).

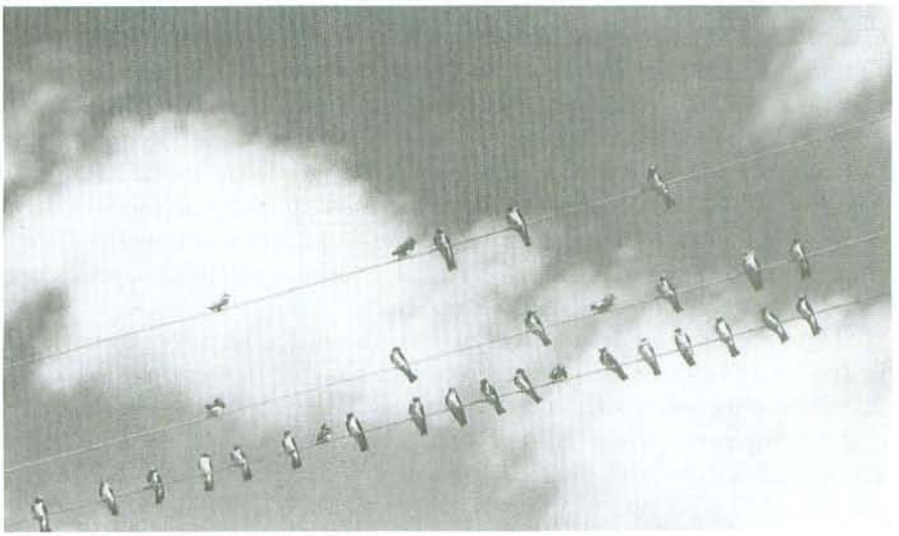


FIGURE 11–1 American Cliff Swallows space themselves at regular intervals on a telephone wire. [*Courtesy of A. Cruickshank/VIREO*]

Territorial Behavior

Territorial behavior is a primary form of aggressive spacing behavior that has intrigued naturalists since Aristotle. H. E. Howard's *Territory in Bird Life* (1920) formally introduced scientific inquiry into the subject. We now understand that territorial behavior includes diverse patterns of aggressive behavior with multiple, often overlapping functions. Not simply categorized, territorial behaviors weave together with complex social interactions that tend to change fluidly and adaptively in space and in time. That said, territorial behavior usually exhibits three major aspects (Brown and Orians 1970):

1. A territory is a fixed area defended continuously for some period of time, even if only hours, in either the breeding season or the nonbreeding season or both. It can move in location if centered on a mobile resource.

2. Acts of display or chases discourage rival birds that would otherwise enter or use the territorial space.

3. Primary if not exclusive use of a territory is thereby limited to the defending individual bird and, perhaps, its mate and progeny.

The simplest territories are those with only one type of resource, such as the food territories of hummingbirds and sunbirds in fields of flowers or those of sandpipers on a beach at low tide. At the other extreme are the all-purpose nesting territories of land birds, which serve for display, courtship, paternity, nest seclusion, and feeding. All-purpose territories enable individual birds to reserve essential resources, to reduce predation, and to control sexual interference by neighbors.

Birds broadcast their presence and intended control of a territory with loud vocalizations (see Chapter 8) or with nonvocal sounds, such as the familiar tree drumming or rapping by woodpeckers. Both males and females may display and defend, sometimes together. Territory residents chase trespassers until they leave, resorting to physical contact as needed. Sometimes these contests for the control of a territory last for hours. Beneath the conspicuous surface of territorial control and ownership exists an inconspicuous underground of subordinate individual birds, which will surface and take charge when the owner is absent or dies (see page 551).

In suitable habitats, territories are usually contiguous areas separated by well-defined, though invisible boundaries. The dense nest territories of colony-nesting Royal Terns actually pack into a hexagonal configuration resembling the cells in a bee's honeycomb (Buckley and Buckley 1977).

The territorial defense of food resources is flexible and dynamic, corresponding to the balance between its costs and its benefits. For nectar-feeding birds, the economics of territorial defense can be measured in terms of the calories invested into defense and the extra calories gained by feeding at protected flowers with more nectar (Box 11–1). Across species, territory size increases directly in relation to body size, energy

BOX 11–1

TERRITORY DEFENSE BY SUNBIRDS DEPENDS ON ECONOMICS

The costs and benefits of the feeding territories of nectar-feeding birds are unusually straightforward and easily defined. Hummingbirds and their African counterparts, the sunbirds, defend clumps of flowers for several days to several weeks or longer. Golden-winged Sunbirds in Kenya, for example, defend about 1600 mint flowers, which produce enough nectar each day to satisfy an individual sunbird's energy requirements (see illustration). Territorial sunbirds benefit by having an assured, adequate food supply. They defend these territories when the energetic benefits exceed the energetic costs of defense (Gill and Wolf 1975, 1979).

A territorial sunbird invests energy at a rate of approximately 12.5 kilojoules per hour chasing intruders. It recovers this investment and more by feeding at nectar-rich flowers on its territory, this feeding time being less than that required at nectar-poor, undefended flowers visited frequently by other sunbirds. Raising the average nectar volume from 1 to 2 microliters per flower cuts feeding time in half. The territorial sunbird, therefore, can spend more time sitting than can a nonterritorial sunbird and save energy. In this example, a defense investment of 20 minutes costing 3.7 kilojoules reduces the sunbird's total costs from 32 kilojoules per day to 26 kilojoules per day, a net savings of 6 kilojoules (Table 11–1). When the projected savings are less than the investment, sunbirds do not defend a feeding territory.

Golden-winged Sunbird, a species that often defends territories of nectar-rich flowers. [*Courtesy of C. H. Greenewalt/VIREO*]

TABLE 11–1 Energy costs of feeding on undefended and defended flowers, for the Golden-winged Sunbird

	Undefended flowers (1 μl nectar/flower)			Defended flowers (2 μl nectar/flower)		
Activity	Time spent (h)	Energy rate (kJ/h)	Energy spent (kJ)	Time spent (h)	Energy rate (kJ/h)	Energy spent (kJ)
Foraging	8	4.0	32.0	4	4.0	16.0
Sitting	—	—	—	3.7	1.7	6.3
Defense	—	—	—	0.3	12.5	3.7
Total energy spent			32.0			26.0

Energy saved by feeding on defended flowers: 6.0 kilojoules

From Gill and Wolf 1975.

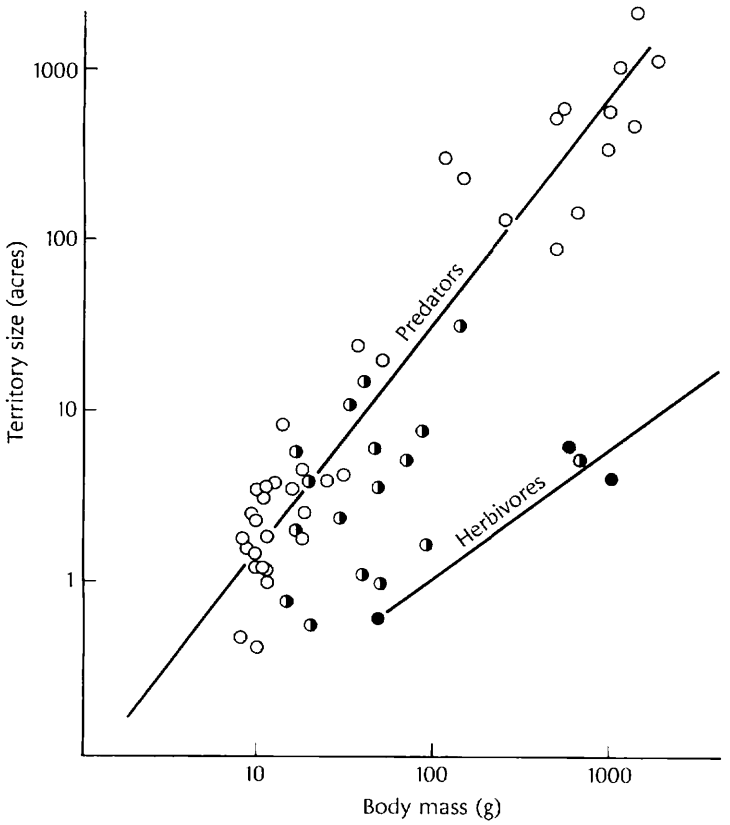


FIGURE 11–2 Territories or home ranges of birds increase directly in relation to body size, energy requirements, and selection of food types. The correlation suggests that territory size is geared to the food and energy requirements of the bird. Predators (white circles) have higher daily energy requirements than do herbivores (black circles), which have correspondingly smaller territories. Half-shaded circles indicate species with mixed diets. [*After Schoener 1968*]

requirements, and food habits (Figure 11–2). This observation suggests a general importance of food resources to the territorial individual bird. Variations within species are even more revealing. Pomarine Skuas, for example, defend small breeding territories when lemmings, their principal food, are abundant and defend large territories when lemmings are scarce (Wiley and Lee 2000). The feeding territories of hummingbirds decrease in size with increasing flower density, and thus the density of nectar.

Birds assert themselves more effectively when they are on familiar ground or on home territories than when they are strangers in a new place. The ability of territorial male Steller's Jays to win fights, for example, decreases with distance from their nesting areas rather than ceasing abruptly at a territorial boundary (Brown 1975). Territory owners usually win encounters with intruders. For one thing, the owner can use familiar details of the territory to its own advantage during high-speed attacks and chases.

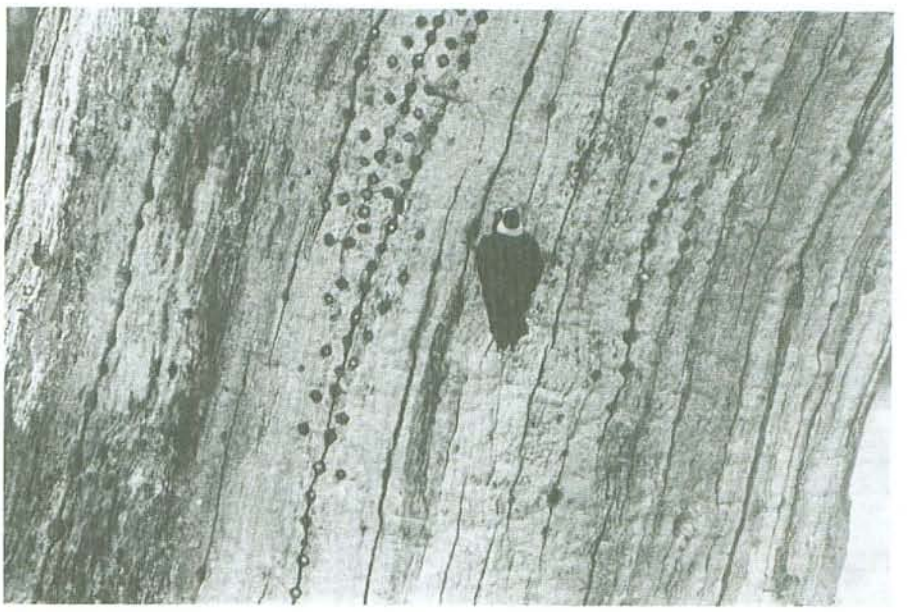


FIGURE 11–3 The granaries of Acorn Woodpeckers are valuable, defensible resources that contain essential supplies of acorns for the winter. [*Courtesy of M. H. MacRoberts and W. Koenig*]

Because territorial owners have an investment to protect, they do not usually give up a fight as easily as a newcomer. Acorn Woodpeckers, for example, vigorously defend their tree granaries against squirrels, jays, and other Acorn Woodpeckers. The granaries hold valuable stores of winter food. In addition, each of the many holes (as many as 11,000 per tree) represents an investment of 30 to 60 minutes of drilling time. These woodpeckers defend trees that are riddled with empty holes as well as those with holes that contain acorns (Figure 11–3).

Territory size also depends on the density of competitors for the available space. When population density is low, nesting American Tree Sparrows regularly use from only 15 to 18 percent of their large territories (Weeden 1965). They concentrate their activities in the core section but also defend a less frequently used buffer zone. In years of high population density and increased competition for breeding space, denser packing of smaller territories eliminates the buffer zones.

Territorial defense not only incurs costs but also produces benefits (Figure 11–4). Conspicuous display can attract predators. The time and energy required to display, to patrol territorial boundaries, and to chase intruders can be a major investment. Territoriality is favored when the resulting benefits outweigh the incurred costs. The central requirement is that adequate resources must be economically defensible (Brown 1964a). Two features of resource distribution—temporal variability and spatial variability—determine whether territories are economically defensible. Resources that change rapidly in time invite opportunistic use, not site-

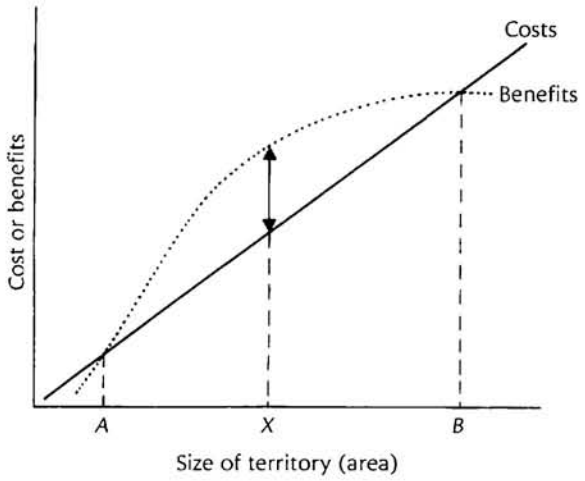


FIGURE 11–4 Territories of intermediate sizes (*A* to *B*) are economically defensible because the benefits exceed the costs. The costs of defense increase as territory size increases. The benefits relative to need (dotted line) increase rapidly at first but then reach a maximum value when needs are filled, as would be the case when food is in excess. Optimum territory size is at *X*, where the net benefit is greatest. [*From Davies 1978*]

specific investment or long-term commitment. Aerial insects whose locations and densities shift frequently, for example, are usually not defensible food resources. Territorial hummingbirds will sit side by side in a bush while they catch passing insects but will chase each other out if one or the other attempts to take nectar from the wrong flower.

Sites rich in resources may also be indefensible because they attract hordes of competitors. No gull would attempt to maintain a feeding territory on a garbage dump where thousands of other gulls vie for the same scraps. Similarly, Sanderlings do not defend their feeding territories on California beaches, when prey is either abundant or scarce (Myers et al. 1979; Figure 11–5). Beach space with dense concentrations of prey (isopods) is not defensible, because no single Sanderling can keep the hordes of other Sanderlings away. Low prey densities also are not worth defending. Sanderlings, however, vigorously defend beach territories at intermediate prey concentrations. The size of the territories they defend is then related to the required defense effort; increased competition forces smaller territories.

The territorial behavior of Sanderlings is affected by two additional factors: tide and predation risk. At high tide, they feed or roost in flocks. In years when Merlins, a small falcon, take up residence in their area, Sanderlings stay in flocks even when intermediate prey concentrations would favor territorial behavior. Isolated territorial Sanderlings would be vulnerable prey (Myers et al. 1985).

Birds typically defend territories against others of the same species. Sometimes, they also expel other species. Territorial hummingbirds defend their territories against a variety of nectar-feeding birds. Wintering

FIGURE 11–5 Sanderlings may defend exclusive feeding territories or feed in large flocks. Note the leg color band. This territorial Sanderling returned each winter to defend its section of a Texas beach. [*Courtesy of A. Amos/VIREO*]

Northern Mockingbirds defend berry-rich feeding territories against other species, especially those that would eat the berries.

Territories may be occupied and defended by a single bird, a mated or cooperating pair of birds, an extended family, or even a group of unrelated individual birds. Small groups of wintering tits and chickadees, for example, defend woodlot territories containing both food and roosting holes. Groups of unrelated Black-capped Chickadees establish common winter territories by late summer (Smith 1991). Group membership, which includes male and female pairs of both resident adults and newly settled first-year birds, is stable throughout the winter. In addition to the protection of food stores for the winter, spring territorial breeding opportunities emerge from the communal winter effort. Group defense of prime territories is also typical of a wide variety of tropical bird species that breed cooperatively (see page 391).

Migrant species returning from winter in the Tropics waste no time establishing their presence on a prime territory for nesting. Returning male Blue-winged Warblers, which winter in Central America, start singing at dawn on the first day of their return, using perches favored the preceding year (personal observation). They also feed actively on insects in the emerging leaflets (to replenish reserves used to fly north) and systematically patrol the outer edges of the territory. Fights between new arrivals may be intense or prolonged, accompanied by active singing, short flights, and aggressive display postures. But, within a week, fights subside, incited mainly by new arrivals looking for territorial openings or willing to challenge an established male. Typically, males arrive a week or more before females, which announce their presence with distinctive buzzing notes. The territorial males then redirect their attention to prospective mates.

Social Rank

Social conflict is a normal part of the daily lives of birds, causing increased concentrations of stress (glucocorticoid) hormones, among other costs (see page 257). Dominance and the aggressive reinforcement of social status reduce this conflict. Individual birds that prevail in aggressive encounters become dominant; losers become subordinate. As social ranks are established in new groups of birds, losers cease challenging dominant birds, with the result that stable dominance relations lower the frequency and intensity of overt hostility.

Dominant birds use threat displays to assert their status and reserve their access to mates, space, and food. They move without hesitation to a feeder or desirable perch, supplanting subordinates and pecking those that do not yield at their approach. Subordinates are tentative in their actions and frequently adopt submissive display postures. Age, sex, physiology, genetics, and possibly parasite load all affect dominance.

Rank has its privileges, advantages, and, potentially, some costs. High-ranking birds obtain options for access to food, reduced risk of predation

BOX 11–2

DOMINANT BLUE TITS ARE MORE CAUTIOUS THAN THEIR SUBORDINATES

Experiments with captive flocks of Blue Tits demonstrated that dominant members were more cautious during periods of danger than were subordinate members. Robert Hegner (1985) flew a model Eurasian Sparrowhawk over his aviary and watched to see which tits were the first to emerge from their hiding places to feed. Low-ranked birds fed first, followed by high-ranked birds. Hegner suggested that high-ranked birds can afford to be cautious because they have the ability to control food sources and thus to ensure adequate foraging, whereas low-ranked birds must take more chances to get to food ahead of their dominant flock mates.

(Box 11–2), and longer residency; low-ranking birds have less access to good feeding sites and are usually the first to leave. The feeding behavior of White-throated Sparrows in winter, for example, is affected both by their dominance status and by the distance of food from protective cover (Schneider 1984). Dominant birds feed more often near shelter than did subordinates, sacrificing their foraging efficiency but reducing their exposure to predators. Dominant members of species such as the Carolina Chickadee and the Tufted Titmouse stay leaner than subordinate members throughout the winter (Pravosudov et al. 1999). They add just enough fat at dusk to get through the cold night. Subordinate birds carry more fat all day long, increasing the risk of predation. The difference between them is that dominant birds can eat when they want, whereas subordinates face a less certain meal schedule.

Social status may have a major influence on stress loads and the ability of individual birds to maintain physiological balance, called homeostasis (Goymann and Wingfield 2004). Deflections from optimal balance cause the release of corticosteroids, stress hormones that are positive in the short run but are detrimental if kept at high levels. If an individual bird must fight others to become dominant and to maintain this status, its stress-hormone levels tend to be high. If, on the other hand, dominance status is inherited or due to logical succession, the hormonal costs of being dominant are minor.

Stable group membership facilitates the development of a dominance hierarchy. Most dominance hierarchies in stable bird groups and flocks are linear—or "peck right"—hierarchies, in which each bird clearly ranks above or below a set of others. Social status is directly related to age and sex. Generally, large birds dominate small ones, males dominate females, and old birds dominate young ones. Within that framework, social rank increases gradually in relation to time, individual tenure, and changes in group composition.

Generally, birds can distinguish among members of their own species by means of variations in plumage patterns, size, voice, and behavior. The extent of yellow on the bills of Tundra Swans and the variable, harlequin

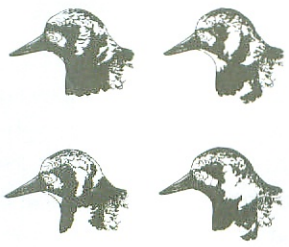


FIGURE 11–6 The harlequin face and neck patterns of Ruddy Turnstones vary among individual birds. [*From Ferns 1978*]

color patterns on the heads of Ruddy Turnstones provide a simple basis for individual recognition (Figure 11–6). Field ornithologists learn to recognize individual birds by these differences and more subtle ones—the extent of plumage wear or a missing feather in combination with eye colors or plumage colors typical of certain age and sex classes. Budgerigar parakeets can learn to discriminate among individual members of their own species in photographs (Trillmich 1976).

The varied plumage colors of Harris's Sparrows serve as badges of their social status (Rohwer 1982; Figure 11–7). Top-ranked, dominant birds have conspicuous, contrasting black markings on the plumage of the head and neck; low-ranked, subordinate birds have few such markings. Many birds are intermediate in appearance. Such variations facilitate individual recognition among the members of the large flocks that these sparrows typically form during winter.

The evolution of the variability seems directly tied to the advantages of being dominant versus the advantages of being subordinate. Dominant birds assert the prerogatives of their rank, including access to food. Conversely, subordinates of plain appearance benefit from flock membership, which they can maintain because they do not threaten the dominant birds having visual badges of high status. When dyed with black to look like a dominant bird, subordinates suffer more frequent attacks but do not rise in status, because they are not inherently aggressive.

Head-color pattern also controls social status and access to communal feeding groups of the Jackass Penguin of South Africa (Ryan et al. 1987; Wilson et al. 1987). Adult penguins, which have bold black-and-white

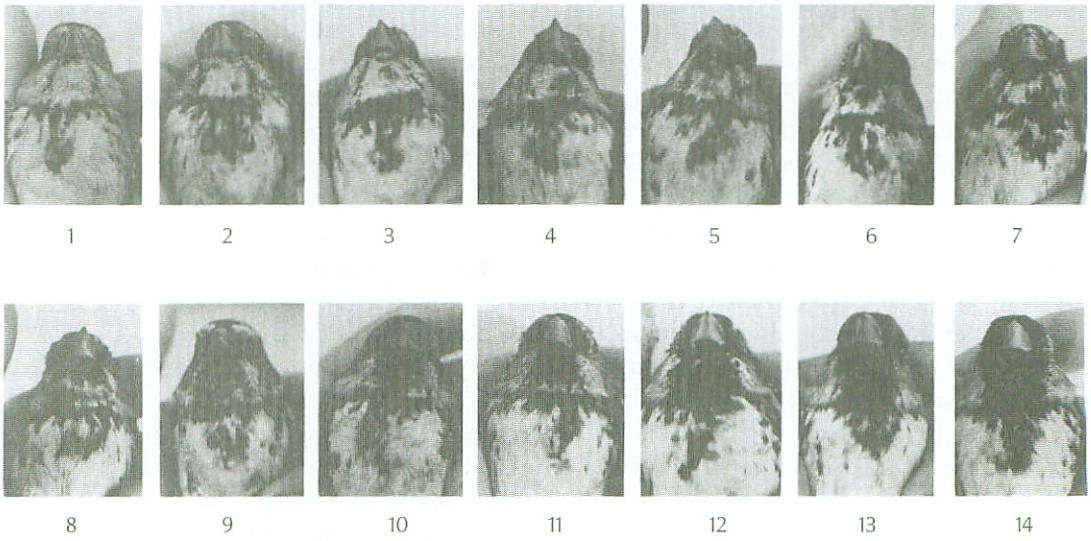


FIGURE 11–7 Plumage variations among male Harris's Sparrows indicate their social status. Dominance is correlated with an increasing extent of black markings on the head and neck: Numbers 1 through 3 are most subordinate; numbers 12 through 14 are most dominant. [*Courtesy of S. Rohwer and Evolution*]

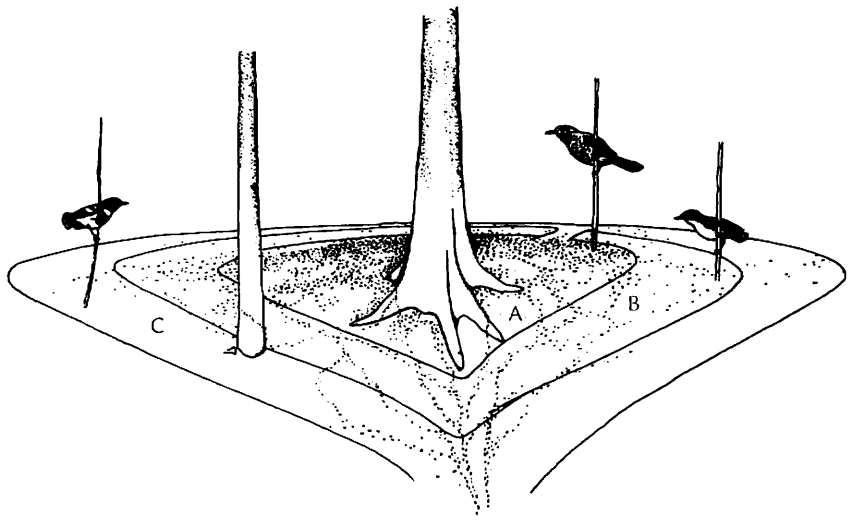


FIGURE 11–8 The hierarchy of interspecific dominance among birds that follow army ants. Large, dominant species such as the Ocellated Antbird control central sites (zone A), where foraging for flushed insects is best; they displace smaller species to outer zones—for example, Bicolored Antbirds to zone B. In turn, the Bicolored Antbirds displace Spotted Antbirds to zone C. Sometimes, a subordinate species can infiltrate the central zone, but only such zone C antbirds as the White-plumed Antbird do this regularly. [*From Willis and Oniki 1978*]

head patterns, feed communally on schools of fish. They aggressively exclude gray-headed juveniles from the communal feeding groups, because juveniles, which are poor swimmers, interfere with the coordinated adult effort. Additionally, the conspicuous black-and-white color pattern of adult plumage causes loose schools of fish to coalesce, making them easier to capture. Some older immatures, however, acquire an adult appearance by undergoing partial head molt, which reduces adult aggression and allows access to exclusive adult feeding clubs.

Even in the absence of social color badges, birds can infer their social rank relative to others by watching who is dominant to whom. Pinyon Jays of the southwestern United States form large flocks with a clear dominance hierarchy. They monitor interactions among other individual birds and decide their appropriate social rank without direct testing (Paz-y-Mino et al. 2004). Simply summarized, Jay X reasons that, if a new bird, called Jay Y, is dominant to Jay Z, known to be a dominant bird, Jay X will respect Jay Y's dominance also.

Dominance hierarchies among different species are a conspicuous feature of the associations of birds that follow raiding parties of tropical army ants. Tropical antbirds and woodcreepers habitually associate with ant swarms. These ant swarms flush large numbers of insects and small reptiles that are usually camouflaged and hard to find. More than 50 species of Neotropical birds are "professional" ant followers; that is, they obtain more than half of their food from the vicinity of ant swarms. Large,

dominant species, such as the large Ocellated Antbird, control the central zone of the ant swarm where prey are most likely to be flushed by the dense, leading columns of ants. Smaller, subordinate species such as Bicolored Antbirds and Spotted Antbirds are chased from this zone, taking up stations in peripheral, less productive foraging zones but moving toward the center when opportunity arises (Figure 11–8).

Agonistic Behavior

When two birds interact, each has selfish purposes that can foster either hostility or cooperation. Birds can manipulate one another to individual or sometimes mutual benefit. Inherent in all social interactions governed by rules is the threat of cheating by those that would take advantage of the existing system. For many years, students of bird behavior have tended to assume the morality of truthfulness in their interpretations. Now it appears that avian social communication may not be as straightforward and honest as once supposed. Individual birds serve their own interests in many ways. The nature of communication between rivals as well as between partners, therefore, invites our attention.

The competitive encounters between rivals—complex mixtures of aggression (attack, threaten) and escape (submit, flee)—are called agonistic behavior. When birds fight over something—mates, food, or territory—they usually avoid direct contact and risk of injury by using threat and appeasement displays.

Threat displays, which emphasize the bill and wings as weapons, herald a real attack if the matter is not resolved quickly. Appeasement or submission displays signal the opposite intent, a willingness to yield on the matter, a signal that defuses the conflict and thereby protects the yielding bird from direct attack (Figure 11–9). Graded or variable displays convey information about the intensity of motivation and the probability of a sender's subsequent actions. The high-crest positions assumed by a defensive Steller's Jay indicate that it will probably attack rather than flee its opponent (Figure 11–10). Often, the submissive bird turns its head and bill away from a threatening rival, a movement that reduces the level of provocation and prevents a physical attack. An appeasing avocet, for example, hides its long bill beneath its back feathers and adopts a sleeping posture. Other species fluff their feathers, in contrast with the sleeked postures associated with threat displays.

Communication of aggressive intent or submission is a central function of the social displays of birds. Even courtship usually starts with aggression by the male toward the female. If the female stays, the actions of the male shift from hostility to appeasement, subordination, solicitation, and, ultimately, the establishment of a pair bond with regular contact and copulation. The courtship of Common Black-headed Gulls illustrates this process (Moynihan 1955). Before the arrival of the females, male Common Black-headed Gulls gather in large areas near the nesting

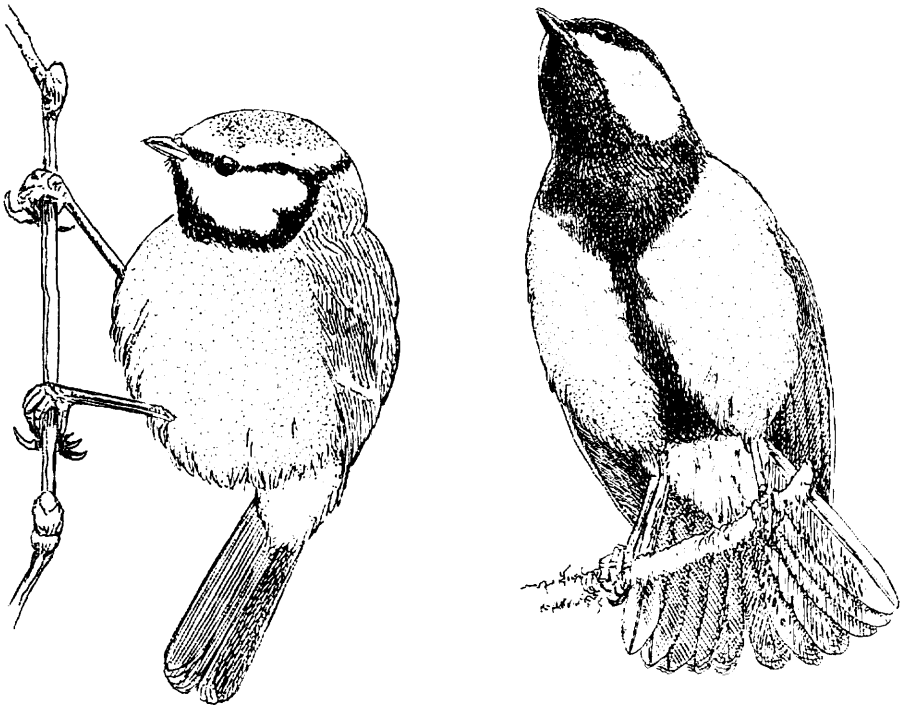


FIGURE 11–9 Threat display of a Great Tit (*right*) and submissive posture of a Blue Tit (*left*).

colony called "clubs," where each bird establishes a small temporary pairing territory. Rival males avoid physical battle and risk of injury by ritualized aggression. As they await the arrival of a potential mate, they threaten each other with the upright-threat display, with the combination long-call display and oblique display, and with the forward display attack posture (Figure 11–11). The contrast between the upright-threat display and normal posture defines unambiguously whether the recipient is welcome. If stylized threats do not succeed, physical attacks may ensue.

Female Common Black-headed Gulls visit pairing territories in the club to find a mate. A male greets an approaching female as a potential rival with the aggressive oblique display and long calls. Instead of fleeing or challenging him as would a rival male, the female gull stretches her neck upward and faces away (facing-away display), revealing her sex and her potential as a mate. In response, the aggressive male reduces the severity of his threat by redirecting the oblique display to the side. The female keeps returning to a selected male and stays longer each time. Ritualized appeasement replaces ritualized aggression. The potential mates engage in mutual displays, such as facing away. Gradually, the female moves closer and begs for food, which the male regurgitates onto the ground in front of her. Copulation follows. The male then deserts his pairing territory and assists the female in nesting and the rearing of young.

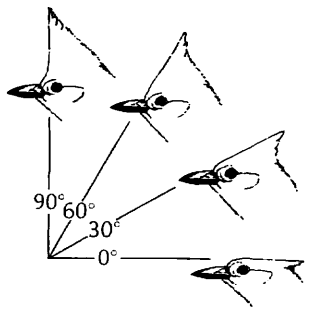


FIGURE 11–10 The positions of the crest of a Steller's Jay signal the likelihood of attack (high crest) or retreat (low crest). [*From Brown 1964b*]

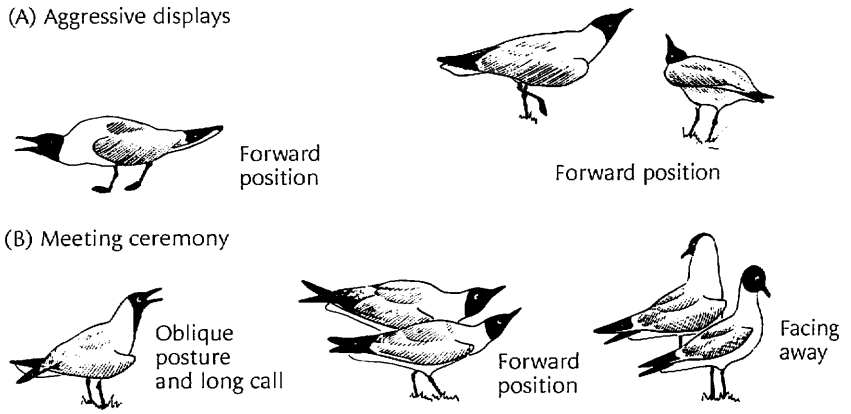


FIGURE 11–11 Displays of the Common Black-headed Gull. (A) Aggressive displays using forward postures. (B) Meeting ceremony display, including oblique display with long-call display (*left*), forward display (*center*), and facing-away display (*right*). [*From Tinbergen 1959*]

Flocks

The large flocks of wintering waterfowl, of migrating shorebirds, and even of roosting blackbirds are spectacles of nature. Flocks range in composition from loose, temporary aggregations to organized foraging associations of diverse species. At one extreme are the millions of blackbirds in the United States or the Bramblings in Europe that converge each evening at traditional roost sites. Temporary feeding aggregations of herons and seabirds also are open gatherings of individual birds responding opportunistically to special situations. Multispecies flocks of tropical birds are closed social systems, similar in many ways to much smaller family units. The members of these flocks feed together as a group throughout the year and they actively exclude new members.

Like territoriality, flock formation is a flexible behavior that includes tradeoffs between its benefits and its costs. On the positive side of the ledger, flocking behavior enables cooperative foraging and reduces the risk of predation. Members of a flock are attentive and sensitive to what their flock mates are doing and adjust their own behavior accordingly. A wealth of information is available from one's neighbors. Which ones find food and where? High on the list of costs are increased competition for limited food supplies, increased risk of disease, and increased aggression to maintain individual distances.

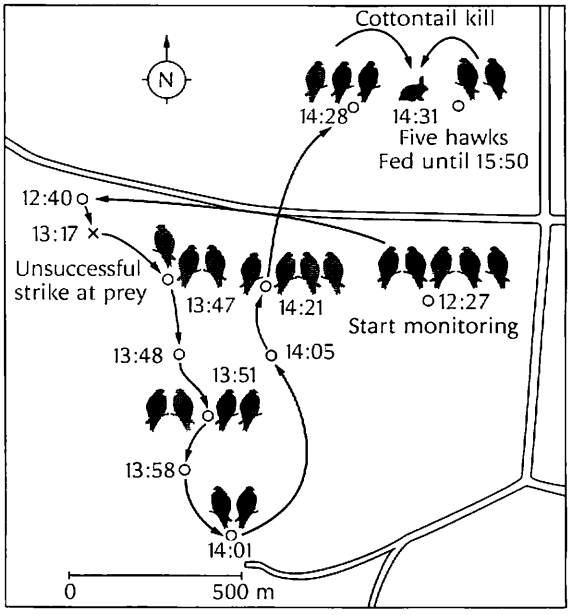
Feeding in Flocks

Casual aggregations of individual birds at rich feeding grounds are fortuitous, but why do unrelated birds form stable foraging partnerships? Some of the advantages are straightforward, practical ones, including cooperative feeding. At one level, flock members may simply benefit from the

BOX 11–3

HARRIS'S HAWKS HUNT IN TEAMS

Family hunting parties of two to six Harris's Hawks cooperate to catch rabbits (Bednarz 1988; and see illustration). The hunting party assembles at dawn and then splits into small subgroups that search for prey by moving in a coordinated "leapfrog" fashion through the desert scrub. They then converge on a rabbit that is spotted and kill it with successive, relay strikes by different hawks. When a rabbit hides in thick cover, the group surrounds the area and waits for one or two of its members to deliberately flush the rabbit into the open. All members of the party then feed on the kill. Team hunting improves the probability of catching a rabbit and raises the average amount of energy available to each hawk relative to that available when hunting alone. Team hunting also enables these hawks to kill larger prey than they could by hunting alone. Before this study was undertaken, cooperative hunting and sharing of prey had been documented only for large social mammals such as lions.



Sequence of movements of Harris's Hawks that culminated in the capture of a rabbit. Although all five hawks in the group remained in view, Jim Bednarz and his assistants specifically monitored a subunit that included hawk number 995, which wore a radio. Perched hawks in this illustration indicate the number of hawks that joined the subunit at each location. Subunit size remained unchanged from the preceding location if no hawks are pictured. [*From Bednarz 1988, with permission from Science*]

"beater effect"; prey that is flushed (and missed) by one bird can be grabbed by another. Ground hornbills in Africa, for example, walk in a line across fields to catch insects flushed by one another. Drongos and flycatchers participate in mixed foraging flocks and specialize in prey flushed by other birds. At a more advanced level, flocks of pelicans deliberately encircle and trap schools of fish in shallow water. At a still more advanced level, predators, from ravens to hawks, hunt cooperatively (Box 11–3).

The advantages of social foraging fall into two main categories: information sharing and producer-scrounger (Giraldeau and Caraco 2000). Sharing successes in finding food defines information-sharing models. All birds in the flock search for food, and then they benefit from a discovery by one of them, as in the subadult ravens (see page 322). This behavior is common among social animals of all kinds (Giraldeau and Beauchamp 1999). Group foraging by pigeons and titmice helps them to find food because members can join successful individual birds at rich

clumps or concentrate their search efforts nearby (Krebs 1973). Groups of four titmice in captivity found more hidden food together than alone. They watched one another's successes and modified the intensity and direction of their searches accordingly.

Information sharing, however, leads to selfish behaviors and cheating. Dominant birds can usurp the sites discovered by subordinate members of the flock or pilfer hidden food (see page 205). Some birds may not look for food themselves but rely on others to find it. The exploitation of actively searching birds defines producer-scrounger models. Some birds (scroungers) don't look for new food patches themselves but, instead, wait for others (producers) to find food and then eat some of it. Competition increases at small food patches and with the number of scroungers trying to take advantage of the discovery. Flocks of Scaly-breasted Munias, also called Spice Finches, typically include both producers and scroungers. Producer munias have definite strategies that match predictions (Beauchamp and Giraldeau 1997). They abandon discovered food more frequently once scroungers arrive when it is easy to discover another patch of food. They also move on predictably when more scroungers are present or when the patch of food is small.

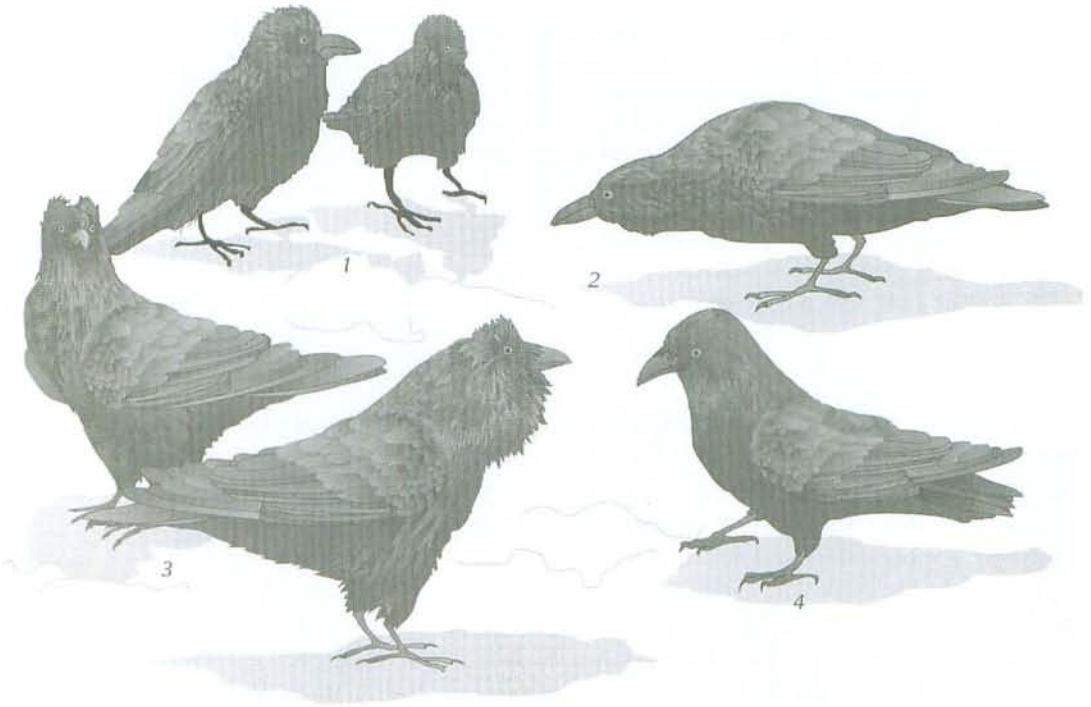


FIGURE 11–12 Postures and feather positions portray a Northern Raven's social status. A vagrant at an adult-protected carcass (1) keeps its head up and the feathers on its head fluffed out. A raven first approaching food (2) lowers its head. When juveniles swamp a carcass, a resident adult performs a dominance display (3), which includes erect posture, raised bill, raised earlike feathers and fluffed-out throat and leg feathers. A raven at an uncontested food source (4) holds its head up and keeps its feathers smooth across its head. [*From Heinrich and Marzluff 1995*]

Groups of young or subordinate birds gain access to defended food sources by outmaneuvering or just overwhelming dominant or territorial birds. Northern Ravens, for example, depend on carcasses of moose or other large animals to survive the winter. Resident adults usurp and defend these valuable finds for themselves (Heinrich and Marzluff 1995; Figure 11–12). They can defend a carcass successfully against fewer than nine subadult ravens. In response, a wandering subadult actively recruits other subadults. It does so by using a loud vocalization, called the "Yell," and by leading others from communal roosts to the food. Typically, the subadult circles a newfound carcass but does not feed. It flies off and returns the next day with a "gang" of 40 other ravens that proceed to overwhelm the adult defenses. In the course of a week, the gang grows to 100 or more ravens drawn to the noise or to their well-fed roost mates. What appears to be altruistic behavior—sharing limited food resources with unrelated ravens—is really in a young raven's self interest. It gets access to the carcass that it spotted and participates in a wide-ranging, all-winter network of carcass discovery and social availability.

Safety in Flocks

Joining a flock theoretically decreases the risk of being caught and eaten, because there is safety in numbers. A bird's chances of being a victim decrease as the number of potential victims in the flock increases, and they decrease even further for birds near the center of the flock (Hamilton 1971; Figure 11–13). Field observations support this logic. The hunting success of a Merlin, for example, varied according to the size of sandpiper flock that it attacked (Page and Whitacre 1975). It fared poorly with medium-sized sandpiper flocks but did well with isolated birds and with large flocks, which were less able to maintain a tight formation.

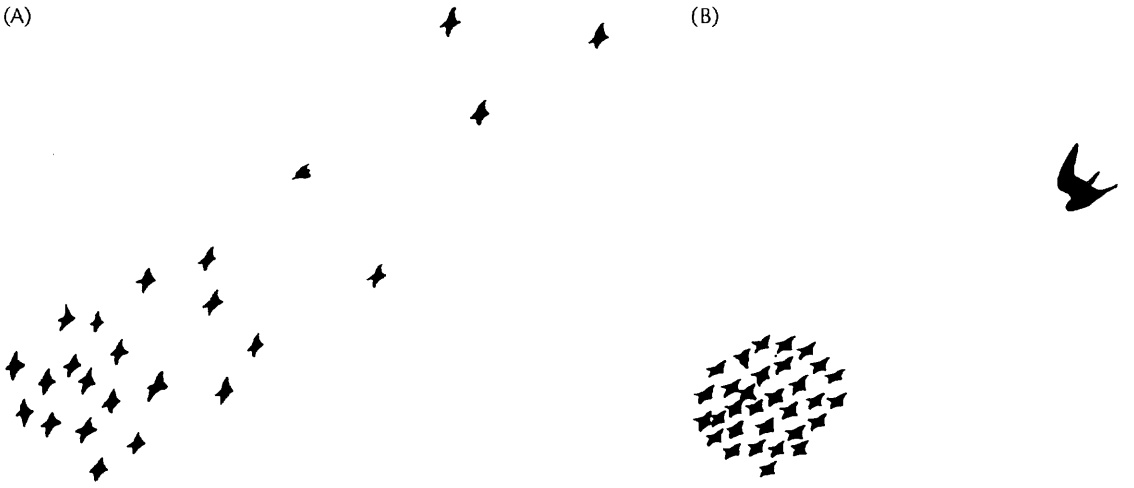


FIGURE 11–13 Common Starlings, which normally fly in (A) loose flock formations, form (B) tight formations when threatened by a hawk. [*From Tinbergen 1951*]

BOX 11–4

OPTIMAL SIZE OF A QUAIL COVEY

Northern Bobwhites feed, roost, and travel in groups called "coveys" in the fall and winter. The coveys hold tight when approached by a predator, including a hunting dog that points them until its master hunter catches up. The coveys then explode as if on cue, causing poor shots by novice quail hunters.

Covey sizes in Kansas range from 2 to 22 quail (Williams et al. 2003). Larger coveys exhibited reduced individual vigilance, increased group vigilance, faster detection of predators, and more time spent in exposed feeding areas. Individual survival was lower in small coveys than in large coveys. However, optimal covey size was only 11 quail. Large coveys also had low individual survival owing to increased competition for food and thus lower body weights, as well as more movement and exposure to predators. The intermediate covey sizes achieved the best individual survival because of the combination of low group movement, improved foraging efficiency, and better individual predator detection.

Predator detection improves in flocks; greater individual security is the result. Ostriches, for example, stick their heads up randomly to look for lions that may be stalking them; at any given time, at least one in the flock functions as a lookout (Bertram 1980). Group vigilance increases with covey size of the Northern Bobwhite, but big coveys are not necessarily best (Box 11–4).

Flock members warn one another of danger so that they can hide or flee at the same time (Box 11–5). Ducks signal one another with head bobs to flush together at the approach of a predator. Alarm calls serve to alert other members of a social group to possible danger. Giving an alarm call would seem advantageous to all but the one that revealed its position by calling. Warning calls thus seem to be heroic or altruistic acts, but they carry benefits for the caller as well if others in the flock are genetic relatives, such

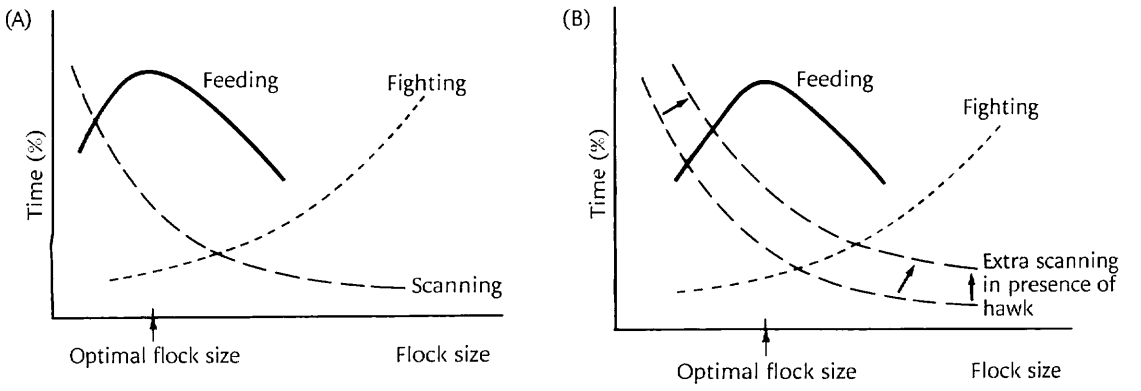


FIGURE 11–14 (A) The optimal flock size theoretically results from a balance between time spent fighting other members of the flock, time spent scanning for predators, and time spent feeding. An intermediate flock size permits the most feeding time. (B) When a predator hawk is present, more time must be spent scanning and the optimal flock size increases. [*After Caraco et al. 1980*]

as siblings, parents, or offspring. Each flock member can also count on a certain degree of reciprocity. Most important, by calling loudly, the potential victim robs a predator of the element of surprise and thereby reduces the likelihood of attack. By warning others in the flock, the vigilant sounder of an alarm reduces its own danger as it alerts kin and neighbors.

By relying in part on such mutual protection, each individual bird in a flock can actually be less vigilant—that is, spend less time looking for predators, as well as more time feeding, than when alone. The time saved by each bird in a flock because of decreased vigilance, however, is offset by aggressive interactions, which increase in frequency with group size (Caraco 1979). The amount of time available for feeding should, therefore, be greatest in flocks of intermediate size. Moreover, optimum group size should increase when predators are near and when each bird must spend more time in surveillance, which was confirmed by Thomas Caraco and his colleagues (1980) in classic studies of Yellow-eyed Juncos in Arizona. In one experiment, average flock size increased from 3.9 to 7.3 juncos when he flew a tame Harris's Hawk regularly over the feeding grounds (Figure 11–14).

BOX 11–5

WANTED: EXPERIENCED PARROT FLOCKS FOR CONSERVATION

The only two parrots native to North America disappeared 50 years ago. Subsistence hunting and habitat degradation exterminated their populations. One of them, the Carolina Parakeet of the eastern United States, is surely extinct, but declining numbers of the other species, the larger Thick-billed Parrot, persist in high mountain refuges in western Mexico. Noel Snyder and his colleagues have undertaken an ambitious conservation program to restore Thick-billed Parrots into the rugged Chiracahua Mountains of southeastern Arizona, where they once lived (Snyder et al. 1999). They used the captive-bred offspring of confiscated Thick-billed Parrots from the illegal pet trade. Their initial efforts were often thwarted because the young parrots lacked predator-avoidance training by experienced flock mates.

Experienced wild Thick-billed Parrots protect themselves from hawks through their wary, vigilant social behavior and through their ability to outfly a pursuer. Northern Goshawks, which are common in the Arizona mountains, found inexperienced, captive-bred parrots to be easy prey because they did not scan the sky for predators, did not freeze or flee when they saw one, and did not react quickly enough to alarm calls of experienced wild birds. The captive-bred birds seemed fearless, despite the fact that they had seen raptors in action from their cages.

Study of their behavior revealed that strong socialization with experienced flock mates is required to learn essential survival skills. The captive-bred birds also required lots of exercise to attain the condition required to keep up with wild flocks and to fly faster than a pursuing hawk. Further, flock mates teach one another to identify pine cones as food sources and how to extract the seeds from them. Finally, well-socialized parrots develop an essential sense of security. Without the sense of security that comes from joining other parrots to feed, pairs of adults seem unwilling to undertake the risks of breeding. The future success of such parrot-conservation programs will depend on the training and gradual release of socially mature flocks of birds that work together to find food and avoid predators.

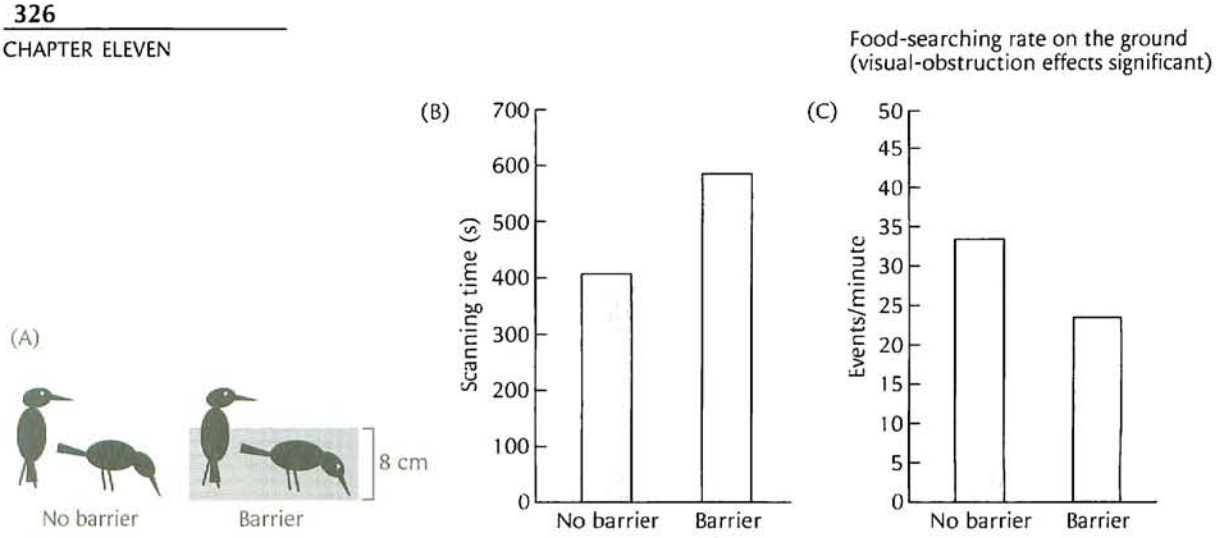


FIGURE 11–15 Blocking the view of their flock mates causes Common Starlings to increase their time scanning and directly checking what their neighbors are doing. This imposes a cost to their foraging time: (A) experimental setup for determining the effect of an 8-centimeter barrier on the ability of a starling to see other starlings while its head is down; (B) effects of the barrier on scanning time when starlings were 3 meters apart; (C) effects of the barrier on food-searching rate (events per minute) when starlings were 3 meters part. [*After Fernández-Juricic et al. 2005*]

The foraging and scanning behavior of Common Starlings is sensitive to that of their flock mates. They increase their search efforts and success at feeding if others in the flock are doing so. They increase their rate of scanning for predators when others in the flock do so. In a clever experiment, Esteban Fernández-Juricic and his colleagues (2005) made it harder for starlings to keep an eye on their neighbors while feeding (Figure 11–15). The starlings spent more time scanning and less time searching for food when a barrier blocked their view while feeding.

When they discover a predator, such as an owl or a snake, birds scold them vocally and sometimes attack them physically. The advantages of mobbing behavior include discouraging or driving away an enemy. In addition, mobbing refines an individual bird's ability to recognize predators, which reduces future risk to self and family. Inexperienced birds quickly associate potential danger with the commotion of mobbing behavior. They then learn to recognize predators by observing the mobbing behavior of their parents or their flock mates. Common Blackbirds of Europe will even learn to attack a detergent bottle if, in experiments, they are tricked into associating the mobbing behavior of others with such an inanimate object (Curio et al. 1978). Species that join mixed-species foraging flocks tend to respond reciprocally to one another's alarm calls and to mob predators cooperatively, possibly sharing their knowledge of potential enemies (McLean and Rhodes 1991).

Mixed-Species Flocks and Social Signals

Flocks are not limited to members of the same species. Rich assemblages of different species form foraging flocks. Flocks of chickadees, titmice, nuthatches, woodpeckers, creepers, and other associates are familiar both in the United States and in Europe, and several species of warblers may join them in the warmer months. Noisy gatherings of antbirds, antwrens, woodpeckers, flycatchers, and honeycreepers surge through the rain forests of South America. Tropical flocks may include 60 birds of 30 different species, whereas temperate flocks average 10 to 15 birds of 6 or 7 species. Curiously, flock size increases primarily as a result of the addition of new species, not more individual birds of a few species. Furthermore, flock composition changes regularly as the flock moves along, a result of new birds joining and others leaving. Individual birds join the flock as it moves through their territory, only to be replaced by neighbors as the flock moves from one territory to the next.

Flock structure is defined by one or more so-called nuclear species that attract other species and that lead the flock's movements. In temperate-zone woodlands of North America, for example, titmice and chickadees are nuclear species. Large antbirds and greenlets take this role in lowland tropical forests. In eastern Peru, the Bluish-slate Antshrike and the Dusky-throated Antshrike assemble 30 other species with their loud rallying calls early every morning. Plain-colored Tanagers and Blue-gray Tanagers are the usual nuclear species in canopy flocks in lowland Panama. Other species, the "followers," join the flocks opportunistically and are subordinate to the nuclear species.

Why do birds of diverse species assemble to feed together? In particular, why do subordinate species join the nuclear species? Reduced predator vigilance and increased foraging efficiency are part of the answer. Downy Woodpeckers, for example, sacrifice feeding time for high levels of vigilance when foraging alone (Sullivan 1984a, 1984b). They stop frequently to look for predators, with a distinctive head-cocking behavior. When they feed with large mixed-species flocks, they cock their heads infrequently and feed at higher rates. The woodpeckers monitor the calls of flock mates to assess their numbers and their tendency to be alarmed by possible predators.

Territorial or rare species that are unable to put together a flock of their own kind can benefit by flocking with other species even though they are subordinate. Their foraging success increases in such flocks. Mixed flocks of several species, each with its own searching skills, increase total scanning efforts for clumped, unpredictable prey. Individual birds of different species monitor one another's foraging success and then modify their search efforts accordingly. Similar advantages accrue to the mixed-species nesting colonies of herons, storks, and ibises. Their combined numbers maximize antipredator behavior, social interactions, and information transfer, but their ecological differences minimize nest competition and food competition (Burger 1981).

TABLE 11–2 Birds that flock together in the mountains of tropical America

Western Panama (black and yellow)	Northern Andes (blue, blue and yellow)	South Central Andes (blue, chestnut)
Yellow-thighed Finch	Blue-and-black Tanager	White-browed Conebill
Yellow-throated Brush Finch	Blue-capped Tanager	Blue-backed Conebill
Sooty-capped Bush Tanager	Santa Marta Mountain Tanager	Chestnut-bellied Mountain Tanager
Silver-throated Tanager	Hooded Mountain Tanager	Black-eared Hemispingus
Slate-throated Whitestart	Masked Mountain Tanager	Golden-collared Tanager
Collared Whitestart	Blue-winged Mountain Tanager	Plushcap
Black-cheeked Warbler	Buff-breasted Mountain Tanager	

From Moynihan 1968.

The advantages of multispecies feeding associations are so marked that, in some cases, unrelated bird species have similar plumage color patterns that promote flock cohesion. Subordinate species increase acceptance by resembling dominant flock members. The color patterns of birds that flock together in the mountains of Central and South America offer striking examples of such social adaptations (Table 11–2). Those species that participate regularly in the montane flocks of western Panama are typically black and yellow, sometimes variegated with brown and white. Bright blue or combinations of blue and yellow prevail, instead, in the humid temperate region of the northern Andes. Farther south, in Bolivia, the flock colors are blue or blue gray above and chestnut below. Such distinctive color patterns possibly serve as flock "badges," which enhance the social integrity of multispecies flocks.

Colonies

About 13 percent of bird species, including most seabirds, nest in colonies (Figure 11–16). Colonial nesting evolves in response to a combination of two environmental conditions: (1) a shortage of nesting sites that are safe from predators and (2) abundant or unpredictable food that is distant from safe nest sites (Siegel-Causey and Kharitonov 1990). Colonial nesting has both advantages and disadvantages (Box 11–6). First and foremost, individual birds are safer in colonies that are inaccessible to predators, as on small rocky islands. In addition, colonial birds detect predators more quickly than do small groups or pairs and can drive the predators from the vicinity of the nesting area; in one classic example, the effectiveness with which Common Black-headed Gulls mobbed predators increased with the number of participants (Kruuk 1964). Because nests at the edges of breeding colonies are more vulnerable to predators than those in the centers, the preference for advantageous central sites promotes dense centralized packing of nests.

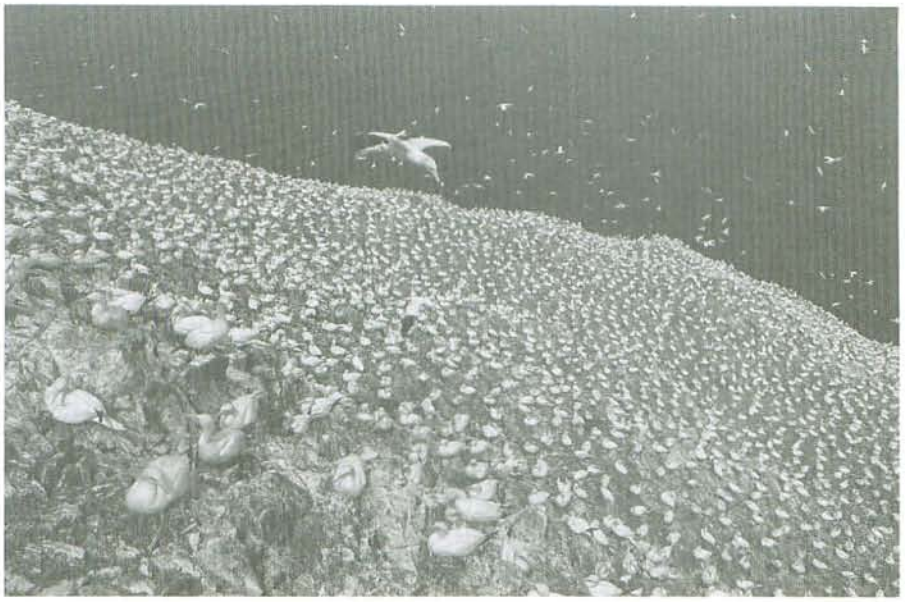


FIGURE 11–16 Northern Gannets, an abundant seabird of the North Atlantic, nest in densely packed colonies on oceanic islands. [*Kevin Schafer/CORBIS*]

Coordinated social interactions tend to be weak in the initial evolutionary stages of colony formation, but true colonies provide extra benefits. Synchronized nesting, for example, produces a sudden abundance of eggs and chicks that exceeds the daily needs of local predators. Additionally, colonial neighbors can improve their foraging by watching others. This behavior is especially valuable when the off-site food supplies

BOX 11–6

COLONIALITY IN YELLOW-RUMPED CACIQUES REDUCES PREDATION

The Yellow-rumped Cacique nests in colonies in Amazonian Peru. These tropical blackbirds defend their closed, pouchlike nests against predators in three ways (Robinson 1985). First, by nesting on islands and near wasp nests, caciques are safe from arboreal mammals such as primates, which destroy more accessible colonies of other birds. Caimans and otters also protect the island colonies by eating snakes that try to cross the open water surrounding the colony. Second, caciques mob predators as a group. The effectiveness of mobbing increases with group size, which increases with colony size. Third, caciques hide their nests from predators by mixing active nests with abandoned nests. Overall, nests in clusters on islands and near wasp nests suffer the least predation. Female caciques switch colonies after losing nests to a predator, usually to sites that offer better protection against that predator. By such mechanisms, the best colony sites accumulate the largest numbers of nests.

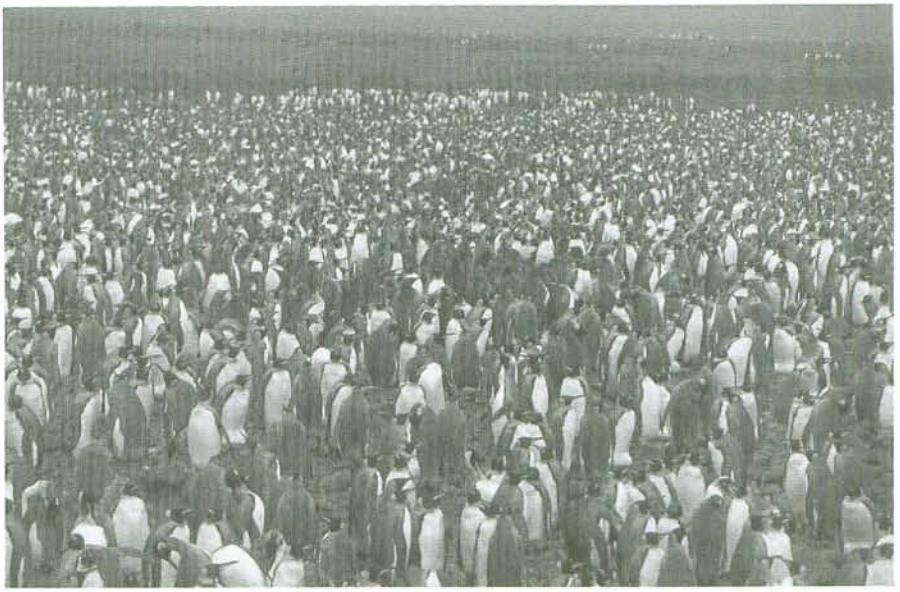


FIGURE 11–17 A large nesting colony of King Penguins on Possession Island, Crozet archipelago. The large, dark "furry" ones in front are young penguins. [*H & J Eriksen/VIREO*]

are restricted or variable in location, as are swarms of aerial insects harvested by swallows or schools of small fish harvested by seabirds (Figure 11–17). The colonies of American Cliff Swallows, for example, serve as information centers from which unsuccessful individual birds follow successful neighbors to good feeding sites (Brown and Brown 1995). Cliff swallows that were unable to find food returned to their colony, located a neighbor that was successful, and then followed that neighbor to its food source. All birds in the colony were equally likely to follow or to be followed and thus contributed to the sharing of information that helped to ensure their reproductive success. As a result of their enhanced foraging efficiency, parent swallows in large colonies returned with food for their nestlings more often and brought more food each trip than did parents in small colonies.

To support large congregations of birds, suitable colony sites must be near rich, clumped food supplies. Colonies of Pinyon Jays and Red Crossbills settle near seed-rich conifer forests, and Wattled Starlings nest in large colonies near locust outbreaks. The huge colonies of Guanay Cormorants and other seabirds that nest on the coast of Peru depend on the productive cold waters of the Humboldt Current. The combination of abundant food in the Humboldt Current and the vastness of oceanic habitat can support enormous populations of seabirds, which concentrate at the few available nesting locations. The populations crash when their food supplies decline during El Niño years.

Among the costs, colonial nesting leads to increased competition for nest sites and mates, increased cuckoldry, the stealing of nest materials,

and increased physical interference. In spite of food abundance, large colonies sometimes exhaust their local food supplies and abandon their nests.

Large groups also attract predators, especially raptors, and facilitate the spread of parasites and diseases (Tella 2002). The globular mud nests in large colonies of the American Cliff Swallow, for example, are more likely to be infested by fleas or other bloodsucking parasites than are nests in small colonies (Brown and Brown 1986). Experiments in which some burrows were fumigated showed that these parasites lowered survivorship by as much as 50 percent in large colonies but not significantly in small ones. The swallows inspect and then select parasite-free nests. In large colonies, they tend to build new nests rather than use old, infested ones. On balance, the advantages of colonial nesting clearly outweigh the disadvantages, given the many times at which colonial nesting has evolved independently among different groups of birds. Still lacking, however, is a general framework for testing different hypotheses for the evolution of coloniality (Danchin and Wagner 1997).

Communal Roosts

Large numbers of some bird species congregate for the night in communal roosts, especially during the nonbreeding seasons. The evening flights of crows and their relatives, herons and waterfowl of many species, Yellow-headed Blackbirds, Common Starlings, and many others converge to their respective roost sites by the thousands—millions in some cases. Communal roosting potentially confers many of the same benefits as does colonial nesting—reduced predation, increased foraging efficiency, and, sometimes, reduced energy expenditures for thermoregulation (Beauchamp 1999). A role as information center emerges as one of the best demonstrated of these benefits.

Experiments with Northern Ravens in Maine illustrate how individual birds learn where to look for food on the day after a carcass discovery (Marzluff et al. 1996; Marzluff and Heinrich 2001). Their interactions at a carcass were described earlier, including the need of young birds to recruit allies to get past adults that defend a carcass. In this experiment, naive ravens released into a roost followed roost mates to their feeding sites the next morning. Conversely, 3 of 20 ravens released at a carcass led roost mates to it the next day. Four additional lines of evidence from this study support the information-center hypothesis:

1. The roosts included knowledgeable and naive foragers.
2. Most roost members departed together in one direction in the morning.
3. The departure direction changed from day to day.
4. The same individual birds switched leader and follower roles, depending on their knowledge of where food was.

Such information exchange increases foraging efficiency and leads to more intricate social interactions, including dominance relations and mate choice, in the complex societies of these intelligent birds.

Summary

The defensibility of a given space, the variability of food resources, and the probability of attack determine spatial relations and social behavior. Territorial behavior is characterized by acts of display intended to discourage the presence of rivals and by the exclusive continued use of a defined area by the defending individual bird and perhaps its mate and progeny. The relative costs and benefits of territorial behavior govern its flexible expression. Dominance status structures the relations among individual birds in flocks, a system that reduces strife. Differences in plumage color may serve as badges of dominance status.

Flock formation reduces the risk of predation and improves foraging efficiency. Flock members benefit from one another's vigilance for danger as well as from one another's prospecting for scarce food. Team hunting improves feeding success in some species. Flocks may be loose opportunistic aggregations or highly structured social systems with closed memberships. Mixed-species flocks increase the benefits of mutual protection without the costs of sharing space or food with competing members of the same species. The advantages of membership in mixed-species flocks may promote convergence in plumage color patterns and social "mimicry."

Many bird species congregate in large numbers to nest in colonies or to roost communally. Reduced predation risk in safe places, by virtue of large numbers and through group defense, is one of the primary benefits. Reduced energetic demands of thermoregulation, especially in cold climates or seasons, is another benefit. Studies of swallows and ravens demonstrate that colonies and roosts also serve as information centers where young or unsuccessful birds can follow others to new food locations.

PART 5

AVIAN LIFE HISTORIES

CHAPTER 12

Mates

The application of molecular genetic techniques has revolutionized our view of avian mating systems.

[Griffith et al. 2002, p. 2195]

The eggs of the flightless Brown Kiwi are huge, each 25 percent of a female kiwi's body size (Figure 12–1). They are an extreme example of a female bird's reproductive investment. In contrast, male kiwis and other birds invest differently, producing vast numbers of tiny sperm, capable of fertilizing many such eggs.

The different investments that males and females make in their gametes drive different options for maximizing individual reproductive success, including their mating opportunities and how best to invest in quality offspring. Most birds form a pair bond with a bird of the opposite sex. They raise their offspring together because both parents are needed to provide adequate care. But, beneath the veneer of cooperation lie major conflicts of interest and cryptic initiatives. Females have an arsenal of ways to protect their investments in large, expensive eggs. Males, instead, must balance the options of mating with extra females against caring for their own young.

Conversely, females can improve the quality of their offspring through extra-pair copulations with high-quality males. DNA fingerprinting analyses reveal chicks fathered by neighbors in most broods. In Red-winged Blackbirds, for example, from 23 to 48 percent of nestlings are sired by a male neighbor, not by the female's mate (Yasukawa and Searcy 1995). In addition, females that consort with neighbors produce more young than do females that are faithful to their mates. Adding further uncertainty to the genetic identity of chicks in a single nest is the possibility of brood parasitism by other females, resulting in nestlings unrelated to either parent.

This chapter starts with a look at the attributes that affect birds' lifetime reproductive success. Front and center are the challenges of mate choice. Pair formation requires critical assessment of potential mates,

FIGURE 12–1 The Brown Kiwi produces an enormous egg relative to its body size. This species provides an extreme example of the great investment of reproductive energy that female birds put into egg production. This x-ray reveals the egg in the oviduct just before laying. [*Copyright 1978 by the Otorohanga Zoological Society, used with permission*]

especially by females, which are able to evaluate traits that may indicate a male's quality. Females can use elaborate male courtship displays and plumages to assess male condition, but these displays and plumages may also help males to achieve dominance and access to females. Featured examples include species that display on communal courtship grounds known as leks, such as manakins and Ruffs, as well as bowerbirds and their artistic crafts. The chapter concludes with an overview of monogamy (one male to one female), the most common avian mating system, with emphasis on the role of the extra-pair copulations that sire a substantial fraction of offspring in most species of songbirds. Alternative breeding systems—polygyny (one male to multiple females), polyandry (one female to multiple males), promiscuity, brood parasitism, and cooperative breeding—are the province of Chapter 13.

Life-History Strategies

Natural selection favors individual birds that achieve the greatest lifetime reproductive success. The acquisition of a prime mate is a first and critical step toward success. Different investments into annual reproductive efforts then add to the diverse life histories of birds. Some birds lay many eggs, whereas others lay just one. Some birds typically live for decades and others for just two or three years.

Inherent in such strategies are tradeoffs between annual reproductive investment and longevity. Individual Common Kestrels that fledge fewer young each year live longer (see Figure 17–9). To maximize their contribution to the next generation, individual birds must achieve optimal combinations of variables that affect their lifetime reproductive output. For example, the costs and often poor results of attempts to breed by yearling or inexperienced birds favor delayed maturity in some species. Recall the costs of prolonged molt incurred by male American Redstarts that invested more time in parental care during the summer (see page 266).

Field experiments demonstrate the interdependence of life-history traits and the expression of sexual plumage badges of male Collared Flycatchers (Gustafsson et al. 1995). Males with large white forehead patches mate with more females and achieve higher lifetime reproductive success than do males with smaller patches (Figure 12–2). However, increased parental effort, imposed by experimentally adding more young to a nest, causes a male's forehead patch to be smaller the following year. Such a male then suffers a reduction in its breeding success in subsequent years, with cascading negative effects.

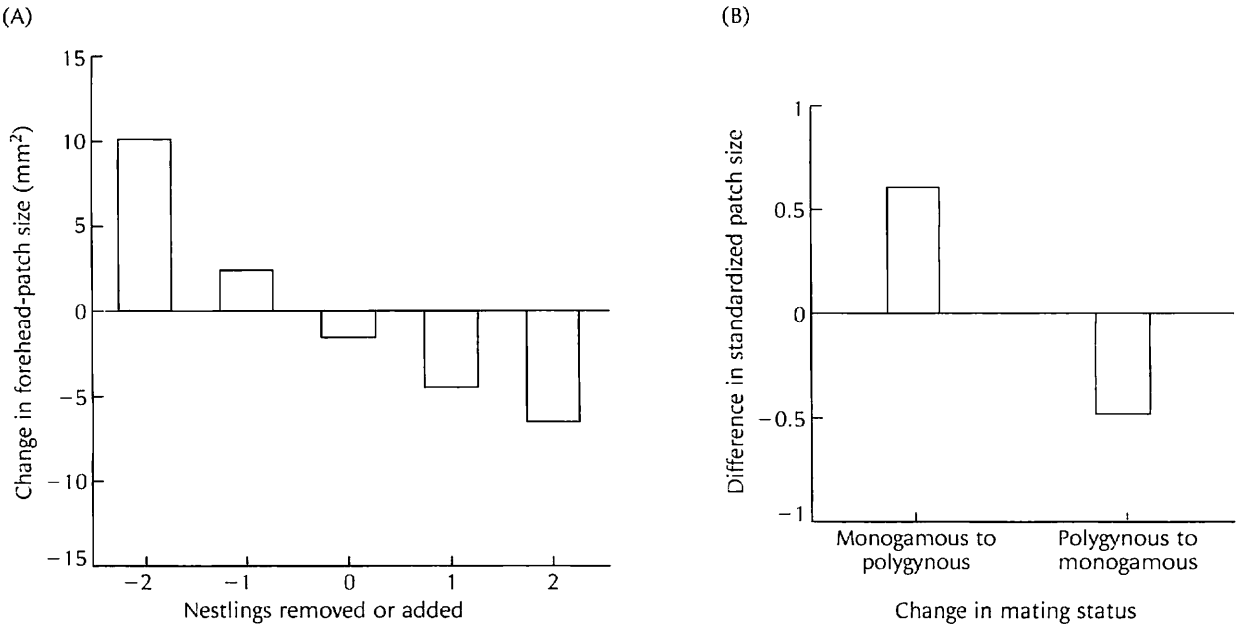


FIGURE 12–2 Collared Flycatcher experiments demonstrate the tradeoffs between reproductive effort and size of their white forehead patch. Males with large patches are more likely to win territorial disputes and produce more young per breeding attempt. But extra reproductive effort in one year leads to smaller sizes of the white-colored forehead patch in the following year. (A) Experimental decreases in the number of young in a nest fostered an increase the next year in the size of the forehead patch of the males that tended those nests. Conversely, experimental increases in the number of young and thus increased parental effort led to smaller patches. (B) Males that switched from one to multiple mates (monagamous to polygynous) the next year also had a larger forehead patch size the second year. [*After Gustafsson et al. 1995*]

Experimentally enlarged broods also affect the quality of the offspring of Collared Flycatchers. First-year males raised in the enlarged broods have smaller patches than those of first-year males raised in small broods. They are then handicapped when they compete for mates the following year. In all these examples, life-history strategies are based on the balancing of the short-term and long-term effects of mate choice.

Mate Choice and Sexual Selection

Striking sexual differences in plumage (and size) are typical of many birds. Darwin concluded that exaggerated sexual differences such as the tail of a peacock or displays of the Wild Turkey evolve as a result of what he called sexual selection—namely, contests among males for mates and female preferences for particular males (Figure 12–3). As potential male reproductive success increases, so does the value of the characteristics—

FIGURE 12–3 Strutting male Wild Turkeys cooperate in courting a hen. Only the dominant male in a coalition of brothers actually mates with the hen. The remaining siblings benefit by virtue of being kin when some of the genes that these siblings have in common with their brother are passed on to the next generation. [*Courtesy of A. Cruickshank/VIREO*]

large size, fancy plumage, intricate songs, and striking displays—that are responsible for the success. The resulting evolutionary process of sexual selection leads to differences between the sexes in size and ornamentation, called sexual dimorphism. Darwin's insights into the evolutionary role of sexual selection are now largely confirmed, but the effects of competition among males, female choice, and resources other than mates intertwine in even more intricate ways than Darwin proposed.

Choice of Superior Mates

Mutual assessment of prospective partners is a vital aspect of the early stages of courtship and pair formation. The ornaments and displays favored and maintained by sexual selection are those that reliably reflect the superior condition of certain males, enabling females to select the best possible mates. For example, House Finch females prefer brightly colored males, which have better survival rates and are better family providers (see Box 4–4). The familiar flight displays of male Bobolinks over lush fields advertise their condition. Females favor males that display longer. Such males have larger fat reserves and consequently fledge more young than their neighbors do (Mather and Robertson 1992; Figure 12–4). Experiments confirmed this female preference: males with clipped wings had shorter flight displays (3.5 s) than those of control males (5.8 s) and acquired significantly fewer mates (average = 0.67) than did control males (average = 1.0).

Studies of birds led to the formulation of robust hypotheses that now guide research on the mating systems of animals of all kinds. Two types of hypotheses explore why females choose males with more elaborate plumage or displays. They are called "good genes" and "arbitrary choice with runaway selection" hypotheses, respectively.

The good-genes hypotheses propose that exaggerated male plumage and courtship displays truthfully signal genetic or physiological superiority. Females should recognize superior males and select them to sire offspring. What aspects of genetic or physiological superiority might exaggerated courtship displays serve to index? One possibility would be a male's superior survival skill. For example, the enormous tail of a peacock might actually be a handicap during flight or escape. So would be bright colors that might attract predators (Zahavi 1975). Males that survive to display such handicaps would have superior stamina or abilities to escape predators. Evolution would tend to favor bigger and bolder badges of this so-called handicap superiority if females preferred to mate with the males that bore such badges.

Another application of the good-genes hypotheses asserts that ornamented plumage provides an index to a male's health, particularly its resistance to pathogens and parasites (Hamilton and Zuk 1982). Females could detect disease-prone males by the lower quality of their display plumage or by their reduced display stamina. Strong evidence now exists for this hypothesis. Among their many effects, parasites reduce the sheen

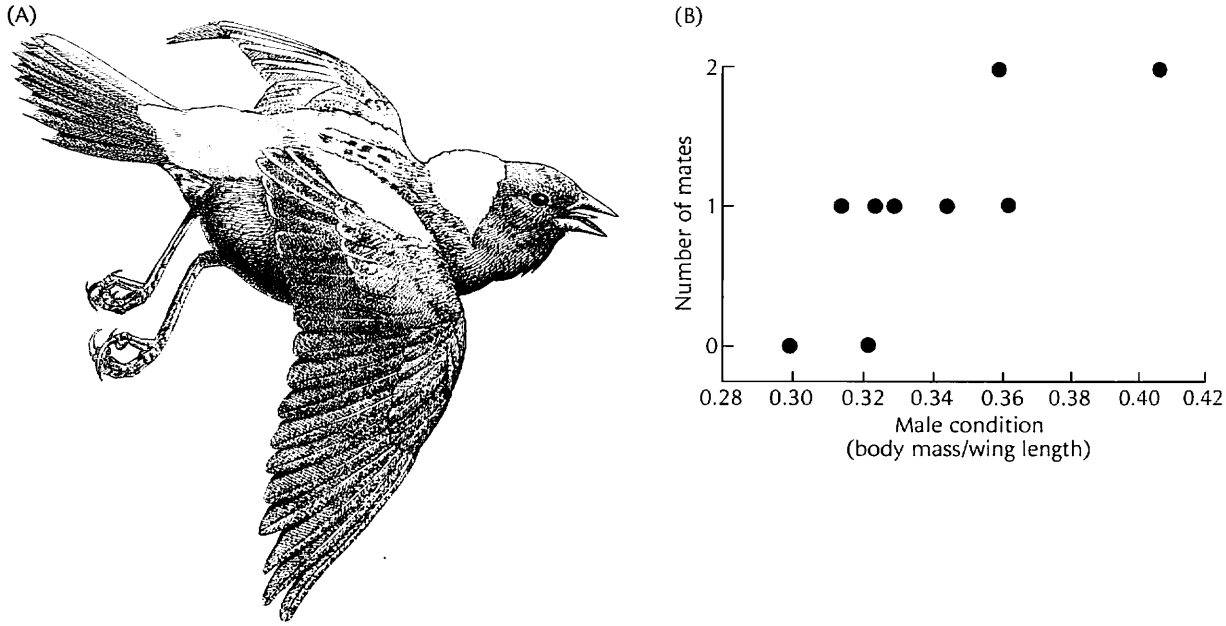


FIGURE 12–4 Honest advertising. (A) Female Bobolinks prefer males in good condition that display their superior condition with longer flight displays. (B) The average number of females that (unaltered) males attracted increased with their relative condition, defined in terms of their total body mass relative to wing length. [*After Mather and Robertson 1992*]

of ultraviolet coloration of bird feathers. The iridescent blue plumage of male Satin Bowerbirds, for example, has a single wavelength peak in the ultraviolet (Doucet and Montgomerie 2003). The visual intensity of this peak predicts the male's level of infection by blood parasites, because ultraviolet sheen decreases with increasing infection. Ultraviolet signals are important for mate choice in bluebirds (see page 100), Blue Tits (Box 12–1), and many other species as well (Siitari et al. 2002).

Other evidence for the use of a bird's appearance as an index to its health comes from studies of Red Junglefowl, which are the ancestors of domestic chickens. Marlene Zuk and her colleagues (1990a, 1990b) first established that hens of the Red Junglefowl mated more quickly with roosters bearing large, fleshy, red combs on their heads. The hens use comb size as an index to the health of a potential mate. Comb size is strongly affected by the level of blood testosterone, which, in turn, affects the bird's physical condition. Intestinal nematode worms reduce comb size, with the result that hens prefer roosters without worms over those that are infected.

Parasites also affect the quality of male ornaments that serve as the basis for female choice in Barn Swallows. The long, forked tail streamers of

the familiar Barn Swallow may be a male's most important ornament (Møller 1994; Evans 1998). Streamers have important aerodynamic functions, including the reduction of flight costs. In addition, the streamers are subject to sexual selection. Male swallows attract females by singing and displaying their outermost tail feathers, which are larger than those of females. Tail length serves as an index to a male's load of ectoparasites, particularly bloodsucking mites, which reduce weight, tail-feather length, the survival of nestlings, and the reuse of nests. Unmated males have more parasites than mated males, and mated pairs exhibit similar parasite loads; that is, males and females with the lowest parasite loads tend to pair with each other. Female swallows mate more readily with males that have longer tails. Often these males are older because tail length increases with age, but females still prefer same-aged males with the longest tails. Once paired, females also prefer longer-tailed, unmated males as partners for extra-pair copulations. Balancing the attractiveness of males with long tail streamers, then, is their reduced ability to guard their mates from other males (Smith et al. 1991). Thus, long-tailed male Barn Swallows are cuckolded more often than their less attractive neighbors.

The large sizes and conspicuous plumages favored in reproductive displays may be liabilities in other regards. Large size itself requires greater energy expenditure. There is some evidence that large male Red-winged Blackbirds are at a disadvantage because they must sacrifice display time for feeding. Among species of North American blackbirds, males that are much larger than females tend to suffer greater mortality as nestlings (Searcy and Yasukawa 1983). Similarly, because they grow twice as fast

BOX 12–1

BLUE TITS CHOOSE MATES IN THE ULTRAVIOLET

Male and female Blue Tits look almost the same to the human eye but not to each other (Andersson et al. 1998; Hunt et al. 1998). The plumage of both sexes includes strong ultraviolet (UV) reflectance, which makes the birds more conspicuous to each other against the background colors of the woods in which they live. Males also have a brilliant purple crown patch that we cannnot see. The males display their ultraviolet crown patch prominently during courtship, especially in the early morning light. Consistent with the process of sexual selection, females prefer males with the brightest crown patches. Females also pair assortatively: those with the brightest UV reflectance in their own plumage pair with the most brightly colored males.

The intensity of the male's crown patch indicates its viability, predicting its survival to the next breeding season (Sheldon et al. 1999). In addition, males that are genetically more heterozygous (at protein loci) have brighter crown patches than those of males with less genetic variability (Foerster et al. 2003). Even more startling, female Blue Tits increase the proportion of male offspring in their broods in proportion to the UV reflectance of their mates. They skew the sex ratio of their young to favor the best males. Experimental masking of the crown patch of their mates erases the bias toward male offspring.

as females to reach their full adult size by the end of their first summer, male Western Capercaillies, a huge species of Eurasian grouse, are more vulnerable than females to starvation when food is scarce (Wegge 1980).

The same bright colors that announce a male's presence to potential rivals or mates may also attract predators. Rock Ptarmigans provide an unusual case study of the tradeoffs between display and risk (Montgomerie et al. 2001). Males of this alpine grouse are bright white and conspicuous when in courtship mode at the beginning of the breeding season. Still in their winter white, which blends with the snow cover, they stand out against the alpine colors when the snow melts. For a while, therefore, they are extremely vulnerable to predators. One in four is eaten in June and July alone. As soon as they pair, however, they soil their finery with mud and dirty water to camouflage themselves until they molt into cryptic brown summer plumage.

Male Quality versus Territory Quality

Most birds are monogamous; that is, they form simple pairs of one male and one female on one territory. Sexual selection is manifest in the initial stages of competition among males for a breeding territory and then in the decisions by females to reside with particular males on their property. Where they can control high-quality territories, some species such as the Red-winged Blackbird of North America are polygynous, often pairing with two or more females. They also exhibit striking sexual dimorphism and large variation in their sexual success (Yasukawa and Searcy 1995).

Male Red-winged Blackbirds are jet black with bright red and yellow shoulder patches, or "epaulettes." Females are smaller and plainer, streaked brown. Males establish and defend large territories in marshes throughout North America. Those with the best territories attract harems of as many as 15 females (Figures 12–5 and 12–6). The male's red epaulettes are essential to winning in competition with other males for quality territories. Males on which the red is experimentally dyed black suffer more frequent challenges and usually lose their territories, although those that are not challenged still attract mates. The epaulettes have evolved in relation to male–male competition, not to female choice.

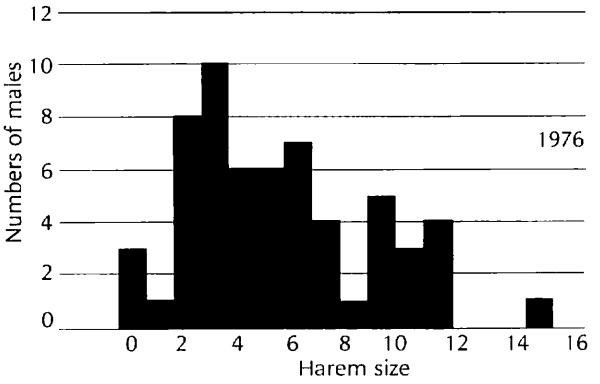


FIGURE 12–5 Male reproductive success varies greatly, depending on the quality of the territory that they defend. Shown here is the variation in the sizes of harems of male Red-winged Blackbirds in Washington State. [*After Searcy and Yasukawa 1983*]

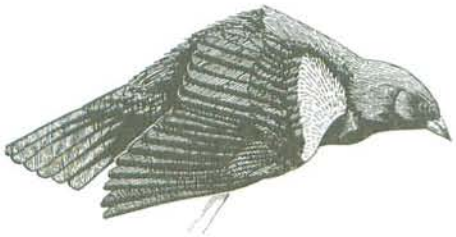


FIGURE 12–6 A territorial male Red-winged Blackbird in aggressive display posture. [*From Orians and Christman 1968*]

Sexual selection among male Red-winged Blackbirds operates through competition for the best territories. Female Red-winged Blackbirds consistently choose high-quality territories rather than particular males. Water level, nest cover, and abundance of food determine territory quality and, therefore, a female's nesting success. A female's nesting success is not lowered by the presence of other females and may actually improve owing to lower risk of predation. Male age is a secondary criterion for female Red-winged Blackbirds in some parts of the country. Females prefer older, more experienced males in Indiana, where males help feed the young, but not in Washington, where males do not help feed the young.

An extraordinary, unrelated counterpart of the Red-winged Blackbird lives in East Africa. The male Long-tailed Widowbird is a convergent species that is jet black with bright red epaulettes. It defends marshland territories in the highlands of Kenya. Sexual selection has gone a step or two further in the enhancement of the male display that is characteristic of this species. True to its name, the Long-tailed Widowbird has an enormous tail, as much as half a meter long. Like female Red-winged Blackbirds, female widowbirds are small, brown-streaked birds. Sexual selection favors the long tail of the male because it enables females to spot him from afar. Humans can spot a displaying Long-tailed Widowbird from more than a kilometer away.

In an elegant experiment, Malte Andersson (1982) increased the tail lengths of some male widowbirds by 25 centimeters and decreased the tail lengths of others by that same amount (Figure 12–7). Males with

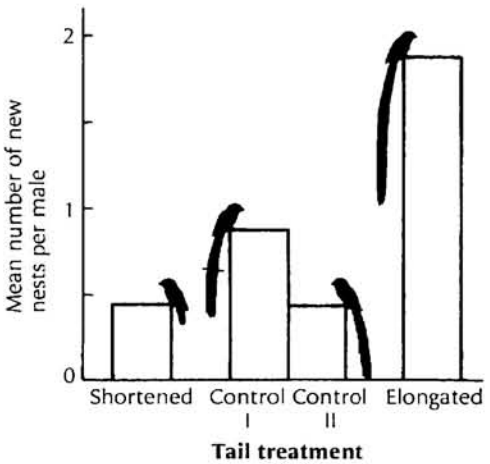


FIGURE 12–7 Female Long-tailed Widowbirds prefer males with long tails. In this experiment, the tails of some males were shortened and the tails of others were extended. Control I males had their tails cut off and then restored, and control II males had unaltered tails. The ability of males to attract females to their territories directly correlated with their tail length. [*After Andersson 1982*]

"super" tails attracted more females to nest on their territories than did males with shorter tails or tails of normal length. These experimental manipulations did not, however, affect a male's ability to hold his territory. Female preference, rather than male competition, was the source of sexual selection in Long-tailed Widowbirds.

Evolution of Displays

Paralleling the good-genes hypothesis for female selection of exaggerated male ornamentation is the concept of arbitrary choice and runaway selection. This concept stresses a more arbitrary process of ornament and display elaboration based on intrinsic female preferences for fancier males—dubbed "fashion icons" (Ridley 1992). Assessment of male quality by a good-genes hypothesis was not part of the original concept, but the two hypotheses potentially overlap and reinforce each other. Once the process of favoring slightly more elaborate displays or plumages begins, it may go to extremes, as in the bizarre plumage displays of birds-of-paradise. Genetic models of runaway selection require the linking of

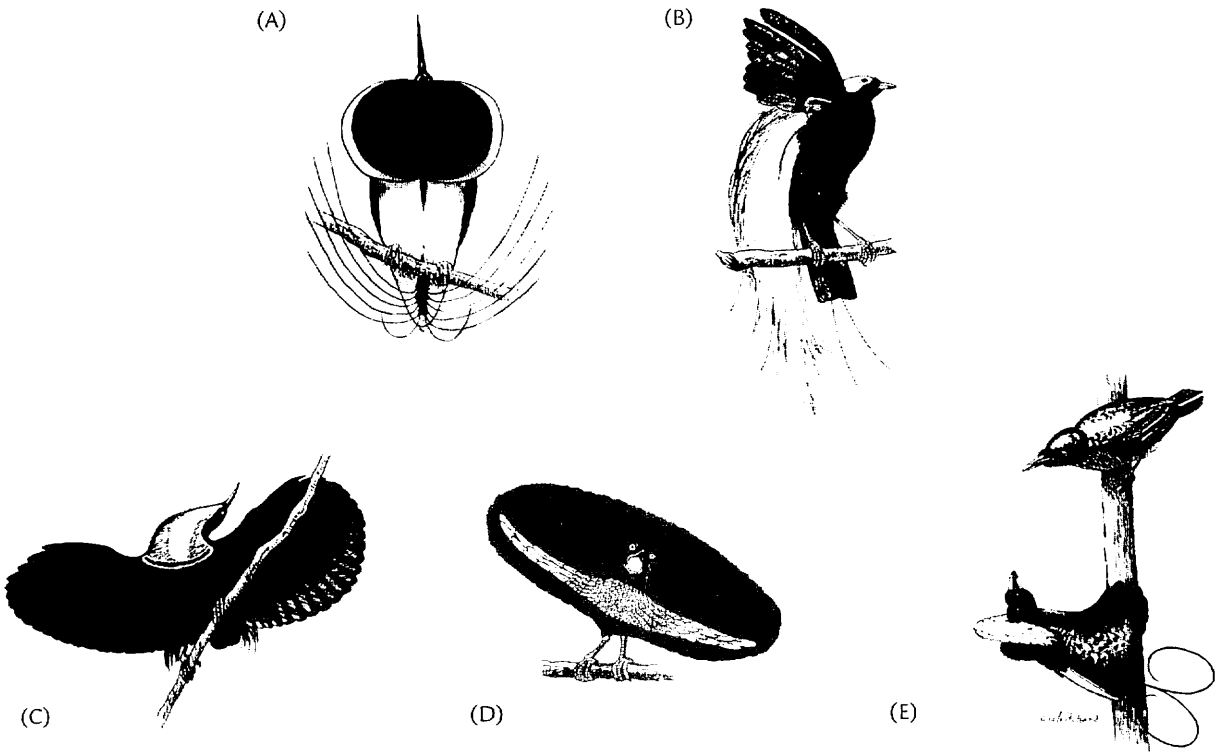


FIGURE 12–8 Elaborate plumages and displays of male birds-of-paradise: (A) Twelve-wired Bird-of-Paradise; (B) Lesser Bird-of-Paradise; (C) Magnificent Riflebird; (D) Superb Bird-of-Paradise; (E) Magnificent Bird-of-Paradise. [*From Johnsgard 1967*]

the genes controlling male traits to the genes controlling female preference for those traits. The process of imprinting in young birds innately fosters adult preferences for new and fancier ornamentation (see Chapter 16).

Sexual selection drives the evolution of courtship displays and other behaviors. In fact, we can infer the phylogeny of behavioral displays in much the same way as we infer the phylogeny of morphological traits. The two tend to evolve in concert. For example, the formidable displays of the birds-of-paradise feature elaborate arrangements of specialized feathers (Figure 12–8; see also Figure 1–1).

Closely related birds tend to have similar display behaviors. Specific displays, for example, distinguish the main groups of pelecaniform seabirds. Members of the Suborder Pelecani—pelicans, boobies, anhingas, and cormorants—have a similar "bowing" courtship display that is absent from the courtship behavior of tropicbirds and frigatebirds. The closely related boobies and gannets have "head wagging" displays, whereas the closely related anhingas and cormorants have "kink throating" and "pointing" displays. Pelicans, however, lack these displays as well as "sky pointing," "wing waving," and the "hop" used by boobies, anhingas, and cormorants (Figure 12–9).

Some displays are evolutionarily conservative, whereas others change in concert with ecology. In the Boat-billed Heron, a shift in feeding ecology prompted the transformation of its displays (Mock 1975). The Boat-billed Heron is a Neotropical night heron with a wide bill evolved for touch-feeding in seasonally flooded lagoons. Its repertoire of social displays differs substantially from that of other herons. For example, its displays emphasize sounds made with the bill. This heron also uses dramatic visual displays such as the tall-rocking display (Figure 12–10). A shift in the Boat-billed Heron's feeding niche fostered the evolution of a wider, more sensitive bill and more sensitive eyes for nocturnal feeding. The ecological and accompanying morphological transformations then led to radical modifications of displays for better communication in the dense nesting habitat where visibility was poor.

Manakins

Courtship displays and structures evolved together in tiny, promiscuous forest birds of the New World tropics, called manakins (Pipridae) (Figure 12–11). Male manakins, as well as a variety of other bird species, display in courtship arenas that contain no resources. They form no lasting pair bonds. The promiscuous males of such species will mate with as many females as possible. Females visit displaying males for one purpose only—fertilization—and then build their nests and raise their young elsewhere by themselves.

Some of the 40 species of manakins perform circuslike, whirling cooperative displays or strut up and down fallen logs (see page 352). Video films of these wonderful behaviors are available on the Web (Google Images: video + manakin). Many components of manakin courtship displays, such as the backward dances of species in the genus *Pipra*, are conserved

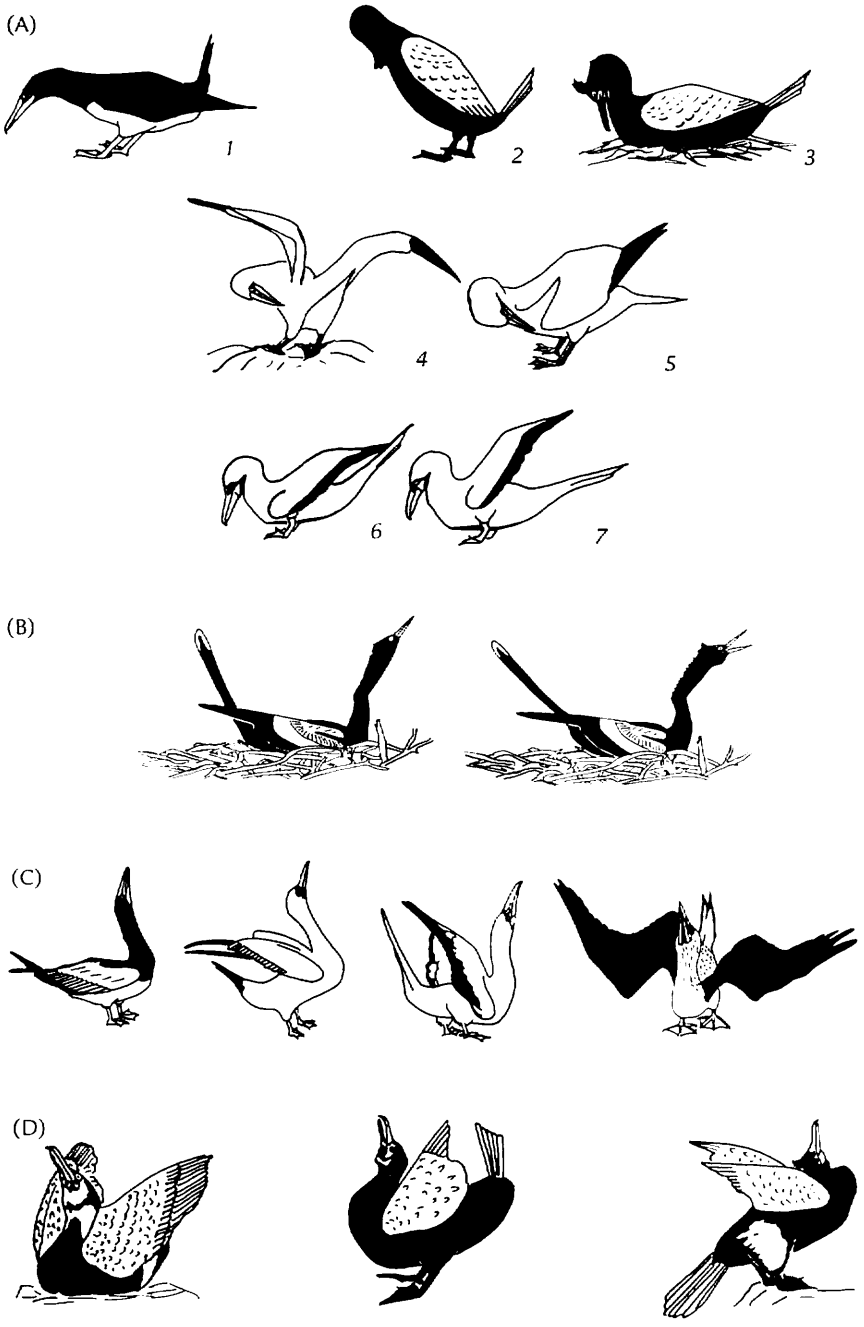
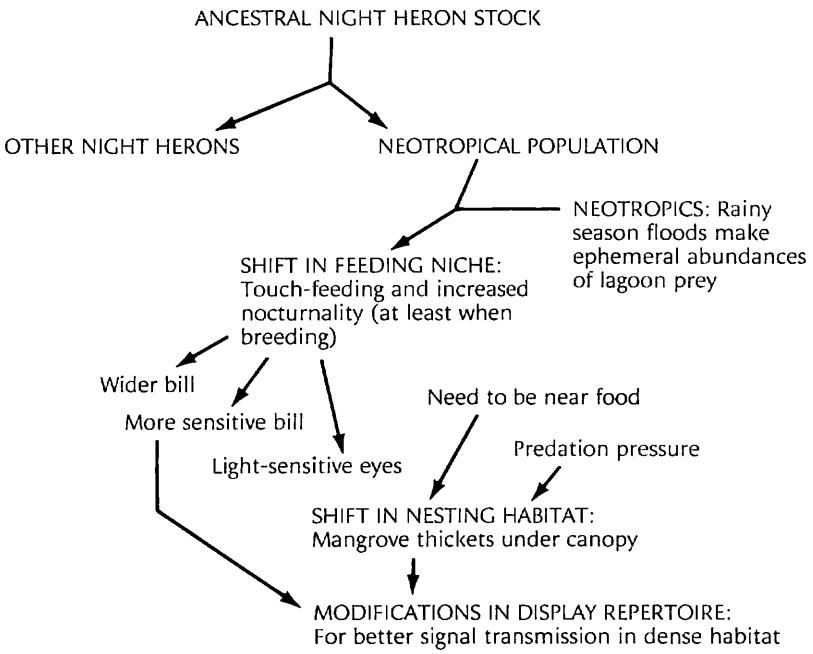


FIGURE 12–9 Displays of pelicaniform birds. (A) Bowing displays: 1, quiver bowing of Brown Booby; 2 and 3, front bowing of Great Cormorant; 4 and 5, wing bowing of Northern Gannet; 6 and 7, front bowing of Red-footed Booby. (B) Pointing (*left*) and kink-throating (*right*) displays of male Anhinga. (C) Sky-pointing displays (*left to right*): Brown Booby, Masked Booby, Red-footed Booby, and Blue-footed Booby. (D) Wing-waving displays (*left to right*): Great Cormorant, Neotropic Cormorant, and Pelagic Shag. [*After Van Tets 1965*]



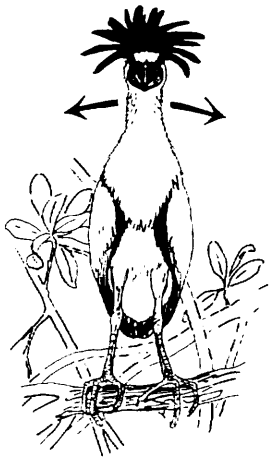


FIGURE 12–10 Tall-rocking display of the Boat-billed Heron (*right*), a species in which shifts in ecology (diagram) have led to major modifications in its repertoire of displays. [*After Mock 1975*]

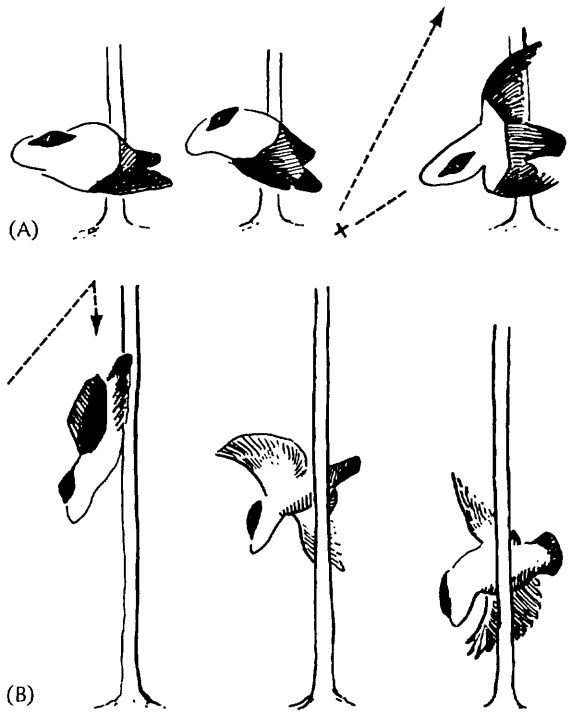
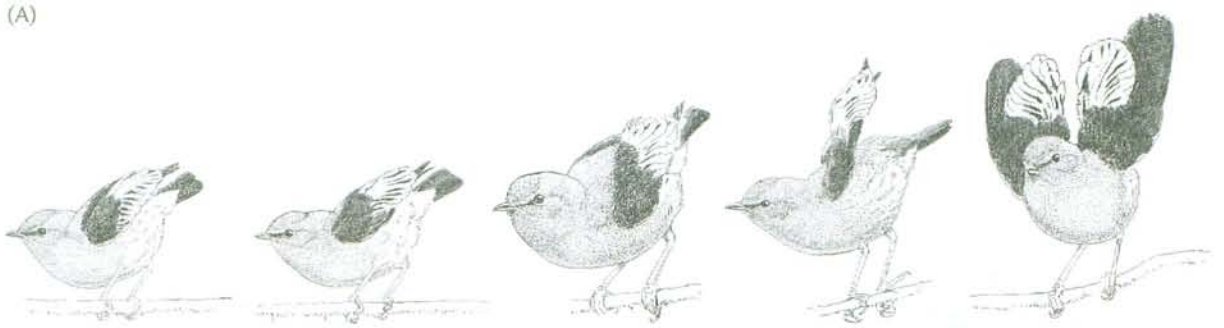


FIGURE 12–11 Displays of the White-bearded Manakin. [*After Snow 1976*] (A) The grunt jump: "Landing transversely on one of the uprights within a few inches of the ground, it becomes momentarily tense, with beard extended—a slowed down film shows the bird quivering as if bracing itself for the effort—then . . . it projects itself at lightning speed headfirst down to the ground, turns in the air to land on its feet for a split second, and with a peculiar grunting noise rockets up to land in a higher position than the one it has just left. The whole evolution lasts about a third of a second." (B) "It may then do what I called its 'slide-down-the-pole': with fanning wings and taking such short rapid steps that it seems to slide, it moves down the perch for a foot or so and remains near the bottom of the upright for a moment, *usually* to resume its to-and-fro leaping and snapping" (Snow 1976, p. 42).

through the evolution of groups of species. The changes trace their evolution history and match the changes of the syrinx (Prum 1990; Bostwick 2000).

As another example, three species—Crimson-hooded Manakin, Band-tailed Manakin, and Wire-tailed Manakin—have in common the primitive "wing shivering" and "about face" displays. The Wire-tailed Manakin enhances these displays with lengthened, paintbrushlike extensions of its tail feathers, which swish back and forth across the face of the visiting female before mating. In each of these cases, and in others as well, evolutionary changes in display behavior tend to precede and to "drive" the evolution of enhancing plumage traits.

Species of *Pipra* manakins and the unusual Club-winged Manakin use modified secondary wing feathers to make mechanical noises with their displays. The Club-winged Manakin is extreme in the modification of the secondaries (see page 85), as well as in the diversity of unique mechanical sounds made during its backward, wing-flash dance (Figure 12–12). Phylogenetic analysis of behavioral and syrinx characters reveals that the Club-winged Manakin evolved its extreme displays and mechanical sounds from homologous characters of the ancestors of *Pipra* manakins. Phylogenetic analysis of manakin relationships also suggests that (1) modifica-



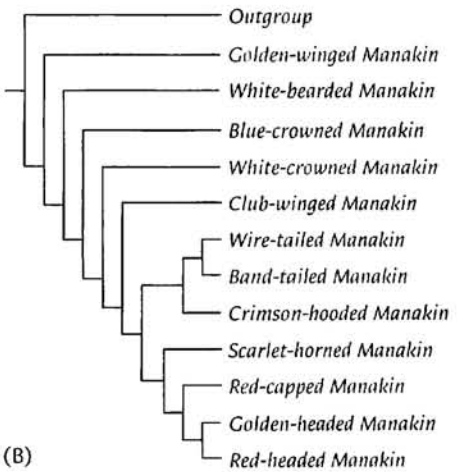


FIGURE 12–12 The displays of the Club-winged Manakin include a backward wing-flash display. (A) In this display, the bird slides back along the branch and then flashes its wings upward, producing at the same time a loud mechanical noise (double ting) by snapping its secondary wing feathers together. (B) Phylogenetic analysis of behavioral and morphological traits (such as syrinx anatomy) reveals that the Club-winged Manakin is most closely related to manakins in the genus *Pipra* (e.g., Wire-tailed to Red-headed in this phylogenetic analysis), which also do the backward dance. Elaborations of the wing feathers of the Club-winged Manakin into castanet-like instruments has led to an unusually diverse repertoire of mechanical sounds that subsitute for the vocal sounds of other manakins, leading, in turn, to the loss and simplification of the syrinx anatomy. [*From Bostwick 2000*]

tion of the wing feathers to produce mechanical sounds by both *Pipra* and Club-winged Manakins followed the evolution of the backward dance and (2) Club-winged Manakins have simplifed the structure of the syrinx through losses and reversals of character change in deference to the use of mechanical rather than vocal sounds.

Lek Displays

> The lek is nature's version of a singles bar. [Sherman 1999, p. 119]

The display grounds of promiscuous birds such as manakins vary from solitary courts to large, communal display grounds, or leks. At one extreme, Great Argus males in Malaysia hold forth on isolated deep-forest courts (Figure 12–13). At the other extreme, dozens of Black Grouse face off on the

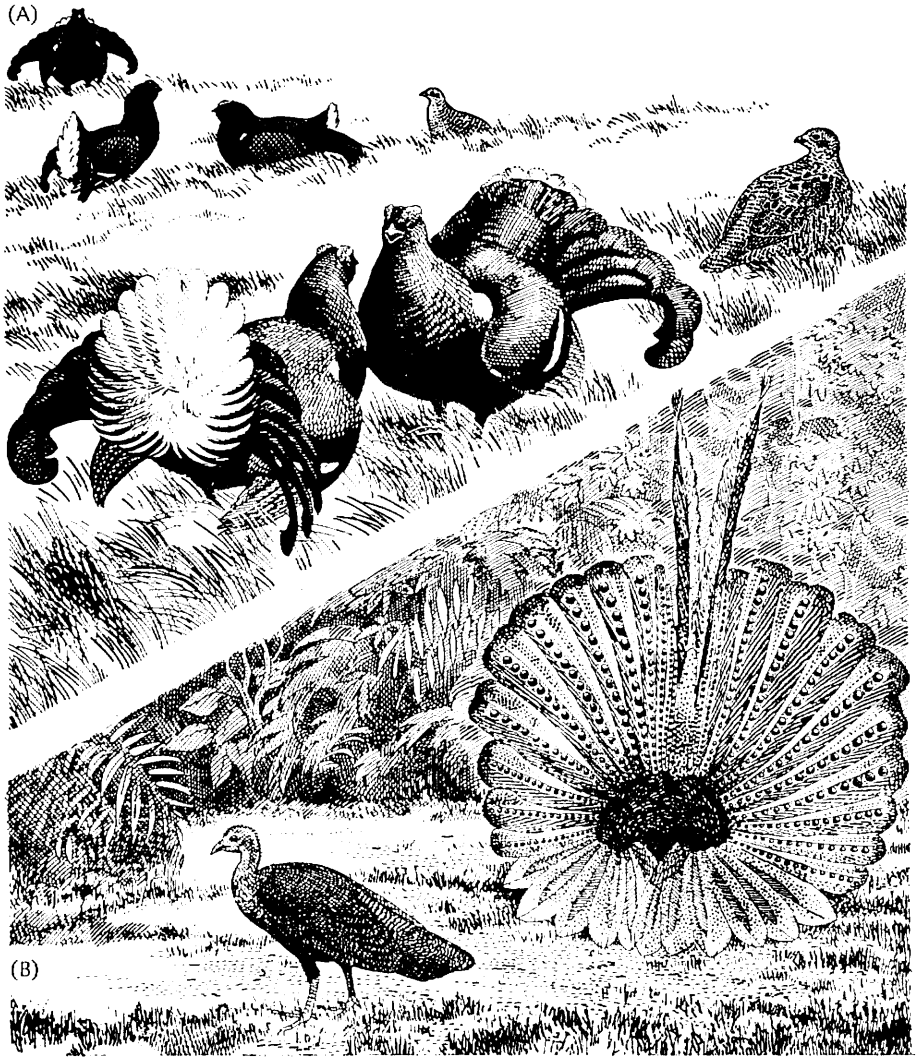


FIGURE 12–13 The mating grounds of promiscuous birds include (A) communal leks of Black Grouse and (B) isolated display courts of the Great Argus. [*From Lack 1968*]

FIGURE 12–14 Andean Cock-of-the-Rock, a brightly colored lek species of the tropical forests of South America.

moors of northern Eurasia. Andean Cock-of-the-Rock males (Figure 12–14) will gather like glowing orange ornaments on leks in the understory of the rain forests of South America, and Sage Grouse strut on the open plains of the western United States (see Figure 3–14). Such avian displays have even provided inspiration for human cultures. The Jivaro Indians of South America copy the Andean Cock-of-the-Rock in a sensual dance ceremony. Blackfoot Indians of the western United States mimic the foot stomping, bowing, and strutting of the Sage Grouse while wearing costumes matching the grouse's spread pointed tail.

Competition among males and hence sexual selection reach extremes in these species. Intense competition ranks males in a dominance hierarchy that determines which males sire most of the next generation. In the well-studied Sage Grouse of western North America, one or two dominant males achieve from 54 to 86 percent of all matings on their leks (Schroeder et al. 1999). One male Lesser Bird-of-Paradise displaying on a lek with six other males made 24 of the 25 observed copulations (Beehler 1983).

Why should promiscuous males gather in leks in which a few dominant birds mate most frequently? The potential costs are substantial. Among them is predictable failure to consummate copulation because of disruption by competitors (Trail 1985).

Field studies on different species support three primary models for the evolution of leks (Sherman 1999). They are (1) the "hot spot" model—males gather at sites where they are most likely to encounter roaming females; (2) the "hot shot model"—males gather around experienced, attractive, or dominant males to increase their chances of being noticed within large aggregations; and (3) the female preference model—females

prefer to visit large clusters of males over small clusters or solitary males. In the first two models, good regional positioning for a male more than offsets the costs of competition within the lek, especially if a male is dominant or has a chance of attaining dominant status. In the third model, the grouping of males allows the female to make safer and more efficient comparisons than is possible with scattered males. More than one of the forces defined by these models may be at work, but experiments that clearly identify the primacy of one over another are difficult to design.

Female comparisons of male quality are an important ingredient. Competition among males produces a dominance hierarchy that aids the process of comparison. Dominance is a matter of age, experience, and ability. By mating with a dominant male, a female may obtain for her offspring the genes responsible for the male's superior traits. The dominance hierarchy, in effect, selects among males and thus simplifies the selection of a good male. In the Sage Grouse, successful males are (1) socially dominant birds that (2) hold central positions on the lek and (3) are more active and visually or vocally attractive or both than are unsuccessful males (Schroeder et al. 1999). They are also in better health: female Sage Grouse prefer males that are free of lice and avian malaria (Johnson and Boyce 1991; Spurrier et al. 1991). Females can identify males with louse infestations by the red blood spots on their air sacs, which the males inflate while strutting.

In the clustering of males on leks, young, inexperienced males gather near older or successful males. In this way, the young males get occasional matings and gradually achieve a controlling position in the system. Extreme cases of such associations are seen in *Chiroxiphia* manakins (Figure 12–15). When an interested female visits the lek, two or three male Blue Manakins line up on a single branch and perform the cartwheel dance. This team performance becomes more and more frenzied and then suddenly stops. The oldest, dominant male does a brief solo precopulatory display and then mounts the female (Foster 1981). Only cooperative group displays attract and excite females, but subordinate males are not being altruistic. They occasionally copulate when the dominant male is absent. More importantly, they establish themselves in a social queue. They so develop their expertise, and some of them eventually attain the status and rights of a dominant male.

Kinship relationships among lekking males have been documented (by using microsatellite DNA comparisons) for several species, most notably Black Grouse, peacocks, and Wild Turkey. In regard to Black Grouse, males on the same lek are more closely related to one another than to males on other leks, possibly the result of wintering together in extended family gatherings. In regard to peacocks, related males tend to display near one another, even when they have been raised separately to prevent prior knowledge of one another (Petrie et al. 1998). How they favor kin is not known for sure, but it seems to be achieved by finding others most similar to self.

In regard to Wild Turkeys, several males routinely court females but only one of them actually mates with a willing female. The original work of Watts and Stokes (1971) suggested that males in the coalition were brothers, but 24 years passed before this relationship was confirmed by Alan Krakauer

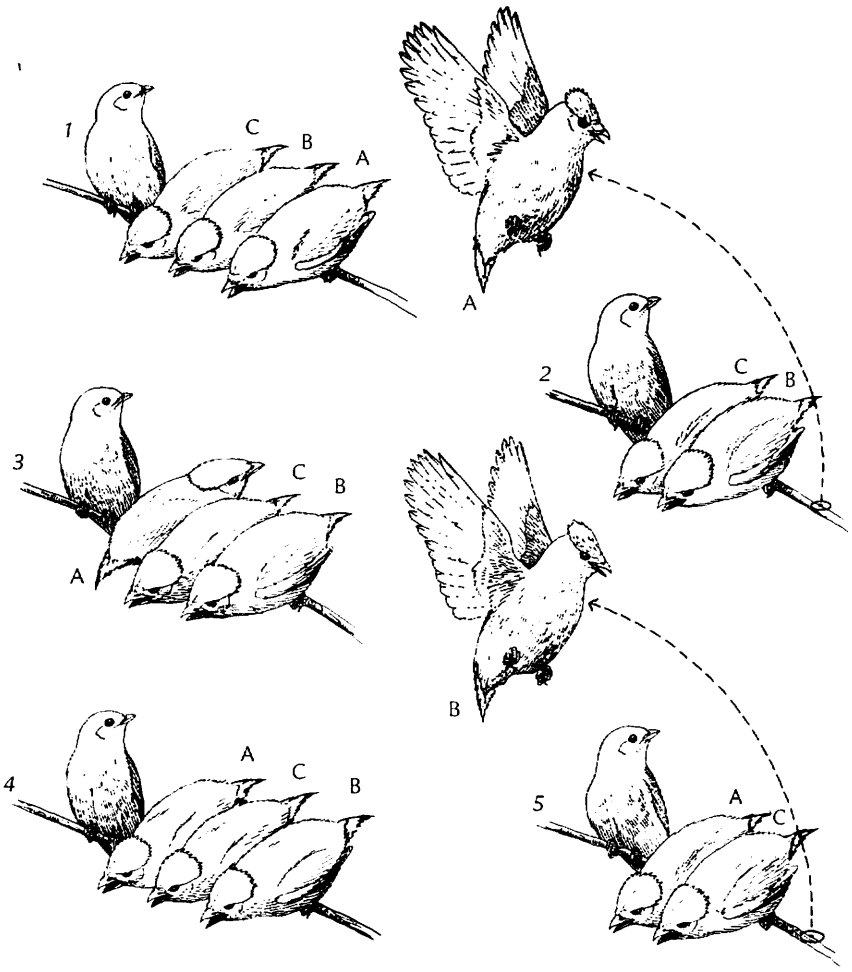


FIGURE 12–15 Cooperative courtship display of the Blue Manakin. Males leap over one another in rapid succession before a waiting female, which may then copulate with the oldest, dominant male. [*After Sick 1967*] Here are the details of this amazing group effort. "The males (blue with red crown, black wings and tail) perch closely side-by-side, in a row, on a slightly sloping (or horizontal) twig, face the same direction, all crouched, tripping [moving back and forth with tiny steps], forming a vibrating mass. They call in the recurrent rhythm of a perfectly synchronized 'frog chorus.' Suddenly the lowest male on the twig [A] rises straight into the air one to two feet and hangs momentarily suspended facing the female. He delivers a sharp dik dik dik, then lands at the upper end of the row of males at the side of the motionless female. He pivots immediately in the direction of the other males and joins the other males in tripping. Now the lowest bird [B] performs in a similar manner and so on. The entire performance occurs rapidly, giving the impression of a turning wheel; the speed varies" (Sick 1967, p. 17).

(2005) with the use of molecular, microsatellite techniques. The microsatellite genotypes of dominant and subordinate members of a coalition were more similar than those of males drawn randomly from the population and were close to the expected value of $r = 0.05$ for full siblings (Figure 12–16A). Next, he documented that dominant males in coalitions achieved more matings and sired more offspring than did solo males (Figure 12–16B).

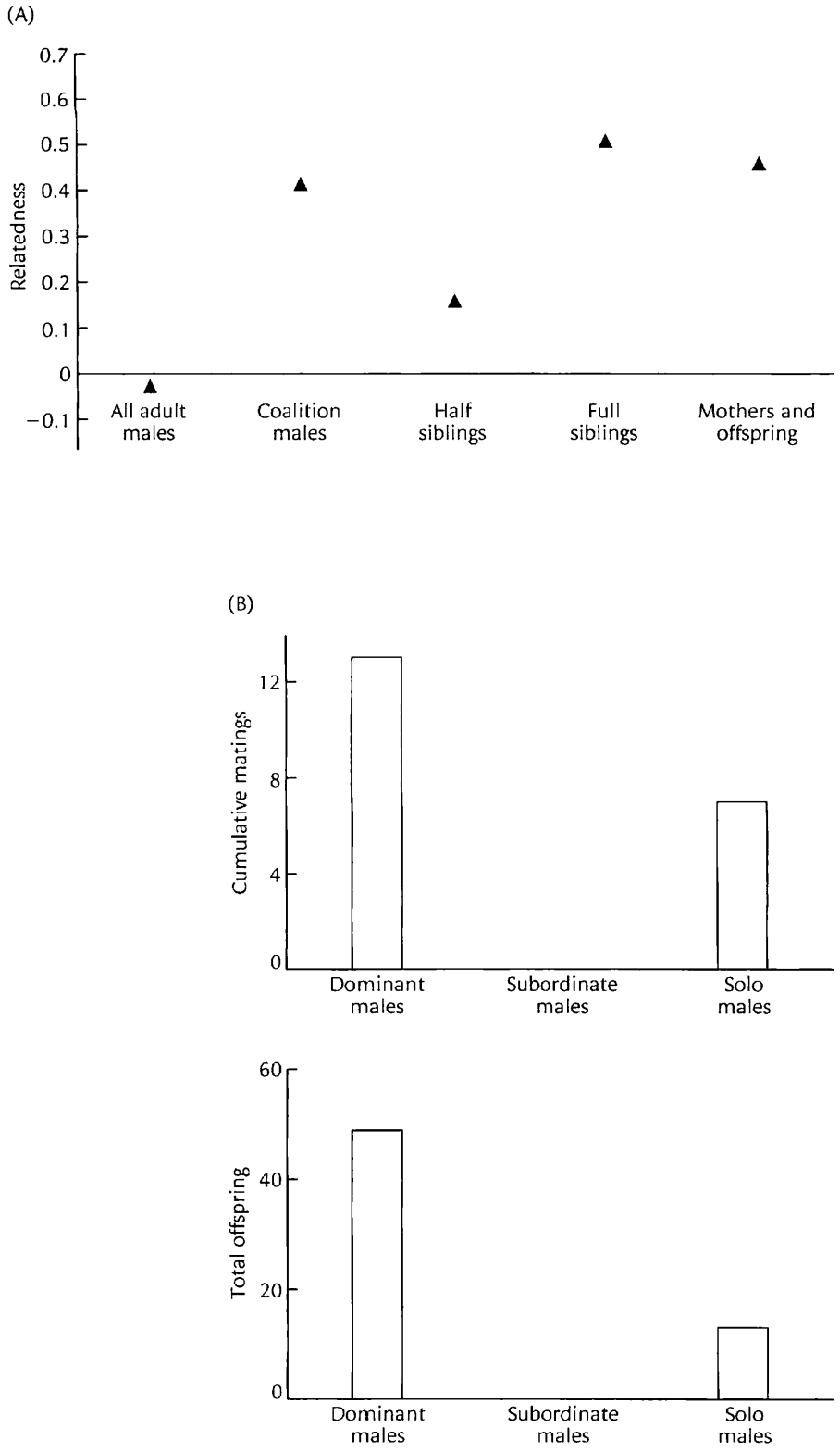


FIGURE 12–16 Kinship and reproductive success in Wild Turkey coalitions. (A) Members of male coalitions are usually brothers. Estimates of their genetic relatedness based on microsatellite comparisons of genotypes are close to those of known siblings and of mothers and their offspring. (B) The dominant male of a coalition achieves more matings and produces more offspring than do solo males that are not part of a coalition. By virture of their brothers' better performance, subordinate males in a coalition achieve a greater net genetic contribution to the next generation than they would have achieved on their own as solitary males. [*After Krakauer 2005*]

The known kinships and improved reproductive success of the turkey coalitions meet two of the three criteria of Hamilton's theory (1964) of "inclusive fitness through kin selection." According to this theory, a bird can promote its own genes by helping kin with some of the same genes. Turkey coalitions also meet the third criterion of this theory—namely, that genetic benefits of helping outweigh the costs of helping compared with trying to breed independently. The cost of helping is basically the sacrifice of reproductive output if alone, which is equivalent to that of the solitary males included in the study, calculated as 0.9 offspring per male. By helping a brother, a subordinate turkey produces the equivalent of 2.6 offspring, for a net benefit of 1.7 offspring.

Ruffs and Reeves

The Ruff is a large sandpiper with an extraordinary social structure (Figure 12–17). Females, which are called Reeves, are "normal" sandpiper brown in color. Males, however, have elaborate breeding plumages—buff, chestnut, black, white, barred—that are as variable as the coat colors of domestic cats (visit David Lank's Web site http://www.sfu.ca/biology/wildberg/ruff.html). The lek mating system of the Ruff fosters a stable set of competing genetic strategies—territorial males versus satellite males—responding to female preferences.

Briefly, here is how it works: the highly variable breeding plumage colors of Ruffs divide into two distinct social classes. The more prevalent dark-plumaged, territorial males defend clustered lek mating courts against other residents. Light-plumaged, nonterritorial satellite males track wandering females and, more importantly, may be recruited as submissive

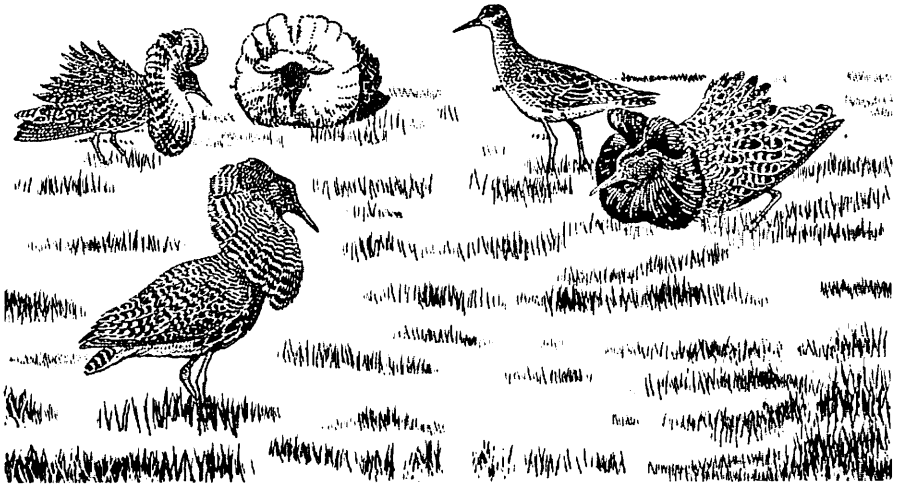


FIGURE 12–17 The Ruff is an unusual species with individually variable male plumage. Two social classes of males associate on the display territories of the lek. The white-ruffed satellite males are subordinate to the variably colored dark-ruffed resident males. [*From Lack 1968*]

partners onto the court of a territorial male. They then share matings with visiting females. Satellite males get an average of 15 percent of the matings. Their low-cost, low-benefit strategy, combined with greater longevity, achieves a lifetime reproductive success equivalent to that of the territorial males (Widemo 1998).

The genetic basis of the difference between territorial and satellite males is well documented (Lank et al. 1999). Controlling the dichotomy (dark versus light plumage) is a simple (autosomal) genetic polymorphism. All territorial males are homozygous recessive, whereas almost all satellite males are heterozygous. Females have the same genes and hence the same plumage color capacities as those of males, but they are not normally expressed. David Lank and his colleagues discovered this fact by implanting testosterone under the skin of Reeves and transforming them into Ruffs, with fancy plumage and male behaviors as well. Removal of the hormone transplant returned these temporary transexuals to being Reeves that bred normally.

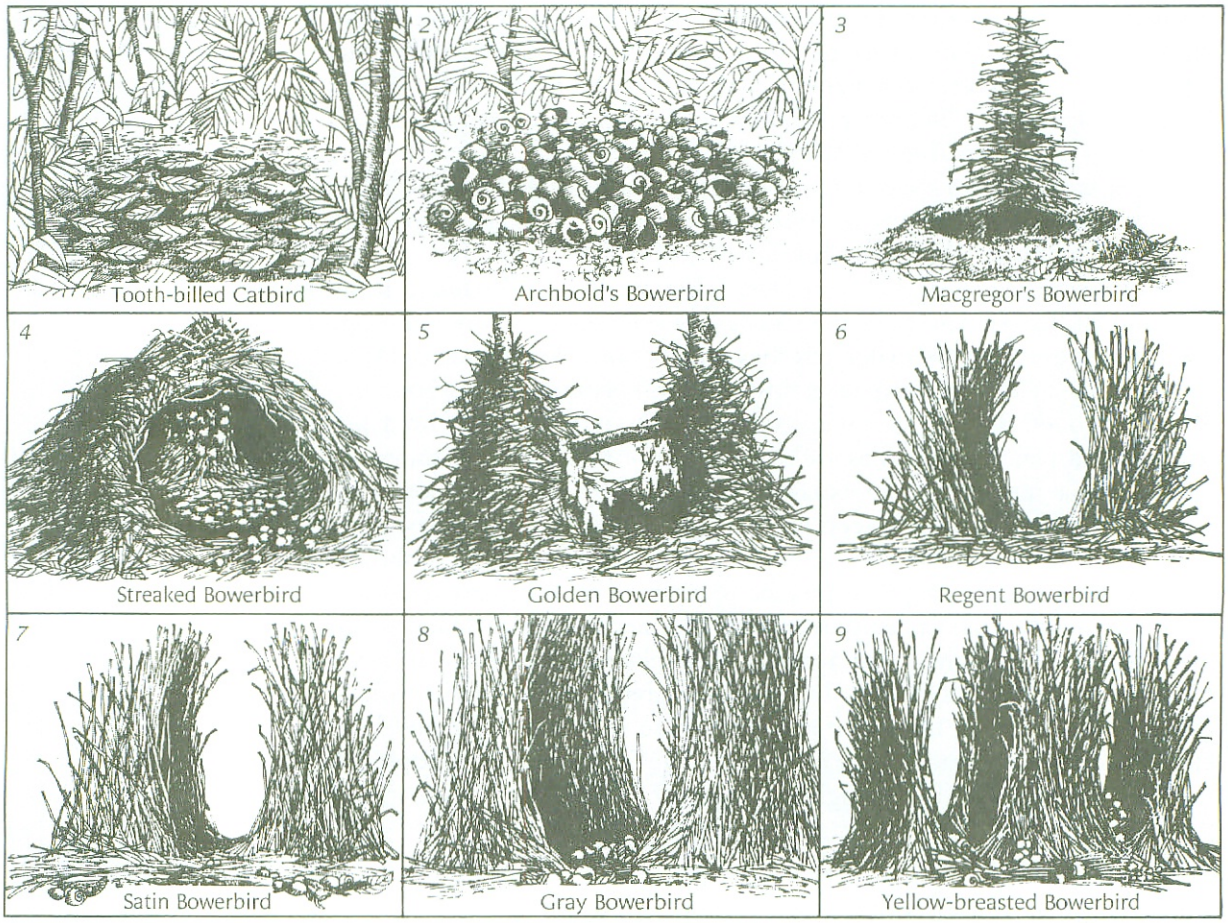
The uneasy alliances between territorial and satellite males persist and lead to the stable social polymorphism, because Reeves visit combos of Ruffs more often (on a per capita basis) than they visit solo territorial males. Territorial males tolerate satellite males because more female visits offset the costs of losing some matings to satellite males. More broadly, Reeves visit multiple leks and favor larger aggregations of males on leks. More than half of the females mate with more than one male and have clutches fertilized by more than one male. The frequency of multiple paternity for this species is the highest known for any lekking bird species (Lank et al. 2002).

The Crafts of Bowerbirds

Bowerbirds are large songbirds found only in New Guinea and Australia. They have display courts on which they construct and decorate architecturally elaborate stick or grass structures, called bowers, that provide platforms for both courtship and copulation (Figure 12–18). Ornithologists initially considered bowers to be ritualized courtship nests, but the origin of bowers probably had little to do with nests (Borgia et al. 1985). Rather, the bowers display a male's social status and ability. In Satin Bowerbirds, both bower quality and plumage color signal male quality (Doucet and Montgomerie 2003). Multiple measures of bower quality predict both ectoparasite load and body size of the attending male.

Male bowerbirds build bowers of two general kinds: maypole bowers and avenue bowers. Maypole bowers consist of sticks built around a central sapling, or maypole. Avenue bowers are walled structures placed on the south side of a display court. Five species of bowerbirds build maypole bowers, and eight species build avenue bowers. Phylogenetic analyses of DNA base-pair sequences indicate that maypole bower builders are nearest relatives of one another. The same is true for the avenue bower builders (Kusmierski et al. 1997; Figure 12–19, p. 358).

Interestingly, in these unique species, the visual aspects of courtship displays have shifted from plumage color patterns, used by most birds, to


1
Tooth-billed Catbird
2
Archbold's Bowerbird
3
Macgregor's Bowerbird
4
Streaked Bowerbird
5
Golden Bowerbird
6
Regent Bowerbird
7
Satin Bowerbird
8
Gray Bowerbird
9
Yellow-breasted Bowerbird

(A)

(B)

the creation of bowers. Thomas Gilliard (1969), an intrepid ornithologist who pioneered the study of the birds of New Guinea, first noticed the transfer of function from plumage elaborations to bower displays. Phylogenetic studies support this "transferrance hypothesis" for avenue builders (Kusmierski et al. 1997). Modestly colored species tend to have more elaborate bowers than do brightly colored species. In addition, the size of a bowerbird's brain correlates with its bower-building behavior (Madden 2001). Bower builders have larger brains than those of nonbuilding species, and species that build complex bowers have larger brains than those of species that build simpler bowers (Figure 12–20).

Bowerbirds decorate their bowers with brightly colored objects. The decorations are as extraordinary as the bower structures themselves, candidates for true art (Diamond 1986). Some species paint the walls of their bowers with fruit pulp, charcoal, or shredded dry grass mixed with saliva. Other species decorate their bowers with mosses, living orchids, fresh leaves turned upside down, or colorful fruits. The birds replace wilted flowers or leaves with fresh ones daily. Modern-day bowerbirds improvise. The Spotted Bowerbird of Australia, for example, is notorious for pilfering household and camp items—scissors, knives, silverware, coins, jewelry, car keys, and even a glass eye snatched from a man's bedside (Marshall 1954). Despite such variety, male Spotted Bowerbirds show strong and consistent preferences for certain objects that increase their mating success (Madden 2003). The male Spotted Bowerbird places these objects, such as green *Solanum* berries, in the most prominent positions in the avenue of the bower and presents them directly as props to visiting females, making sure that they will be seen.

Males of another species, the Satin Bowerbird, which has brilliant blue eyes, decorates its large avenue bowers with anything blue that it can find (see Figure 12–18B). Originally confined to natural objects, including parrot feathers and flowers, this species now exploits human trash. One bower was decorated with glass fragments, patterned crockery, rags, bus tickets, candy wrappers, a child's blue mug, a toothbrush, hair ribbons, and a blue-bordered handkerchief.

Constructing a bower and provisioning it with fresh decorations require experience and considerable effort. By monitoring the activity at bowers with video cameras triggered by infrared sensors, Gerald Borgia

FIGURE 12–18 (A) The bowers of bowerbirds include (1) simple forest clearings with ornaments on the ground; (2) a mat of lichens decorated with snail shells; (3 through 5) a maypole built of sticks about a central sapling or fern and surrounded by a raised, ornamented court; and (6 through 9) a decorated avenue built with varying complexity of stick walls opening onto a platform.

(B) The male Satin Bowerbird builds an avenue bower of sticks (*top left*), at which it courts visiting females (*top center*). Females judge bower quality and then may solicit copulation by crouching in the bower (*top right*). Other males destroy the bower in the absence of the owner (*bottom left*) and may try to interrupt copulation (*bottom center*). Mated females lay their eggs and rear their young without male help at nest sites away from the bower (*bottom right*). [*From Borgia 1986, with permission from Scientific American*]

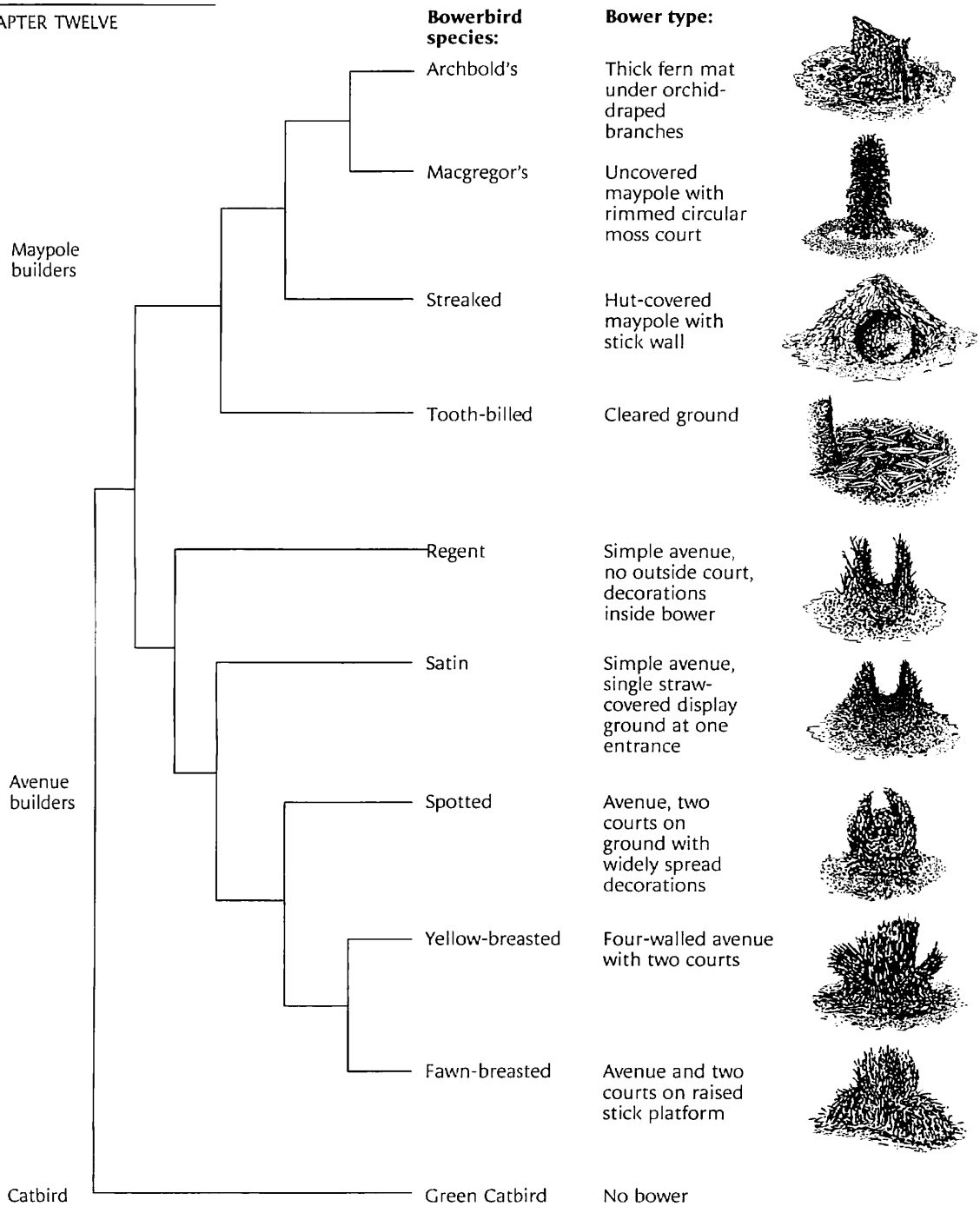


FIGURE 12–19 Cladogram of bower evolution. Phylogeny of the species is constructed from sequences of mitochondrial DNA. The catbirds, represented here by the Green Catbird, are basal in the phylogeny and do not build bowers. [*From Madden 2001*]

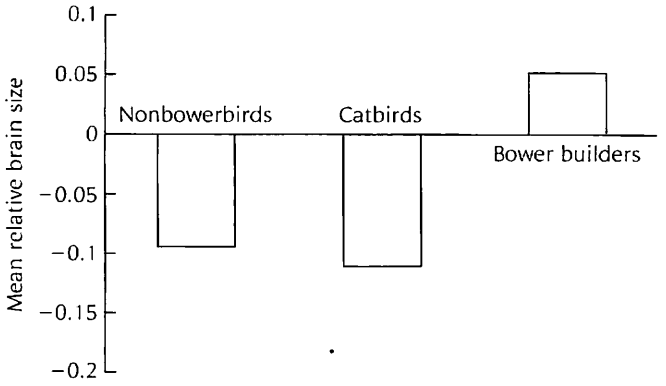


FIGURE 12–20 Bowerbirds that build bowers have larger brains than those of the related catbirds that don't build bowers and other species of passerine birds. [*After Madden 2001*]

and Mauvis Gore (1986) discovered that male Satin Bowerbirds tear one another's bowers apart, if they can, and steal prized decorations of rival males. Decorations that are rare in the environment, such as blue parrot feathers in northern Queensland, are particularly prized and subject to theft. Dominant males, better able to protect their bowers, have more time to visit and degrade the bowers of nearby competing males, which must constantly rebuild and struggle to keep up a minimally acceptable bower. The quality of the bower, in this respect and others, indicates the ability and status of a male.

Borgia and Gore's video cameras also recorded the bower visits and the preferences of female Satin Bowerbirds for well-made and well-decorated bowers (Borgia et al. 1985). A female Satin Bowerbird visits an average of 3.6 bowers in a local area before mating with a particular male. The females clearly prefer well-made bowers with special decorations. Of 22 males, 5 accounted for 56 percent of the 212 copulations recorded in 1981. These 5 males had the most blue parrot feathers, snail shells, and leaves as decorations, as well as the best bower structures, judged in regard to symmetry, stick size, stick density, and quality of construction. Males whose leaf decorations were experimentally removed from their bowers obtained fewer matings than did control males.

Monogamy

The preceding examples of elaborate displays and sexual selection include species that are subject to the most intense sexual selection because they are promiscuous or polygynous (one male to multiple females). Only a minority (less than 10 percent) of bird species adopt such mating systems, which we explore in further detail in Chapter 13. Most birds are monogamous, at least superficially so. An introduction to monogamy provides the foundation for further understanding avian mating strategies.

Monogamy refers to a prolonged pair bond with a single member of the opposite sex for purposes of raising young. Birds are classically among the most monogamous of organisms. Traditionally, ornithologists have viewed monogamy as the mating system of choice. Most birds spend weeks or months tending their eggs and young. In contrast, most reptiles simply lay their eggs and leave them. Not only do avian eggs and chicks require more parental care than do the offspring of most vertebrates, but the participation of both sexes is frequently essential.

The parental-care roles of monogamous male birds can be substantial. Defense of the territorial space, usually by the male, secures food supplies for the female and young. Most monogamous males also help their mates build nests and feed young, and some share incubation. Hence, a monogamous female bird should assess her prospective mate's commitment and ability to sustain efforts in raising young. Some year-old Barnacle Geese even sample prospective mates by forming trial liaisons before making a final, lifelong choice when two to three years old (van der Jeugd and Blaakmeer 2001). As a result, they achieve greater lifetime reproductive success than that of birds that pair right away.

Monogamous pair bonds may last for a breeding season or for life. Most pairs of parrots, eagles, and pigeons sustain lifelong associations. Long-lived birds—including swans and geese, albatrosses, and some shorebirds—also rarely divorce, which would penalize their reproductive output (Ens et al. 1996). Even long-distance migrant shorebirds maintain their partners. Paired male and female Black-tailed Godwits migrate and winter separately, but they return at the same time (within three days) to their nesting territories in Iceland and renew their pair bond (Gunnarsson et al. 2004). Failure to arrive together (more than eight days apart) leads to divorce.

In other species, divorce initiated by the female increases her reproductive success. Female oystercatchers, for example, leave their mates to move to better nesting sites close to good feeding grounds (Heg et al. 2003). They produce more chicks as a result. Abandoned partners remate and continue to commute from the nest to the mud flats to feed, thereby exposing offspring to predation and new mates to opportunities for infidelity.

Similarly, female Blue Tits and Black-capped Chickadees typically divorce for better options. Blue Tits form pair bonds that endure many breeding seasons on the mainland of Europe. On the island of Corsica in the Mediterranean, however, females leave their mates 59 percent of the time (Blondel et al. 2000). Breeding sites vary greatly in quality on this island; so, when there are openings, female tits shift to habitats with more food, denser vegetation, and fewer parasites. Reproductive performance with their former mates is not an issue. A study found that, in North America, female Black-capped Chickadees typically left their partners between the first and second breeding seasons for males of higher social rank and did not leave on the basis of previous reproductive success (Ramsay et al. 2000). The females that left their partners, however, had a more significant tendency toward broods of mixed paternity before divorce than that of females that stayed with their first partners.

Cuckoldry and Promiscuity

> Well over nine-tenths (93%) of all passerine subfamilies are normally monogamous. . . . Polyandry [multiple male mates] is unknown. [Lack 1968, p. 35; see Griffith et al. 2002]

These statements by David Lack—the father of avian life-history theory—summarize the working assumptions of 40 years ago. Since then, research with the use of the latest DNA technologies has brought about a dramatically different view of monogamy among most birds. Monogamy is a social relation between members of opposite sex that is built on the assumption that the offspring are truly their genetic offspring. Yet this assumption is only rarely true. Only 14 percent of socially monogamous bird species studied to date are also genetically monogamous. Instead, the broods of most species exhibit mixed paternity due to copulations by females with additional males—called extra-pair copulations. On average, more than 11 percent of offspring are sired by males other than the social father (Griffith et al. 2002; Figure 12–21). The proportion of chicks sired through extra-pair copulations may be more than 50 percent in some Tree Swallow populations (Lifjeld et al. 1993). Extra-pair copulations are also a significant source of sexual selection for bright plumage and other indicators of male quality (Moller and Birkhead 1994). These startling statistics result from the application of a variety of DNA "fingerprinting" technologies (Griffith et al. 2002).

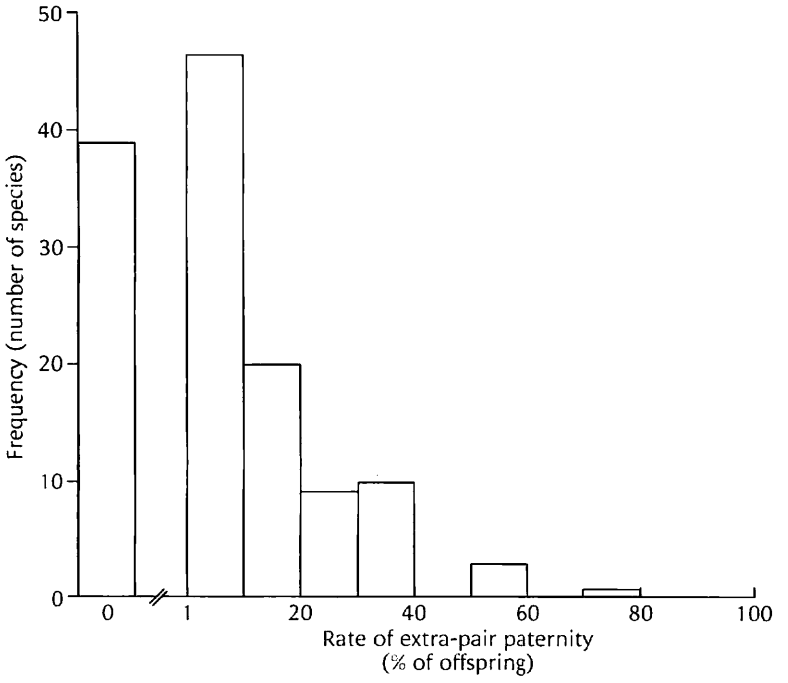


FIGURE 12–21 Frequency of extra-pair paternity (percentage of offspring that are fathered outside the pair bond) in 130 species of birds. [*From Griffith et al. 2002*]

Cuckoldry in Purple Martin Colonies

The social life of the colonial Purple Martin, a favorite backyard species throughout North America, has been unveiled (Wagner et al. 1996; Brown 1997). Native Americans used to attract Purple Martins by hanging hollow nesting gourds. Elaborate, multistory, white condominiums—sometimes with hundreds of nest chambers—now attract local colonies of martins (Figure 12–22). Appreciation of his backyard martins piqued Smithsonian ornithologist Eugene Morton and his colleagues (1990) to learn more about social life inside his 24-room backyard martin mansion. Among his findings was rampant cuckoldry.

This cuckoldry begins when older, experienced males arrive first and take charge of the top floors, where the nests are safest from predators. After establishing themselves with their mates in the best available condominiums, the experienced male martins sing a special song high in the dark predawn sky to attract late-arriving yearling males to the colony. The older males then concentrate on copulating with the mates of their naive, young neighbors—with much success. Through their extra-pair copulations, adult males added to their reproduction scorecard an extra 3.6 fertilized eggs to the 4.5 eggs produced by their own mates. They fathered 43 percent of the offspring in the nests of yearling males. In some years, a single older male is responsible for most or all of the cuckoldry (Wagner et al. 1996). Conversely, yearling males fathered only 8 percent of the offspring in the nests of a few of the older males.

Female purple martins are active participants in these social interactions. Those that pair with older males generally avoid extra-pair copulations, whereas those that pair with the younger males actively accept

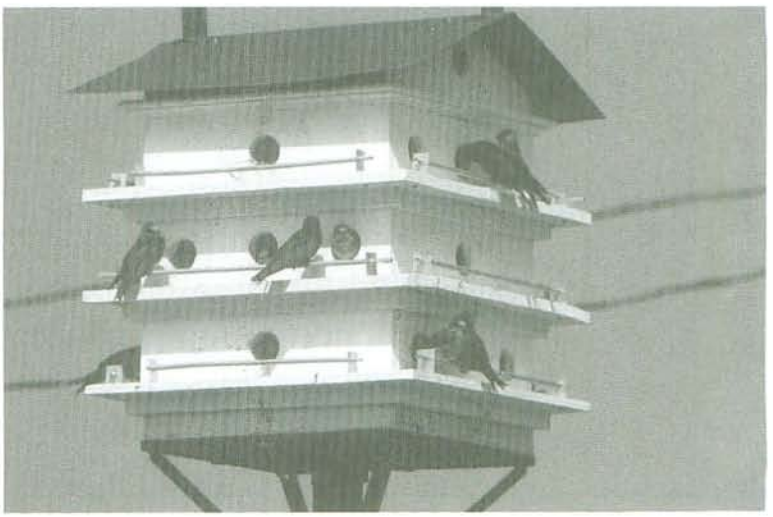


FIGURE 12–22 Colony of Purple Martins, a species in which older males recruit young males to the colony and then exploit the weak mate-guarding abilities of these young males to increase their own reproductive fitness. [*Leonard Lee Rue III/Photo Researchers*]

extra-pair copulations by older males, cuckolding their young mates. How successful these females are in mixing the paternities of their offspring depends on the guarding efforts of their mates. Young males that are larger than their mates and that actively guard them are better able to prevent extra-pair copulations by their mates and to achieve higher levels of paternity of their offspring. Regardless, some offspring are better than none at all. More importantly, with time, yearling males inherit the prime nest chambers and sing their predawn songs to attract junior neighbors to the suites below.

Quality Offspring

Socially monogamous female birds may actively seek extra-pair copulations to increase the quality of their offspring—the broad conclusion of many studies of paternity in birds (Petrie et al. 1998; Griffith et al. 2002). Whereas males can increase their reproductive success by siring additional offspring, females are limited by their clutch size. Quality rather than quantity improves a female's lifetime reproductive success.

How then do extra-pair copulations improve the quality of one's offspring? Insurance against the infertility of one's mate is one possibility (Krokene et al. 1998). Increased genetic variability, however, is the principal source of improvement. Genes from multiple males can improve the quality of offspring through improved immunocompetence (Johnsen et al. 2000) and, more generally, through the fitness advantages of heterozygosity. Across a variety of bird species, the proportion of extra-pair offspring directly correlates with genetic variability among males and, hence, variability in the quality of potential male mates (Petrie et al. 1998).

Blue Tits of Europe provide one of the best examples of how females improve their breeding success through extra-pair copulations (Foerster et al. 2003). In a long-term study of two populations of Blue Tits, one in Germany and the other in Norway, distant males less related to the female than her mate or her neighbors sired half of the offspring. Deliberate outbreeding with genetically different males increased the heterozygosity of those offspring, which, as a result, were more likely to survive their first winter and to breed locally. Heterozygous young sired by distant males were most likely to beat the low odds (1/11) of making it to the next spring. In addition, heterozygous young males in this study had brighter ultraviolet crown patches, which also confer advantages (see Box 12–1).

Female Blue Tits also consort with neighboring males that do not, on average, increase genetic diversity. But the females chose quality neighbors with "good genes," specifically those that were larger and older than their social mates. Thus, females increased the diversity and quality of their broods by two initiatives—deliberate outbreeding and selection of superior neighbors. Studies of the related Black-capped Chickadee revealed that a female also listens carefully when her mate engages a neighbor in a dominance-controlling singing contest. If the mate loses, the female chickadee is more likely to consort and copulate with other males,

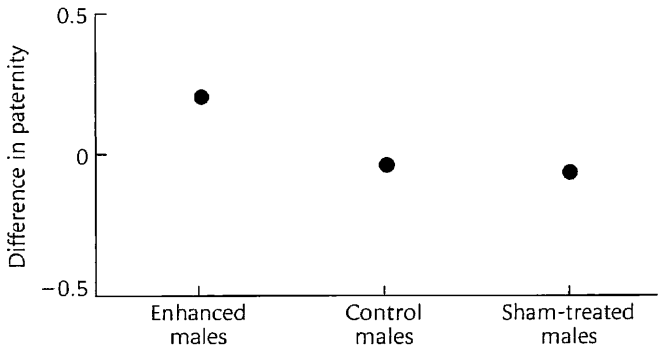


FIGURE 12–23 Experimental enhancement of the intensity of the rusty belly coloration of male Barn Swallows increased their paternity of replacement young in their own nests. [*After Safran et al. 2005*]

thereby increasing the number of extra-pair young in the brood (Minnell et al. 2002).

Barn Swallows provide a final example of ways that birds adjust the genetic composition of their offspring. Levels of extra-pair paternity in Barn Swallows change dynamically from clutch to clutch in relation to the intensity of the rusty breast and belly coloration of a male swallow (Figure 12–23). Belly coloration of North American Barn Swallows is a sexually selected trait, like the length of tail streamers in the Barn Swallows of Europe. In a series of elegant experiments Rebecca Safran and her colleagues (2005) enhanced the rusty coloration of some randomly chosen but already paired males. They surveyed the levels of extra-pair paternity of embryos in the first clutch of eggs of each pair and removed that clutch to induce the production of a replacement clutch. Males with experimentally enhanced plumage increased their paternity of young in their nests, compared with control and sham-treated males. Whether female mates of the enhanced males were more faithful to them or the enhanced males guarded their mates better to achieve these results is not yet known.

Reproductive Strategies

While being assessed as a prospective mate by a female, a male must judge during courtship how receptive the female is. Most of all, he must strive to be the father of the chicks that he will care for. The advantages to the female of mating with other males, combined with the imperfections of mate-guarding behavior, make it likely that the sperm of several males will compete to fertilize a newly released ovum.

Sperm competition is intense in Smith's Longspurs, a sparrowlike bird of the subarctic tundra with the highest copulation rate known for any bird backed by enormous testes (Briskie 1993). High copulation rates in Smith's Longspurs help to displace the sperm of other males. During the peak week in June, a female longspur copulates frequently with one to

three different males. Females solicit copulations an average of seven times per hour and are mounted by their mates three times per hour. An average of 365 copulations precedes each clutch of eggs laid. Such extraordinary sexual effort probably evolved as an adaptation to sperm competition in which frequent copulations dilute or displace the ejaculates of rival males.

The next chapters consider sperm competition and other features of birds' reproductive strategies in a continued but expanded context of life-history theory. The complexities and conflicts between what is best for males versus females, sperm versus egg, and groups versus individual birds foster diverse breeding systems that range from competitive to cooperative to parasitic.

Summary

Natural selection favors individual birds that achieve the greatest lifetime reproductive success. The investments of males and females in small sperm and large eggs, respectively, drive different options, including their mating opportunities and how best to invest in quality offspring. Most birds pair with a single mate and both then raise the offspring together. Both parents are needed to provide adequate care for their young. Females strive to protect their investments in large, expensive eggs. Males must balance the options of mating with extra females against caring for their own young. Conversely, females can improve the quality of their offspring through extra-pair copulations with high-quality males.

Competition for mates fosters sexual selection for elaborate courtship displays and sexual dimorphism in size or plumage. The bowerbirds of Australasia compete by constructing and decorating mating arenas. Distinctive male features are favored by female choice, especially if the male features convey information about the quality or health of the male. Competition for mates and therefore sexual dimorphism is especially intense in lek species, ranging from open-country grouse such as the Sage Grouse to tropical forest species such as the birds-of-paradise and manakins.

Monogamy is the most common avian mating system. But the social pair bond is often not mirrored by sexual fidelity or genetic monogamy. Instead, extra-pair fertilizations usually initiated by the female sire a substantial fraction of offspring in most species of songbirds. Through extra-pair paternity, females improve the quality of their offspring by increasing heterozygosity and by adding the genes of superior male neighbors to some young.

CHAPTER 13

Breeding Systems

The Reverend F. O. Morris (1856) encouraged his parishioners to emulate the humble life of the dunnock, or hedge sparrow Prunella modularis. . . . *Had his congregation followed suit, there would have been chaos in the parish.*

[Davies 1992, p. 1]

The pair bonds of birds vary from brief sexual unions to sustained mutual associations. For many species, the raising of young requires a major and consuming effort by two or more adult birds. Males and females may share the parental effort equally or unevenly. They may allocate their time to several broods. At stake are their individual selfish best interests, which often conflict with each other's and with the interests of their offspring.

From an evolutionary perspective, all that really counts in the end is a bird's genetic contribution to future generations. There are two primary ways to do so: (1) directly by producing young with one's own genes and (2) indirectly by helping relatives to raise young that possess some of one's own genes. Many birds do both.

Microsatellite DNA analyses, however, reveal that extra-pair copulations, leading to extra-pair fertilizations, increase the genetic diversity of many broods, as stated in Chapter 12. The prevalence and patterns of extra-pair fertilizations blur the classical distinctions of breeding systems based on the overt social relations of individual birds. Similarly, birds can increase their lifetime reproductive success by helping kin. Studies of inclusive fitness expose new depths of the social behavior and extended family structures of birds.

This chapter shifts our attention from sexual selection and the social veil of monogamy, discussed in Chapter 12, to the diversity of avian breeding systems themselves. We begin with the diversity of the so-called mating systems of birds, their relation to the availability of food, and their adjustments to the requirements for the parental care of offspring. Then, we look more closely at overtly polygynous bird species (one male to multiple females) and overtly polyandrous bird species (one female to multiple males). Close study of breeding behavior often reveals a complex reproductive fabric that weaves together elements of different systems.

Next, we consider brood parasitism. The females of many species lay extra eggs in other birds' nests. Obligate brood parasites such as cowbirds and cuckoos take this behavior to extremes. The final sections explore cooperative breeding and the roles of helpers, which are often young birds that stay at home rather than disperse to establish their own breeding territories. Concluding the chapter, the elaborate family structures of bee-eaters of Africa illustrate the potential complexities of the relationships among kin in cooperative-breeding systems.

Diversity

The diversity of avian breeding systems is rooted deeply in the evolutionary history of major taxa and has been refined in response to local ecological opportunities (Ligon 1999). The ability of each sex to monopolize or control access to members of the opposite sex helps to define the principal mating systems of birds. Table 13–1 presents an ecological classification of mating systems.

Guiding the evolution of alternative systems are life-history tradeoffs between current and future efforts, as well as uncertainties about parentage. Some individual birds cheat, whereas others help. Cuckoldry and brood parasitism are normal behaviors.

The options for mating and parenting are likened to an evolutionary game in which each parent has to choose between taking care of the young or abandoning them and seeking additional mates (Maynard Smith 1977). At one extreme, reduced confidence of paternity can promote desertion or infanticide. Tree Swallows, for example, practice deliberate infanticide. Intense competition among males for nest sites results in a floating population of unmated males. In one study, five of seven such males replaced males that were experimentally removed. The replacement males then killed the nestlings of their predecessors (Robertson and Stutchbury 1988). One of the killers mated with the widowed female, but two others brought in new mates.

At another extreme, the facade of a cooperative social order often hides a swirl of competition, strife, and harassment. Helpers may deliberately interfere with parental reproduction to increase turnover and thereby increase their own chances of breeding. Conversely, adults may sabotage the initial breeding efforts of young to increase the incentives for the young to stay at the nest as helpers. Young helper males sometimes mate with their stepmothers, and helper females sometimes slip an egg of their own into the parental clutch.

In a different direction, cooperative social interactions appear to be altruistic but are actually selfish. Individual selfishness prevails beneath the surface of communal breeding by Groove-billed Anis, large black cuckoos of the New World Tropics that form social units of one to four monogamous pairs. All members of the unit lay their eggs in a single nest, and all the birds in the unit help incubate and feed the communal brood. The main advantage of communal nesting in this species is in sharing the

TABLE 13–1 An ecological classification of mating systems

Monogamy (Greek: *mono*, single; *gamos*, marriage) The predominant avian mating system in which neither sex has an opportunity to monopolize additional members of the opposite sex. Shared parental care maximizes reproductive success.

Polygamy (Greek: *poly*, many; *gamos*, marriage) Any mating system including multiple mates of the opposite sex. Only 3 percent of all birds practice polygamy.

Polygyny (Greek: *poly*, many; *gyna*, woman) The kind of polygamy in which males frequently control or gain access to two or more females. It is called bigamy if the male pairs with only two females. For polygynous birds, the breeding success of males is more variable than that of females. About 2 percent of all birds are polygynous.

Resource defense polygyny Males control access to females indirectly by monopolizing critical resources.

Female (or harem) defense polygyny Males control access to females directly, usually by virtue of female gregariousness.

Male-dominance polygyny Mates or critical resources are not economically monopolizable. Males compete for females by sorting out positions of dominance or by directly demonstrating quality through display or by both. Extreme aggregation (leks) occurs. Where female home ranges are mobile, a female pursuit strategy may develop.

Polyandry (Greek: *poly*, many; *andros*, man) The kind of polygamy in which females frequently control or gain access to multiple males (i.e., the opposite of polygyny). Each male may tend a clutch of eggs. For classically polyandrous birds, female breeding success is more variable than that of males. Fewer than 1 percent of all birds are polyandrous. Extra-pair fertilizations due to socially monogamous females lead to clutches with mixed paternity and blur the distinction between monogamy and polyandry.

Polygynandry (Greek: *poly*, many; *gyna*, woman; *andros*, man) The kind of polygamy in which several females and several males form a communal breeding unit. The males defend territories and provide parental care to broods in proportion to their confidence of paternity. This mixed mating system, which is common among fishes, is characteristic of tinamous, the flightless ratites (ostriches, rheas, emus), and some unusual songbirds—Smith's Longspurs, Dunnocks, and Bicknell's Thrush. Male ratites and tinamous incubate mixed clutches of eggs from several females, which deposit eggs successively with different males.

After Oring 1982.

high nocturnal predation risks during incubation and brooding, thereby improving individual survivorship (Bowen 2002).

Female anis, however, compete among themselves to ensure the success of their respective contributions to the clutch. Because one nest cannot hold all the eggs, the females throw one another's eggs out to make room for their own. Young subordinate females start laying first. The older females toss out some of these eggs to make room for their own eggs, which make up most of the clutch. Subordinate females counter these actions by increasing the total number of eggs that they add to large clutches. They do so by prolonging the interval between eggs laid and by producing a "late egg" as the clutch size nears completion. There are natural limits to a subordinate female's attempts, because the last-born nestling is the smallest and most vulnerable member of the brood.

Generally, monogamy prevails when male help is essential for raising young or when males cannot commandeer the resources that they need to support extra mates. How young birds develop influences their need for biparental care and thus the evolution of alternative breeding systems. When one sex alone can take care of young, multiple mates become a viable option. Individual birds that are able to control the best territories attract the most mates.

Arctic sandpipers, for example, produce a fixed brood of four young. Their fixed clutch size and reduced parental-care requirements favor increasing the number of clutches produced through nonmonogamous mating systems (Ligon 1993). As a result, they exhibit a diversity of mating systems: monogamy, polygyny, and polyandry. Fifteen species are monogamous, with shared incubation at a single nest. Two or three species are socially polygynous or polyandrous, and different birds incubate successive clutches. Two or three other species feature polygynous males that provide no parental care. Three species are lek species, such as the Ruff described in Chapter 12.

Extra-pair copulations and mixed paternities of broods blur the distinction between monogamy and alternative mating systems, as noted in Chapter 12. Extra-pair paternity is a core theme in each of the mating systems. Females increase the genetic diversity of their offspring by mating with multiple males, regardless of which sex actually cares for the young. What amounts to covert polyandry is widespread.

A comprehensive view of avian breeding systems embraces the full diversity of social systems that describe individual efforts to maximize their lifetime reproductive success. Different roles affect individual reproductive output. Female birds can increase their reproductive success by offloading some or all of the parental care and by producing additional clutches. Conversely, males can allocate energy to extra-pair fertilizations or to varied levels of sustained parental care. The expansion of the breeding system from a pair of mates to a cooperative family group adds the matters of ecological constraints, such as the availability of territories, and inclusive fitness, or the value of siblings (Emlen 1995a).

Polygyny

Careful vigilance of color-marked birds often reveals a few bigamous males in an otherwise monogamous species. Only 2 percent of all birds, however, are overtly polygynous. In North America, these birds include 14 of the 278 breeding songbird species, 11 of which nest in marshes or grasslands (Ford 1983). Throughout the Tropics, birds that nest colonially in "safe" trees or in marshes with abundant or easy-to-find food tend to be polygynous (Figure 13–1). Females of many marsh-nesting blackbirds, wrens, European warblers, and sparrows care for their young with little or no help from males by exploiting aquatic insects emerging on prime territories.

Control of quality resources leads to the evolution of what is called resource-defense polygyny. Clumped resources are easier to monopolize

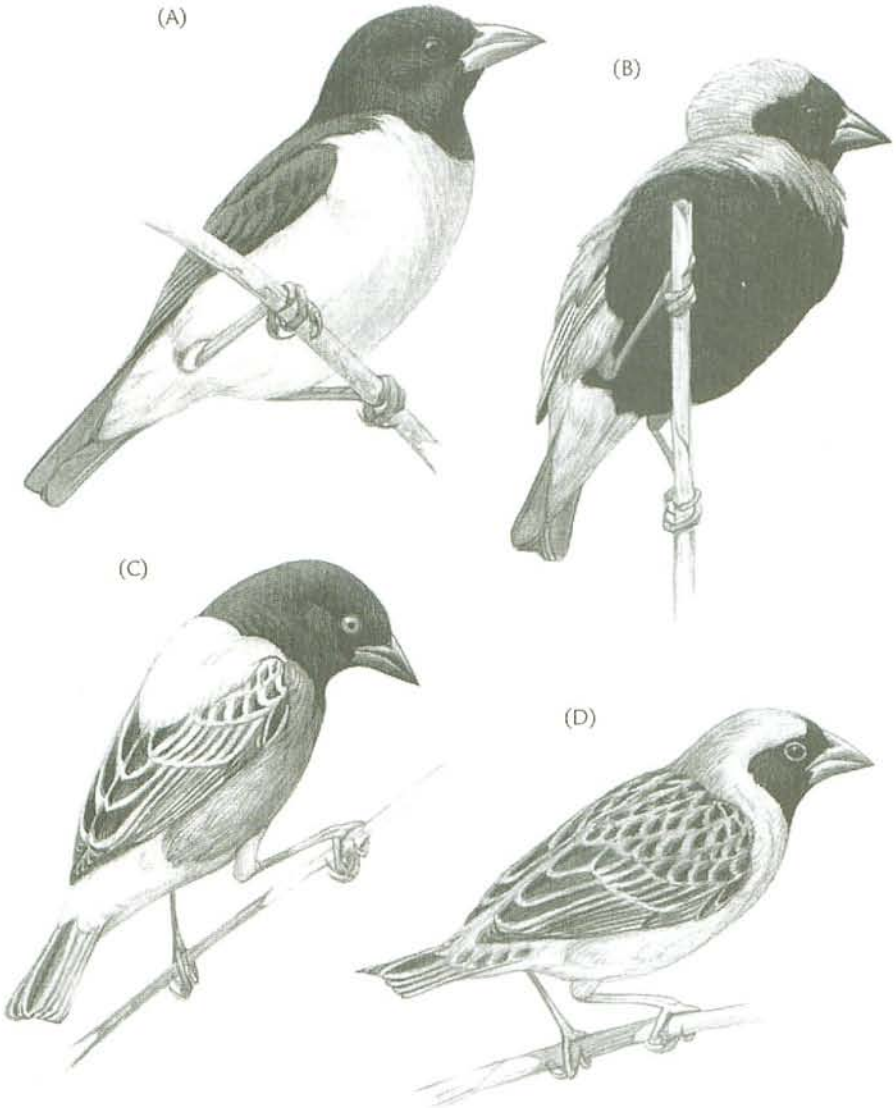


FIGURE 13–1 African weavers have different breeding systems. (A) The Dark-backed Weaver and other species of stable forest habitats with uniform food distributions tend to be territorial, solitary, and monogamous. (B) The Southern Red Bishop, a territorial polygynous species, and (C) the Golden-backed Weaver, a colonial polygynous species, both live in highly seasonal or unpredictable savanna habitats. They practice resource-defense polygyny. Males of these species can control the limited safe nest sites near good food supplies. (D) The most abundant of the savanna weavers, the Red-billed Quelea is monogamous even though it nests near abundant food. Queleas nest in colonies so large that their members deplete nearby food stores during nesting and must commute farther and farther to gather food for their young. Male assistance becomes essential to ensure that older nestlings are fed.

than are uniformly distributed resources. Extending Brown's concept of economical defensibility (see Chapter 11), the environmental potential for polygyny increases with clumped resource distributions. Variation in quality of controllable territories therefore leads to polygyny. Females that join a harem do so because they can do as well as or better than when paired alone with a male on a territory of poorer quality. Polygynous male Marsh Wrens, Red-winged Blackbirds, and Indigo Buntings, among others, all control better-quality territories than do unmated or monogamous males in the same area. The mating success—number of mates—of male Marsh Wrens, for example, increases with the proportion of the territory that provides good nest sites (Kroodsma and Verner 1997).

Females in a harem share male help—at a cost. Among Great Reed Warblers, for example, more nestlings of polygynous males die from starvation than those of monogamous males (Dyrcz 1977). Starvation is most

frequent during cold, wet spells when food is scarce and the young depend on food delivered by the male as well as by the female parent. Belonging to a harem is still advantageous because reduced nest predation on polygynous territories with better nesting sites offsets losses to starvation.

Fruit diets favor the evolution of polygynous mating systems in birds. Males of many tropical, fruit-eating birds do not help care for their young. Fruit and floral nectar are conspicuous food sources that require little searching. After a bird has located them, regular revisitation minimizes foraging effort. Incubating females can easily slip off the nest to feed quickly. As long as the energy requirements of nestlings can be mostly satisfied with fruit, one parent can raise them successfully. Males of these species devote themselves, instead, to display to attract additional mates. Most species of birds-of-paradise, therefore, are polygynous. They feed on predictable, highly nutritious fruits, and so females can raise their young alone.

Extra-pair fertilizations are frequent in polygynous species, as they are in monogamous species. Two working hypotheses describe the tradeoffs between the number of mates that a male has versus the frequency of extra-pair fertilizations that he can attain. They are the male tradeoff hypothesis and the female choice hypothesis. Support exists for both.

The male tradeoff hypothesis predicts that polygynous males should experience more frequent cuckoldry than do monogamous males because polygynous males opt to attract new mates rather than to guard their current mates from neighbors (Hasselquist and Sherman 2001). In support of this prediction, polygynous male Rock Sparrows spend less time guarding their mates during their fertile period than do monogamous males. The polygynous males were cuckolded more frequently as a result. About half of the young in the nests of polygynous males were sired by another male, compared with only 6 percent of the young in the nests of monogamous males of this species (Pilastro et al. 2002). More generally, the overlapping of the fertile periods of females in a harem increases the probability of cuckoldry because their shared mate cannot guard them as effectively (Neudorf 2004).

The alternative female choice hypothesis predicts the opposite result—namely, less frequent cuckoldry in polygynous species. According to this hypothesis, a female can pair with the (best) male of her choice. Males with multiple females, therefore, have less incentive to seek extra-pair copulation. In support of this hypothesis, extra-pair chicks are twice as frequent in monogamous species (in north temperate species) as in polygynous species—0.23 percent compared with 0.11 percent (Hasselquist and Sherman 2001).

Serial polygyny with successive females sets up a different option. To acquire extra females, males of the hole-nesting Eurasian Pied Flycatcher set up side territories where they advertise for an additional late-arriving females (Alatalo and Lundberg 1984). The male flycatchers sing on their secondary territories after their first mate starts laying and incubating the eggs. Their extra territories are typically far enough away from their primary territory to allow them to project themselves as unmated males,

tricking secondary females into an unfavorable situation. Secondary females get less male assistance than the do primary females and fledge fewer young as a result.

Conversely, female flycatchers widowed during incubation solicit copulations from neighboring paired males. A female thereby entraps her neighbors into helping to raise offspring fathered by her former, deceased mate (Gjershaug et al. 1989).

Polyandry

Females control and pair overtly with several males in only a few bird species. Their males then incubate the eggs and take care of the young. Such females defend territories, compete for males, and take the lead in courtship. In some cases, sex-role reversal has led to the evolution of large and brightly colored females. Female phalaropes, a kind of sandpiper, for example, are the brightly colored sex. They compete for males in congregations at productive feeding sites and initiate courtship with males. Males incubate the resulting clutch of eggs by themselves and do not tolerate the female near the nest after the clutch is complete. Females then lay additional clutches for other males.

Classic polyandry has evolved primarily in two orders of birds. In the Order Gruiformes, the buttonquails, roatelos, and some rails are polyandrous. In the Order Charadriiformes, the jacanas, painted snipes, the ploverlike Eurasian Dotterel, the Plains Wanderer of Australia, and a few sandpipers are polyandrous.

The Spotted Sandpiper of North America provides a classic case study of avian polyandry (Oring et al. 1997). Female Spotted Sandpipers are 25 percent larger than males. They defend large nesting territories and fight one another for the available males (Figure 13–2). Initially, females pair monogamously, and many, but not all, share parental duties. As additional

FIGURE 13–2 With raised wings, a polyandrous female Spotted Sandpiper defends her territory against a neighboring female. [*Photography by S. J. Maxson, courtesy of L. Oring*]

males arrive on breeding grounds, females compete for them. A female's reproductive success increases directly with her ability to obtain extra mates. At some locations, Spotted Sandpipers breed monogamously, and females help care for young. At other locations, including Minnesota, some females become polyandrous and attract as many as four males. In this case, a female lays separate clutches of four eggs each sequentially for her primary male and for one to three secondary males. Each male assumes most of the parental care. It incubates its clutch of eggs, defends a surrounding territory against other males, and cares for the brood. When a male loses its clutch of eggs to a predator, the female quickly replaces the clutch with a new set of eggs. One female produced five clutches for three males in 43 days.

Changes in the levels of hormones that mediate aggression and parental behavior match the reversal of sex roles in this sandpiper (Oring and Fivizzani 1991; Figure 13–3). Levels of the sex hormone testosterone are lower in males than in their aggressive females. Testosterone also inhibits incubation behavior. Low levels of this hormone in male Spotted Sandpipers facilitate their increased incubation effort. Conversely, high levels of the hormone prolactin promote incubation and other parental behavior.

Male incubation seems unlikely to evolve unless the male is confident of his paternity of the clutch that he parents (Oring et al. 1997). Cuck-

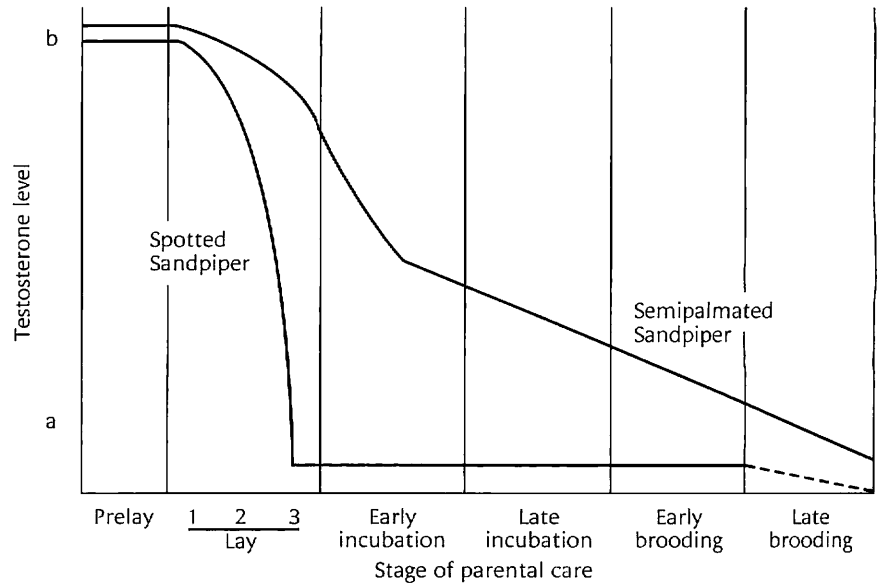


FIGURE 13–3 Seasonal changes in the circulating testosterone levels of male Spotted Sandpipers and Semipalmated Sandpipers. In male Spotted Sandpipers, which perform all or most of the parental care, testosterone levels drop sharply from (b) the elevated levels that support sexual activity before eggs are laid to (a) basal levels at the onset of incubation. Numbers above the word "Lay" indicate first, second, and third eggs of a four-egg clutch. In male Semipalmated Sandpipers, which share incubation with their mates, testosterone levels decline gradually throughout the parental-care period. [*After Oring and Fivizzani 1991*]

oldry accounts for about 10 percent of Spotted Sandpiper young. Females store sperm for as long as a month and use it to fertilize some eggs in later clutches. Mixed paternities therefore are the result of fertilization by sperm that females store from their primary mates. Experienced, older male Spotted Sandpipers speed to the breeding grounds before younger males and compete vigorously to be a female's primary mate.

Paternity assurance accrues for both primary and secondary males in several ways. First, within-pair copulation rates peak when females are most likely to be fertilized—on the day before the first egg is laid. Second, mates copulate frequently within 1 minute when they are reunited after a separation. Third, females usually reject attempts at extra-pair courtship (Oring et al. 1993). But, in the end, younger, secondary males incubate and then parent some young that are not their own. Doing so is better than not reproducing at all. And, as if to compensate, they get more assistance from the female than does the primary male. All's fair it seems.

Sex-role reversal is even more striking in the jacanas (Family Jacanidae), long-toed marsh birds of the Tropics. They provide the most extreme examples of reverse sexual size dimorphism among birds (Emlen and Wrege 2004). Females are from 50 to 83 percent larger than males in seven of the eight species in the family. Female Wattled Jacanas also have more elaborate ornamentation (facial shield and wattles) and weapons (wing spurs) than do males, which they dominate physically. Males and females of another species, the Lesser Jacana, are the same size and share equally in all aspects of parental care. In the remaining species, males build the nest, incubate, and raise their young (Jenni and Mace 1999).

Female Northern Jacanas and the closely related Wattled Jacanas bond with as many as four males simultaneously in rich habitats with high densities of males. Each male defends its own nesting territory, aided by the female. When Stephen Emlen and his colleagues (1989) removed resident females—thereby creating opportunities for new females to take over the undefended territories and associated males—the takeover females killed or evicted three of four existing broods of chicks. They solicited copulations from four of the five "widowed" males to start all over again with their own young.

As with Spotted Sandpipers, multiple males in the harems of female Wattled Jacanas sustain a substantial cost of cuckoldry in the young that they raise (Emlen et al. 1998). Chicks sired by a male's co-mates (the other males in a female's harem) make up as much as 74 percent of the broods. They constitute as much as 29 percent of all chicks each year. In contrast with Spotted Sandpipers, however, stored sperm from the primary male is not the source of this cuckoldry. Rather, the female copulates frequently with all the males of her harem during the production and laying of eggs. The risk of cuckoldry increases with the number of males in the harem (Figure 13–4). Single mates of monogamous females experience no cuckoldry. The result is that male jacanas compete with one another not only for the receipt of a clutch but also for copulations. They compete to fertilize both the eggs in their primary clutch and the eggs tended by other males in the harem.

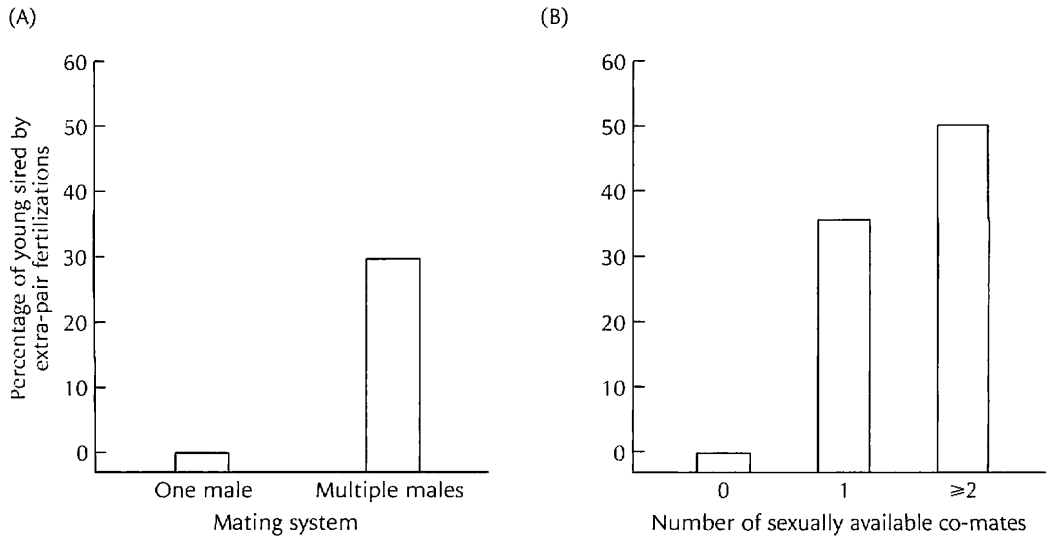


FIGURE 13–4 Risk of cuckoldry increases with polyandry in jacanas. Single mates of monogamous females tended broods that were their own offspring. (A) Almost 30 percent of broods tended by males of polyandrous females included young that were fathered by a sexually available co-mate—that is, a male not yet incubating or tending small young. (B) The more sexually available co-mates there were, the more broods there were that included young sired by extra-pair fertilizations. [*From Emlen et al. 1998*]

Diverse species practice cooperative polyandry, in which several males cooperate to assist one or several females. Such species include hawks (Galápagos Hawk, Harris's Hawk), gallinules (Dusky Moorhen, Tasmanian Nativehen), a woodpecker (Acorn Woodpecker), and a songbird (the Dunnock).

The games of allocation of resources to parental care motivated by the probability of paternity reach their zenith in the complex mating systems of the Dunnocks, a drab, sparrowlike songbird that lives in the dense hedgerows of Europe. The complex sexual relations of Dunnocks include monogamy, polygyny, polyandry, and polygynandry (Davies 1992; see also Gibson 1993).

Dunnocks eat the tiniest soil arthropods in dense cover, where exclusive nesting territories are difficult to maintain. Only the female incubates. The sexes establish independent, but overlapping, territories in relation to food density. The patterns of overlap prescribe the varied pair bonds. Where food is dense, one male may overlap the small territories of one female (monogamy) or two (bigamy). At lower food densities, however, males cannot monopolize the food resources required by females and their chicks. Females then have large territories that overlap with two (unrelated) males. Because they fledge the most chicks when they have two males helping them, such females solicit copulations from both males, which increases the commitment of each male to the parental care of her

chicks. The experimental addition of food causes reductions in territory size and can promote polygyny rather than polyandry. More complex groups of two or more females may share two or more males, depending on the arrangements of their feeding territories.

Contrary to the female's best course, Dunnock males fare best as bigamists. The resulting conflicts lead to intense copulation rates (as in Smith's Longspur; see Chapter 12 and Box 14-3) and sperm competition. Preceding copulation is an elaborate display in which the male Dunnock pecks the female's cloaca, thereby stimulating her to eject sperm from previous matings and simultaneously increasing the probability of egg fertilization by the latest—namely, his—ejaculate. Underneath that complexity, each sex adjusts its personal and parental relationships in ways that optimize reproductive success. To tell whether they are the fathers of certain young and, therefore, how much they should feed them, the males monitor the appearance of eggs in the nests of the females with which they have mated.

Brood Parasitism

The demands and conflicts of parental care invite both cheating and cooperation. Brood parasitism—the surreptitious addition of eggs to another female's nest—is a common form of cheating. It allows females to increase the number of eggs that they lay without increasing their costs of parental care. It also dilutes the genetic relationship between parents and their dependent offspring.

Brood parasitism among birds takes place both within species and between species. Many species practice intraspecific brood parasitism; that is, they lay extra eggs in the nests of other females of the same species as a supplement to those tended in their own nest. Some species, called obligate brood parasites, never build their own nests or raise their own young. Instead, they depend on other species for the services of parental care.

Intraspecific Brood Parasitism

Intraspecific brood parasitism is widespread among birds, being reported in at least 234 species in 16 orders (Yom-Tov 2001). The habit is most prevalent among waterfowl, but the practitioners also include grebes, fowl, gulls, ostriches, pigeons and doves, and songbirds. American Cliff Swallows nesting in large, dense colonies in southwestern Nebraska regularly lay their eggs in one another's nests (Brown and Brown 1995). Careful daily monitoring of the number of eggs in nests revealed that at least 24 percent of the nests in colonies of more than 10 pairs of swallows received eggs from neighbors. Parasitic females quickly deposited eggs in host nests when the hosts were away; in one instance, it took only 15 seconds to do so. Such parasitism reduced the reproductive success of host females, which acted as though the parasitic eggs were their own and laid fewer eggs themselves.

Common Starlings commonly lay eggs in nests other than their own. Like those of the cliff swallows, one of every four early nests in both New Jersey and Britain acquires foreign eggs (Evans 1988; Cabe 1993). Breeding females guard against parasitism by removing foreign eggs deposited before they themselves start to lay. After a female has started her own

BOX 13–1

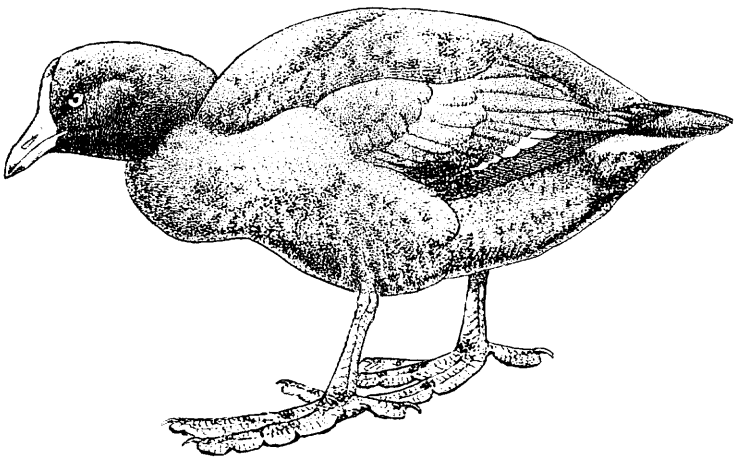
COOTS COUNT

American Coots are almost comical, ducklike rails whose name also refers to a simpleton or stupid person. Quite the opposite. They are champions of the game of optimizing their allocation of eggs to their own nests versus the nests of neighbors. They even keep count of how many eggs are in their own nests (Lyon 2005).

Intraspecific nest parasitism is high in British Columbia, where 41 percent of coot nests include eggs placed there deliberately by other females. Thirteen percent of all eggs laid were in the nests of other females. Female coots recognize about half of the parasitic eggs by the timing of their appearance and, in some cases, by distinctive color patterns. They either kill such an egg by burying it in the nest material or move it to an inferior incubation position in the clutch, which delays hatching and increases the likelihood that the chick will not survive.

Faced with the likely addition of parasitic eggs to the clutch, the female coot keeps an ongoing count of how many eggs in the nest she recognizes as her own. She continues to add eggs to the optimal clutch size. Her count excludes eggs that have been added by others but that she later rejects. She doesn't spot all the parasitic eggs, however, and counts some of them as her own. She lays one egg fewer of her own for each accepted parasitic egg to reach her correct clutch size.

Deciding when it pays to put some eggs in the nests of neighbors rather than in the female's own nest adds more complexity to the game. Generally, coot chicks from the earliest laid eggs in a clutch survive best. A female coot parasitizes another nest when an early addition to the neighbor's clutch has a better chance of succeeding than does a late addition to her own clutch.



An American Coot.

clutch, however, it cannot distinguish the parasitic eggs. Often, a roaming, parasitic female removes one of a host's eggs and replaces it with her own. In addition to making detection more difficult, egg removal by the parasite keeps the clutch size closer to the optimal number (six) for nest success, to its own benefit as well as that of the host. At least one species, the American Coot, optimizes its clutch size by keeping count of its own eggs versus distinguishable parasitic eggs (Box 13–1).

Intraspecific parasitism could be the first step in the evolution of obligatory brood parasitism. Occasional, or facultative, parasitism of the nests of related species would be the next step. The Black-billed Cuckoos and Yellow-billed Cuckoos of North America, for example, parasitize each other, particularly when abundant food encourages the production of extra eggs (Hughes 2001). The acceptance of a parasite's eggs and successful raising of its young then lead logically to increasing parasitism and possibly to obligatory interspecific brood parasitism.

Obligate Brood Parasites

Cowbirds and cuckoos are the most familiar of North American birds that relinquish care of all their young to foster parents of other species (Davies 2000). Such obligate brood parasites always lay their eggs in the nests of other birds (Figure 13–5). This breeding strategy is unusual. A few fish and social insects, but no mammals, also are obligate brood parasites. Among birds, the practice has evolved in cowbirds (Icteridae; 5 of 6 species), honeyguides (Indicatoridae; 18 species), cuckoos (Cuculidae; 53 of 135 species), African brood parasitic finches (Viduidae; 19 species), and one duck (Anatidae) (Payne 1998).

FIGURE 13–5 Foster-parent Dunnock (*right*) feeding a parasitic young Common Cuckoo. [*Stephen Dalton/Minden Pictures/NHPA*]

By reducing their costs, risks, and commitments, birds that are obligate brood parasites are able to lay more eggs each season. Additionally, by not putting all their eggs into one nest, brood parasites improve the chances that some of their offspring will escape predation. Female Brown-headed Cowbirds lay from 30 to 40 eggs per season in weekly sets of 2 to 5 eggs (Lowther 1993). Most host nests have only 1 cowbird egg, but some may have as many as 12 as a result of visits by multiple female cowbirds. African cuckoos of several species lay from 16 to 25 eggs per season in clutches of 3 to 6 eggs, but they lay only 1 egg per nest (Davies 2000).

The eggs of parasitic cuckoos have thick shells and are resistant to cracking. Females drop their eggs into deep nests, sometimes damaging the hosts' eggs rather than their own.

Some obligate brood parasites are highly specialized birds that target specific hosts. To minimize detection and destruction by the host, cuckoo eggs have come to resemble or mimic those of their primary hosts. In Africa, the eggs of the Dideric Cuckoo are so similar to those of its host, the Vitelline Masked Weaver, that one ornithologist resorted to chromosome analysis to distinguish them (Jensen 1980). The eggs of the Red-chested Cuckoo, and perhaps other species, closely match their hosts' eggs in the ultraviolet spectrum and other aspects not visible to the human eye (Cherry and Bennett 2001).

Throughout Europe, Common Cuckoos parasitize a variety of host species that have eggs with different color patterns. In these cases, the Common Cuckoos' eggs mimic those of their different hosts (Figure 13–6). For example, the blue eggs of the Common Cuckoo in Finland match those of its primary hosts, the Common Redstart and the Whinchat, whereas, in Hungary, Common Cuckoos lay greenish eggs with dark markings, similar to those of the Great Reed Warbler. Female cuckoos of such egg "races," or *gentes,* occupy different major habitats in Scandinavia and central Europe, but they coexist in some parts of central

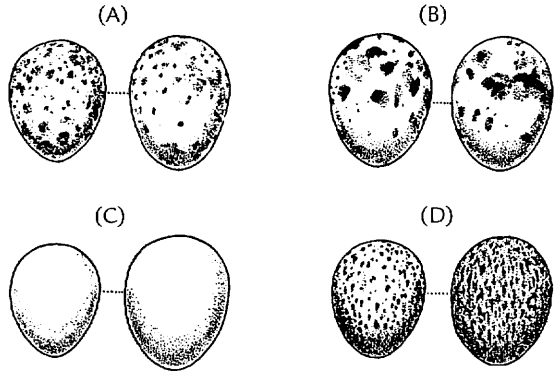


FIGURE 13–6 Matched pairs (joined by dotted line) of the egg "races" of the Common Cuckoo (*right*) and their hosts (*left*). Identity of hosts: (A) Garden Warbler; (B) Great Reed Warbler; (C) Common Redstart; (D) White Wagtail. [*From Rensch 1947*]

FIGURE 13–7 Baby brood parasites dispose of their competitors. A hatchling Common Cuckoo (*left*) pushes the eggs of the host from the nest, and a hatchling Greater Honeyguide (*right*) kills host nestlings with the hooklike tip of its bill. [*After Lack 1968*]

Europe. Females of each race are genetically distinct, carrying the genes for egg type on the female-specific W sex chromosome (Gibbs et al. 2000). Although females that specialize on particular hosts coexist in central Europe, they are not different species. They cross-mate with males that are not genetically distinct, uniting all as a single species.

The eggs and subsequent chicks of brood parasites are normally the same size or larger than those of their hosts, thereby increasing their dominance over the host's chicks. Some baby brood parasites are aggressive. It is not uncommon for a hatchling cuckoo to shove the unhatched eggs of its host out of the nest. Baby honeyguides have fanglike hooks at the ends of their bills for killing their foster nest mates (Figure 13–7).

Nestling cowbirds do not evict their foster nest mates, as do many cuckoos and honeyguides. Why not? The reason is that they benefit from higher rates of food delivery by parents if some host young are in the nest. Experiments with Eastern Phoebes revealed that cowbird nestlings grow faster with nest mates than alone, garnering more than half of the food delivered 2.5 times as frequently (Kilner et al. 2004). Two host young appear to be optimal for the cowbird. More encroach on the cowbird's share of the food.

As a rule, the eggs of brood parasites require less incubation time (from two to four days less) than do those of the host. This timing ensures earlier hatching and dominance by the young parasite. The Pied Bronze Cuckoo and Common Cuckoo incubate eggs in their oviducts for as long

as 18 hours before laying, which gives them an extra head start. Hatchling parasites also grow faster than nonparasites, enabling them to garner most of the parental attention. Common Cuckoo chicks are even more direct (Kilner et al. 1999). They stimulate the host parent Great Reed Warblers to bring more food faster by imitating the begging calls of warbler nestlings. Parents increase food deliveries in proportion to the volume of begging calls. Therefore, a cuckoo chick imitates not just one of its foster nestlings but a chorus of "si . . . si . . . si . . . si" calls from the entire brood. Initially, the cuckoo chick's loud begging calls are equal to the calls of four foster warbler nestlings. As the cuckoo chick grows, the volume of its robust begging call grows, too, ultimately matching that expected from eight warbler nestlings.

The brood parasitic finches of Africa and their hosts are sources of deep insight into the evolutionary dynamics of brood parasitism in birds (Sorenson and Payne 2001; Sorenson et al. 2004). First of all, the practice of brood parasitism in this group evolved only once, a long time ago. The 18 species of indigobirds and whydahs *(Vidua)* and the distinct Cuckoo Weaver *(Anomalospiza)* had a single, ancient origin in Africa about 20 million years ago. Together, they are the sister group of the grass finches that are their hosts. The two related sets of species, one parasitic on the other, have evolved and speciated in a long and enduring association. Whereas all the *Vidua* finches specialize on species of grass finches, the Cuckoo Weaver shifted to certain Old World warblers as its hosts.

The species of *Vidua* finches are host specialists that mimic the distinctive nestling mouth color and markings of their single grass finch hosts (Estrildidae) as well as the adult songs (Figure 13–8). The mimicry of

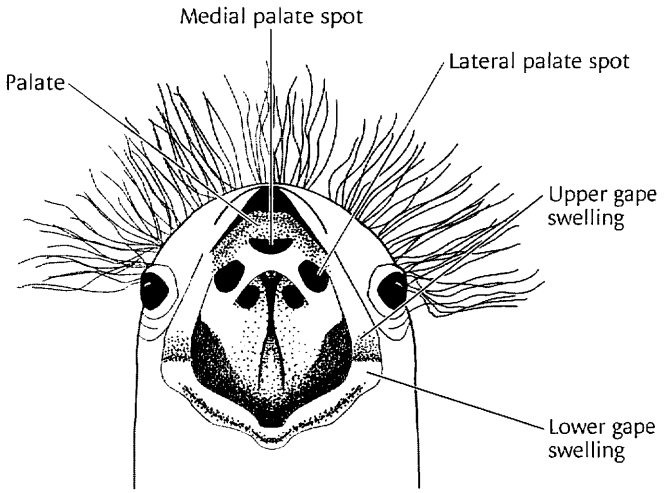


FIGURE 13–8 The mouth pattern of a nestling of the host Cut-throat Finch includes a ring of five large black spots against a bold white palate and large white gape swellings. The area anterior to the spots is yellow, and behind shades to reddish black. The lower mouth is black and the tongue is pink with a broad black band. [*From Payne 2005*]

mouth color and markings of their host's nestlings favors young *Vidua* brood parasites in receiving food from their foster parent (Payne 2005). The mimicry of adult songs fosters the fidelity of successive generations of the parasite to their specific host. How? Briefly, both males and females imprint as nestlings on the song of their host. Males of each *Vidua* species later sing the host song to attract females, which were raised by the same host. The females then lay their eggs in the nests of the same hosts, which the females identify by the familiar song.

How, then, did the different host-specific species of *Vidua* finches come to be? Did they co-speciate—split, speciate, and coevolve in concert with their grass finch hosts? Or did some females switch hosts opportunistically and start a new host-specific lineage? Analysis of the patterns and timings of speciation in both grass finches and *Vidua* finches suggests that co-speciation did not take place. Rather, the colonization of new hosts (like the colonization of a new island) was the principal way that the indigobirds evolved into new host-specific species.

Bob Payne and his colleagues (2002) documented a recent switch to a novel host species by one species, the Village Indigobird. This species normally mimics and parasitizes the Red-billed Firefinch. But one population on the Zambezi River in southern Africa parasitizes the nests and mimics the song of the Brown Firefinch. It is the only population of Village Indigobirds known to do so. Nestlings of this pioneering population have mouth markings that match those of their traditional hosts. The two host-specific races, old and new, coexist as distinct breeding populations.

Effects of Brood Parasites on Their Hosts

Brood parasites severely limit their host's breeding success, at least in the short term. Parasitized nests rarely fledge young of the host itself. For example, the well-studied Brown-headed Cowbird parasitizes from 20 to 40 percent or more of the nests of local host species (Payne 1998). Host productivity drops from 10 to 20 percent, mostly because the cowbird removes one host egg for each one that it adds to a nest. Then the cowbird nestling takes most of the food delivered by its foster parents to the nest, often causing nest mates to starve. For smaller hosts, one cowbird nestling is equivalent to 3.4 host nestlings in its energy intake (Kilpatrick 2002).

The local, short-term effect of brood parasitism can be substantial (Robinson et al. 1995). Abundant cowbirds parasitize three-fourths of the nests of Neotropical migrants in small forest fragments in Illinois. Combined with high rates of nest predation, few nests succeed. The control of cowbirds is an important tool for the management of highly endangered species such as the Black-capped Vireo in Texas, Bell's Vireo in California, and the Kirtland's Warbler in Michigan.

Cowbirds were believed to be responsible for the precipitous decline of the endangered Kirtland's Warbler in Michigan (Mayfield 1992). In 1957, parasitism was high (about 55 percent), and 75 percent of the nests examined between 1957 and 1971 were parasitized. In just one decade,

the number of singing male Kirtland's Warblers dropped from 502 (1961) to 201 (1971), and parasitized nests produced nearly 40 percent fewer young than unparasitized nests. Emergency removal of cowbirds started in 1972 but caused nest parasitism to drop to only 3 percent. The warbler population stablized at about 200 pairs but did not increase until 1990, when it grew in response to new habitat created by a wildfire. Cowbird control may be a short-term, expensive management tool for endangered species, but it cannot substitute for the acquisition and management of quality habitat (Rothstein and Robinson 1994).

The long-term effect of brood parasitism by cowbirds may not be severe in species that have several broods of young a year (Payne 1998; Payne and Payne 1998). For example, rearing a cowbird nestling has little effect on the lifetime reproductive success of an adult Indigo Bunting. It does not affect the bunting's ability to nest again in the same season. Nor does it affect adult survival and reproductive success in future years.

How do host birds themselves respond to brood parasitism? In general, they respond adaptively. Some host birds accept the eggs of a brood parasite, but others do not. Stephen Rothstein (1975) placed artificial cowbird eggs in 640 nests of 30 species of North American birds. Twenty-three of these species usually accepted the eggs (meaning that they threw them out less than 30 to 40 percent of the time), whereas 7 species usually rejected the different eggs. "Rejectors" typically threw out the parasite eggs as a natural extension of nest sanitation behavior, albeit at some risk to damaging their own eggs. Some cuckoo hosts are more likely to eject a cuckoo egg from their nests if they have seen a cuckoo nearby (Lotem et al. 1995). Some birds, such as the American Yellow Warbler, respond to the discovery of a cowbird egg by deserting the nest or by burying the entire clutch in additional nest materials and laying a fresh clutch of eggs on top. Others desert the nest and start over again (Payne 1998).

The rejection defenses of American Robins against cowbird parasitism vary with location (Briskie et al. 1992). In Churchill, Manitoba, north of the range of cowbirds, American Robins are more likely to accept a parasitic egg than in southern Manitoba, where cowbirds have parasitized local birds for centuries. One-third of the southern robins rejected an experimental egg placed in their nests by "parasitic" ornithologists, whereas all Churchill robins accepted them.

Egg rejection is tricky business when a female experiences both intraspecific brood parasitism and the attentions of an obligate brood parasite. Rejecting eggs from multiple sources increases the host's risk of damaging some of her own eggs. Conversely, the one duck that is a brood parasite, the Black-headed Duck, suffers substantial costs to its own eggs owing, incidentally, to the host coots' responses to their own high levels of intraspecific brood parasitism (Lyon and Eadie 2004). The Black-headed Duck parasitizes mainly two species of coots in South America. Unlike those of all other brood parasitic birds, the Black-headed Duck young leave the nest upon hatching and require no parental care from the host.

Yet the eggs are rejected at high rates (38–65 percent), and few of those that remain will hatch. Like the related American Coot, South American coots experience frequent brood parasitism by their neighbors, and so they are vigilant for foreign eggs. They reject the duck eggs at high rates as a result of their vigilant rejection of any other coot's eggs.

Cooperative Breeding

Brood parasitism and cooperative breeding lie at opposite ends of the spectrum of breeding-system practices among birds. Obligatory brood parasites are selfish cheaters whose evolution is consistent with Darwin's theory of natural selection. Individual advantages are not as obvious in cooperative breeding, in which "helpers" care for young that are not their own.

The apparent altruism of cooperative breeding challenges the basic tenets of evolution by natural selection: Charles Darwin himself offered the discovery of altruistic behavior as a way to disprove his theory. A century later, V. C. Wynne-Edwards (1962) shocked the evolutionary biology establishment when he concluded that individual organisms place the good of their populations or species above their individual well-being. In particular, helpers at the nest seemed to offer the most compelling cases of altruism. Do helpers really sacrifice their own reproductive potential to help others? Or do they perpetuate their own genes in some way?

The possible routes of reconciliation are many. First, helpers might directly enhance their reproduction by delaying their own dispersal to breed independently. Second, helpers might obtain indirect benefits, either by enhancing their own lifetime reproductive success through the production of genetic relatives, called kin selection, or by obtaining help in return, called reciprocal altruism. Kin selection is one way of understanding complex social behavior in ants, bees, and wasps, in which sterile castes help their mother produce sisters. Reciprocal altruism could be in an individual organism's best interest as long as there is no cheating. Field studies of cooperative breeders show increasingly that helpers achieve both direct benefits and, in some cases, indirect benefits.

The phenomenon of "helpers at the nest" was first reviewed by Alexander Skutch (1961). We now know that hundreds of bird species breed cooperatively and that cooperation is a core feature of the breeding biology of birds (Koenig and Dickinson 2004). In Florida Scrub Jays, one of the best-known cases, helpers are an integral part of the social system (Woolfenden and Fitzpatrick 1996; Figure 13–9). The basic social unit is a breeding pair with as many as six helpers that stay for one to seven years. About half of the breeding pairs have helpers, which defend a territory throughout the year. The helpers also protect and feed the nestlings. More generally, helpers contribute to parental care in a diverse array of cooperative-breeding systems.

Surveys of varied bird species consistently indicate substantial testosterone activity in helpers, albeit at lower levels than in breeding adults

FIGURE 13–9 The Florida Scrub Jay is one of the most thoroughly studied species of cooperative-breeding birds. [*Courtesy of A. Cruickshank/VIREO*]

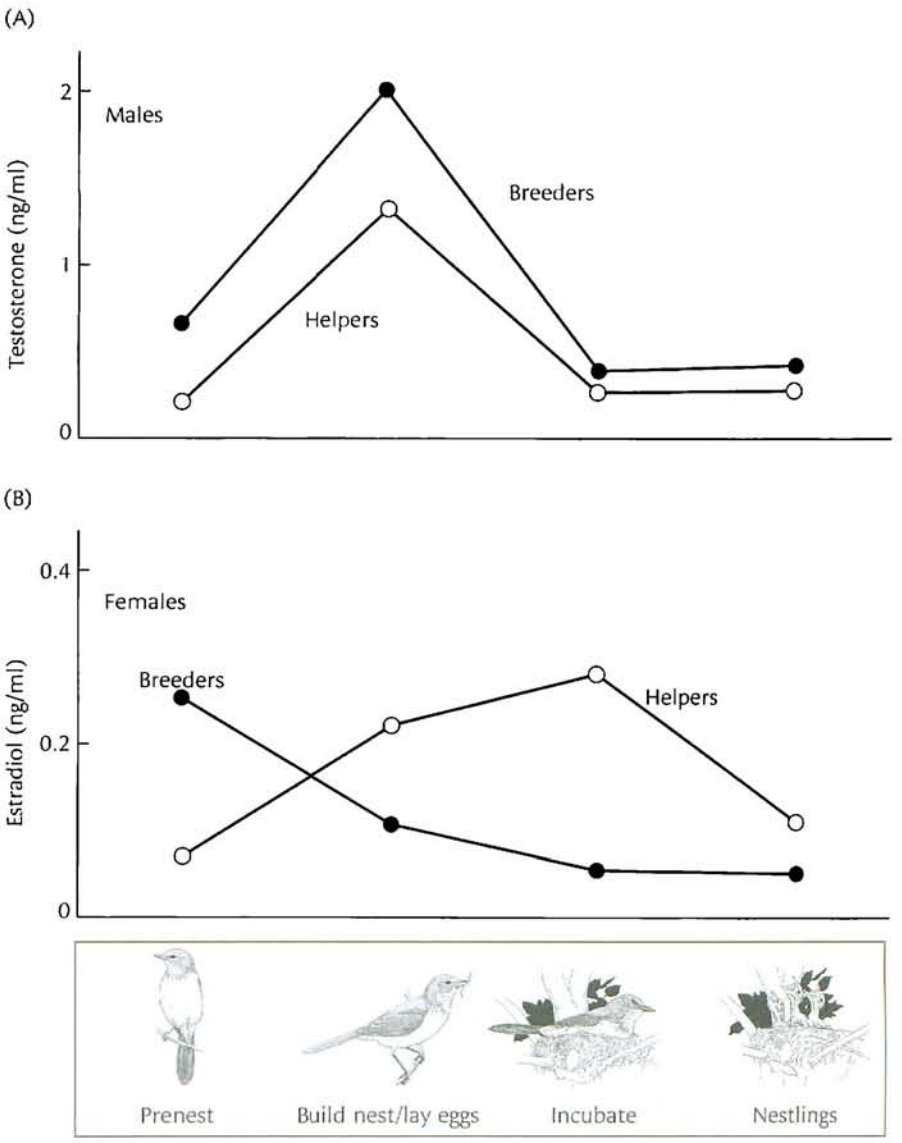


FIGURE 13–10 Changes in sex-hormone levels during the breeding season in male and female Florida Scrub Jays. The graphs show sex-hormone levels in helpers (white circles) compared with nonhelpers, or breeders (black circles). (A) Levels of testosterone in the blood are higher in breeding males than in helper males. Testosterone levels increase in both groups during the early stages of the nest cycle but then drop to low levels during incubation and care of the nestlings. (B) Levels of the estrogen estradiol drop steadily in breeding females but increase in helper females during the later stages of the nest cycle, when helper females tend to disperse in search of their own territory. [*From Schoech 1998*]

(Schoech et al. 2004: Figure 13–10). Neither males nor females are psychologically or hormonally neutered. The reproductive axis—from hypothalamus to pituitary to gonad—is fully functional. Helpers of both sexes of Florida Scrub Jays, for example, are reproductively capable (Schoech 1998). No abnormal hormone profiles are evident. Testosterone levels of helpers increase and then decrease in parallel with those of parents. Levels of prolactin, which mediates incubation and other parental behavior, average lower in helpers than in parents, but they increase in all participants to maximal levels during incubation and nestling stages of the nesting cycle.

Ian Rowley (1965) pioneered the field study of cooperative nesting in Australian birds, specifically in the Superb Fairywren (see Figure 1–16E).

Most breeding groups consist of a female and as many as five males, which provision a group's young cooperatively. Rowley's discovery that helpers are young from preceding broods has been confirmed in other species: most helpers help either genetic parents or stepparents to raise siblings or half-siblings. The functional social units are essentially extended families, and the production of genetically related siblings is consistent with the evolutionary theory of inclusive fitness.

The cooperative social system of the Superb Fairywren is also highly promiscuous. As many as 95 percent of nests contain young sired by males outside the cooperative social group (Mulder et al. 1994). Solicitation and copulation with the large number of receptive females available in the population outside the cooperatively breeding group sustain high levels of testosterone in all males of a social group (Peters et al. 2001, 2002). Individual fairywrens increase their fitness directly and indirectly.

Help or Nuisance?

Do helpers really help? Or do they just hang out and interfere or compete for resources because they lack of a place of their own? Most studies show that helpers truly help, rather than hinder, the parents in their social unit (Figure 13–11). Parental tolerance of grown offspring on their natal territories is a key step in the evolution of cooperative-breeding systems. Reasons to tolerate the continued presence of young from preceding broods center on their helpful contributions to reproduction as well as to the survival of the breeding pair itself.

Many field studies document that the number of young fledged increases with the number of helpers. In a classic study, breeding pairs of Florida Scrub Jays with helpers fledged more young per season than did groups without helpers, principally as a result of better group defense

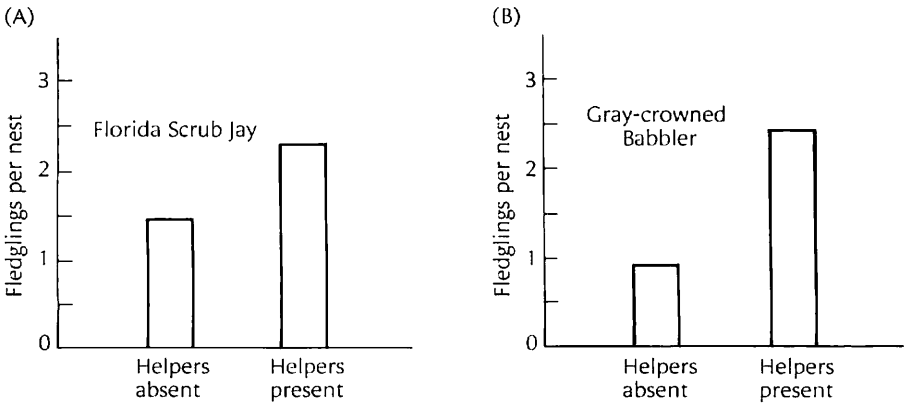


FIGURE 13–11 Groups with helpers fledge more young. (A) Groups of Florida Scrub Jays with helpers produce more fledglings per nest than do pairs without helpers. (B) The experimental removal of helpers from breeding groups of Gray-crowned Babblers reduces the average number of young fledged per nest. [*(A) After Woolfenden 1981. (B) After Brown et al. 1982*]

against snakes, the primary predator on young jays. Temporary removal of helpers from some territories at the beginning of the breeding season showed that breeding pairs with helpers produced more young that fledged from the nest (2.2 versus 1.6) and lived longer after they left the nest than did breeding pairs without helpers (Mumme 1992). In addition to increasing the production of surviving fledglings, helpers improved the survival of the breeding parents. More breeding Florida Scrub Jays with helpers survived than did those without helpers. Hence, helpers increased the lifetime reproductive success of the breeders in this system.

Ecological Constraints and Delayed Dispersal

It may be in the parents' best interests to have helpers, but why do the helpers themselves not disperse from their natal territory and breed elsewhere on their own? Young Florida Scrub Jays achieve three times the individual reproductive success when they breed on their own compared with helping parents produce half-siblings. Yet these young birds delay dispersal and reproduction on their own for several years, even though they may be physiologically capable of breeding.

Stephen Emlen (1984) proposed the general hypothesis that ecological constraints limit successful dispersal and reproduction of young birds entering the breeding population (Figure 13–12). Unpredictable or difficult breeding conditions favor cooperative breeding in some birds. For example, many species that live in the dry forests of Africa and Australia breed cooperatively. Some are nomadic. Others, such as the White-fronted Bee-eater of East Africa, are resident and colonial. Nestling bee-eaters often starve when adequate rains and good supplies of insects fail to materialize. Helpers increase the rate of food delivery. Helpers could start their own nests, but they can raise young successfully by themselves only in environmentally good years. Consequently, the size of cooperative groups

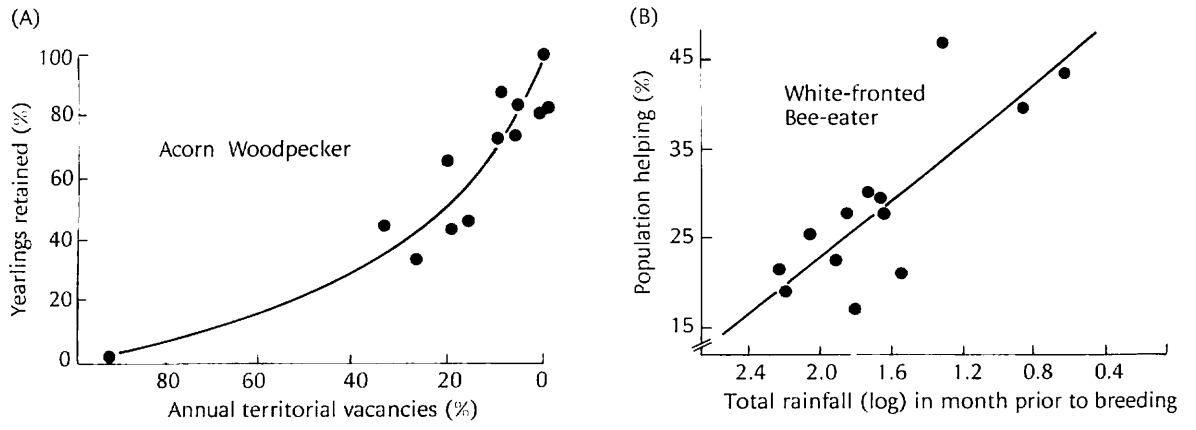


FIGURE 13–12 The retention of young may result from ecological constraints, such as (A) territory shortage, in regard to the Acorn Woodpecker, and (B) environmental harshness (lack of rain) in regard to the White-fronted Bee-eater. [*After Emlen 1984*]

increases with environmental harshness, as measured by low rainfall and poor food availability in the month preceding the onset of breeding.

Uli Reyer's (1980) pioneering studies of Pied Kingfishers on Lake Naivasha and Lake Victoria in Kenya illustrate the importance of local ecology in the acceptance of helpers. A breeding male kingfisher's acceptance of unrelated male helpers is directly related to its need for help in delivering fish to their young. On Lake Victoria, where fishing is difficult, a single helper doubles the average fledging survival rate from 1.8 to 3.6 young per nest. On Lake Naivasha, where fishing is easier, helpers have less effect, and the survival rate only increases from 3.7 to 4.3 young per nest. Most breeding pairs on Lake Victoria have helpers, at least one of which is not their own progeny. On Lake Naivasha, however, few pairs have helpers, and almost all the helpers are the pairs' own young.

Delayed dispersal and group living, it turns out, reflect both extrinsic ecological constraints, such as habitat saturation, and intrinsic social benefits, such as improved survivorship and the acquisition of essential skills. The shortage of quality territories, however, is the primary constraint that discourages and delays dispersal, leading to helping one's parents instead of going it alone (Box 13–2).

BOX 13–2

ALTRUISM BYPASSES INFIDELITY IN AN ENDANGERED ISLAND WARBLER

The Seychelles Warbler is an endangered species, confined until recently to the tiny island of Cousin in the Seychelles islands of the western Indian Ocean. The territories of this drab island species consumed all the available habitat, and young warblers had no choice but to wait as helpers until a breeding adult died.

As a part of the program to prevent the extinction of the Seychelles Warbler, Jan Komdeur (1991) transplanted breeding adults from 16 territories to the nearby and much larger island of Aride, in the hope of establishing a new population. All the vacancies created on Cousin were quickly filled, sometimes within hours, by birds that had been helpers. The transplanted pioneers started to breed on Aride without help. Their 61 young dispersed and bred independently on territories of their own the next year. Given opportunities to breed on their own, they did not serve as helpers. In addition to being a conservation success story, this experiment demonstrated that lifting the ecological constraint of habitat allows the birds to shift to the first-choice practice of breeding rather than helping.

With time, the territories of transplanted warblers and their progeny saturated the habitat available on Aride, restoring the conditions that favored helping. Young females, particularly, stayed home and helped the parents that fed them to raise half-brothers and half-sisters (Richardson et al. 2003). But they provisioned their young kin mainly when the primary female, their mother, rather than the primary male, was present on a continuing basis. This practice increased the odds that they would raise genetically related half-siblings, because the high frequency of extra-pair copulations by their mother severely reduces the odds that young females have genes in common with their social father. Their altruistic helping behavior, therefore, tends to propagate their mother's genes, some of which are certainly the same as those of the half-siblings that they help to raise.

Breeding status may be difficult to obtain on an exclusive territory when established pairs defend most of the available habitat. This situation is most common in species that reside in stable environments and that have specialized habitat requirements and high adult survivorship. Florida Scrub Jays, for example, are restricted to undisturbed oak–palmetto scrub habitat in central Florida. It exists only as small islands of scrub surrounded by other vegetation. This available habitat is saturated by occupied territories. Female helpers wait for openings. They monitor nearby groups and move quickly to replace breeding females that disappear. Males, however, wait to inherit breeding positions on their natal territories. The dominant (usually oldest) son replaces its deceased father, stepfather, or brother.

Alternatively, helper males may take over a separate part of the family territory for their own breeding purposes. The territories tend to expand with group size. When the expanded territory is large enough, one part is ceded to the oldest male helper, which then recruits a female from outside the family unit, thus preventing inbreeding.

Delayed dispersal increases the lifetime reproductive success of male Siberian Jays. These birds have limited access to quality habitat in the boreal forests of northern Sweden (Ekman et al. 1999). Young males that delay dispersal until a quality territory becomes available breed for more years on average than do males that disperse in their first year (3.27 versus 2.73, and to a maximum of seven years versus five years). Males that stay home initially also produce significantly more offspring of their own on average than do those that disperse early: 4.72 versus 1.4 offspring, respectively (Figure 13–13).

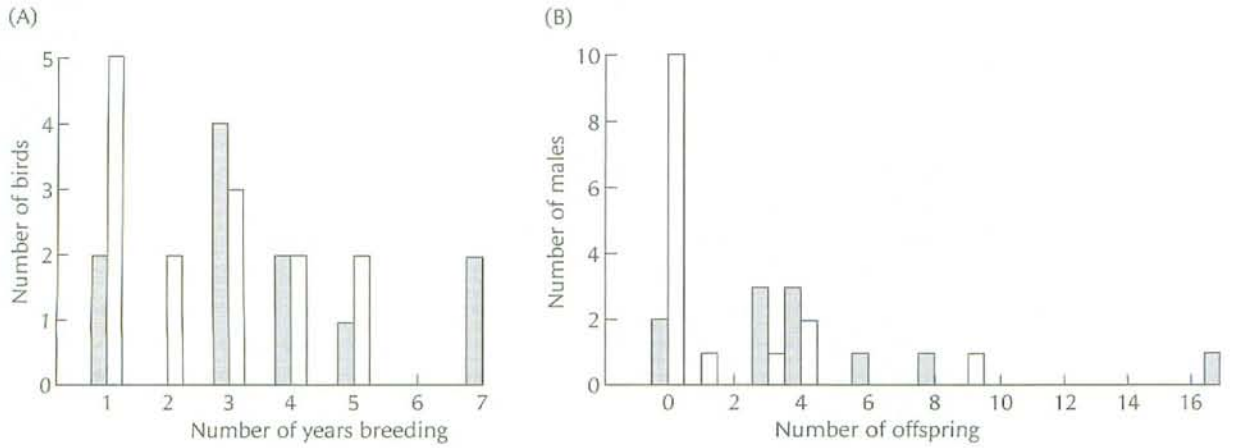


FIGURE 13–13 Lifetime reproductive success of male Siberian Jays that delayed dispersal from their natal territory (gray bars) compared with males that immigrated to a territory after dispersal in their first year of life (white bars). (A) Males that stayed bred more times in significantly more years. (B) Males that stayed produced significantly more offspring in their lifetimes. [*After Ekman et al. 1999*]

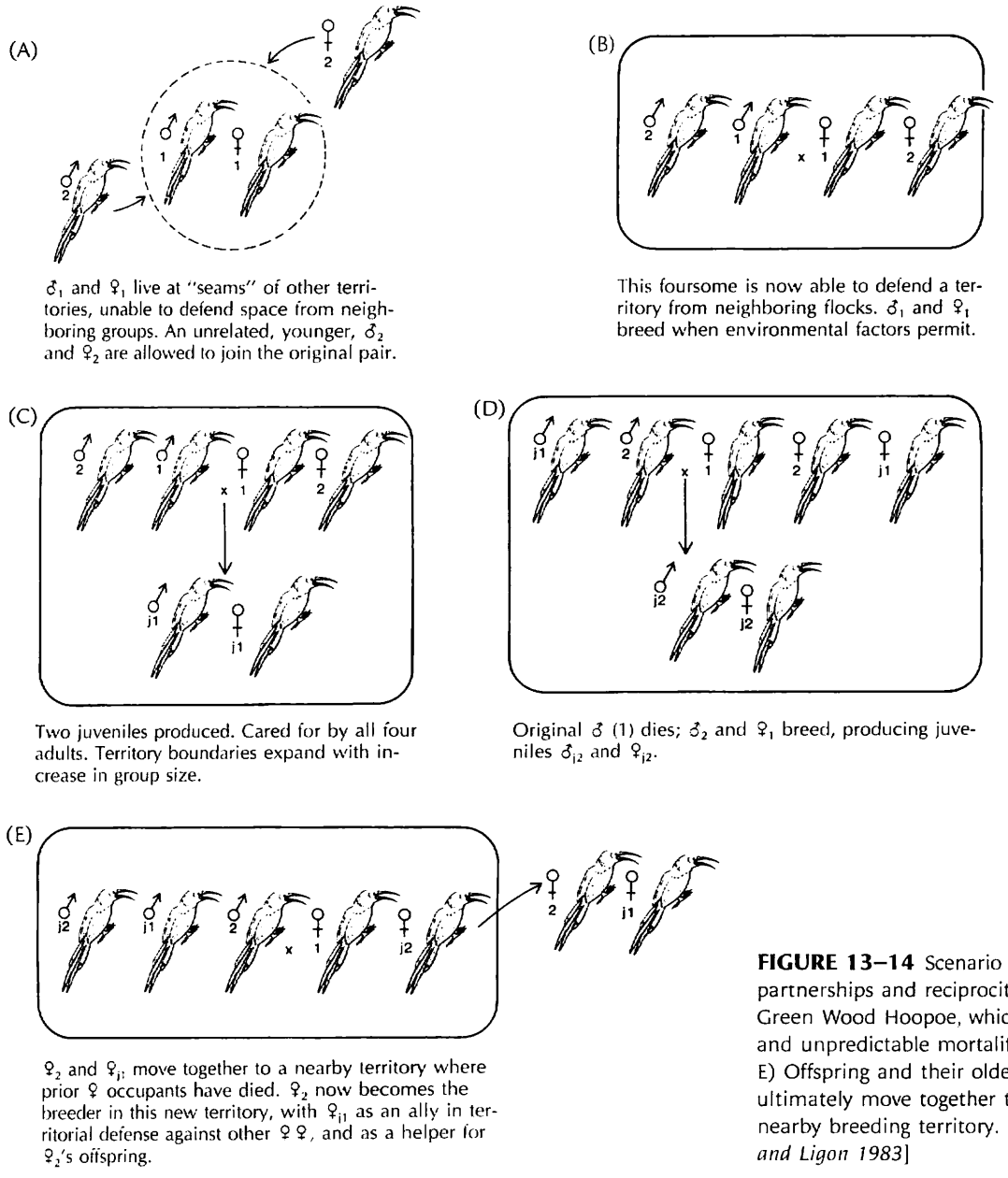
Parental nepotism is a key factor in delaying dispersal by young male Siberian Jays (Ekman and Griesser 2003). Parents are more tolerant of their own offspring than they are of immigrant birds that try to join a family group. Experimental removal of fathers led to their replacement by despotic immigrant males and the departure of the retained sons. By blocking unrelated males from joining a group, fathers favor their sons and provide them with a safe haven of high quality with minimal competition for resources.

Many potential benefits favor delayed dispersal. These benefits include participating in a large cooperative social unit for several years and assisting parents in the raising of siblings or stepsiblings. In addition to waiting for a territorial opening in saturated habitats, a young bird might stay in a home territory that contains key resources not readily available elsewhere. For example, acorn storage granaries are the key resource for Acorn Woodpeckers (see Figure 11–3), and tree holes for nesting and roosting are a key resource for the endangered Red-cockaded Woodpecker. Both of these species of woodpeckers are cooperative breeders that employ young helpers from preceding broods.

Young birds might not be able to breed on their own until they achieve the behavioral skills and social status required to control territorial space, acquire mates, and feed young. The acquisition of such critical skills during a period of apprenticeship favors delayed dispersal and prolonged membership in an extended family unit. For example, White-winged Choughs, an Australian crowlike bird, take almost seven months to acquire the foraging skills needed for independence (Heinsohn 1991). Young choughs depend on food provided by helpers while acquiring essential skills. Conversely, helpers develop their own breeding skills by observing and practicing on their siblings.

The recruitment of help from younger siblings is sometimes a side benefit of cooperative-breeding systems. Green Wood Hoopoes, medium-sized hole-nesting birds of the African savannas, live in extended family groups of helpers (Figure 13–14). Large roost holes in dead trees are a key resource for these cold-sensitive birds. They stay warm at night by sleeping together inside a deep hole (Williams et al. 1991). Where suitable roost holes abound in some habitats in southern Africa, young wood hoopoes disperse readily to new territories, leaving pairs of adults to breed on their own (DuPlessis 1990).

In the lakeside forests of the Rift Valley of East Africa, however, roost holes are scarce and competition for territories containing them is keen. There, pairs of young wood hoopoes, usually an older and a younger sibling or half-sibling, cooperate to secure new breeding space. In the avian version of the television series *Survivor*, young male wood hoopoes recruit help from their former charges to take control of a quality territory. In this way, the initial cooperation leads to long-term working alliances between siblings. The alliance is in the younger sibling's interest because it will eventually replace its partner as the breeding male of the new unit.



δ_1 and $♀_1$ live at "seams" of other territories, unable to defend space from neighboring groups. An unrelated, younger, δ_2 and $♀_2$ are allowed to join the original pair.

This foursome is now able to defend a territory from neighboring flocks. δ_1 and $♀_1$ breed when environmental factors permit.

Two juveniles produced. Cared for by all four adults. Territory boundaries expand with increase in group size.

Original δ (1) dies; δ_2 and $♀_1$ breed, producing juveniles δ_{j2} and $♀_{j2}$.

$♀_2$ and $♀_{j1}$ move together to a nearby territory where prior ♀ occupants have died. $♀_2$ now becomes the breeder in this new territory, with $♀_{j1}$ as an ally in territorial defense against other ♀♀, and as a helper for $♀_2$'s offspring.

FIGURE 13–14 Scenario of cooperative partnerships and reciprocity in the Green Wood Hoopoe, which suffers high and unpredictable mortality. (A through E) Offspring and their older helpers ultimately move together to take over a nearby breeding territory. [*From Ligon and Ligon 1983*]

Bee-eaters and Families

The potential for complex social relations is greatest where contacts with large numbers of birds are frequent and predictable, as for colonial breeding birds. The White-fronted Bee-eater is a case in point (Emlen et al. 1995; Figure 13–15). These bee-eaters are strictly monogamous. They breed in large colonies in the Rift Valley of East Africa, but they function on a daily basis in clans or extended families of 3 to 17 members from several generations. A colony usually includes from 15 to 25 fami-

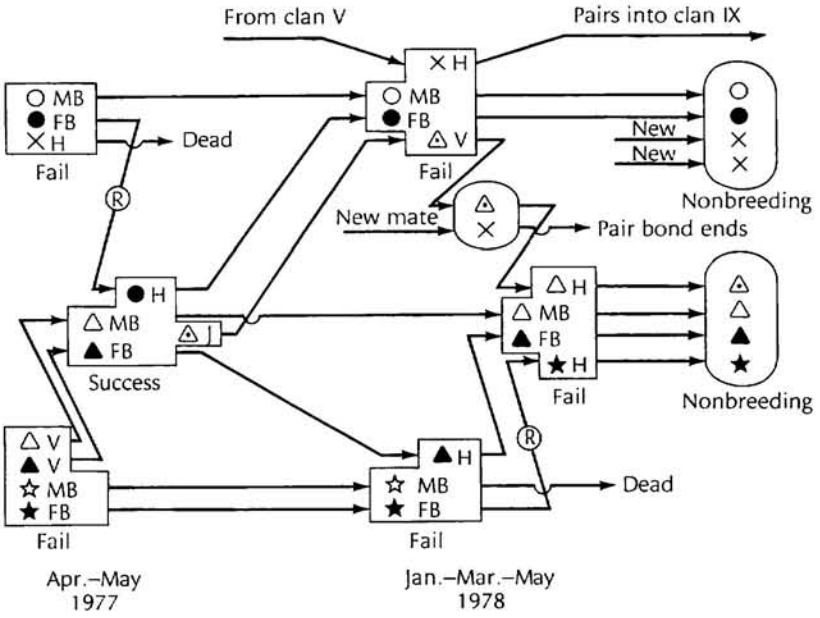


FIGURE 13–15 The social relations of members of a clan of White-fronted Bee-eaters illustrate the complexity of a cooperative-breeding system, as well as ornithologists' ability to follow the behaviors of known, color-marked individual birds. Core members of the clan are identified individually by symbols (circles, triangles, stars). Connecting lines trace their social movements over time. Temporary associates are indicated by ×.

In 1977, the clan consisted of three monogamous pairs and their associates. Two of the pairs failed in their breeding attempts and one succeeded. Each box represents a breeding or roosting chamber in the colony: MB, male breeder; FB, female breeder; H, helper; V, visitor (i.e., a bee-eater that roosted in the chamber but did not help in the nesting effort); J, juvenile. Note the rearrangements of the associations within the clan: redirected helping (R) by breeders whose own efforts failed; and the reciprocal helping between females represented by the solid star and solid triangle. [*After Hegner et al. 1982; photograph courtesy of S. Emlen and N. Demong*]

lies. Each family includes an assortment of the possible relatives: grandparents, uncles, aunts, nephews, and nieces as well as parents, brothers, and sisters. Death or divorce of one member of the two or three mated pairs in the family leads to replacement by a stepparent and the production of stepsiblings. Members of different families pair, and one member of a pair relocates to become an in-law in its mate's family.

Members of each family feed, roost, and breed cooperatively. They defend a group territory within 20 miles of the colony. Family units exhibit both stability and instability. Membership in a family provides great benefits and exacts significant costs.

The fabric of the complex bee-eater society is a "mixture of openness and fluidity of group memberships on the one hand, with stability and fidelity of certain social bonds on the other" (Emlen 1981, p. 224). Individual birds appear to remember past associations. They leave groups to join other groups but return months or years later to roost or nest with old associates. Those that breed usually require help in feeding young. The open cooperative-breeding system of the White-fronted Bee-eater is adapted to the unpredictable environment of the Rift Valley. In some years, pairs can breed successfully by themselves, but, in other years, they cannot do so without help.

Despite their flexibility and fluidity, personal relations based on individual recognition and long-term memory are the social foundations of extraordinary levels of social complexity. Bee-eater society includes subtle forms of reciprocal altruism, social manipulation, and kinship responses (see Figure 13–15). The nonbreeding male members of the family help the most closely related breeding pair. They practice kin selection, even opting not to help if no close kin are available (Figure 13–16). This choice requires some ability to recognize kin versus nonkin (Box 13–3).

Unlike closed cooperative-breeding systems in saturated stable environments, where young cannot disperse and must compete with established

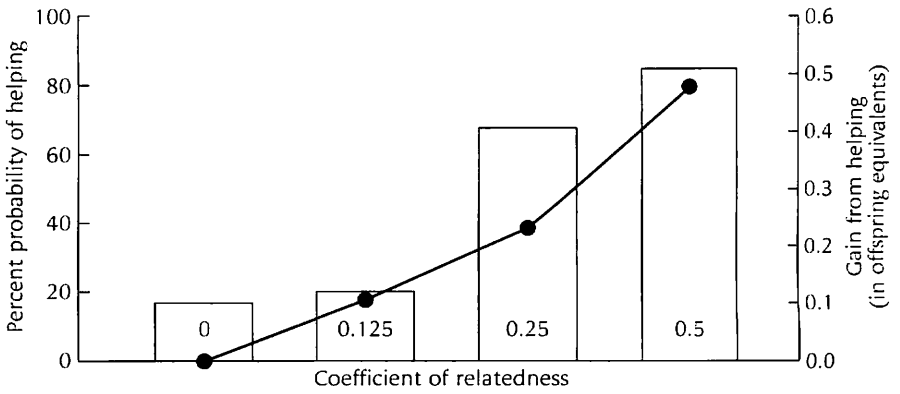


FIGURE 13–16 Helper White-fronted Bee-eaters chose to help the most closely related breeding pairs, thereby increasing their inclusive reproductive fitness. Their gain in indirect reproductive benefits (line) increases with their degree of genetic relatedness to the juvenile bee-eater that they help. [*After Emlen et al. 1995*]

BOX 13–3

KNOWING KIN BY THEIR CALLS

Like the White-fronted Bee-eaters of Africa, the Long-tailed Bushtits of Europe help their kin. Helping in this system has a different basis: the redirection of efforts by those birds that lose their nests to predators late in the breeding season. Unable to nest themselves, failed breeders gain substantial fitness benefits indirectly by increasing the brood productivity of their close relatives. By tracking exactly which birds a failed breeder helped, Stuart Sharp and his colleagues (2005) showed that helpers chose nests of a sibling that had been fed in preceding seasons by the same parents or by related helpers. They found these kin by their distinct contact calls. Cross-fostering experiments demonstrated that the Long-tailed Bushtits learned their parents' call signatures while in the nest. Unrelated foster siblings reared together ended up with call characteristics more alike than true siblings reared apart (Figure 1).

In another set of experiments, Sharp and his colleagues unveiled this system of kin recognition by measuring the responses of the bushtits to playbacks of recordings of the "churr" contact call. They broadcast churr calls from known relatives and from nonrelatives. They also manipulated the calls by erasing the highest and lowest frequencies of the call. The bushtits responded more strongly to the unmanipulated calls of their relatives than to those of nonrelatives (Figure 2). They also responded to manipulated calls of kin as if they were nonkin. This result suggests that the bushtits use the high and low frequencies of the calls to identify their kin.

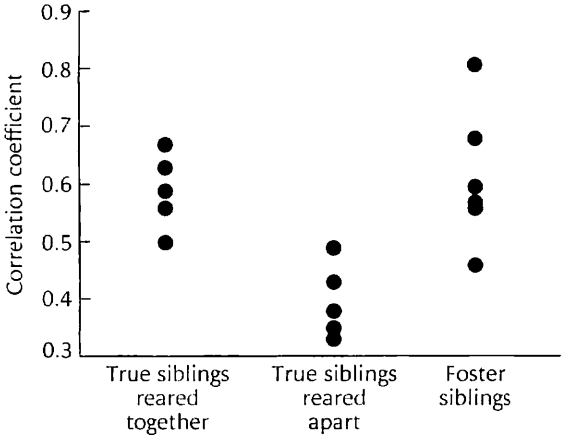


FIGURE 1. Cross-fostering experiments demonstrate that the calls of Long-tailed Bushtits raised together in the same nest acquire similar "churr" calls, whether or not they are genetically related siblings.

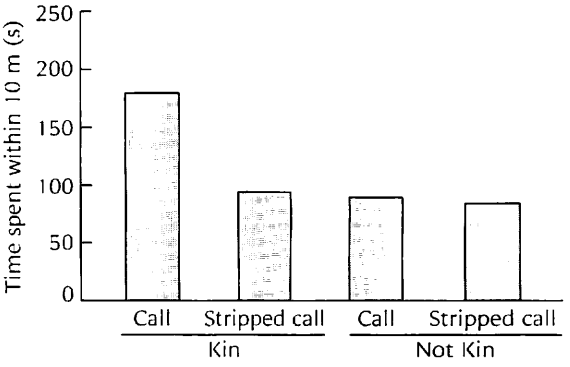


FIGURE 2. Adult Long-tailed Bushtits respond more strongly to playback broadcasts of the churr calls of known relatives than to those of nonrelatives or to playbacks of relatives' calls that were stripped of the highest and lowest frequencies.

birds for breeding status, adult bee-eaters have less control over the breeding options of potential helpers. They resort to coercion and temptation. Male bee-eaters actively harass their sons, blocking the nest chamber or doing whatever it takes to disrupt their early nesting attempts. They then recruit their young sons as helpers for a couple of years before the sons achieve the dominance required to breed successfully on their own. To

TABLE 13–2 Predictions of an evolution theory of the family

The study of family structure in the White-fronted Bee-eater and other cooperatively breeding bird species has led to a general evolutionary theory of the family based on four key parameters: (1) genetic relatedness, (2) social dominance, (3) benefits of group living, and (4) probable success of independent reproduction (Emlen 1995a). In addition to its application to the diversity of cooperative family systems among birds, social insects, and many mammals, this theory has application to human families and to the social sciences generally (Emlen 1995b). Studies of birds support 14 of 15 predictions in four categories. A few case studies do not support 3 of these 14 predictions. No data are available in support of prediction 11 or against it. The number of x's in a cell indicates whether the number of species totals less than 10 (x), 10–99 (xx), or more than 100 (xxx).

	Birds do?	
Category followed by prediction	Yes	No
Family formation: The importance of delayed dispersal		
1 Family groups will be unstable, disintegrating when acceptable reproductive opportunities materialize elsewhere.	xx	0
2 Family stability will be greatest in those groups controlling high-quality resources. Dynasties may form.	xx	0
Family dynamics: Kinship and cooperation		
3 Help with rearing offspring will be the norm.	xxx	x
4 Help will be expressed to the greatest extent possible between closest genetic relatives.	x	x
5 Sexually related aggression will be reduced because incestuous matings will be avoided. Pairings will be exogamous.	xx	
6 Breeding males will invest less in offspring as their certainty of paternity decreases.	x	
Family dynamics: Disruption after breeder loss or replacement		
7 Family conflict will surface about filling the reproductive vacancy created by the loss of a breeder.	x	
8 Sexually related aggression will increase because incest restrictions do not apply to replacement mates.	x	
9 Replacement mates (stepparents) will invest less in existing offspring than will biological parents. Infanticide may occur.	x	
10 Family members will reduce their investment in future offspring after a parent pairs again after the loss of a mate.	x	x
11 Stepfamilies will be less stable than biologically intact families.	??	
Family structure: Reproductive sharing leads to extended families		
12 Decreasing ecological constraints will lead to increasing reproduction by two or more members of the same sex in the family (sharing of reproduction).	x	
13 Increased social equality of potential cobreeders will lead to increased sharing of reproduction.	x	
14 Potential cobreeders that are siblings, rather than parents and their grown offspring, will foster increased sharing of reproduction within the family.	x	
15 Decreasing genetic relatedness will lead to increased sharing of reproduction. Reproductive suppression will be greatest among closest kin.	x	

From Emlen 1995a and 1995b.

recruit helpers, potential breeders must sometimes allow helpers to share the paternity or maternity of group clutches to attract their assistance.

Young females help only as a last resort. The first goal of a young female is to pair with a male that has the status and ability to attract or coerce others in the family to help. If she fails at that, she switches to the tactic of brood parasitism by inserting her own eggs into the clutch of her mother or a close relative. Breeding females actively discard parasitic eggs, challenging a parasite both to overcome her active defenses and to add the parasite egg within a two- or three-day period when the host female is laying her own eggs and can't afford to make a rejection mistake.

Flexible helping and complex social relations are not restricted to colonial bee-eaters. More than 300 bird species exhibit family structures, defined as social groups in which offspring continue to interact with their parents into adulthood (Emlen et al. 1995). Unable to relocate to optimal conditions, birds that reside in permanent, fixed territories and defend them must respond flexibly to different circumstances each year. Social flexibility with continuity enables them to keep their options open and cooperate with kin as needed. But, for birds as well as humans, the internal challenges of optimizing relations with half-kin and nonkin, as well as with real parents versus stepparents, may destabilize the family structure (Table 13–2).

Summary

Most birds raise young that require extended and substantial amounts of parental care in both time and energy. Guiding the evolution of alternative breeding behaviors are tradeoffs between current and future efforts, conflicts between parents and their offspring, uncertainties about parentage, and opportunities to cheat or to cooperate. How much effort a bird theoretically should invest in protecting and nurturing its chicks is basically a tradeoff between the increased survival rate of chicks and the cost of a parent's survival or additional mating opportunities. Deliberate infanticide is known in some bird species.

The reproductive courses available to males and females differ, and uncertainties about genetic parentage govern each partner's commitment to care of the young. Polygyny is a viable system when females can take care of young without the assistance of males. Species that tend to be polygynous include those with precocial young (which are relatively developed when they hatch, compared with other hatchlings, and are soon mobile) and those that feed on easily accessible resources such as fruit. Polyandry, found primarily in the Orders Gruiformes and Charadriiformes, is a system with competitive, territorial females, which are generally larger than their male counterparts.

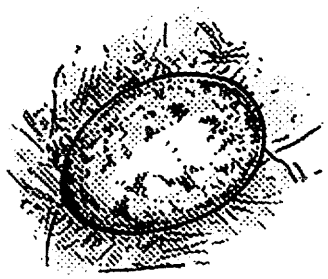
Brood parasitism and cooperative breeding lie at opposite ends of the spectrum of parental-care strategies among birds. Brood parasites lay their eggs in the nests of other birds. Cooperative breeders help other breeders

(usually parents or stepparents) to raise young while waiting for an opportunity to breed themselves.

Intraspecific brood parasitism—leaving eggs in nests of other females of the same species—is proving to be quite common among birds. Facultative parasitism of other species is the next step toward the evolution of obligatory brood parasitism. Cowbirds and cuckoos are the most familiar obligate brood parasites, but this practice has evolved along at least seven separate lines among birds. Adaptations for brood parasitism include egg mimicry, nestling mimicry, host mimicry, egg size and hardness, and the destruction of host eggs and young. A high incidence of brood parasitism is responsible for the decline of some host populations. Countermeasures evolved by hosts include egg recognition and nest abandonment.

Although cooperative breeders may appear to act altruistically, they actually act in their own best interest. Cooperative breeding evolves under conditions of ecological constraint—for example, when lack of breeding territories delays dispersal and prevents young birds from breeding on their own. Intrinsic benefits, such as learning behavioral skills, also may favor delayed dispersal. By helping to raise other broods, these birds enhance their own chances for breeding through the inheritance of a territory or through other forms of territory acquisition. Breeding pairs with helpers fledge more young than do those without helpers, primarily because they suffer less stress and hence survive longer and are more likely to renest. White-fronted Bee-eaters are remarkable for their complex, cooperative social systems that feature the value of kinship family relationships for increasing lifetime reproductive success in the unpredictable environments of East Africa.

CHAPTER 14



Bird Sex

I think, that, if required, on pain of death, to name instantly the most perfect thing in the universe, I should risk my fate on a bird's egg. [T. W. Higginson 1863, p. 297]

A bird's egg is one of the most complex and highly differentiated reproductive cells achieved in the evolution of animal sexuality. The many sizes, shapes, tints, and textures of birds' eggs fascinated the earliest ornithologists and inspired naturalists to collect them (Figure 14–1). Interest in the avian egg also helped to develop ornithology as a comparative science. Nineteenth-century ornithologists published enormous monographs illustrating the eggs of British and African birds, and serious students of oology—the study of eggs—undertook detailed studies of the microscopic structure of eggshells and embryos.

The avian egg is closed, or cleidoic—the type of egg that freed the reptiles from the aquatic mode of life of their amphibian ancestors. It contains all the nutrients, especially water, required by the embryo for its early development. The embryo inside the egg is not isolated from the external environment. Its survival requires an active exchange of oxygen, carbon dioxide, and water vapor through the shell membranes. Its growth and well-being depend on the egg's provisions and on its temperature. Its chances of hatching depend on the ability of the parents to regulate the egg's immediate environment within narrow limits.

This chapter reviews the fundamentals of sexual reproduction in birds, including their sex organs, or gonads; their sex chromosomes; their ova and sperm; copulation and fertilization; and the production of a fully formed egg in the oviduct. Included are descriptions of avian sexuality from the usual "cloacal kiss" to unusual genitalia. Then follows a detailed review of the structure and functions of the fully complete external egg that costs the female much to produce and, having been laid, demands

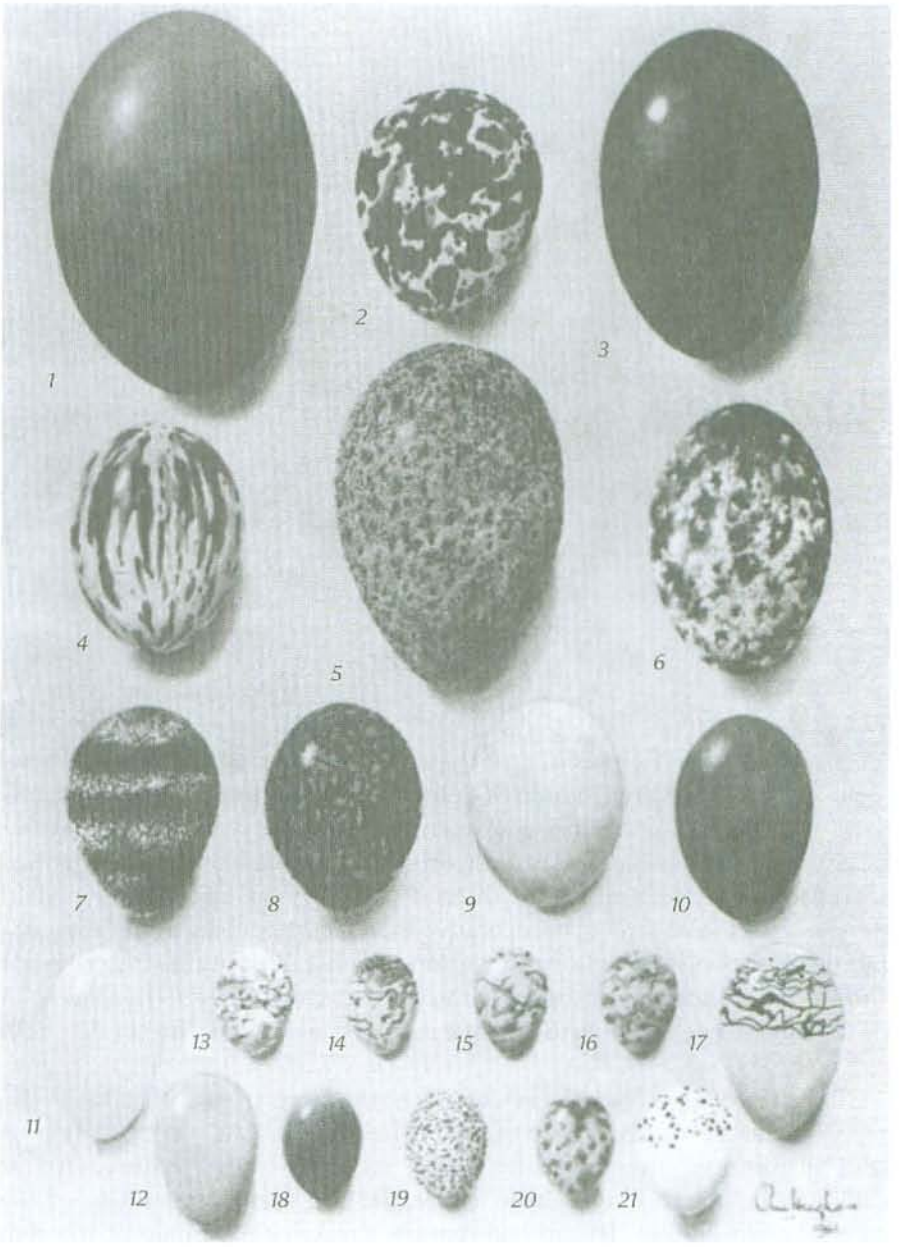


FIGURE 14–1 Eggshell patterns: (1) Patagonian Tinamou; (2) Bronze-winged Courser; (3) Chilean Tinamou; (4) Lesser Bird-of-Paradise; (5) Cape Crow; (6) Gray-necked Picathartes; (7) Three-banded Plover; (8) African Jacana; (9) Stripe-backed Bittern; (10) White-throated Laughingthrush; (11, 12) Brown Babbler; (13, 14, 15, 16) Tawny-flanked Prinia; (17) Grayish Saltator; (18, 19, 20) Winding Cisticola; (21) Yellow-green Vireo. [*From Winterbottom 1971; painting by A. Hughes*]

continued parental care. Subsequent chapters examine the nests and incubation behavior of birds (see Chapter 15) and the development of young birds, along with the challenges of parental care (see Chapter 16).

The Sexes

Birds are strictly bisexual animals, with separate male and female organisms. Hermaphroditism—both sexes in one individual organism—is a

familiar condition among reptiles, fish, insects, and plants but is virtually unknown in birds. Birds also do not change sex with age, as some members of other animal species may do. Rather, the sexual identities of birds are defined for life at fertilization. Different gene activities and hormone balances govern separate sexual roles and life-history strategies. In addition, contests take place between the sperm of different males for fertilization, and females can manipulate egg quality through different doses of testosterone.

Gonads and Chromosomes

The males and females of some species of birds are dramatically different in coloration or size, usually as the result of sexual selection (see Chapter 12). The sexes of many other bird species, from flycatchers to penguins, are indistinguishable externally. Unlike mammals and many reptiles, birds typically lack external genitalia. The gonads—paired testes in the male and usually a single ovary in the female—are located deep inside the body cavity on the surface of the kidneys (Figure 14–2; see also Figure 6–26). These sex organs produce gametes and secrete sex hormones.

Like mammals, birds have distinct sex chromosomes (Figure 14–3). The avian sex chromosomes—W and Z—evolved independently of mammalian sex chromosomes from a pair of autosomal chromosomes (Fridolfsson et al. 1998). They differ from the mammalian X and Y sex chromosomes in genetic structure as well as in origin. Female birds, rather than males, are the sex with different sex chromosomes (WZ). Male birds have two Z chromosomes (ZZ). Patterns of inheritance of sex-linked traits correspond to these chromosomal identities.

Geneticists don't yet know how the W and Z sex chromosome of birds interact to determine sexual identities (Ellegren 2002). In mammals, genes on the Y chromosome trigger the development of males. One (dominant) gene inactivates part of the X chromosome. Another gene, called *SRY*, starts the development of the testis and, in turn, sexual differences in the brain.

Occasionally, subsequent to an aberration in the first (mitotic) division of the fertilized ovum, half of a bird embryo becomes female, ZW, and the other half becomes male, ZZ (Figure 14–4). Called bilateral gynandromorphs, these birds have a testis on one side of the body and an ovary on the other. Externally, they have male and female plumages on the corresponding right and left sides of the body, with a sharp division down the center. Bilateral gynandromorphs have been reported among a wide variety of bird species, including an Orchard Oriole, a Black-throated Blue Warbler, Evening Grosbeaks, American Kestrels, and House Sparrows (Patten 1993). Nothing is known about the breeding activities of such birds in the wild.

Sexual differences in both avian and mammalian brains are thought to be controlled by hormones from the gonads. Studies of a bilateral gynandromoph Zebra Finch revealed that genes on sex chromosomes also act directly on the neural circuitry of the brain (Agate et al. 2003). The Zebra Finch was male on the right side of its body and female on the left

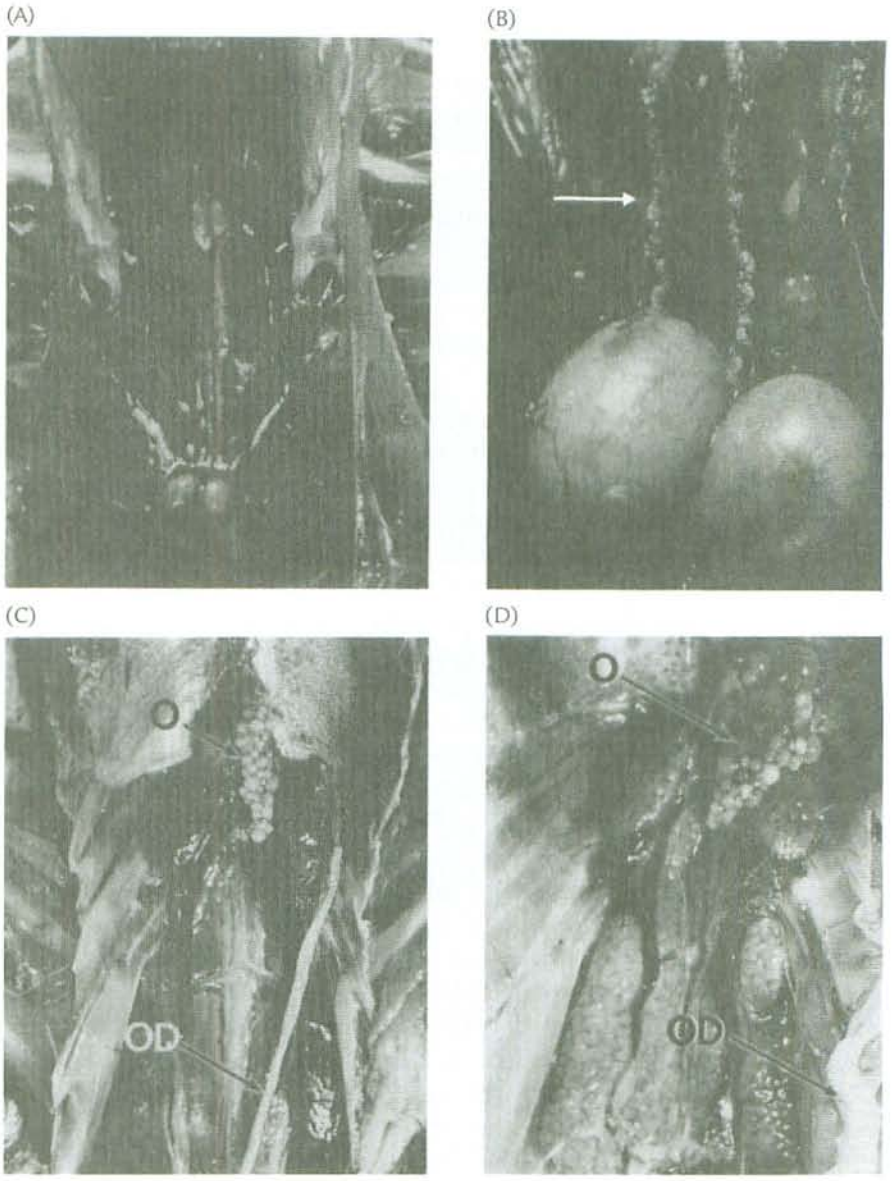


FIGURE 14–2 Avian reproductive systems. Testes of the male Eurasian Tree Sparrow (A) in winter and (B) at full size during the breeding season. Note the enlarged vas deferens indicated by the arrow (magnification of A and B, ×5). Ovary (O) and oviduct (OD) of the female Eurasian Tree Sparrow (C) in winter and (D) during the breeding season (magnification of C and D, ×4). [*Courtesy of B. Lofts*]

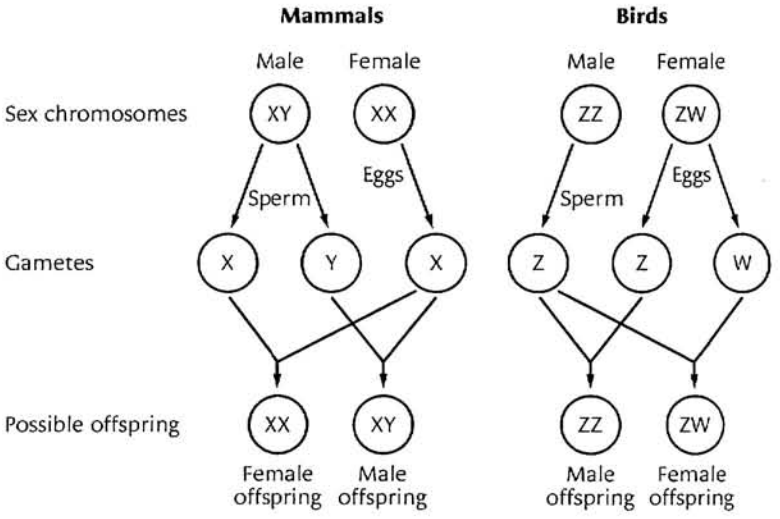


FIGURE 14–3 Sex chromosomes. Birds and mammals differ in the bases of sex determination. Their sex chromosomes are of different origins and hence are given the letters Z and W in birds rather than X and Y as in mammals. Male birds are the sex with two of the same sex chromosomes (ZZ), and female birds are the sex with one of each (ZW), the converse of mammals. [*After Evans and Heiser 2004*]

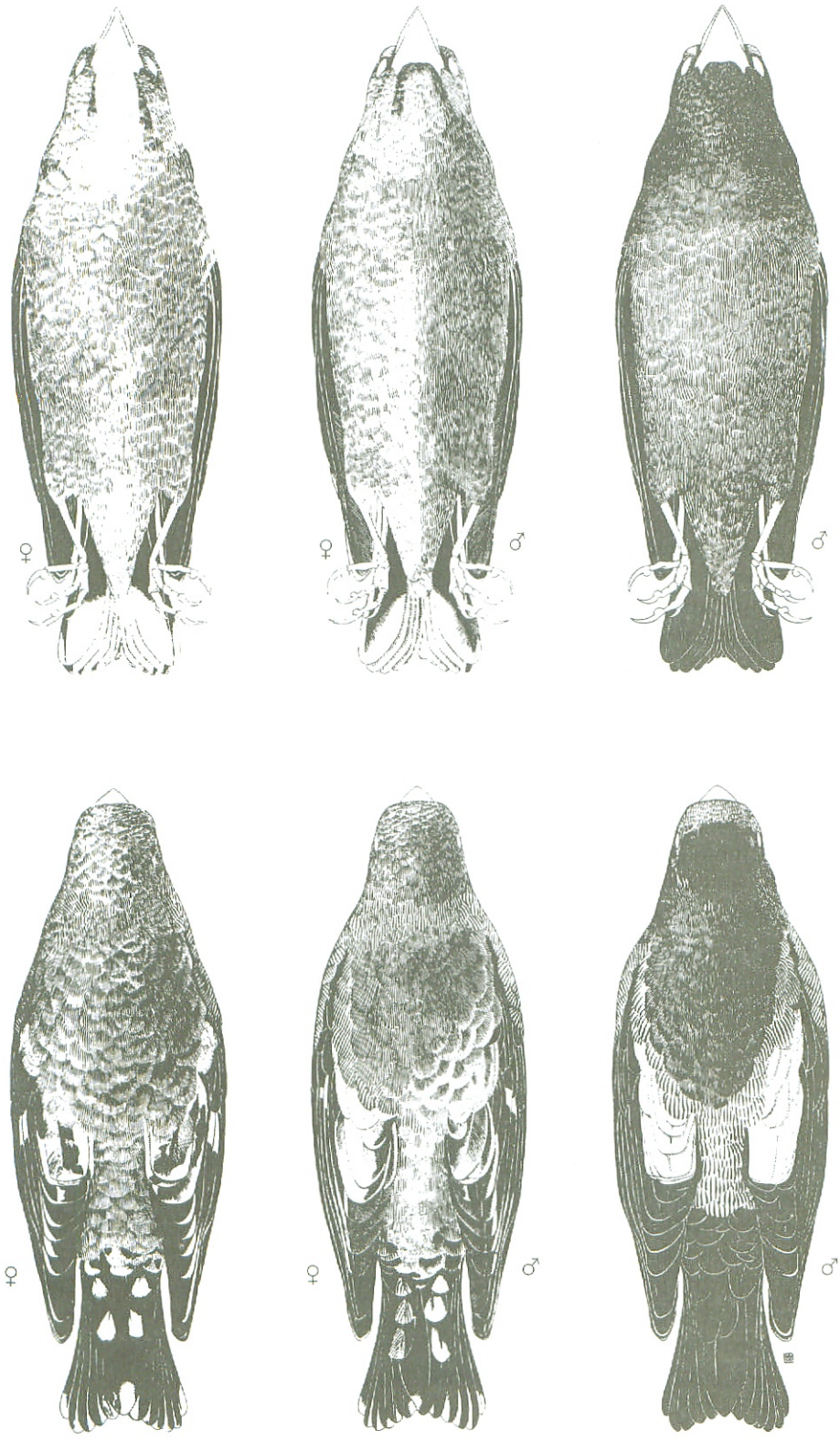


FIGURE 14–4 Rare individual Evening Grosbeaks are male on one side and female on the other as a result of an aberration in the first cell division of the fertilized egg. These birds are called bilateral gynandromorphs (*middle bird, both top and bottom*). Such gynandromorphism is not seen in mammals, in which hormones override the genetic differences between right and left sides. [*From Laybourne 1967*]

side of its body. Despite the infusion of male and female hormones into both sides of its brain, enlarged male song circuitry developed only on the right side of its brain. The enlarged circuitry was a direct response to gene activity in cells that were ZZ (male). A double dose of one protein (TrkB) known to mediate neural development is likely to be implicated (Chen et al. 2005).

Sex Hormones

The brain regulates the secretion of sex hormones through the hypothalamus and, in turn, the pituitary gland (see Figure 9–10). Two hormones secreted by the anterior pituitary control the gonads: follicle-stimulating hormone regulates gamete formation, and luteinizing hormone regulates hormone secretion by the testes and the maturation of follicles in the ovary. The gonads themselves secrete two principal steroid sex hormones—testosterone and estrogens—that directly activate gamete production.

The action of the principal sex hormones on specific receptors in the brain also induces reproductive behaviors. These behaviors include aggression, courtship, nest building, and parental care. Although testosterone is well known as the male hormone and estrogen as the female hormone, both hormones are present in males and females. The proportions of the two hormones and the ways in which body tissues react to each of them cause male or female attributes.

Testosterone and estrogen affect sexual distinctions in plumage, body size, and vocalizations. For example, testosterone causes the bills of Common Starlings to turn bright yellow in the breeding season, whereas estrogen causes the red bills of female Red-billed Queleas to turn yellow in the breeding season. Testosterone also promotes the growth of the red head ornaments—wattles and combs—of roosters and the bill ornaments of breeding auklets.

Males acquire their breeding plumage as a result of increased amounts of testosterone in their blood. The experimental injection of testosterone triggers the growth of colorful feathers in either sex. Recall the experiments on the plumage genotypes of Reeves (see Chapter 12). Conversely, castration prevents Ruffs from acquiring their fancy neck feathers. Phalaropes offer another such case. They are unusual sandpipers in that the bright-plumaged females defend breeding territories and the less colorful males assume the duties of incubation and parental care. Female phalaropes normally have higher concentrations of testosterone than do males, whose maximum levels of testosterone remain below the threshold required to produce colorful feathers. In a similar case, males of some breeds of chickens have femalelike feathers because the cellular chemistry in the skin actively converts testosterone into estrogen. When castrated, they grow male feathers. The injection of testosterone into these castrated males causes them to revert to the female type of plumage (George et al. 1981).

The elaboration of secondary sex traits by steroid hormones has costs. In particular, testosterone tends to reduce the immune response in birds

and to make them more susceptible to disease or parasitic infection. Experimental elevation of testosterone suppresses antibody production or cell-mediated immunity in Dark-eyed Juncos and in House Sparrows (Casto et al. 2001; Evans et al. 2000). The prolonged elevations of testosterone in polygynous male songbirds may exact a substantial cost. Still uncertain, however, is whether testosterone directly suppresses the immune system or whether it does so by increasing levels of corticosteroid stress hormones, which, in turn, suppress disease resistance as well as some aspects of reproduction (see Chapter 9).

Ovary and Ovum

The avian ovary resembles a small cluster of grapes. Most birds have only one ovary, the left one with its associated oviduct. Two functional ovaries are typical of many raptors and of kiwis. They are also occasionally present in pigeons, gulls, and some passerines.

In early development of the embryo, primordial germ cells migrate to the site where the gonads will develop. More of these germ cells settle on the left side than on the right, leading to an unpaired left ovary in most female birds and a testis on the left side that tends to be larger than the one on the right side in males.

The primordial germ cells first generate what is called medullary tissue. It becomes the primary tissue of the testes and a secondary tissue of the ovary. Ovarian medullary tissue normally becomes more active with age in females. In extreme cases, the increased activity causes overt masculinization of older females. For example, with age, somber female Golden Pheasants acquire the spectacular plumage of males as a result of this phenomenon.

A second phase of cell proliferation creates the cortex, the principal tissue of the ovary. Primary oocytes—the cells that give rise to ova—are already present in the cortex of a hatchling bird, but distinct ova do not appear until the bird is older. Each maturing ovum resides within a follicle. At maturity, the microscopic ovarian granules of the immature bird increase in size 10 to 15 times. The total number of primary oocytes in a wild bird is at least 500, and often there are several thousand, many more than are actually used to produce functional eggs.

Maturation of the Ovum

The development of a mature ovum includes two different yet interdependent processes: (1) the formation and deposition of yolk layers and (2) the differentiation, growth, and maturation of the germ cell itself. The infusion of yolk, the deposition of egg white, or albumen, and the shell layers all contribute to the growth and maturation of the ovum. The yolk is added to the ovum before ovulation. The rest of the components of the egg are added as the egg passes through the oviduct.

The period of yolk formation, or follicular maturation of the ovum, lasts from 4 to 5 days in passerine birds, from 6 to 8 days in larger birds

such as ducks and pigeons, and as long as 16 days in some penguins. The ovum swells to its functional size, more than 1000 times its original microscopic volume.

Yolks vary in color from pale yellow or light cream to dark orange red or even brilliant orange. Within a species, such variations are partly due to diet. Hens that eat red peppers rich in carotenoid pigments, for example, lay eggs with red yolks instead of the normal yellow yolks (Fox 1976).

The yolk is not homogeneous (Figure 14–5). Rather it comprises alternating layers of yellow yolk in large globules (0.025–0.15 mm in diameter) and white yolk in smaller globules (0.004–0.075 mm in diameter). The layers correspond to daytime (yellow) and nighttime (white) yolk deposition. These layers can be counted like a tree's growth rings to determine the time required for yolk formation (Roudybush et al. 1979). The center of the yolk, or central latebra, is composed of a fluid, white substance called vitellin, which extends to the periphery through a distinct, narrow passage. A thin vitelline membrane encases the yolk, separating it from the albumen to be added later.

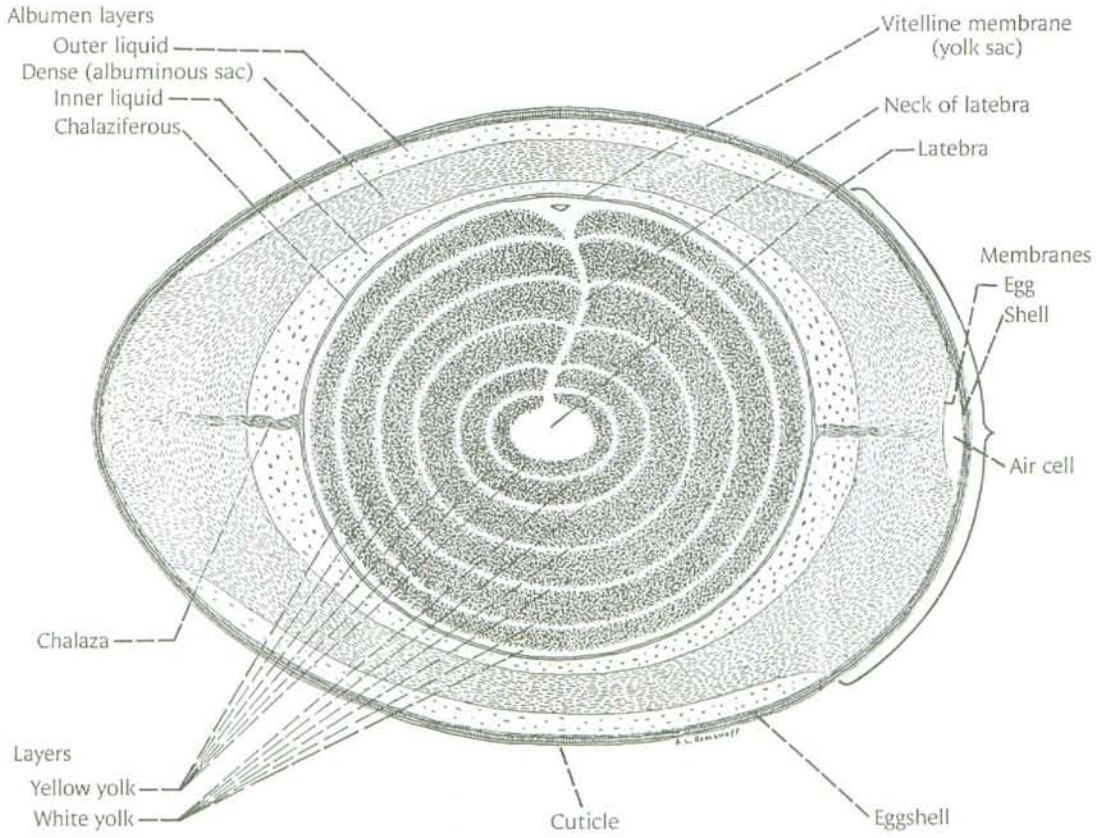


FIGURE 14–5 Structure of a freshly laid hen's egg. Note alternating layers of white yolk and yellow yolk. The components of egg structure are discussed throughout this chapter. [*After Romanoff and Romanoff 1949*]

BOX 14–1

MANIPULATING EGG QUALITY AND BROOD MATES

Female birds vary the provisions that they add to eggs in a clutch and thereby control their quality and the offspring that hatch from them. For example, they adjust the amount of testosterone that they add to the egg yolk. Some ova get more than others. Additional testesterone changes the behavior of the nestlings, with some cost in reduced immunity to disease and parasites.

In the original study of this phenomenon by Hubert Schwabl (1993), female canaries added more testosterone to each successive egg in the clutch. The social rank and aggressiveness of the nestlings increased accordingly, helping to equalize last-hatched nestlings in the competition for food deliveries. Conversely, White Storks and Cattle Egrets short the dose of testosterone in the last egg of a clutch; the Cattle Egret does so by half (Sasvari et al. 1999; Schwabl et al. 1997). These species practice brood reduction (see Chapter 16). The last chick to hatch is a weakling that often does not survive, especially in years of low food availability.

Most of the nutrients and energy supplies in the completed egg are added before ovulation. Females also transfer hormone and health functions to their offspring through the egg contents (Box 14–1). They put substantial amounts of immune factors, including carotenoids, immunoglobins, and lysozymes, into the egg yolk (Saino et al. 2002a, 2002b). These factors improve the immune systems and the fitness of developing embryos and chicks after hatching. Bright yellow and orange yolks are rich in carotenoids. Carotenoids are not just pigments that add color to the yolk and to feathers; they are also precursors of vitamin A. They protect DNA and lipid molecules from oxidative damage (like antioxidants in our diets), and they enhance immune functions (Surai et al. 2001). Higher carotenoid concentrations in the yolk of Barn Swallow eggs, for example, increase T-cell-mediated immune function in their nestlings (Saino et al. 2003).

Swollen with yolk and nutrients, the full-sized ovum is ready to be transferred to the oviduct and to pass through it. Only a few ova actually make it to this stage. Many follicles, called atretic follicles, stop developing in the early stages of maturation and are resorbed (Figure 14–6).

Sex of Offspring

A female's condition affects the quality of her eggs, which, in turn, causes embryos to differ in their growth and their survival. Differences in the survival of the embryos favor one sex or the other and thus the relative numbers of males and females that hatch, called the primary sex ratio (Arnold et al. 2003). Females in poor condition tend to produce eggs with female embryos (Royle et al. 2002).

Selecting the sex of their offspring is a most important strategy available to parents, at least in theory. Previously, only wasps and bees were known to control directly the production of male versus female offspring.

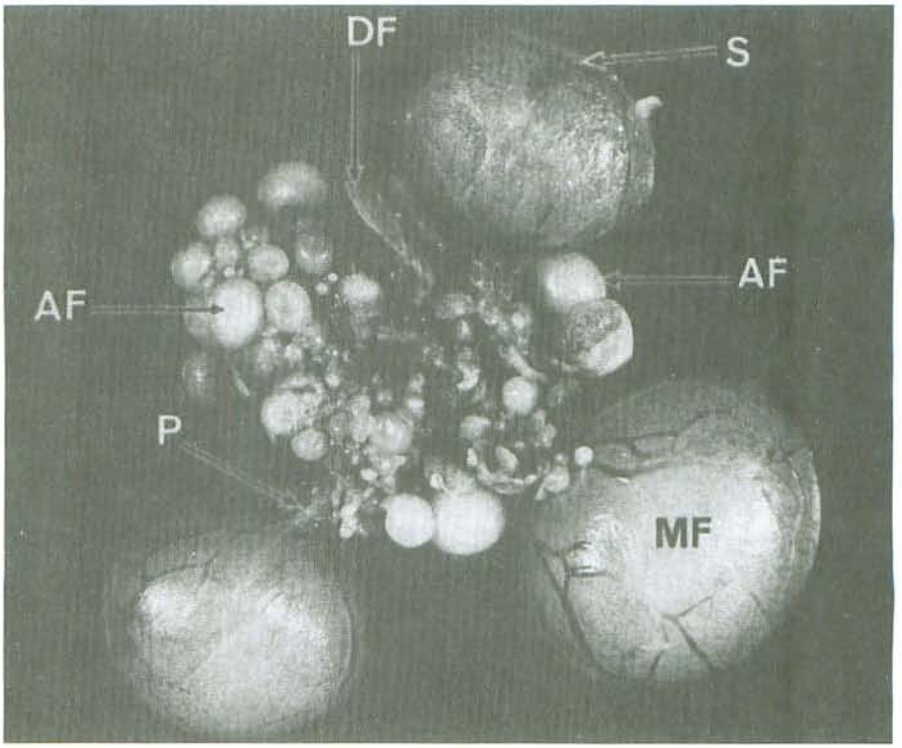


FIGURE 14–6 The ovary of a sexually mature chicken showing mature follicles (MF) with basal stalk, or pedicel (P), resorbed, or atretic, follicles (AF), and a recently discharged follicle (DF). The letter S indicates a stigma, the scarlike area where the follicle will rupture during ovulation. [*Courtesy of B. Lofts and R. K. Murton*]

Birds can apparently do so, too. Advances in technology for the early sexing of bird nestlings have catalyzed a burst of field studies of brood sex ratios in birds (Hasselquist and Kempenaers 2002). How females control the sex of the eggs that they ovulate is unknown, but several studies now indicate that they can do so.

The cooperatively breeding Seychelles Warbler (see Box 13–2), for example, favors female offspring through the selective release or production of female ova (Komdeur et al. 2002). Recall that, in this species, parents engage helpers on high-quality territories, where helpers increase their parents' reproductive success. Only daughters from preceding broods help their parents. In this species, daughters are the valued sex when conditions are good. Sons, the dispersing sex, are valued to garner new territories when conditions are poor and when help by daughters is not advantageous. Adult female warblers switch production as predicted (Komdeur et al. 1997). Of the offspring of breeding pairs on low-quality territories without helpers, 77 percent were sons, whereas, of the offspring of pairs on high-quality territories without helpers (and therefore in need of daughters), only 13 percent were sons. Breeding pairs transplanted from low-quality territories to empty high-quality territories switched to pro-

ducing female eggs instead of male eggs. They did so by changing the sex of their eggs when ovulated, again by means unknown.

Recall also that the female Blue Tits paired with males that have intense ultraviolet coloration produce mostly male young (see Box 12–1). They do so at ovulation by means unknown, but not by absorbing or aborting female eggs after ovulation (Sheldon et al. 1999).

Ovulation

In ovulation, the egg is released from the ovary. The follicle enclosing the mature ovum ruptures at the stigma—a layer of smooth muscle fibers. The enlarged ovum pops out and falls into the ovarian pocket—an irregular cavity formed around the ovary by the surrounding organs.

Entry into the oviduct is not simply a matter of chance. The open upper end of the oviduct, called the infundibulum, actively pulses back and forth toward the new ovum, partly engulfing it and then releasing it for as long as half an hour, before finally taking it in. Finally inside the infundibulum, the ovum is ready for fertilization.

Parthenogenesis, the development of unfertilized eggs, is a regular event in reptiles but is a rare phenomenon in birds. Some unfertilized eggs develop normally in domestic turkeys. Between 32 and 49 percent of infertile eggs may begin so-called parthenogenetic development, but their embryos usually die (Johnson 2000). All surviving parthenogenetic turkey chicks are males (because they have the duplicated ZZ sex-chromosome combination) and have a full diploid set of chromosomes. They may even be sexually competent.

Testes and Sperm

The testes of most mammals and reptiles reside in external sacs, or scrota, away from internal body heat because sperm are sensitive to high temperatures. The testes of birds are housed, instead, inside the abdominal cavity at body temperature. To compensate for the extra body heat, the formation and development of sperm take place primarily at night when body temperature is slightly lower. New sperm are then stored closer to the body surface in swollen seminal vesicles that are several degrees cooler than internal body temperatures.

The testes of birds are internal, bean-shaped organs that are attached to the dorsal body wall at the anterior ends of the kidneys. They usually are cream colored but are dark gray or even blackish in some species. Initially only a few millimeters long in small birds, they swell rapidly at the beginning of the breeding season, often reaching from 400 to 500 times their inactive mass. The testes of a mature Japanese Quail, for example, increase from 8 to 3000 milligrams in just three weeks. Fertility in domestic geese is directly related to the weight of their mature testes (Szumowski and Theret 1965).

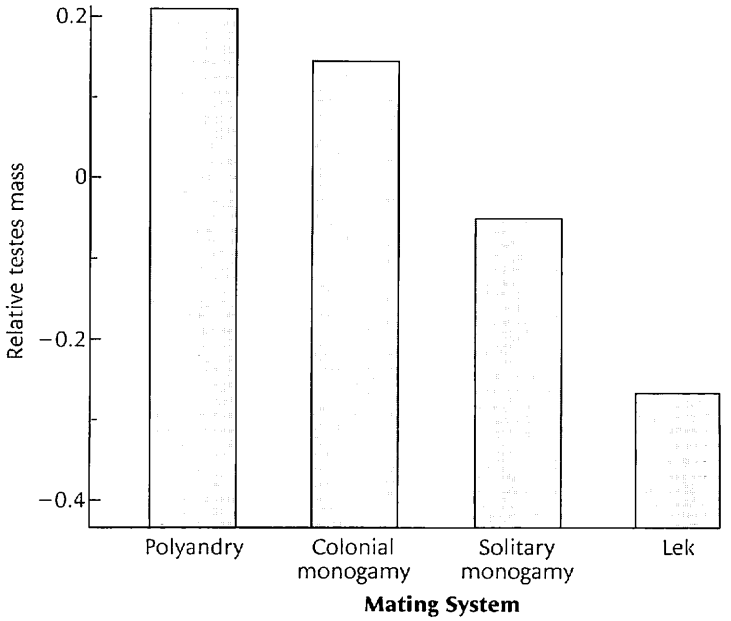


FIGURE 14–7 The sizes of bird testes differ among mating systems. Lek species have small testes relative to their body size. Males in polyandrous and colonial nesting monogamous species tend to have large testes relative to their body size. Values are means. [*After Birkhead 1995*]

Testis size relative to body size increases with the intensity of sperm competition (Pitcher et al. 2005). Among birds, testis size is highest in polyandrous species and next highest in colonial species that are monogamous (Figure 14–7). Lek species have smaller testes sizes than those of solitary, monogamous species.

The thick, outer fibrous sheath of the testis encases a dense mass of convoluted tubules, called seminiferous tubules. Lining the tubules are active germinal epithelia that produce sperm. Both Sertoli cells, which line the tubules, and Leydig cells, which are packed between the tubules, secrete the sex-hormone testosterone. These cells undergo well-defined seasonal cycles in the accumulation of lipid and cholesterol used in the development and formation of sperm. Cells of the germinal epithelia transform into mature sperm in synchronous waves down the tubule. The entire length of a seminiferous tubule produces sperm at the same time in strongly seasonal breeders, such as Arctic shorebirds. Mature sperm quickly leave the testis through a series of other thin tubules—rete tubules, vasa efferentia, epididymis, and vas deferens (Figure 14–8).

A typical bird sperm consists of three sections, as in other vertebrates (Figure 14–9). The head (acrosome and nucleus) contains the genetic material. The midpiece provides metabolic power. The tail (axial filament and tail membrane) propels the sperm forward.

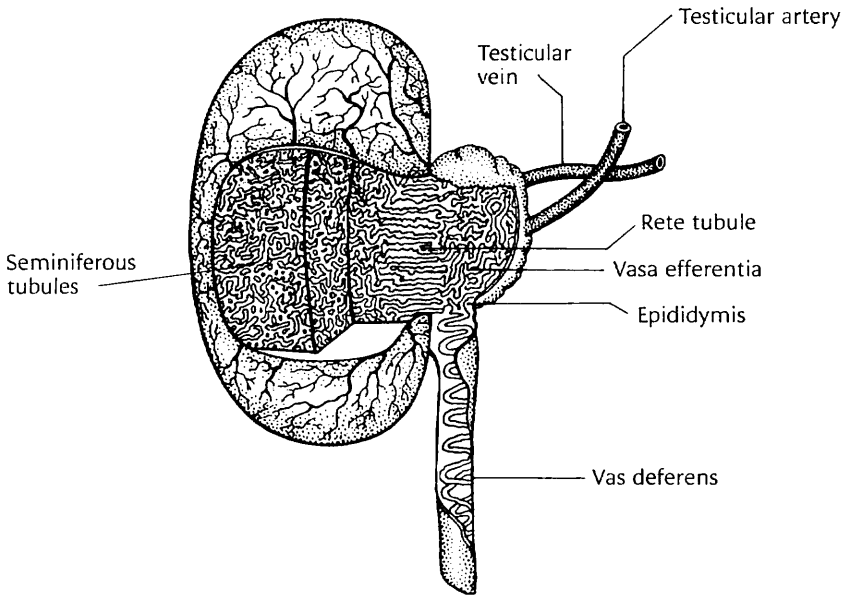


FIGURE 14–8 Internal anatomy of the avian testis. [*From Marshall 1961*]

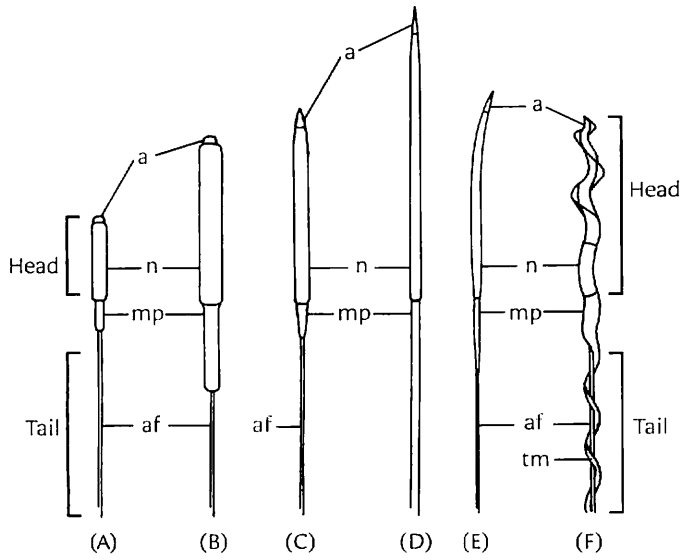


FIGURE 14–9 Structural differences in spermatozoa characterize the orders of birds. (A) Collared Trogon (Trogoniformes); (B) Great Black-backed Gull (Charadriiformes); (C) Common Eider (Anseriformes); (D) Blue Ground Dove (Columbiformes); (E) domestic chicken (Galliformes); (F) Yellow-rumped Warbler (Passeriformes). Abbreviations: a, acrosome; af, axial filament; mp, midpiece; n, nucleus; tm, tail membrane. [*From McFarlane 1963*]

Distinctive sperm structures characterize different groups of birds and some species. Nonpasserine sperm are generally long and straight like those of mammals. Passerine sperm are distinct, with a spiral head and a long, helical tail membrane (see Figure 14–9F). Instead of swimming by beating the flagella-like tail, they spin. The relative proportions and lengths of the sections are inherited traits that vary among male Zebra Finches (Birkhead et al. 2003).

The seminal vesicles are the expanded bases of the two ductus deferentia, which swell with accumulated semen awaiting discharge. They are responsible for the conspicuous cloacal protuberances of breeding male passerine birds (see Figure 14–12A). In mammals, the seminal vesicles and accessory glands, such as the prostate, add nutritious ingredients to the semen. In birds, the seminal vesicles supply few nutrients, and the other glands are absent (Kirby and Froman 2000).

Copulation

Most birds lack external genitalia, with some impressive exceptions. Mating typically requires only brief cloacal contact, often described as a "cloacal kiss." Standing or treading precariously on a female's back, a male twists his tail under hers and she, in turn, twists into a receptive position (Figure 14–10). The male may slip off while trying to maintain contact for the few seconds required. Swifts copulate in midair. Some species take longer (Box 14–2).

Sperm are transferred when each partner's cloaca everts. Tiny papillae protruding into the cloaca from the posterior walls of the male's sperm sacs come into contact with the opening of the female's oviduct. Ejaculation follows. In chickens, average concentrations of sperm are 3.5 million per cubic millimeter of semen. A single ejaculation passes from 1.7 billion to 3.5 billion sperm (with records ranging from 7 billion to 8.2 billion by roosters). The concentration of sperm, however,

BOX 14–2

PROLONGED COPULATION

Some mammals, including minks—the aquatic weasel with wonderful fur used for coats—are notorious for their lengthy copulations that last for hours. The prolonged copulation of the Aquatic Warbler also is extraordinary compared with that of other birds (Schulze-Hagen et al. 1995). This species has the highest known level of multiple paternity per brood of any bird species. Rather than the normal 1 to 2 seconds, copulation in this species lasts 25 minutes. The male and female lie together on the ground, male atop the female, holding on to her head feathers with his bill. The male inseminates the female repeatedly just before and after egg laying. This behavior ensures that his sperm will be positioned to fertilize the next ovum released from the ovary. Such attention is required to win a share of the intense competition for paternity.

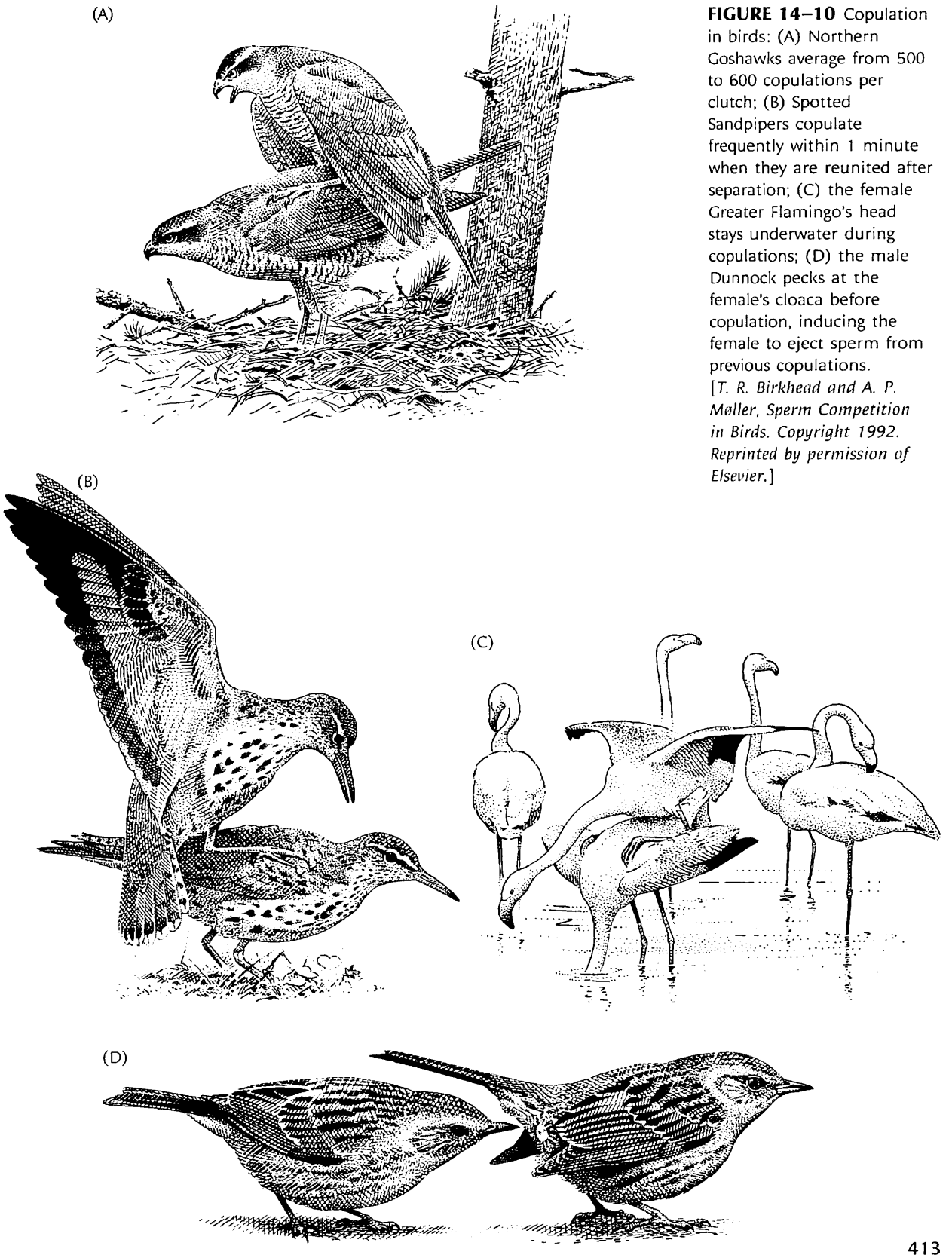


FIGURE 14–10 Copulation in birds: (A) Northern Goshawks average from 500 to 600 copulations per clutch; (B) Spotted Sandpipers copulate frequently within 1 minute when they are reunited after separation; (C) the female Greater Flamingo's head stays underwater during copulations; (D) the male Dunnock pecks at the female's cloaca before copulation, inducing the female to eject sperm from previous copulations. [*T. R. Birkhead and A. P. Møller, Sperm Competition in Birds. Copyright 1992. Reprinted by permission of Elsevier.*]

FIGURE 14–11 Bridling, a postcopulatory display of the male Mallard, at left. The male then swims around the female, at right. [*Courtesy of F. McKinney*]

drops rapidly after three or four ejaculations. A minimum of about 100 million sperm is required for the proper fertilization of hens (Kirby and Froman 2000).

Some birds have elaborate postcopulatory displays. Immediately after copulation, for example, a male Mallard flings his head upward and backward, called the bridling display, and gives a whistled call (Figure 14–11). Then he swims around the female, holding his head low to the water, called nod swimming. These displays apparently announce successful intromission (Hailman 1977).

Enlarged cloacal protuberances of male passerine birds function as copulatory organs (Figure 14–12A). The size of the protuberance varies among species with the intensity of sperm competition (see page 416). The cloacal protuberance of the male Bearded Reedling of Europe everts during copulation into a large red phalluslike structure (Briskie 1998; Sax and Hoi 1998). Unlike that of other species, this protuberance does not store sperm. It serves solely as a copulatory organ. The size of the organ indicates a male's reproductive status. It also matches the fertility cycle of its mates.

Formal study and an understanding of the diversity of avian genitalia have been slow in coming, apparently owing to a long-standing Victorian prudishness (Briskie 1998). A few birds have an erectile, penislike intromittent organ, which is a special modification of the ventral wall of the cloaca (Figure 14–12B). The list of species so endowed includes tinamous, most waterfowl, screamers, curassows and chickens, some parrots, and ostriches. The fully extended, bright red penis of an ostrich may be 20 centimeters long. The mating ritual of these large flightless birds is a dramatic event: intromission and ejaculation last a full minute. Both chickens and turkeys have small penises, which enlarge with lymph fluid that adds to semen in the vas deferens. This fluid is ejaculated through a longitudinal phallic groove.

The waterfowl penis probably facilitates sperm transfer underwater. However, the Ruddy Duck and its close relative, the Lake Duck of South America, have extraordinary copulatory organs owing to sexual selection (McCracken 2000). The spiny penis of the Lake Duck is the greater of

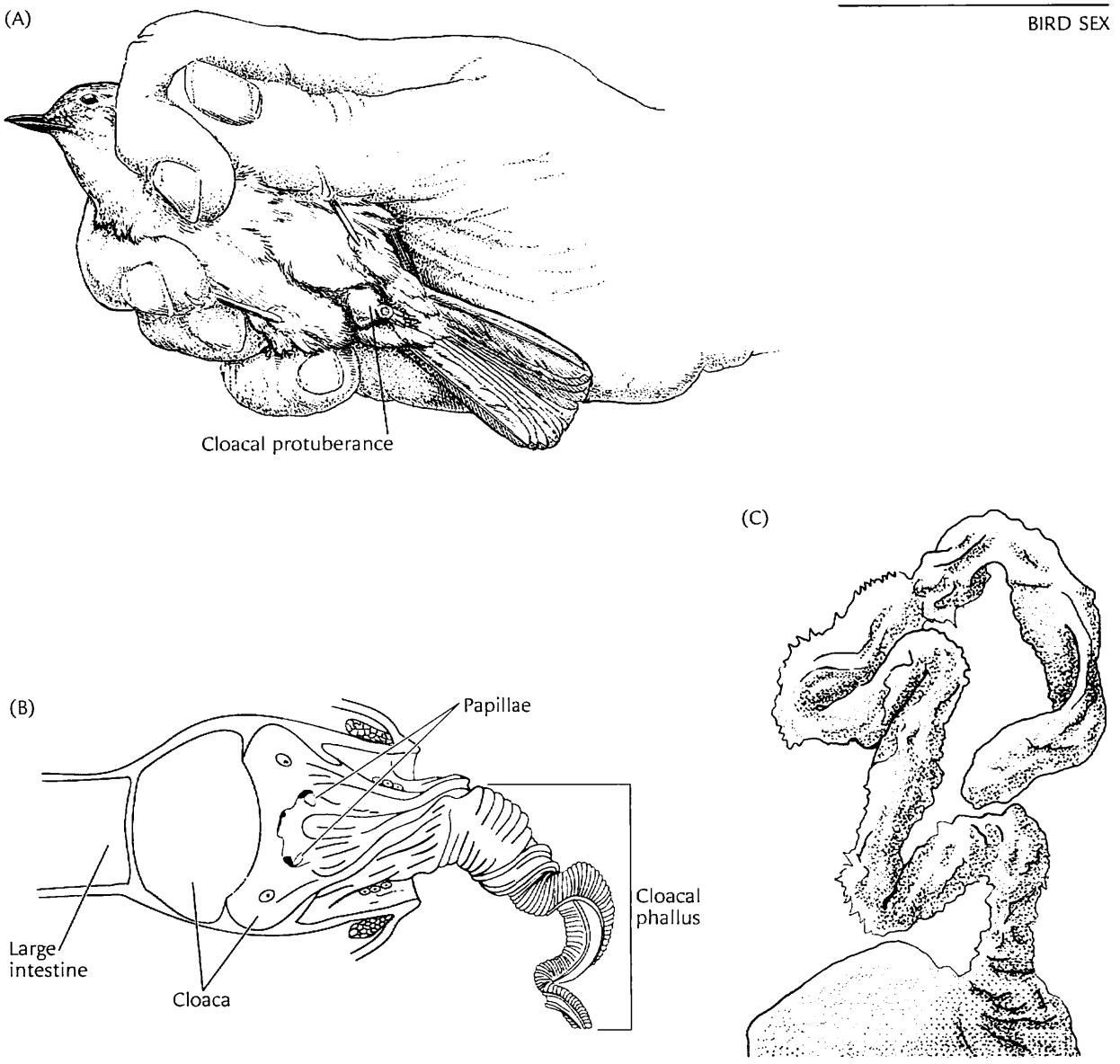


FIGURE 14–12 Phallic organs of male birds. (A) Cloacal protuberance of a male Dunnock. (B) The cloacal phallus of a domestic duck. (C) The longest known penis (42.5 cm) of a bird is a feature of the Lake Duck of South America.

the two, extending 20 to 42 centimeters long, almost the length of the duck's own body and rivaling that of an ostrich (Figure 14–12C). This organ stays coiled inside the body until activated. The duck then waves it before a potentially receptive female. Size matters. Females of a related species, the White-headed Duck in Europe, prefer the exaggerated displays of introduced male Ruddy Ducks to the modest organs of males of their own species. As a result, hybridization with Ruddy Ducks is increasing and now endangering the lesser native species.

Buffalo weavers are the only passerine birds known to have a phalluslike organ. Extra-pair paternity and sperm competition are intense in this colonial species, which practices polygynandry and polygyny: 63 percent of broods examined had multiple sires. Located anterior to the cloaca, the phalluslike organ is not inserted during copulation but serves, instead, as a unique stimulatory organ (Winterbottom et al. 2001). Endurance—18 minutes of prolonged stimulation and protracted copulation—leads to an orgasm that is a prerequisite to ejaculation and probably to better retention of the sperm by females in this highly competitive sexual society.

Fertilization and Sperm Competition

Avian sperm swim directly to the upper end of the oviduct, where they may encounter the ripe ovum. They can reach the infundibulum in less than 30 minutes. But then there is only a narrow window of opportunity for fertilization. The ovum quickly adds protective barriers against fertilization by more than one sperm.

Female birds of many species have special sperm-storage tubules (Birkhead 1995; Figure 14–13). The primary storage tubules are located at the junction of the uterus and vagina of the oviduct above the cloaca (see Figure 14–17). Secondary, short-term storage tubules are sited at the infundibulum itself. The number of tubules varies greatly among species—from 500 to 20,000. Large birds have more tubules. The tubules can hold the sperm for weeks, albeit with some passive loss, and then release sperm at a constant rate shortly before ovulation. Last sperm in are the first ones out.

Normally, eggs are fertilized within a few days of copulation, but some sperm remain viable for weeks. Domestic chickens and turkeys, in particular, can produce fertile eggs from 30 to 72 days after copulation. For most birds, the probability of laying fertile eggs decreases rapidly from one to two weeks after copulation. Some unpaired birds mate on migration and continue onward carrying stored sperm. In one set of studies, the presence of viable cloacal sperm during spring migration revealed that at least 25 percent of the females of North American migrant passerines copulate before they reach the breeding grounds (Quay 1989).

Female birds tend to mate with more than one male, even if socially monogamous, as noted in preceding chapters. For this reason, the sperm of different males may be in the storage tubules or in the oviduct at the

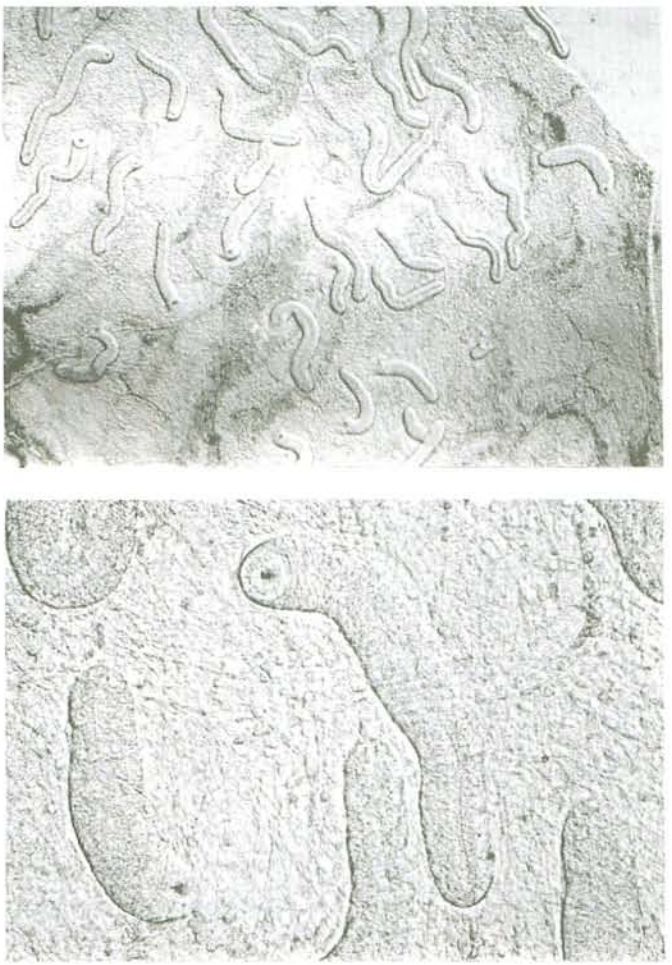


FIGURE 14–13 Photographs showing the sausagelike sperm-storage tubules of a Japanese Quail at two levels of magnification. [*From Birkhead and Møller 1992*]

same time. If so, they compete to fertilize the ova released from the ovary. Such so-called sperm competition is prevalent among animals. It is an important element of sexual selection. Male adaptations to sperm competition include large testes, large sperm stores, long sperm, the guarding of mates, and frequent copulations (Birkhead 1998; Pitcher et al. 2005; Box 14–3). Females, however, control the pace, timing, and probability of paternity.

Mating order and, to a lesser extent, the interval between copulations determine which male wins paternity of offspring (Birkhead 1998). Last male sperm precedence is the rule, especially if sequential copulations are separated by more than 4 hours. Relative numbers of sperm determine the probability of fertilization by a particular male's sperm. After insemination, sperm are passively lost from the female's storage tubules at a constant rate for days or weeks. For this reason, the interval between two inseminations increases the probability that the second one will be better represented by more sperm in the oviduct. On the other hand, females

BOX 14–3

SPERM COMPETITION AMONG SMITH'S LONGSPURS

The Smith's Longspur, a bunting of the subarctic tundra, offers an extreme example of sperm competition (Briskie 1993). Each female pairs and copulates with two or three males for a single clutch of eggs. Males do not defend territories; instead, they pair and copulate with two or more females and compete for copulations and paternity of the offspring. They practice polygynandry. The male that copulates most on the day of ovulation usually fertilizes that ovum. It does so by diluting or displacing ejaculates of rival males, thereby putting its own sperm in position when a new ovum is released. The huge testes of the Smith's Longspur—twice the size of those of the related, but monogamous, Lapland Longspur—support its frequent copulations and supply its many ejaculates.

actively eject most new sperm when they defecate after copulation. This act is part of the mating ritual in some species. In another polyandrous species subject to extreme sperm competition, the male Dunnock pecks at the exposed cloaca of the receptive female just before they copulate (see Figure 14–10D). In response, the female ejects a droplet of the sperm from a previous copulation (Davies 1983).

Last male sperm precedence is also responsible for most extra-pair fertilizations in monogamous species (Birkhead 1998). Despite frequent copulations with a mate, the sperm of extra-pair males prevail for two reasons. First, females solicit extra-pair copulations when they are about to ovulate and so achieve optimal timing. Second, males tend to participate in extra-pair liaisons after they have completed siring their own broods and when they copulate less frequently with their mates. Because they are "rested," they achieve higher densities of sperm in larger ejaculates.

The Complete Egg

Fertilization converts an ovum into an embryo, which then begins its passage through the oviduct to complete the formation of the cleidoic, or closed, egg. Before accompanying the egg on its formative passage, we should examine the major features of the completed egg (see Figure 14–5).

Cleidoic eggs evolved from the naked, amniotic eggs of ancestral reptiles, presumably in response to predation by soil invertebrates and microbes (Packard and Packard 1980). The flexible shell membranes of primitive reptilian eggs were water permeable, but the harder, calcified avian eggshells are less so. The increased calcification of the avian eggshell provided better protection for eggs. Sacrificed was their ability to absorb the water needed by an embryo. To compensate, birds added water to the egg contents in the form of albumen (the egg white).

The albumen consists primarily of water (90 percent) and protein (10 percent). Besides being the embryo's water supply, the albumen is an elastic, shock-absorbing cushion that protects the embryo when the egg is

moved or jolted. It insulates and buffers the embryo from sudden changes in air temperature and slows the cooling rate when the parent is not incubating. Albumen constitutes from 50 to 71 percent of the total weight of the egg.

In addition to the albumen, the freshly laid avian egg contains the yolk, which is an energy-rich food supply for the embryo. Lipids constitute from 21 to 36 percent of the yolk, and proteins make up another 16 to 22 percent. The rest is primarily water. The yolk sac, or vitelline membrane, functions as the early analogue of a stomach and intestines. This sac is ultimately absorbed into the embryo's body cavity. The yolk initially cradles the tiny embryo in a small pocket.

Bird eggs vary greatly in composition, especially in the amount of yolk that they contain relative to their size (Sotherland and Rahn 1987). Most clearly, yolk increases from a low of about 15 percent in the eggs of gannets (Sulidae) to a high of 69 percent in the eggs of kiwis. The water content of the egg decreases as the yolk content increases. This spectrum of increasing yolk corresponds to the chicks' maturity at hatching, ranging from helpless (altricial mode of development) to mobile and sometimes independent (precocial) (Figure 14–14). Chapter 16 looks at these

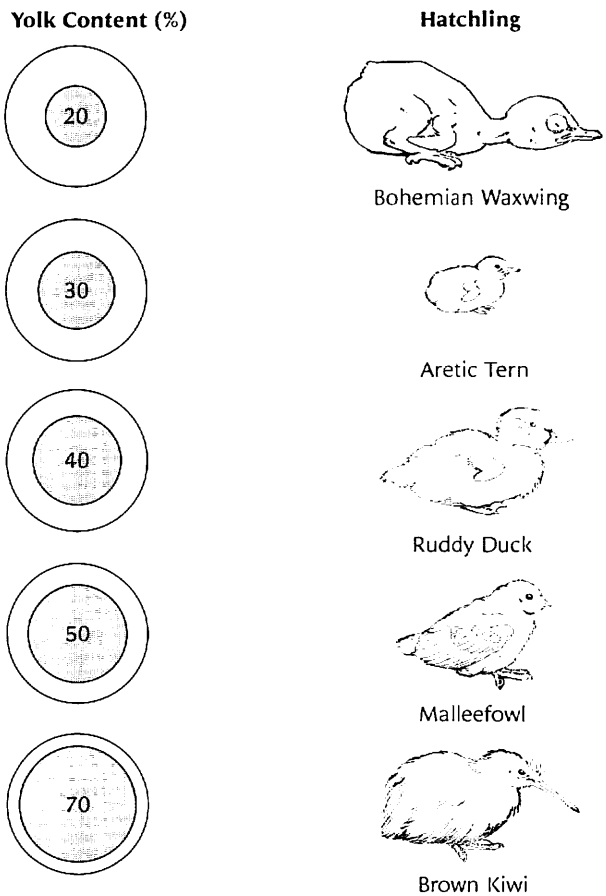


FIGURE 14–14 Differences in the relative amount of yolk in the eggs of different birds. Typical hatchlings are (*from top to bottom*): Bohemian Waxwing (altricial); Aretic Tern (semi-precocial); Ruddy Duck (precocial); Malleefowl (precocial); Brown Kiwi (precocial). [*From Sotherland and Rahn 1987*]

different modes of development, including different rates of growth of the embryos in the eggs and the implications for the early life of birds and care by their parents.

Eggshells

Above all, the hard eggshell provides structural support and protects the egg from soil invertebrates and microbes. The external shell layers shield the embryo, conserve food and water, and facilitate the respiratory exchange of gases. Eggshells vary in thickness from paper thin in small land birds to as much as 2.7 millimeters thick in ostriches. They are strong enough to withstand the weight of an incubating adult but delicate enough to allow the chicks to break out. The shell usually constitutes from 11 to 15 percent of an egg's total weight—as much as 28 percent in extreme cases.

Among the most endearing qualities of birds' eggs are the varied and often intricate colors of their shells. Only birds lay eggs with pigment-colored shells. Most eggs laid in open nest sites are exquisitely colored and patterned. Shaded ground colors, superficial blotches, and fine specklings or scrawls provide camouflage, helping to blend the smooth contours of an egg into its background.

The eggs of some ground-nesting species, such as nightjars, are conspicuously white. In these exceptional cases, the well-camouflaged incubating parent shields them from the eyes of potential predators. The eggs of hole- or burrow-nesting species tend to be dull white. The need for camouflage is minimal in such nest sites. Enhanced visibility of the white eggs in the dark interior of the nest cavity may reduce accidental breakage by the parents. The whitish eggs of grebes are camouflaged by brownish stains from mud and rotting nest vegetation.

A variety of birds, such as American Robins, lay bright blue eggs. The brightest blue eggs of all are those of the Great Tinamou of Central and South America. The function of blue coloration is still not known (Underwood and Sealy 2002). Remember that most mammalian predators don't see color and that birds themselves don't see colors exactly as we do.

Besides providing camouflage, brown speckling may strengthen the eggshell (Gosler et al. 2005). The amount of speckling on the eggs of Great Tits, caused by the addition of protoporphyrin pigments, varies with the thickness of the eggshell. Darker spots mark thinner and more permeable parts of the eggshell itself. The intensity of brown speckling also varies among locations according to the availability of the calcium needed by birds to produce the eggshells. Eggs produced in locations with reduced calcium are both thinner and more intensely speckled. Andrew Gosler and his colleagues suggested that the protoporphyrin pigments responsible for the brown speckles make the thinner eggs less brittle by lubricating the crystalline microstructure of the eggshell.

Different shell textures characterize the various families of birds. Accentuating the bright blues, greens, and violets of tinamou eggs is their polished, enamel-like texture. The eggs of ibises and megapodes, in con-

trast, have dull, chalky textures, whereas duck eggs are oily and waterproof. The eggs of cassowaries are heavily pitted, and the eggs of jacanas appear lacquered.

Eggshell textures are the result of a porous microstructure that regulates the passage of water vapor, respiratory gases, and microorganisms between the inside of the egg and the external world. The eggshell is permeated by thousands of microscopic pores (Figure 14–15). An ordinary hen's egg has more than 7500 pores, mostly at the blunt end of the egg.

The shells of most avian eggs have simple, straight pore canals that widen slightly toward the openings on the exterior surface. The eggshell pores of swans and ratites, however, branch from their origins near the shell membrane into a more complex network (Tyler and Simkiss 1959). Covering the exterior openings of the pore canals of all avian eggshells except those of pigeons and doves are tiny plugs or caps, which may act as pressure-sensitive valves.

The structure of eggshells could limit the altitudinal or geographical distributions of birds (Carey 1991). Rates of potential water loss are high in dry habitats, where relative humidity is low, or at high altitudes, where barometric pressures are low. Such water loss would limit the hatchability of eggs without some adjustment in pore density or length. Domestic chickens change their eggshell microstructure with altitude (Rahn et al. 1982). There is also some compensation for altitude in the eggs of swallows (Carey 1980). The degree to which eggshell microstructures vary as a form of environmental adaptation invites new research.

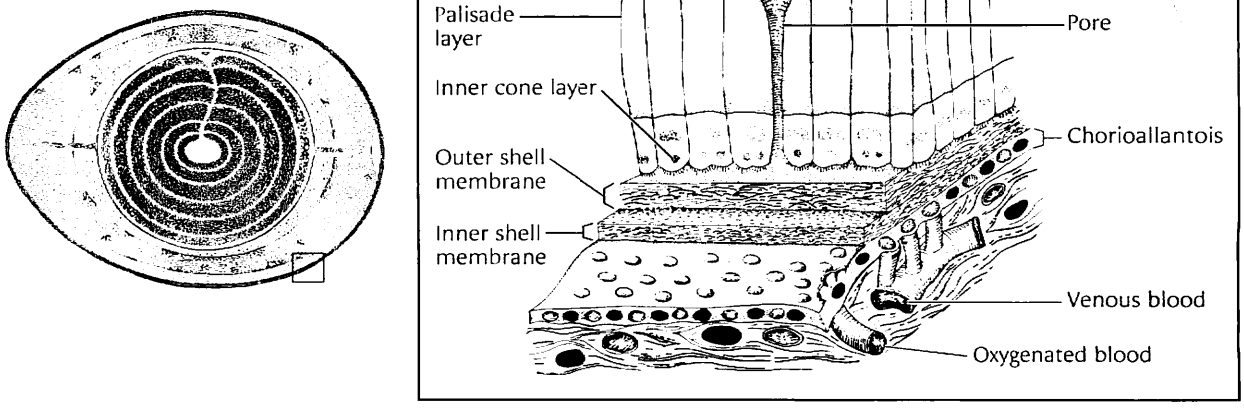


FIGURE 14–15 Pore canals allow gas exchange through the eggshell. Oxygen enters the eggs through pores in the cuticle and passes through columns of crystals to the permeable shell membranes. Carbon dioxide and water vapor escape to the outside environment through these same pores. Blood vessels in the capillary bed of the chorioallantois link the developing embryo to the gas-exchange pathway. [*After Rahn et al. 1979, with permission from Scientific American*]

Egg Sizes and Shapes

Modern bird eggs vary in size from the tiny (0.2-g) pea-sized eggs of hummingbirds to the enormous (9-kg), half-gallon eggs of the extinct elephant birds (Aepyornithidae) of Madagascar. Although egg size increases with body mass, small birds lay much larger eggs relative to their body mass than do big birds. Most birds lay eggs ranging from 11 percent to only 2 percent of body mass, with some dramatic exceptions. Kiwis, as mentioned in Chapter 12, lay unusually large eggs. The Brown Kiwi lays two, sometimes three, 500-gram eggs, each of which is 25 percent of the female's own mass. It lays these enormous eggs at four-week intervals (see Figure 12–1, page 336). Occasionally, birds lay dwarf, or runt, eggs that are less than half the size of their normal eggs. Most of these eggs lack a yolk and result from aberrant stimulation of the oviduct by an object such as a blood clot.

The term "egg shaped" brings to mind a rounded structure, longer than it is wide and slightly more pointed at one end than at the other. The familiar hen's egg is an example. Some factors influence the shapes of the eggs of domestic hens, but sex is not one of them. Males do not come from pointed eggs; nor do females come from more rounded ones, as Aristotle once suggested and popular wisdom would have it. Eggs vary from the nearly spherical eggs of petrels, turacos, owls, and kingfishers to the pointed (pyriform—literally "pear shaped") eggs of plovers and murres. Between these shapes are the ellipsoidal, or biconical, eggs of grebes, pelicans, and bitterns.

What determines egg shapes? They are a compromise between structural advantages, clutch volume, and egg content. Spherical eggs maximize shell strength, the conservation of heat, and the conservation of shell materials because they maximize volume relative to shell surface. Pointed eggs—for example, those typically laid by shorebirds—further enhance the volume or content of large eggs within the limits set by the area that an incubating parent can cover with its body. The pointed eggs of murres and other cliff-nesting birds have an additional advantage: they roll only in a tight arc, which lessens their chance of falling from nest ledges (Figure 14–16).

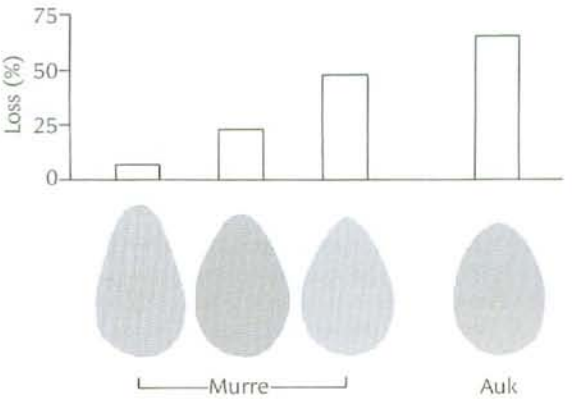


FIGURE 14–16 Pointed eggs such as those of the Common Murre are less likely to roll off a cliff ledge than are the more rounded eggs of auks such as Razorbills. Data presented here are from 400 trial experiments in which eggs of each type were pushed gently on a nesting ledge. [*After Drent 1975; Tschanz et al. 1969*]

Egg Formation in the Oviduct

A freshly laid egg consists of (1) the ovum, if unfertilized, or an embryo, if fertilized; (2) a full supply of food to nourish the embryo; and (3) protective layers to safeguard the internal environment. These components are assembled in an orderly way in the egg's trip down the oviduct.

The egg's passage through the oviduct usually takes about 24 hours but may require a week. After only a brief stay in the infundibulum (20 minutes), the egg of a chicken enters the main length of the oviduct, where it remains for 3 to 4 hours, progressing at a rate of 2.3 millimeters per minute, as if on an assembly-line conveyor belt. The albumen is added in this period. The membranes of egg and shell are added next, in a 1-hour passage through the isthmus section of the oviduct at a rate of about 1.4 millimeters per minute. Shell formation in the uterus then takes from 19 to 20 hours.

The oviduct is a long, convoluted tube with elastic walls able to accommodate the egg as it enlarges (Figure 14–17). Peristaltic contractions of smooth-muscle layers propel the egg from the infundibulum to the vagina. A glandular epithelial lining adds the albumen, shell membranes, and pigmentation in successive distinct sections.

As a first step, the anterior section of the oviduct, called the magnum, adds four layers of albumen. The yolk rotates gently in response to the slight spiral arrangement of the cellular ridges that line the oviduct's interior. Twisted strands of albumen, called chalazae, form as the yolk rotates (see Figure 14–5). They act as small built-in springs that help stabilize the yolk position and keep the embryo on the dorsal side of the finished egg.

Covered with albumen, the egg enters the isthmus of the oviduct, which surrounds the albumen first with an inner membrane and then with an outer shell membrane. This pliable and tough outer membrane is usually firmly attached to the shell itself. It is riddled with tiny pores that allow the passage of gases and liquids by osmosis and diffusion. Small amounts of pigments added to the shell membrane may impart a pinkish hue.

The final stage of egg production is the addition of a hard shell. It consists mostly of calcium carbonate ($CaCO_3$) in the form of calcite crystals. The shell is added in the uterus section of the oviduct. Eggshells are made of inorganic calcium and magnesium salts (carbonates and phosphates) embedded in a network of delicate, collagen-like fibers (Johnson 2000).

Two distinct layers make up the shell microstructure: (1) an inner cone layer with basal protuberances that adhere to the shell membrane and (2) a palisade layer that makes up most of the shell material (see Figure 14–15). Crystalline calcite is the principal construction material. This inorganic salt will gradually be taken from the shell and used as calcium for bone growth by the embryo.

Covering the outer surface of the eggshell is the cuticle, a thin, proteinaceous froth of air bubbles that blocks invasion by microorganisms.

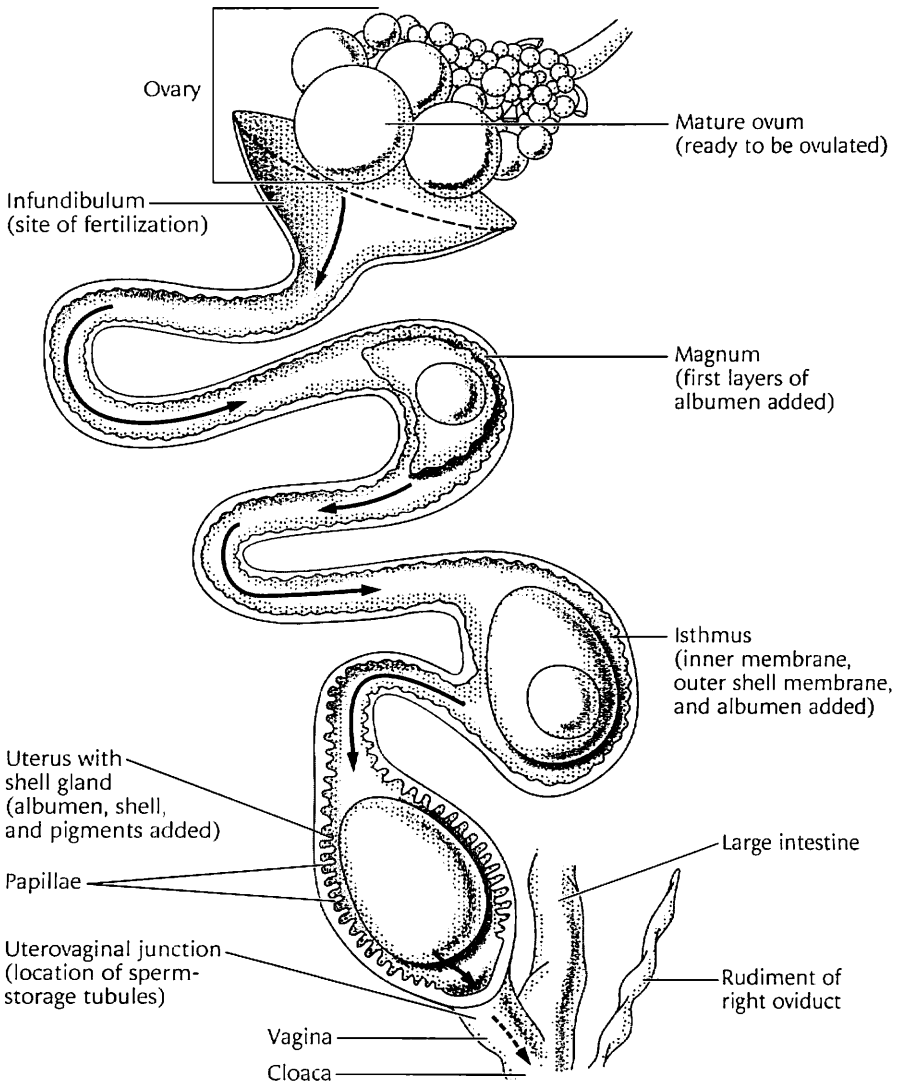


FIGURE 14–17 Formation of the complete egg in the oviduct, starting with the release of a mature ovum into the infundibulum. Layers of albumen and the shell membranes are added as the egg proceeds down the oviduct. The shell gland of the uterus adds pigments as a final step. Sperm-storage tubules are located at the uterovaginal junction of the oviduct. [*After Evans and Heiser 2004*]

The chemical elements that make up eggshells are extremely stable. For example, with proper calibration for past temperatures, fossil ostrich eggshells can be used to estimate the ages of archaeological sites as old as 1 million years (Brooks et al. 1990).

Magnesium and phosphate are minor components of the shell structure, but even slight variations in their concentrations affect the strength and thickness of the shell, altering the delicate balance of gas and water exchange required by the embryo. Magnesium is usually concentrated in a very thin layer of the inner shell, where it plays a role in the reclamation of eggshell salts by the embryo.

Pesticides also affect shell thickness, causing serious declines in raptors, water birds, and others high on the food chain. Pesticides, such as DDT and DDE (a breakdown product of DDT), affect normal eggshell formation by increasing magnesium and phosphate levels—with fatal consequences. For example, the normal level of magnesium in Common Tern eggshells is 1.54 percent, and the normal phosphate level is 0.25 percent. Exposure to DDT and DDE increases these concentrations to 2.1 percent and more than 0.6 percent, respectively, causing denting and developmental failure (Fox 1976). An even higher phosphate level (0.86 percent) has been associated with dead embryos.

In the 1960s, these pesticides were responsible for the widespread eggshell thinning and reproductive failure of Brown Pelicans (see Figure 18–24), several species of raptors, and penguins. Many eggs were so thin that the weight of the incubating parent crushed them. Reduced pesticide use led to improved eggshells and rebounds of endangered species.

At the end of the egg's journey through the oviduct, the shell gland adds shell colors, first as pigments deposited in the course of shell formation—the ground color—and later as superficial markings in the cuticle, the thin transparent coating of protein molecules that covers the entire shell. The shell pigments are porphyrins (see Chapter 4), which derive from the hematin of old blood cells that have been broken down in the liver and transformed into bile pigments.

No bird retains and nurtures a fertilized egg inside its body and bears live young. All birds lay a shelled egg for external incubation—a trait called oviparity. The high body temperatures (40°–42°C) of birds preclude the retention of eggs inside the body cavity and mandate the rapid expulsion of the fertilized egg to cooler temperatures outside the body, followed by external incubation in nests.

Birds eject the finished egg voluntarily with their powerful vaginal musculature. The large size of most eggs precludes the retention of more than a single egg. Larger retained clutches would increase the energy cost of flight and make females more vulnerable to predators. Most birds lay their eggs early in the morning, probably to avoid the risks that daytime activity could pose to a bird carrying a heavy, fragile egg in its oviduct.

As a rule, the laying interval between eggs is from one to two days. Most passerines, ducks and some geese, hens, woodpeckers, rollers, small shorebirds, and small grebes can lay an egg a day. At the other extreme, moundbuilders require from four to eight days to produce one of their huge eggs. Ratites, penguins, and large raptors take from three to five days, and boobies and hornbills take as many as seven days.

The Embryo

Three extraembryonic membranes support the life and growth of the avian embryo (Figure 14–18). The amnion surrounds only the embryo, which floats in a contained environment of water and salts. The chorion is a protective membrane that surrounds all the embryonic structures. The allantoic sac functions in both respiration and excretion. This sac increases

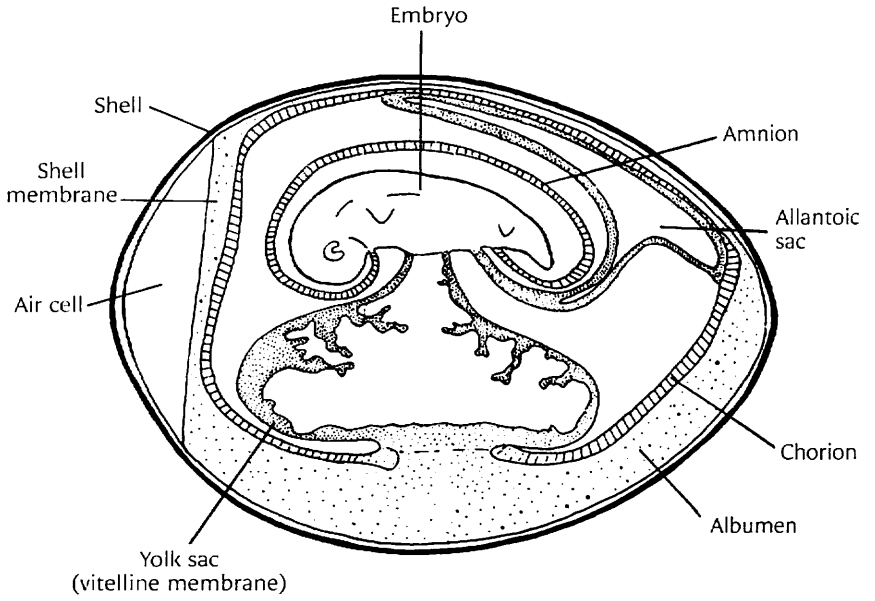


FIGURE 14–18 The developing embryo and the extraembryonic membranes. [*After Bellairs 1960*]

in size as development proceeds. A growing network of fine capillaries keeps it well supplied with blood. Pressed tightly against the chorion and the shell membranes, the resulting "chorioallantois" is the site of export of carbon dioxide produced by the embryo and import of oxygen from the outside world (see Figure 14–15). The allantois also acts as a sewer for the storage of poisonous nitrogenous wastes.

The avian egg provides a secure, self-contained environment for embryonic development. It also imposes restrictions on the kind of nitrogenous waste that the embryo can produce. Ammonia is not a suitable waste product, because the embryo, confined in its shell, cannot excrete it. Unexcreted ammonia would rapidly reach toxic concentrations. Nor is urea, a water-soluble compound, acceptable. The egg lacks the space required to store large volumes of this dilute waste. Birds, both embryonic and adult, have an excellent solution to their waste-disposal problem. Uric acid is a nonsoluble form of nitrogenous waste that can be deposited safely as tiny crystals inside the allantois. It is not toxic, and it does not require large volumes of water to flush it from the adult system.

Diffusion through the shell membranes allows the exchange of water vapor and gases, which are vital to embryonic life. Eggs breathe passively. No active, regulated exchange is known; nor is it required to account for the known rates of exchange of gas and water vapor. The density of pores is an exquisite compromise between the optimal high densities that would facilitate rapid gas exchange and the low densities that would minimize water loss.

The dynamics of gas exchange change as incubation progresses. The eggshell thins progressively as calcium is removed from it and incorporated into the embryonic skeleton. This thinning increases the rate of gas

exchange at a time of increasing respiration by the growing embryo. The permeability of the shell membranes to oxygen also increases as they dry out, and oxygen moves inward more rapidly as the growing embryo draws increasing amounts of oxygen from the chorioallantois.

Clutch Size

The number of eggs that a bird lays in one set, called the clutch, is subject each season to the availability of energy and other resources (Box 14–4). As already noted, avian eggs are elaborate structures, and each one requires a substantial investment of energy and nutrition. The production of a full clutch within a short time interval is a major feat that can strain a female's daily energy budget. Food shortages can reduce or stall egg production and thus affect clutch size.

Generally speaking, the amount of energy transferred to the egg varies from 4.2 kilojoules per gram in passerine birds to as much as 8.4 kilojoules per gram in the fat-rich eggs of waterfowl. The efficiency of energy transfer is only about 20 percent. A laying female passerine bird, for example, must eat 5 kilojoules of food for every kilojoule that is transferred to her eggs. Estimates of the daily costs of egg production range from 45 to 60 percent of basal metabolic rate for passerines, from 80 to 130 percent for shorebirds and fowl-like birds, to more than 200 percent for waterfowl (Carey 1996). How ornithologists should best measure the direct costs of egg production is an ongoing debate (Williams 2005), but all agree that these costs are significant ones.

Egg production also requires sources of protein and of minerals, such as potassium and calcium. Poor supplies of these nutrients may limit egg

BOX 14–4

DETERMINATE VERSUS INDETERMINATE EGG LAYERS

Historically, in the study of birds, a distinction has been made between determinate layers—species that lay a fixed number of eggs—and indeterminate layers—species that lay extra eggs if some are removed from the nest early in incubation. A classic example of an indeterminate layer is a prodigious female Northern Flicker that laid a total of 71 eggs in 73 days to replace those removed as soon as they were laid (Bent 1939). Domestic hens and Japanese Quails can produce an egg a day all year long.

In contrast are the determinate layers, which do not replace eggs removed from their nests. Shorebirds and gulls are usually classified as determinate layers, but they do replace eggs that are removed as soon as they are laid. Pheasants and ducks lay a full complement of replacement eggs if all but one egg of the original clutch is removed as soon as laying is complete.

The importance of genetic, nutritional, and psychological factors controlling the production of replacement eggs needs study, and the basic concept of determinate versus indeterminate laying ability needs to be reevaluated (Winkler and Walters 1983). No clear classification of species can be made until all the species being compared are subjected to the same experimental regimen.

production, especially in birds that eat fruit and seeds. Providing females with extra protein causes egg size or clutch size or both to increase in many species. The importance of calcium for eggshell production was noted earlier.

The greatest costs of egg formation are incurred during the period of yolk production. The peak daily energy expenditure for total egg production depends on the amount of overlap in the growth cycles of separate ova and on the number of follicles growing simultaneously. For a Fiordland Penguin, for example, the peak occurs on day 20 as it adds albumen to the first egg at the same time as it adds the last of the yolk to the second egg (Grau 1982).

The resources required for egg production come from stored reserves supplemented by increased daily intake. Species such as waterfowl, which draw heavily on stored energy and nutrient reserves to produce their large, expensive eggs, are called "capital breeders." Wood Ducks, for example, lay large clutches of about 12 richly provisioned (and, therefore, energy-expensive) eggs at a total metabolic cost of 6000 kilojoules (Drobney 1980). A hen's fat reserves provide most of this energy (88 percent). The protein content of the eggs, however, comes from invertebrates eaten by the hen during the laying period, which requires an additional investment of energy from her fat reserves. The use of stored reserves for egg production by passerine birds is not yet well studied (Williams 2005).

Other birds are "income breeders." These species ingest, on a daily basis, the resources that they need for egg production. Brown-headed Cowbirds are income breeders. They do not use stored reserves despite their great egg production—approximately an egg a day for more than a month. Instead, they obtain the nutrients for egg production directly from the diet (Ankney and Scott 1980).

Arctic shorebirds also are income breeders. Ornithologists once assumed that female Arctic shorebirds carried most of the resources that they would need for egg production when they migrated north. They supposedly built up these reserves at their refueling stopovers enroute to the breeding grounds. Analyses of carbon isotopes, however, showed it not to be the case (Klaassen et al. 2001). The carbon-isotope signatures of eggs and natal down of the hatchlings do not match those of estuarine ecosystems. Instead, they are typical of the Arctic tundra, demonstrating the direct transfer of resources ingested after arrival in the Arctic.

Laying females draw some of the calcium needed for eggshells from their own bone tissues. They also supplement that source with extra calcium intake. Rodent teeth and small bones on the forest floor are important sources of calcium for egg production. So are snails, wood lice, and millipedes (Bure and Weldinger 2003). These essential natural sources of calcium are declining in some forests owing to acid rain, which dissolves the calcium in the litter on which land snails, for example, depend for their shells (Graveland et al. 1994). Declines in the abundance of land snails then cause poor reproduction by forest birds. Experimental supplements of calcium can reverse reproductive decline by improving egg volume, eggshell thickness, the onset of breeding, and chick health (Mänd et al. 2000).

Other costs of egg production may not be resource based and are more subtle and mostly speculative. For example, decreases in breast muscle and increases in body weight during the egg-laying period may impair a female's ability to fly and hence her ability to avoid predators (Veasey et al. 2001). Female Blue Tits are 14 percent heavier and fly 20 percent more slowly during the egg-laying period than they do after the eggs hatch, but males stay the same (Kullberg et al. 2002). Another potential cost may stem from the elevated levels of estradiol hormone associated with egg laying. This hormone inhibits the production of red blood cells and reduces the red-blood-cell count of laying females, potentially impairing their ability to fly and their general aerobic performance (Williams 2005).

Non-resource-based costs of egg production may be more important than resource-based costs (Ketterson and Nolan 1999; Williams 2005). Reproductive hormones have a broad effect on the body, affecting immunocompetence, organ size, and the protection of blood vessels and nerves. Minimizing such costs in the short term by limiting reproductive investment potentially increases longevity and lifetime reproductive success. Linking these short-term constraints to long-term costs and benefits remains a major challenge for students of avian life-history strategies.

Optimal clutch sizes are subject to long-term tradeoffs that affect lifetime reproduction success (see Chapter 17). The results take many forms. The "insurance" eggs of certain seabirds are one example. Penguins, boobies, and other seabirds lay an extra egg to back up the first egg to offset chronically poor hatching success due to infertility, early embryonic failure, or predictable loss to predation. Rockhopper Penguins and the Macaroni Penguins typically lay two eggs of different sizes (del Hoyo et al. 1992). The second egg is from 20 to 70 percent larger than the first and tends to hatch first despite being laid as much as a week later. The penguins do not start incubation until both eggs are laid. The smaller, later-hatching chick from the first, smaller egg then usually starves to death within a few days after hatching.

How can we explain this situation? Two intriguing hypotheses are available. One suggests that the first eggs laid by these penguins are often lost to predators or pushed out of the nest in fights with neighbors before the parents settle down to incubation. For example, 54 percent of the pairs of Macaroni Penguins lose their first egg this way before they lay their second egg. Such losses, combined with high mortality during incubation, favor a two-egg clutch containing one insurance egg. Alternatively, the other hypothesis suggests that *Eudyptes* penguins could be evolving from a two-egg clutch to a one-egg clutch, and what we see is a snapshot of evolution in action.

Summary

Birds reproduce sexually. The gonads consist of paired testes in males and (usually) a single ovary in females. Avian testes are located internally, attached to the dorsal body wall at the anterior ends of the kidneys. The avian ovary, which resembles a cluster of grapes, comprises hundreds,

sometimes thousands, of oocytes. The gonads are controlled by two hormones secreted by the anterior pituitary: follicle stimulating hormone, which regulates gamete formation, and luteinizing hormone, which regulates hormone secretion by the testes and the maturation of follicles in the ovary. Estrogen and testosterone control sexual distinctions in plumage, body size, voice, and behavior.

The two sex chromosomes (W, Z) controlling sexuality in birds evolved independently of the mammalian sex chromosomes (X, Y). Female birds have two different sex chromosomes (WZ), and males have two similar sex chromosomes (ZZ). Gene activity in the sex chromosomes directly affects the neural circuitry of the brain as well as the development of the gonads.

Most birds lack external genitalia. Copulation normally entails only brief cloacal contact. Females store viable sperm for weeks in special storage tubules. Females also mediate competition among sperm received from different males. Sperm swim directly to the upper end of the oviduct, where fertilization takes place, usually within a few days of copulation.

The avian egg is one of the most complex and highly differentiated reproductive cells achieved in the evolution of animal sexuality. It provides not only nourishment for the developing embryo but also ventilation, insulation, resistance to rapid heating or cooling, and protection. The avian eggshell evolved to protect the embryo from soil invertebrates and microbes. Pores that permit gas exchange and water loss permeate the microstructure of the eggshell.

After fertilization, the egg with its tiny embryo passes through different regions of the oviduct, a process that generally takes about 24 hours. Albumen, yolk, egg and shell membranes, and a hard shell made of calcium carbonate are added in the journey down the oviduct. Egg formation takes from one to seven days, depending on the species. Females transfer to their eggs immune factors and steroid hormones in variable doses that affect the quality and competitive ability of their offspring. Some birds have fixed clutch sizes, but others do not. Energy requirements, food supplies, egg size, and parental-care requirements, as well as genetics, all influence clutch size.

CHAPTER 15

Nests and Incubation

The great diversity of nests built by birds of the order Passeriformes helps explain their success . . . and their occupation of most terrestrial habitats over the world.

[Collias 1997, p. 267]

No bird gives birth to live young. Instead, birds prepare nests to cradle their eggs and then their young. Caring first for the eggs and then for the young requires a major commitment of time and energy, often by both sexes. The associated risks also are great. The vulnerable eggs, nestlings, and attending parents tempt a host of predators. Costs of reproduction include high mortality of incubating parents and low survival of eggs and nestlings. Competition for prime, safe nests, therefore, fosters the evolution of diverse nest architectures and social arrangements.

Successful reproduction also requires attention to the narrow thermal tolerances of the embryos and, later, to those of nestlings. The incubation behaviors of parents correspond to the requirements of their offspring. Embryos inside the eggs need heat from their parents' bodies to grow to hatchlings. They must also be protected from excessive heat or lethal cold.

These needs present a conflict: incubating birds must balance the costs of caring for eggs in the nest against the benefits of fending for themselves away from the nest. Additionally, activity at the nest—comings and goings to and from rest breaks or feeding a mate on the nest—draws attention to the nest and increases the risk of predation.

This chapter starts with a review of the nests and nesting behaviors of birds. Then follow the challenges of the incubation of eggs that contain developing embryos. The first of these two major topics surveys the adaptive architectures and construction materials of bird nests, followed by more detailed discussions of how nests thwart predators, how birds build their nests (including the role of experience), and the importance of nest microclimates. The second section is on incubation behavior and presents

evidence that birds adjust their behavior sensitively to the risks of predation as well as to the basics of keeping eggs warm, cool, and viable. Variable incubation periods support different patterns of embryo development as well as different ways that mates share the costs and risks of this stage of parental care. The chapter concludes with the ways in which chicks hatch from the eggs, with a feature on the nests and hatchlings of the highly precocial moundbuilders of the Australasian region.

Nests

In general, nesting success increases in northern latitudes, in hole-nesting species, and in large species with hardy young. The principal causes of nest failure, in descending order of importance, are: predation, starvation, desertion, hatching failure, and adverse weather.

Predation causes by far the greatest number of annual nest losses, in all habitats and on all continents. Predation on nests and their contents severely reduces breeding success: more chicks may leave the nest through the stomach of a predator than on their own. This powerful force influences nest architecture, nest placement, and the evolution of life-history traits such as clutch size. Nest predation also forces species to compete locally for limited safe nest sites and thereby affects whether they can coexist (Martin 1988a, 1988b).

Nicholas Collias (1997), the dean of bird-nest ornithology, suggests that the building of elaborate nests was a key feature of the adaptive radiation and evolutionary success of the songbirds (Order Passeriformes). The generally small body sizes of songbirds, combined with their strong powers of flight and flexible nesting behaviors, allowed them to compete with the hole nesters, which prevailed first in terrestrial habitats. Songbirds competed by hiding their smaller nests in diverse sites, including green plants overhanging water and the outer twigs of bushes and trees, or by suspending them from vines. Domed nests that hide the contents from predators overhead came to characterize many of the smallest songbird species throughout the world. Also providing safety from predators, the burrows of nocturnal auklets and petrels riddle the hillsides of oceanic islets. The woven nests of caciques and weavers dangle from crowded tall trees, often over water.

The diverse nesting behaviors of birds correspond to their diverse solutions to the local challenges of reproduction. Most birds build isolated, hidden nests. Many of their nests remain unknown to science. At the other extreme are conspicuous, open-breeding colonies, some with millions of pairs. In Africa, from 2 million to 3 million pairs of the sparrow-like Red-billed Quelea nest in less than 100 hectares of thornbush savanna. On the Peruvian coast, black-and-white Guanay Cormorants pack together at densities of as many as 12,000 nests per acre and attained colony sizes of 4 million to 5 million birds.

Birds build nests to protect themselves, their eggs, and their young not only from predators but also from adverse weather. Structure and func-

tion are inseparable in nest architecture (Hansell 2000). Conspicuous nest features provide protection. Subtle features aid in the regulation of temperature and humidity.

Nest Materials and Architecture

Other animals build nests, but birds do so in an extraordinary variety of forms, materials, and sites. Bird nests range from precarious constructions on bare branches to enormous communal apartments and from simple scrapes on the ground to elaborate stick castles (Figure 15–1). In size, they range from the few sticks assembled by some doves to the gargantuan aeries of eagles. One Bald Eagle aerie weighed more than 2 tons when it finally fell in a storm after 30 years of annual use, repairs, and additions (Herrick 1932).

Many birds nest in colonies, but only a few actually build compound, communal nests divided into individual compartments. In contrast with most parrots, instead of nesting in excavated cavities or burrows, as many as 15 pairs of the Monk Parakeet of Argentina occupy huge, communal, stick nests, which also house nesting pairs of Speckled Teal and Spot-winged Falconets (Martella and Bucher 1984). These nests are now a familiar sight in Florida and other states, where introduced Monk Parakeets are increasing in numbers.

The nests of the Sociable Weaver of southwestern Africa are the largest and most spectacular of all communal avian nests. Each one resembles a large haystack in a thorny tree. The weaver pairs that will occupy the structure share in building the common roof that covers 100 or more separate nest chambers. These chambers are cool by day and warm by night. The geographical distribution of this species is limited to the extremely arid sections of southwestern Africa, probably because rain would saturate the nest and create an insupportable weight.

Nests may be casually constructed from ready-for-use pebbles and sticks or laboriously woven from natural fibers. Animal products, plant matter, and inorganic materials, including mud pellets, rocks, tinfoil, and ribbons, are used in nest construction. Selected aromatic plant materials provide fumigants to repel parasites (Box 15–1). Birds go to extremes to get prime materials, which may be in short supply. Thievery is common, especially in large seabird, heron, and penguin colonies. It is often much easier to steal than to collect fresh materials.

Entirely self-sufficient are the Edible-nest Swiftlet and its relatives *(Collocalia)* of Southeast Asia. They make their nests almost entirely of their own (hardened) saliva. A sticky form of glycoprotein is the critical ingredient of this oral cement that holds the fragile nest together and attaches it to a cave wall. The glycoprotein is the primary ingredient of bird's nest soup, a gastronomic delicacy that supports a substantial trade in harvested nests for sale to the Asian food industry (Medway 1963).

Beyond basic construction materials, birds use spider webs for mooring or adhesion and feathers and hairs for the final lining. Great Crested Flycatchers and their relatives sometimes add snake skins to their nests,

(A)

(B)

(C)

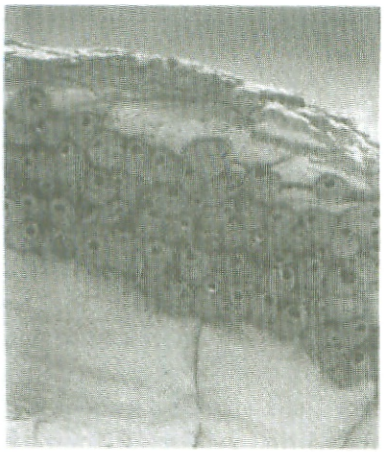
(D)

(E)

FIGURE 15–1 The nests of birds vary from simple to elaborate, large to small. (A) Floating platform nest of Western Grebe; (B) sandy scrape nest of Wilson's Plover; (C and D) down-lined, camouflaged nest of Cinnamon Teal; (E) mud nest of Rufous Hornero.

prompting speculation that they help protect the nest from predators. Feathers are often a major component of the nest and, especially, the nest lining. The nests of Long-tailed Bushtits and Goldcrests in Europe may contain 2000 or more feathers. Waterfowl pluck down from their own breasts, and the Superb Lyrebird plucks down from its flanks to line the nest. Many birds pluck hair, also a premium nest-lining material, from livestock. Galápagos Mockingbirds snatch hair from the heads of surprised tourists.

In one remarkable example of unusual nest materials, Black-eared Sparrow-Larks of southern Africa add to the edges of their nests the scarlet-colored lids that cover the burrows of a particular species of trap-door spider (Hockey et al. 2005). The geographical distribution of this sparrow-lark coincides closely with that of the spider. Whether this addition is some form of competitive cultural decoration akin to the bowers of bowerbirds (see page 355) or a defense against predators or vermin is not known.



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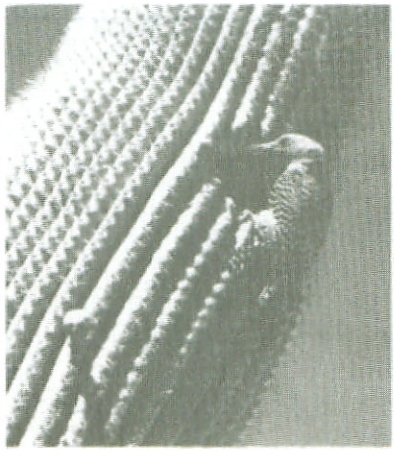

(G)

(H)

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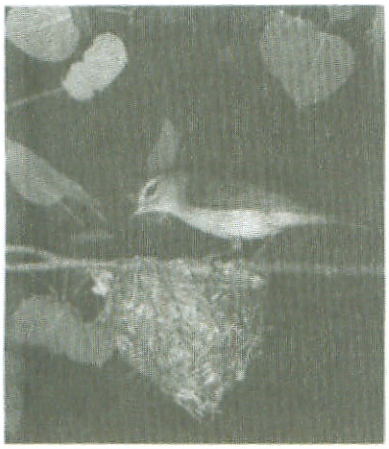

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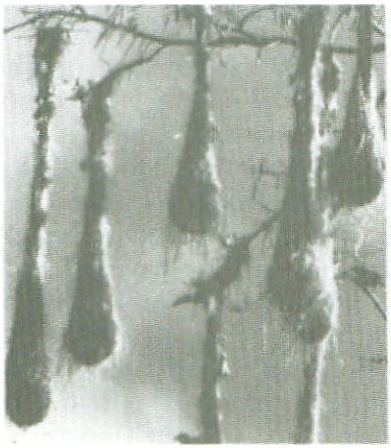


(M)

(N)

(F) Mud nests of American Cliff Swallows; (G) hole nest (in cactus) of Gila Woodpecker; (H) straw nest of Cactus Wren; (I) stick nests of Great Blue Herons; (J) stick nest of Rufous-fronted Thornbird; (K) cup nest of Broad-tailed Hummingbird; (L) suspended cup nest of Warbling Vireo; (M) suspended nests of Crested Oropendolas; (N) intricately woven nest of Cassin's Malimbe. [*Courtesy of (A–D, F–H, K, and L) A. Cruickshank/VIREO; (E and M) O. Pettingill/VIREO; (I) T. Fitzharris/VIREO; (J) P. Alden/VIREO; (N) E. Collias and N. Collias*]

BOX 15–1

FRAGRANCE HELPS

Nests made of plant matter may contain twigs, grass, lichens, and leaves. Some birds add green vegetation that helps to combat disease and ectoparasite infestations (Baggott and Graeme-Cook 2002). In general, hole nesters incorporate fresh, green vegetation more regularly into their nests than do open nesters. Common Starlings, in particular, select by odor certain plants, such as red dead nettle and yarrow, which contain volatile chemical compounds that inhibit the growth of bacteria and the hatching of the eggs of arthropod nest parasites (Clark 1991). The experimental removal of these green plant materials leads to a dramatic increase in the populations of bloodsucking mites, tiny parasites that can drain the blood volume of a starling chick.

Blue Tits on the island of Corsica also add fragrant plants to their nests (Petit et al. 2002). They select by odor fragments of as many as five herb species that Corsicans themselves use to make aromatic house cleaners and herbal medicines. The birds also refresh the bouquet of odors, selectively replacing, by using olfactory cues, herbs that wane or are removed.

With respect to architecture, passerine songbirds construct the most diverse and the most elaborate nests of all. Their nests fall into three basic categories: (1) cavity or hole nests (in the ground or in a tree); (2) open-cup nests (outside of holes); and (3) domed nests (with a constructed roof). All three types were present early in the evolution of songbirds (Collias 1997). Secondary radiations of diverse nest architectures followed the initial theme of domed structure as features of the evolution of some songbird families. Many birds build enclosed or pensile (hanging) nests to discourage predators. Tropical passerines build globular or enclosed nests, often with an entrance tube on the sides (see Figure 15–1H and M). Eggs in a covered nest are less visible to potential predators when parents are absent than are eggs in an open nest. Snakes cannot easily reach pensile nests or easily crawl inside protruding entrance tubes.

Recall the diverse nest types of swallows, which map well on the phylogenetic relationships among genera (see Chapter 3). Even more dramatic is the architectural variety of the nests of the ovenbirds (Family Furnariidae) of South America. This group of suboscine birds is one of the most diverse families of (suboscine) songbirds in morphology, behavior, and nests (Zyskowski and Prum 1999). Some species resemble larks; others resemble jays, tits, creepers, nuthatches, wrens, thrushes, thrashers, dippers, or warblers. Ovenbird nests are similarly diverse in their structure and in siting (Figure 15–2). Like their close relatives the woodcreepers (Dendrocolaptidae), the ancestral ovenbirds nested in cavities. Derived from and replacing cavity nests are diverse domed nests made of vegetation, ranging from modest grass nests to huge stick piles. The horneros *(Furnarius)* sculpt novel, domed, ovenlike structures made of mud (see Figure 15–1E).

Pensile nests are among the most elaborate of specialized nests. Some hang delicately by silky cobwebs or by wiry, black fungal fibers. Some are suspended far below a main branch. Others, such as those of the Bal-

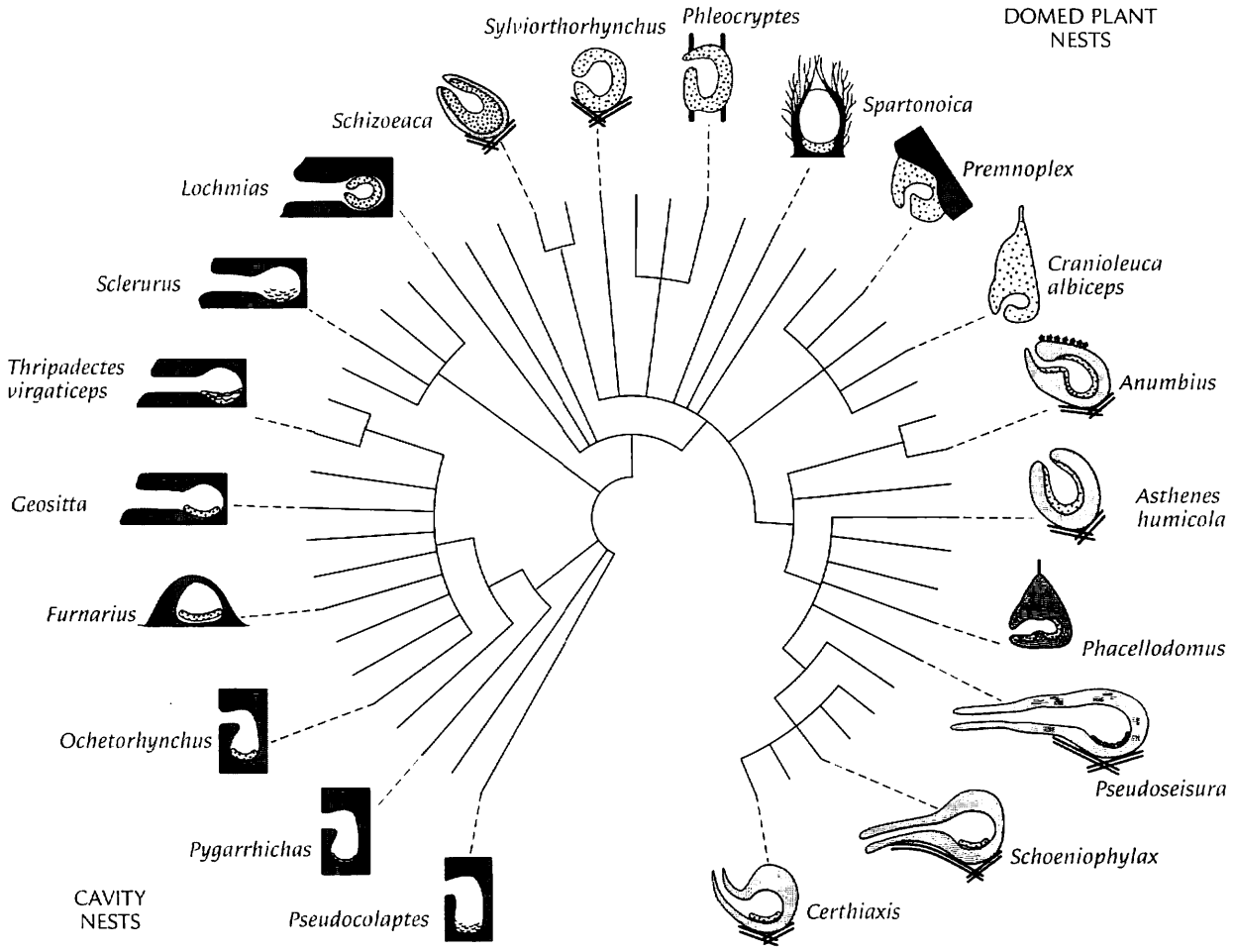


FIGURE 15–2 Adaptive radiation of nest architectures of the genera of ovenbirds (Furnariidae) of South America. Diverse domed nests made of plant matter followed the original mode of cavity nesting. Black exterior materials indicate cavities in trees or the ground. The Sharp-tailed Streamcreeper *(Lochmias)* and its relatives build domed plant nests inside cavities. The clay ovenlike nests of horneros *(Furnarius)* are unique replacements of a cavity nest. [*After Zyskowski and Prum 1999*]

timore Oriole, hang from the thin, outermost branches of large trees. The integrity of pensile nests derives from their tightly woven construction, tough knots, and strong binding materials. The intricately woven, meter-long nest of Cassin's Malimbe, a West African weaver, may well be the pinnacle of avian nest construction (Collias and Collias 1984; see Figure 15–1N).

Nest Safety

Invisibility, inaccessibility, and impregnability all contribute to nest safety. The camouflaged color patterns of incubating nightjars and of shorebird eggs render them nearly invisible. The lichen decorations on the sides of a hummingbird's nest do the same.

Some nest sites are clearly safer than others. Cryptic sites in dense clumps of grass, vine tangles, or hidden crevices minimize the chance of discovery. Seabirds that nest on sheer cliffs (Box 15–2) and swifts that nest in deep caves or behind waterfalls achieve safety through inaccessibility. Horned Coots pile up stones in the middle of high Andean lakes to build their own nesting islands out of reach of terrestrial predators (Figure 15–3A and B), and many grebes build nests of floating vegetation. Nests on the ground are more vulnerable to mammalian predators than are nests in trees or bushes. Tooth-billed Pigeons once nested on the ground on Samoa, but they shifted to the trees after whalers introduced cats to this South Pacific island (Austin and Singer 1985).

BOX 15–2

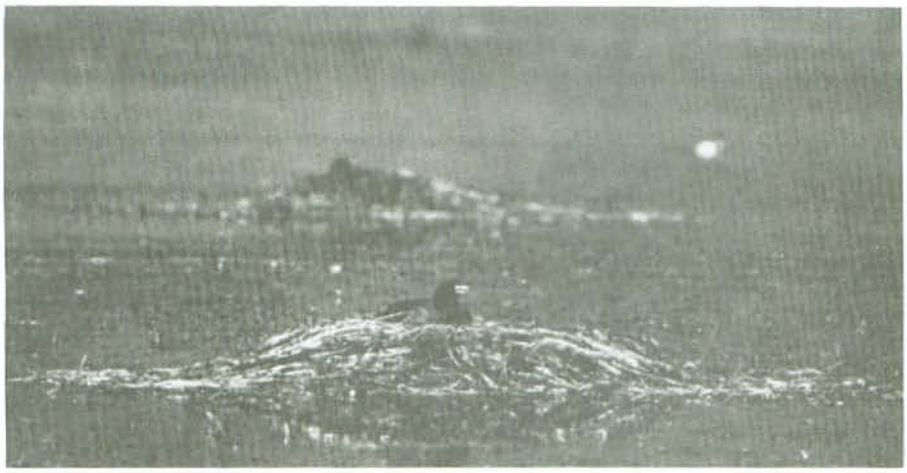
KITTIWAKES ADAPT TO CLIFF NESTING

Most gulls nest on the ground, where they are vulnerable to predation by crows, mammals, and other gulls. Black-legged Kittiwakes, however, nest on narrow, predator-free ledges on windswept, seaside cliffs (see illustration). The selection of these relatively safe nest sites broadly molds the behavior and morphology of these kittiwakes. They cling to their safe nest sites, using strong claws and toe muscles. Reduced nest predation has also fostered the loss of antipredator behaviors evident in other gulls, including alarm calls, predator mobbing, and the removal of eggshells from the nest site. Young kittiwakes, which are a conspicuous silvery white, stand still and hide their beaks when frightened, rather than running and hiding as the cryptically colored chicks of ground-nesting gulls do.

The physical restrictions of a kittiwake's narrow nesting ledge have also favored aggressive and courtship displays that differ from those of other gulls. Instead of using the long call (see Chapter 9), for instance, kittiwakes announce territorial ownership with a modest choking display. Aggression between males is expressed by bill jabs from a fixed position and does not extend to the flamboyant charges of other species. Females commonly hide their beaks to minimize the likelihood of attack and physical displacement from the narrow ledge. A courting male does not regurgitate food onto the ground in front of a female (there is no place to do so) but, instead, gives it to her directly.

Unlike most other gulls, Black-legged Kittiwakes nest on cliffs. [*Gordon Wiltsie/ Peter Arnold*]

(A)



(B)

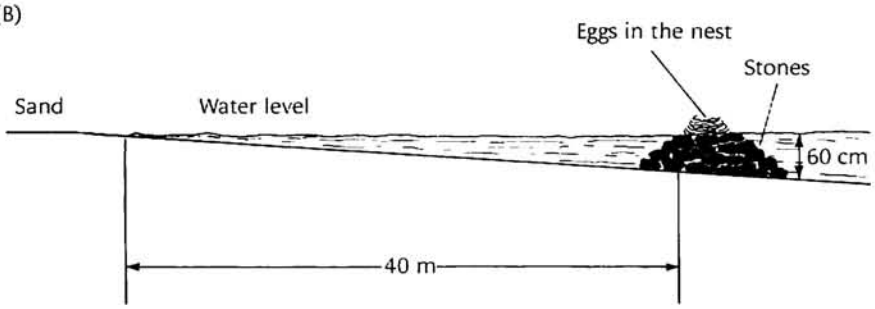


FIGURE 15–3 Some birds go to extremes to build nests that are less vulnerable to predation. Horned Coots build their nests on stones, which they assemble in piles in high-altitude Andean lakes. (A) Horned Coot on nest. (B) Diagram of nest structure. [*(A) Courtesy of P. Canevari/VIREO. (B) After Ripley 1957*]

The Yellow-rumped Cacique is one of the many species that builds a hanging nest. It nests in colonies in Amazonian Peru. These tropical blackbirds defend their closed, pouchlike nests against predators in three ways (Robinson 1985). First, by nesting on islands and near wasp nests, caciques are safe from arboreal mammals such as primates, which destroy more accessible colonies of other birds. Caimans and otters also protect the island colonies by eating snakes that try to cross the open water surrounding a colony. Second, caciques mob predators as a group. The effectiveness of mobbing increases with group size, which increases with colony size. Third, caciques hide their nests from predators by mixing active nests with abandoned nests. Overall, nests in clusters on islands and near wasp nests suffer the least predation. Females switch colonies after losing a nest to a predator, usually moving to sites that offer better protection against that predator. In such ways, the best colony sites accumulate the largest numbers of nests.

Even within a species, some nest sites are more vulnerable than others. Thomas Martin and colleagues (2000) compared predation rates in

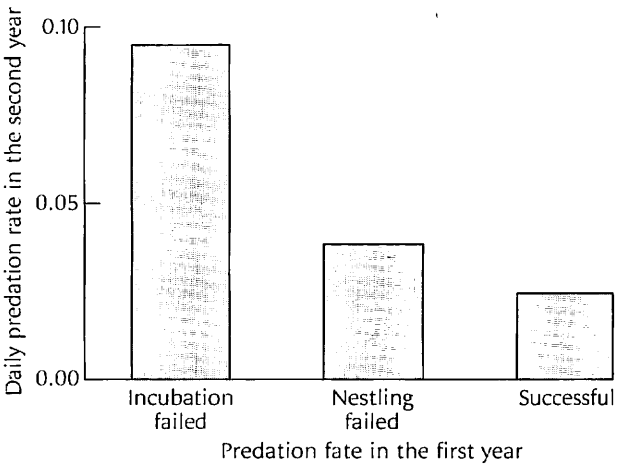


FIGURE 15–4 Some ground-nesting sites are more vulnerable to predation than are others. Daily predation rates at nest sites baited with Zebra Finch eggs were highest at sites that had been attacked by predators during the incubation stage in the first year. Daily predation rates were lowest at sites that were successful in the first year. [*After Martin et al. 2000*]

successive years at specific sites used by several species of ground-nesting Arizona birds (Figure 15–4). Nest sites that failed during incubation in the first year suffered the highest rates of predation in the next year. Nest sites that were successful in the first year suffered the lowest rates of predation in the following year.

Cavity nesting is safer than open nesting. Half of the avian orders, among them all parrots, trogons, and kingfishers and their relatives, nest in cavities or holes. Owls, parrots, and Australian frogmouths nest in natural cavities, and trogons, titmice, and piculets excavate cavities in the soft or rotten wood of old trees. Woodpeckers are the preeminent primary cavity excavators. Some species drill holes in hard, living trees. Most species select wood softened by fungal infections, which they spread to other trees by carrying fungal spores on their bills (Jackson and Jackson 2004). Other birds, unable to make their own holes—thus called secondary cavity nesters—compete intensely for abandoned woodpecker holes.

The excavation of valuable nest holes by woodpeckers and their use by other species creates a complex web of community interactions (Figure 15–5). In central British Columbia, the Northern Flicker emerges as the keystone species (Martin et al. 2004). The nest holes that it creates, especially in aspens, provide housing for more than 13 mammal and bird species, ranging from rodents and weasels to owls and ducks.

Some birds nest in an area protected by large animals or stinging insects. Common Starlings and House Sparrows nest on the fringes of Spanish Imperial Eagle aeries. The Eurasian Stone-curlew, a ploverlike bird of Africa, nests on sandy shores beside nesting crocodiles. Bananaquits of the West Indies reduce rates of nest predation by nesting in association with wasps (Wunderle and Pollock 1985). At least 49 tropical bird species, in-

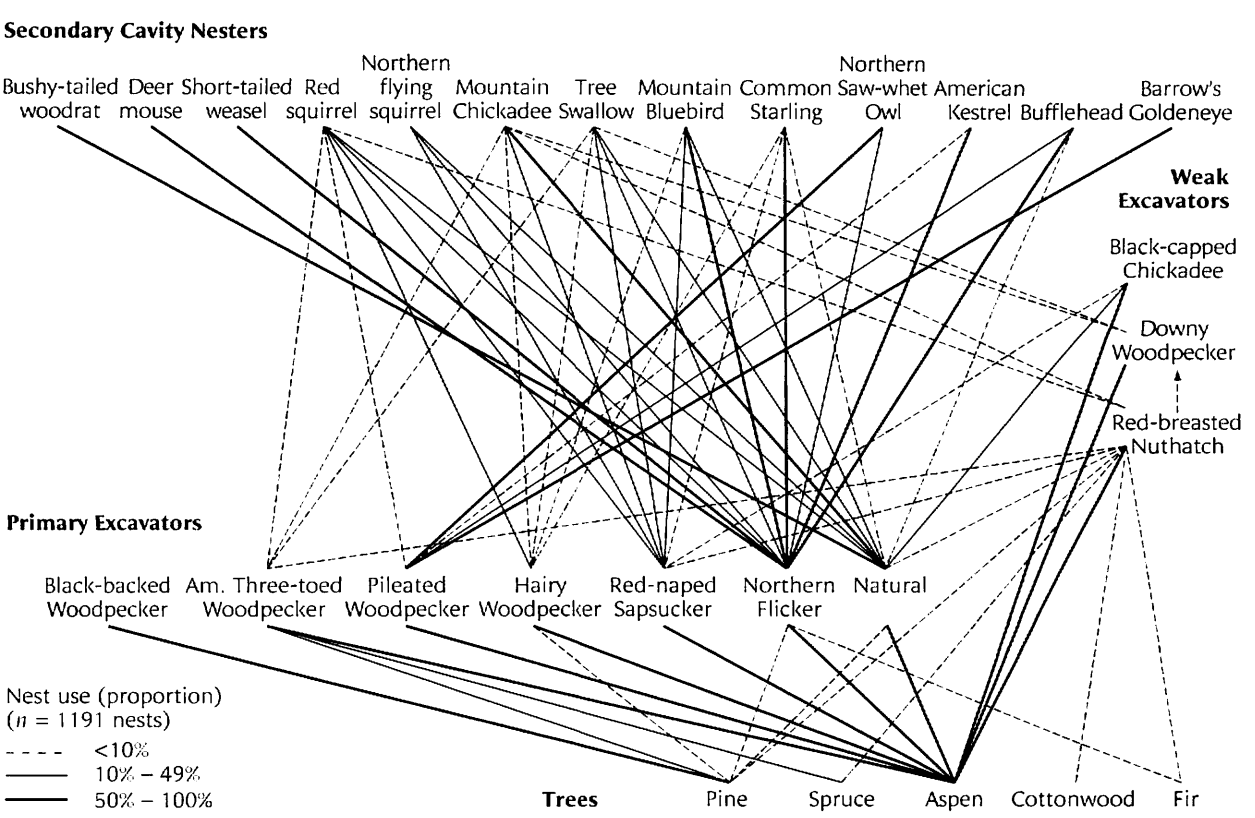


FIGURE 15–5 Diverse species compete for the prime nest cavities. This web diagram illustrates secondary cavity nesters' use of nest cavities (and trees) excavated by six primary excavators, all woodpeckers, and three species of weak excavators in interior British Columbia. For example, as the different types of lines show, Bufflehead ducks primarily used flicker cavities, secondarily used Pileated Woodpecker cavities, and occasionally used natural cavities. [*From Martin et al. 2004*]

cluding 25 percent of all kingfishers, excavate nest cavities inside the mounds, called termitaries, of social termites (Hindwood 1959). The Orange-fronted Parakeet of Central America nests exclusively in the termitary of one species, *Eutermis nigriceps*. The geographical distribution of this parakeet is restricted to that of its termite host.

Many birds directly attack trespassers. Eastern Kingbirds chase anything that violates nearby airspace. Northern Mockingbirds, Blue Jays, and Arctic Terns can draw blood and bits of fur from cats that come too close to their nests or young. They may attack people as well. Large owls and eagles with powerful feet and sharp talons can seriously wound climbers.

A parent flushed from the nest may attempt to draw a predator's attention away from the nest site with distraction displays. The two most common displays are the injury flight and the rodent run (Figure 15–6). By using the injury-flight display—feigning a broken wing and calling in great alarm—an adult plover can easily draw a fox away from its nest. To keep the fox's attention, the plover may then switch to the rodent-run display—running in a low crouch—an action that appeals to the mouse-catching instincts of the fox. Distraction displays are risky, but, more often

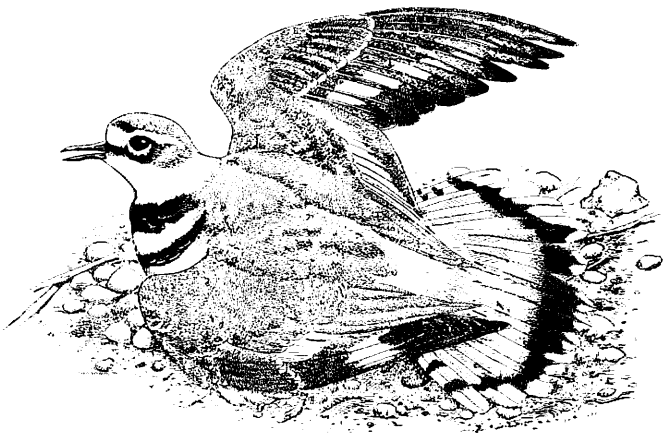


FIGURE 15–6 Distraction display of a Killdeer feigning injury. [*Barry Kent McKay*]

than not, the parent escapes and the predator loses track of the original nest location.

Nest Building

Either member of a pair of birds may build their nest or they may do so jointly during courtship and pair formation. Most monogamous male North American passerines contribute to the nest-building effort. A male's presence at the nest site in the earliest stages of nesting, however, may be primarily to protect his mate from insemination by other males (to guard his paternity).

Nest-site selection is an integral part of pair formation, often accompanied by special displays. Wrens and weavers construct nests for evaluation by prospective mates. If prospective mates reject a nest, Village Weavers tear it down and build a new one. A male Marsh Wren may build more than 20 nests for comparison by a prospective mate (Kroodsma and Verner 1997). The unused nests also serve as dummy nests that help to distract nest predators.

Nest building itself varies from the simple accumulation of materials to elaborate construction. The nonincubating parent may simply toss materials in the direction of the nest site, creating a mound of debris or a conspicuous rim near the eggs and leaving the incubating parent to delineate the nest site by drawing the materials toward itself. The deliberate transport of suitable materials to the nest site was a major step in the evolution of nest-building behavior among birds (Collias and Collias 1984). It led to the modification and design of the nest site and to more complex nest architecture, which can be a strenuous undertaking.

Birds usually carry nest materials in their bills or feet. Some lovebirds, which are small African parrots, transport their nest materials in an unusual way that is genetically determined (Dilger 1962). The Yellow-collared Lovebird carries one strip of nesting material at a time in its bill, but the related Rosy-faced Lovebird tucks the ends of several strips beneath its rump feathers and flies to the nest with the strips in tow

(Figure 15–7). Hybrids between these two species try to tuck strips into their rump feathers but cannot do so correctly. Sometimes, the hybrids fail to complete the tuck. More often, they hold the strip by the middle instead of the end, fail to let go of the strip after tucking it, or tuck it into the wrong place, and so many strips do not reach the nest box. The hybrid's genetic program for carrying nesting material apparently contains conflicting instructions.

Bills and feet are the nest-building tools. Bills serve as wood chisels and drills, as picks for digging into the ground, as shuttles for weaving, as needles for sewing, as trowels for plastering, and as forceps for plucking and inserting (Skutch 1976). Birds also build nests by stamping, scraping, kneading, and scratching as their reptilian ancestors did. Burrow nesters dig by kicking loose soil backward. They then mold the internal nest dimensions by using their bills, breasts, and feet.

The cup nests of small arboreal land birds are usually built from the bottom up. Others, such as the open-cup nests (suspended by the rim) of vireos, are built by wrapping nest materials around the supporting twigs first and then by looping strands of material from side to side to form the framework of the cup. The long, hanging nests of tropical flycatchers begin as an accumulation of materials stuffed into a tangled mass. The flycatcher forces its way into the center and gradually expands the nest cavity from the inside out, and then it reinforces and lines the hollowed-out cavity (Skutch 1976).

Weavers and New World orioles weave elaborate hanging nests. The male Village Weaver, for example, begins with a vertical ring, to which it adds in succession a roof, the walls of the main nest chamber, an antechamber, and finally the finished entrance (Figure 15–8). The structural features of these nests are woven into their final positions with the use of special knots. The types of knots used are species specific. Some weavers tie simple knots, whereas others tie half hitches and slipknots (Figure 15–9).

Most passerine birds build nests with architectural features so distinctive that we can identify the genus or species of the builder. How, then, does a young bird know how to build a complex nest similar to the one built by its parents? A male Village Weaver, hand-raised in isolation without ever seeing a nest, can build a nest that is typical of its species. This ability suggests a strong genetic control of this behavior.

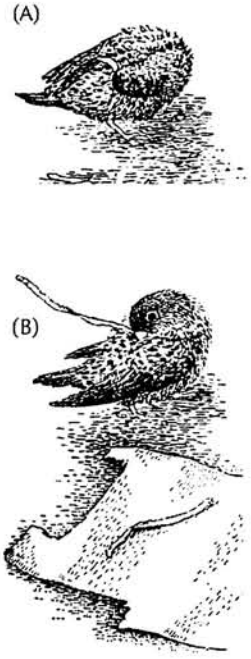


FIGURE 15–7 Lovebirds carrying nest strips. (A) The Rosy-faced Lovebird tucks them into its rump feathers, whereas the Yellow-collared Lovebird (not shown) carries them in its bill. (B) Hybrids of these two species try to tuck strips but usually fail. [*From Dilger 1962, with permission from Scientific American*]

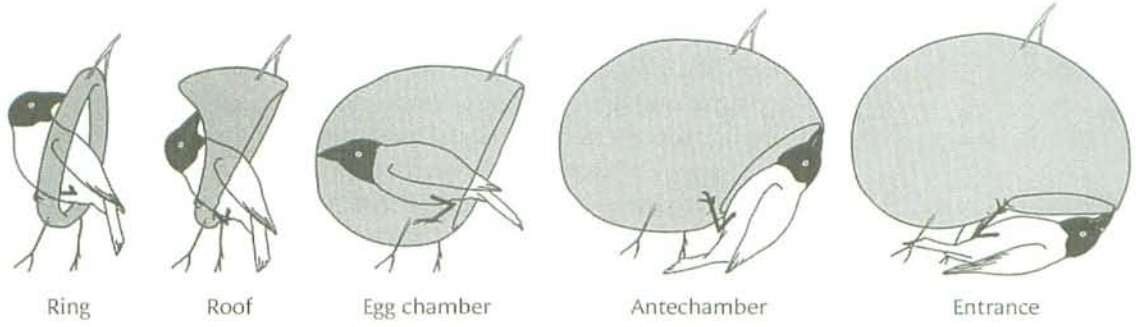


FIGURE 15–8 Stages of nest construction by the male Village Weaver. [*After Collias and Collias 1964*]

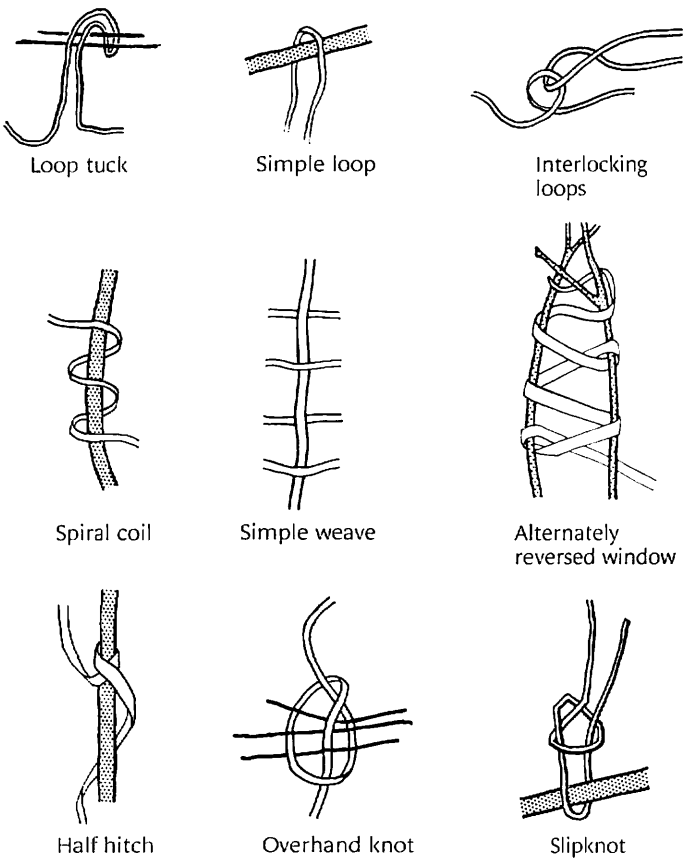


FIGURE 15–9
Some knots and stitches used by weavers in constructing their nests. [*From Collias and Collias 1964*]

Early experiences also play a role. Improvement in nest construction is particularly evident in the Village Weaver and other species that build elaborate nests (Collias and Collias 1964). Although immature males build crude structures at first, they become more skilled in the arts of tying knots and weaving. Older males build refined products.

When nesting for the first time, the Western Jackdaw, a small European crow, rapidly improves its skills. It starts by making clumsy movements with inappropriate nest materials and progresses to efficient construction with a range of suitable nest materials. At first, the inexperienced young jackdaw tries to shove almost anything into the nest platform. Sticks of the right size and texture insert easily and firmly into the matrix, but objects, such as light bulbs, do not. By the time the nest is complete, the range of materials gathered narrows to the types of twigs that are most suitable for nest construction (Lorenz 1969).

Raptors imprint on their natal nest sites. Consequently, they choose a similar situation several years later when they reach maturity (Temple 1977). Understanding this process is critical to the conservation of endangered species. The Mauritius Kestrel, for example, nested in tree cavities that were vulnerable to predation by introduced monkeys. As a result, the kestrel population declined to only a few endangered pairs in the 1960s. One of the last pairs of kestrels switched to a cliff ledge, out of reach of

the monkeys, and raised young successfully. This change started a new tradition that helped the population recover, providing hope for the survival of the species.

Nest Microclimates

The microclimate of a nest is crucial to the successful incubation of the eggs and to the later health of baby birds. Nest microclimate also influences the daily energy requirements of the adults and, in turn, the amount of time that they spend on the nest incubating eggs and brooding young. The warmth of the nest is usually determined by the thickness of insulation and the heat produced by the incubating parent. The outstanding insulating properties of breast down used by eiders and other waterfowl, for example, greatly reduce the cooling rate of eggs that are not covered by the parent. Nest insulation also reduces the time that an incubating parent must be on the nest by reducing its own costs of thermoregulation and, in turn, the amount of time spent feeding itself (Figure 15–10).

The great thermal inertia of the enormous communal nests of the Sociable Weaver in southern Africa keeps them cool in the daytime and warm at night. Temperatures inside the nest at night remain from 18° to 23°C above external temperatures. The warm nighttime temperatures are due partly to heat absorbed during the day and partly to heat generated by the bodies of large numbers of roosting birds.

Placing a nest in or out of the sun, shade, or wind has a major effect on its microclimate and, therefore, on a pair's breeding success. Early in the season in Arizona, Cactus Wrens build nests where they are protected from cool winds and are bathed in the warm morning sun. Later in the

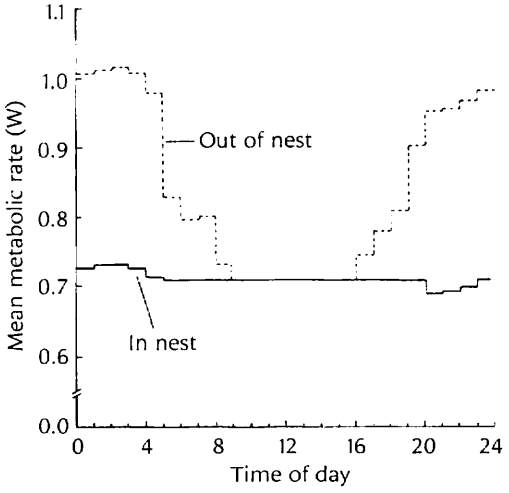


FIGURE 15–10 The effect of insulated nest microclimates on the energy expenditures (in watts) of a Red-winged Blackbird. The mean metabolic rates of birds perched outside the nest at night are higher than those while incubating inside the insulated nest. [*From Walsberg and King 1978*]

season, when it is hot, they build well-shaded nests that are exposed to cooling breezes (Proudfoot et al. 2000).

Placing nests in cavities and burrows also conserves energy. Like the haystack nests of Sociable Weavers, cavity nests and burrow nests buffer eggs, parents, and young against fluctuations in external temperatures. For another example, the temperatures inside the burrows of European Bee-eaters remain close to 25°C despite an outside temperature range of almost 40°C (Ar and Piontkewitz 1994).

Deep, cool burrow and cavity nests, however, have their drawbacks. Poor ventilation limits the amount of time that parents can spend inside with growing young (Ar et al. 2004). On windless days, ammonia and carbon dioxide tend to build up as a result of decaying excreta amid unsanitary nest conditions, and oxygen levels occasionally decline until the occupants have difficulty breathing. Offsetting this problem, the diffusion of gases through the soil and the nest tunnel helps ventilate the air in the nest chamber. The movements of adults in and out of the nest pump air in and out, as a moving piston would (Ar and Piontkewitz 1994).

Nest microclimates, particularly the relative humidity of the air, also affect the rate of water loss from the eggs and hence their hatchability. Water loss from an egg and its embryo is inevitable because of differences between the water-saturated interior of the egg and its unsaturated external environment. During incubation, eggs lose from 10 to 23 percent of their weight, primarily as a result of the loss of water vapor, especially in deserts and at high altitudes. Excessive water loss may fatally dehydrate the embryo. On the positive side, the space vacated inside the egg becomes the air cell at the blunt end of the egg, which is the source of air for a chick as it starts to break out of the egg. An adequate volume of air must be available for the chick's first critical breaths.

Nest Sanitation

Fouling of a nest is common. The nests of many pigeons, raptors, and carduelline finches, such as the House Finch, are well known for their unseemly conditions. Many other birds are fastidious, regularly removing feces and other debris to prevent the nest from becoming a breeding ground for disease and insects and other parasites. Some young birds instinctively eject liquid feces away from the nest, and others eliminate feces accurately through nest hole openings. Adult female hornbills defecate through the narrow slit remaining in the mud-sealed opening. The larvae of a particular moth species help to clean the nests of the Golden-shouldered Parrot of Australia.

The young of most passerine birds and woodpeckers excrete fecal sacs, which facilitate nest sanitation. Fecal sacs are packages of excrement surrounded by a gelatinous membrane. The parent can easily pick up the sac and drop it away from the nest (Figure 15–11). Incomplete digestion by nestlings leaves some residual food in their fecal sacs, which are often eaten by parents for nutrition as well as sanitation purposes. In one study, fecal sacs provided 10 percent of the daily energy requirements of adult White-crowned Sparrows (Morton 1979).

FIGURE 15–11 American Robin removing fecal sac from nest. [*John T. Fowler/Alamy*]

Incubation

Birds incubate their eggs externally with a minor exception: some cuckoos jump-start incubation internally before laying their eggs in the nest of another species. The parents' task is to maximize the hatching success of their eggs by controlling the environment of the eggs steadily for several weeks (Deeming 2002a). The narrow temperature and hydration tolerances of embryos inside the eggs demand rigorous attendance by their parents. Increased energy expenditures required to thermoregulate at cool temperatures (and to heat larger clutches of eggs) challenge incubating parents (Tinbergen and Williams 2002). Yet the need to stay at the nest compromises the parents' ability to feed themselves.

The hormone prolactin mediates the incubation behavior of birds (Vleck 2002). The levels of this hormone circulating in the blood rise sharply the day before incubation starts (Figure 15–12). Circulating blood levels of prolactin correspond to the incubation roles of males and females. Where one sex contributes most of the parental care, it has relatively high levels of prolactin. Conversely, the sex hormone testosterone, which mediates aggressive and sexual behavior, inhibits the expression of parental behavior in birds. Blood levels of testosterone in male birds that incubate drop sharply after egg laying has begun.

Incubation Shifts

The term "attentiveness" refers to the percentage of time spent by a parent on the nest incubating eggs compared with the time spent off the nest feeding or, in some cases, reducing heat stress. Both sexes incubate in a

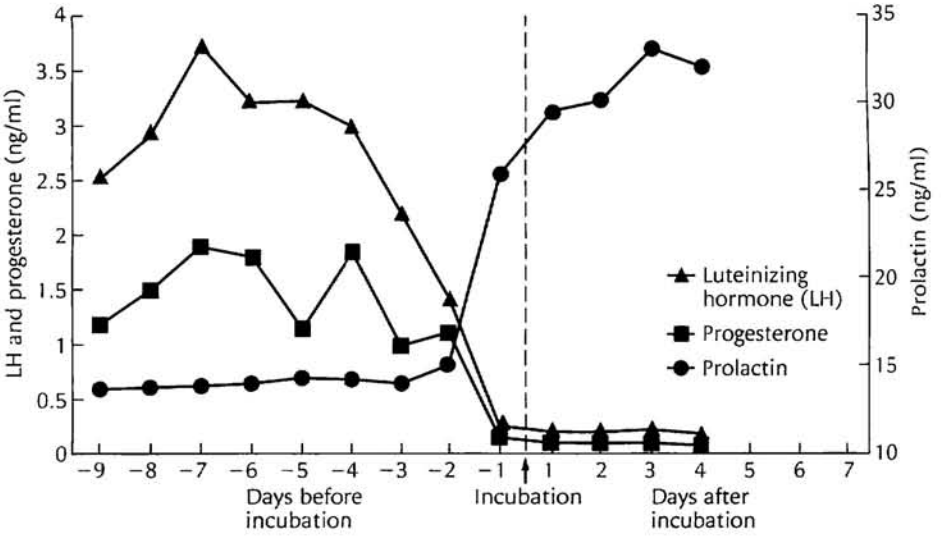


FIGURE 15–12 Daily changes in plasma hormone concentrations at onset of incubation. Abbreviation: LH, luteinizing hormone. The rise of prolactin is associated with incubation behavior. [*From Lea and Klandorf 2002*]

majority of avian families. The female incubates alone in about 37 percent of the families, and the male incubates alone in only 6 percent (Figure 15–13). The parents take regularly alternating shifts and achieve nearly continuous coverage of the eggs in many groups, including some penguins, woodpeckers, doves, trogons, hornbills, hoopoes, and antbirds. Incubation shifts may last for 1 or 2 hours; for 12 hours when one sex incubates by day and the other by night; for 24 hours when each sex takes a day at a time; for several days for many pelagic seabirds; and for more than a month for penguins.

Females that incubate alone often need their mates to bring food to them. Hornbills provide an extreme example. The male provides all the food for its mate, which is imprisoned in the nest cavity. A female Red

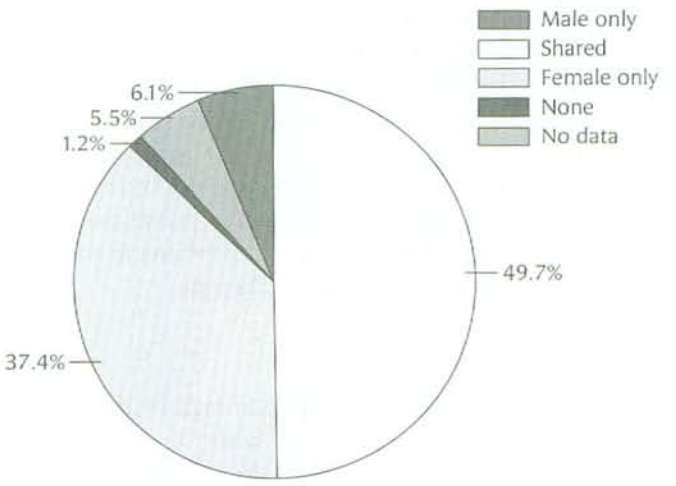


FIGURE 15–13
Distribution of different patterns of incubation in 163 families of birds. Both parents incubate in about half of the families. [*From Deeming 2002b*]

Crossbill also receives all its food from its mate, an arrangement that enables this species to incubate continuously in the middle of winter.

In some cases, the male may guard the nest against predators while the female leaves to feed. Each egg is important to the endangered Seychelles Warbler, which has one clutch with one egg each year and no time to replace an egg lost to predators (Komdeur and Kats 1999). Yet nest predation by another bird—the finchlike Seychelles Fody—is severe on two of the little islands on which the warbler persists. Egg loss at unguarded nests is seven times that at guarded nests. Therefore, males sacrifice their own feeding time and body condition to guard. When some of these males were transplanted to Aride, a nearby island without fodies, the males stopped guarding, foraged more for themselves, and improved the condition of their own bodies.

The risks of predation decrease with reduced parental activity at the nest (Martin et al. 2000; Figure 15–14). Birds should be sensitive to this risk and should adjust their daily behavior appropriately. In the longer term, natural selection should favor risk-averse behavior most strongly in those species that are subject to high predation rates. As a rule, open-nesting birds are subject to more nest predation than are hole-nesting species. Birds that nest in the Tropics are subject to more nest predation than are birds that nest in the temperate zones.

Observations and experiments support these predictions. For example, North American bird species that endure high nest predation employ long on–off shifts, rather than frequent short shifts (Conway and Martin 2000). This pattern reduces their activity at the nest. To explore this further, Thomas Martin and his colleagues placed models of predators near nests. They then measured the sensitivity of nesting birds to the simulated predation risk by measuring changes in their attentiveness and incubation

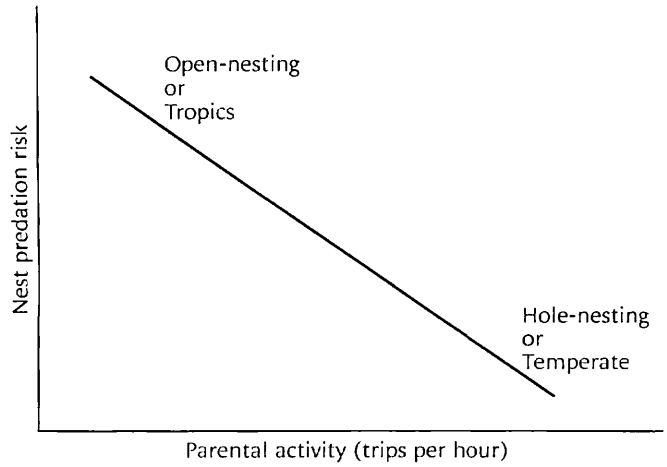


FIGURE 15–14 Relation of risk of nest predation to parental activity at the nest. Within a species, the daily probability of nest predation increases with parental activity. Natural selection more strongly favors the evolution of breeding behaviors that reduce parental activity near the nest in species that are exposed to higher predation rates (open nesting versus ground nesting, the Tropics versus temperate zones). [*After Martin et al. 2000*]

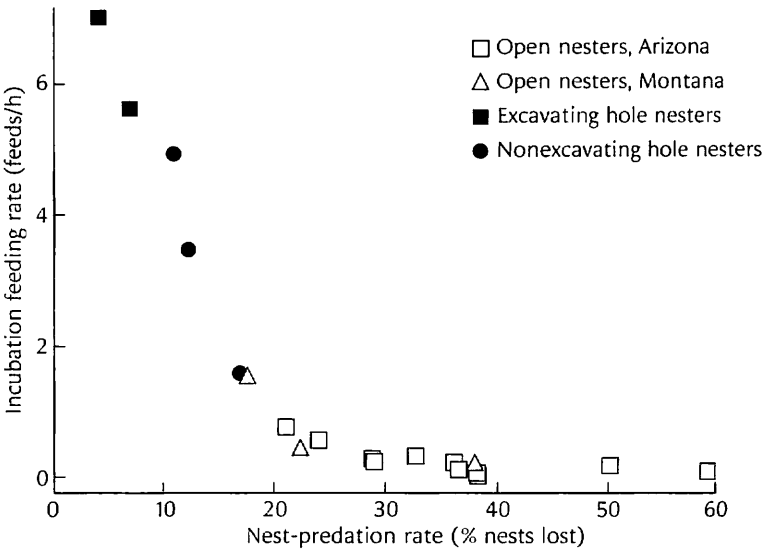


FIGURE 15–15 Males of hole-nesting bird species (black symbols), which are subject to low nest-predation rates, feed their incubating mates on the nest more frequently than do males of open-nesting bird species (white symbols), which are subject to high predation rates. Owing to the lower rates of feeding by their males, female open nesters are less attentive during incubation than are female hole nesters. [*From Martin and Ghalambor 1999*]

feeding behavior. Males of both open-nesting and hole-nesting species reduced their deliveries of food to the incubating female when risk of predation increased (Martin and Ghalambor 1999; Figure 15–15). Females then left the nest more often to feed themselves, reducing their own attentiveness. In further support of the hypothesis of sensitivity, males of open-nesting species that experienced high rates of nest predation reduced their rate of visitation more than did males of species that experienced low rates of nest predation (Ghalambor and Martin 2002).

Changing shifts may be surreptitious or highly animated. Most small land birds lack conspicuous relief ceremonies, slipping on and off the nest surreptitiously to prevent detection by predators. Meadowlarks land some distance from the nest and sneak back to it through the grass, by using one of several indirect routes. Bearded Reedlings pretend to look for food as they get near their nests and then enter rapidly if they perceive that the coast is clear. The female Long-tailed Hermit, a tropical hummingbird, behaves similarly. On returning from foraging, she searches intensively for spiders on the buttresses of large trees before quickly slipping onto her nest and sitting very still.

Other birds have highly ritualized relief ceremonies. When changing the guard, Pied-billed Grebes touch bill tips lightly. Least Bitterns erect their crown feathers and rattle their bills. Some herons present a stick for the nest to their mates, and terns offer a freshly caught fish. Penguins have elaborate changeover rituals that facilitate individual recognition and reinforce the pair bond, as described here for one species:

> As a Yellow-eyed Penguin approached his incubating partner, she broke into an "open yell." He ran up with arched back and beak to the ground. Then both put their heads together to perform a hearty welcome ceremony, in which a great volume of sound issued from their widely opened mouths as they faced each other, standing erect close together. After several less-intense displays of mutual affection and three repetitions of "welcome," the female resumed her position on the eggs, then rose to relinquish them to her mate. [Skutch 1976, p. 171, from Richdale 1951]

Because their foraging time is limited, incubating birds sometimes must fast and depend on their fat reserves for supplementary food. A female Snow Goose, for example, subsists on the reserves remaining after egg production. Inadequate reserves cause some females to desert their eggs during incubation and others to die of starvation (Figure 15–16). Similarly, male Emperor Penguins and King Penguins start incubation with

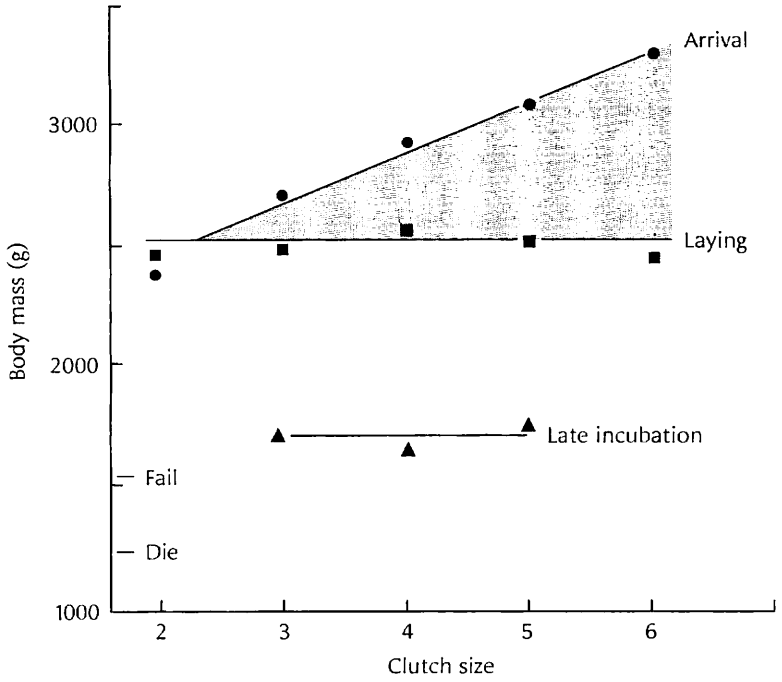


FIGURE 15–16 Relation of fat reserves of the female Snow Goose arriving on Arctic breeding grounds to its projected clutch size. Females use some reserves (measured by loss of body mass) to produce eggs and then use more reserves during incubation. The number of eggs that a female lays is directly related to its reserves. Most females finish laying and start incubating with approximately the same body mass and, hence, similar reserves. Females that start incubation with inadequate reserves may abandon their eggs to prevent starvation, but sometimes they do not do so in time. Circles, squares, and triangles indicate mean values of body mass of females weighed on arrival, while laying, and in late incubation, respectively. [*After Drent and Daan 1980, from data in Ankney and MacInnes 1978*]

substantial reserves that allow them to fast for as long as four months, in the Emperor Penguin's case. They lose substantial weight in the process. Male King Penguins depend on relief from their mates before they lose too much weight. If their mates fail to return on schedule, the males fast an extra eight days and metabolize body protein before abandoning their eggs in the interest of self-preservation (Robin et al. 2001).

Incubation Periods

The incubation period is the time required by embryos to develop in freshly laid eggs that receive normal attention by incubating parents. It is defined as the interval between the laying of the last egg of a clutch and the hatching of that egg.

Most birds delay the onset of incubation until the clutch is complete. This behavior ensures that the embryos begin to develop and later hatch at roughly the same time, even though some eggs are laid earlier than others. Pigeons and doves, for example, sit on the first egg before the second is laid but do not bring it up to the temperatures required for incubation. Owls and raptors, on the other hand, begin incubation before the clutch is complete, with the result that young hatch at intervals. To maintain the viability of the eggs in their large clutches, female ducks increase attendance as laying progresses. The development of embryos starts slowly after the second egg is laid. Increased warming by the hen then accelerates the development of later embryos. As a result, the ducklings hatch together at about the same time (Loos and Rohwer 2004).

Incubation periods vary from as short as 10 days for some woodpeckers, cuckoos, and small songbirds to as long as 80 to 90 days for albatrosses and kiwis. Longer incubation periods increase the risk that a predator will find the nest. Offsetting the increased risk are strategic advantages tied to life-history strategies, brain size and cognitive abilities, and the maturation of embryonic tissues (Ricklefs and Starck 1998). Chapter 16 reviews these advantages in relation to the different modes of development of the hatchling chick.

Embryos

Adaptive, genetically controlled differences govern the developmental programs of embryos. Growth rates of embryos vary with egg size and with incubation period, but they have little to do with a species' position in the spectrum from altricial to precocial modes of development. Similar-sized eggs of different taxa differ greatly in the amount of time that they take to hatch and in the chick's state of development on hatching.

A broad survey of 47 families and subfamilies of birds revealed that incubation periods relate directly to how long adult birds live (Ricklefs 1993). Incubation periods also correlate with the probability of predation. Species that nest in holes tend to have longer incubation and nestling periods than do species that nest in less safe, open sites. Long incubation

periods produce active, precocial chicks with advanced muscular and sensory development.

From fertilization to hatching, the avian embryo undergoes a standard sequence of stages of development, regardless of the length of the incubation period (Ricklefs and Starck 1998: Figure 15–17). The sequence includes 42 stages that experts distinguish by the morphology of

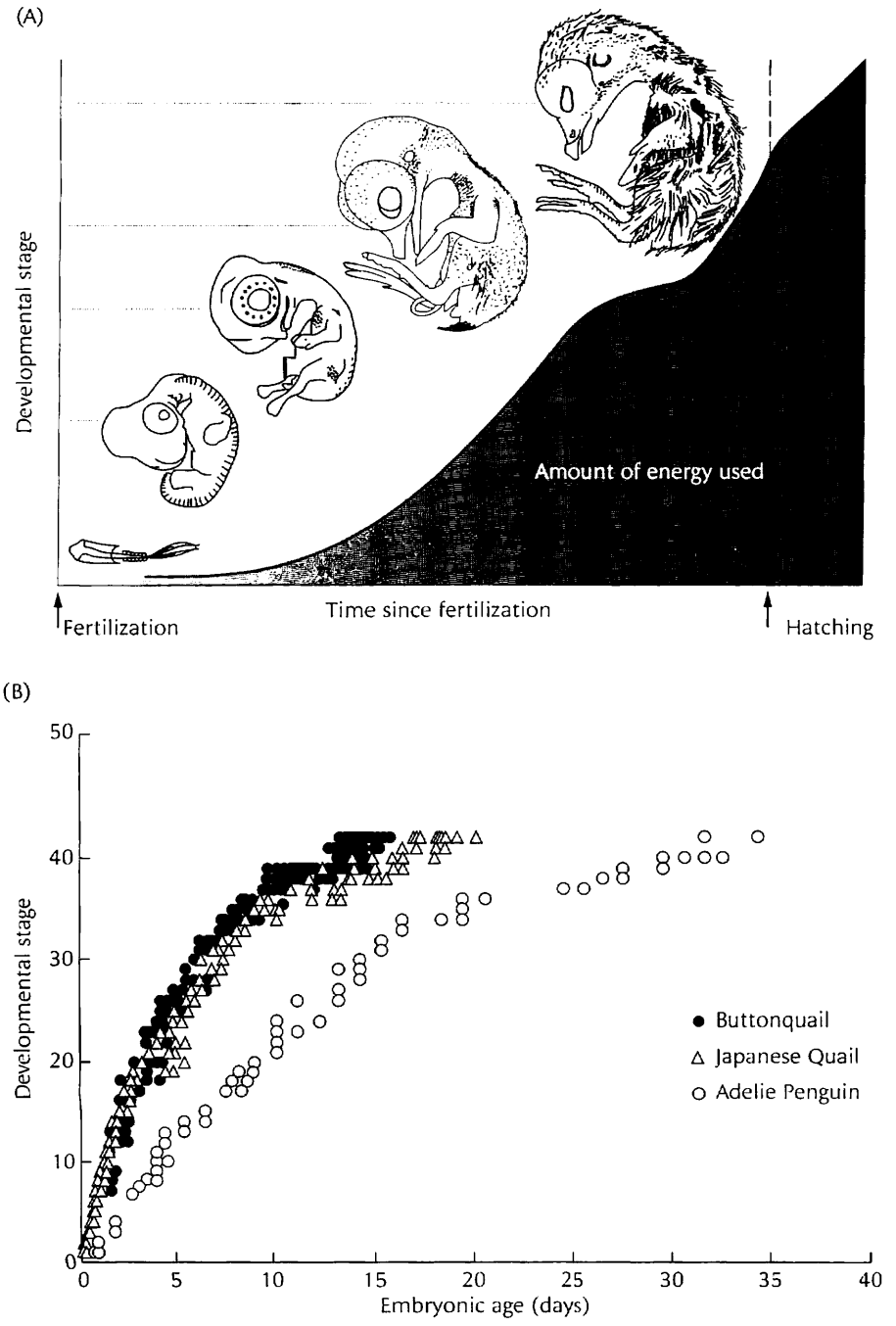
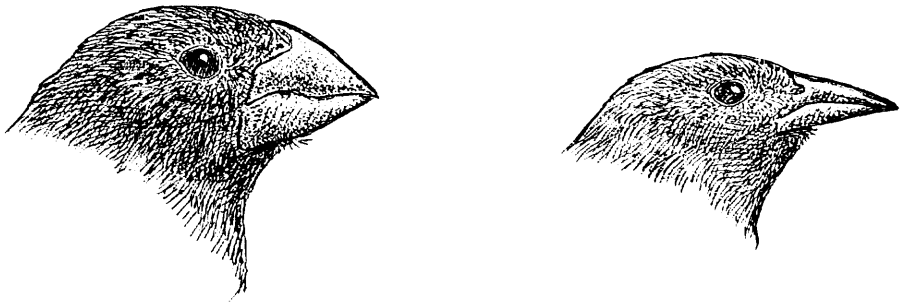


FIGURE 15–17 (A) The development of the avian chick proceeds through a well-defined sequence of morphological stages from fertilization to hatching. (B) Although the sequence of stages is the same among species, the rate of morphological change, the amount of energy used, and the length of each stage vary among species. [*(A) From Starck 1993. (B) From Ricklefs and Starck 1998*]

BOX 15–3

BONE-MAKING PROTEIN CHANGES FINCH BILLS

Different patterns of protein activity in later stages of development are responsible for some of the features that finally distinguish even closely related species. The well-known Galápagos finches, for example, differ dramatically in their bill shapes and sizes, which evolved in response to different food choices (see Chapter 1; and see illustration below). Changes in gene activity responsible for the bone-making protein Bmp4 accompanied the speciation and diversification of these finches (Abzhanov et al. 2004; Pennisi 2004). Earlier and greater activity of this Bmp4 protein produces the larger bills of ground finches compared with the slender bills of cactus finches. Among different species of ground finches, Bmp4 activity starts earliest to produce the large grosbeaklike bill of the Large Ground Finch.



The grosbeaklike bill of the Large Ground Finch (*left*) compared with the slender, conical bill of the Large Cactus Finch (*right*).

the embryo. The first 33 stages vary little among different species from songbirds to penguins. The body plan develops, tissue begins to differentiate, and organs begin to form. The basic systems of life are established, including a feathered integument, a skeleton made first of cartilage and then gradually calcified, a brain that may continue to enlarge and build internal neural networks, and a digestive system that will set limits to energy intake.

The lengths of the final stages of development vary with features that are specific to different species (Box 15–3). Stage 39, for example, is prolonged in species, such as the moundbuilders and penguins, that hatch in advanced physical condition. The same stage (39) is abbreviated in birds as different as buttonquails and songbirds.

Brood Patches

Birds transfer body heat to their eggs through brood patches, or incubation patches, which are bare, flaccid sections of skin on the abdomen or breast. This area may be a single median patch, as in most birds, or two lateral patches, as in most shorebirds, gulls, and quails (Figure 15–18). Most birds lose feathers to form an incubation patch for the purpose of

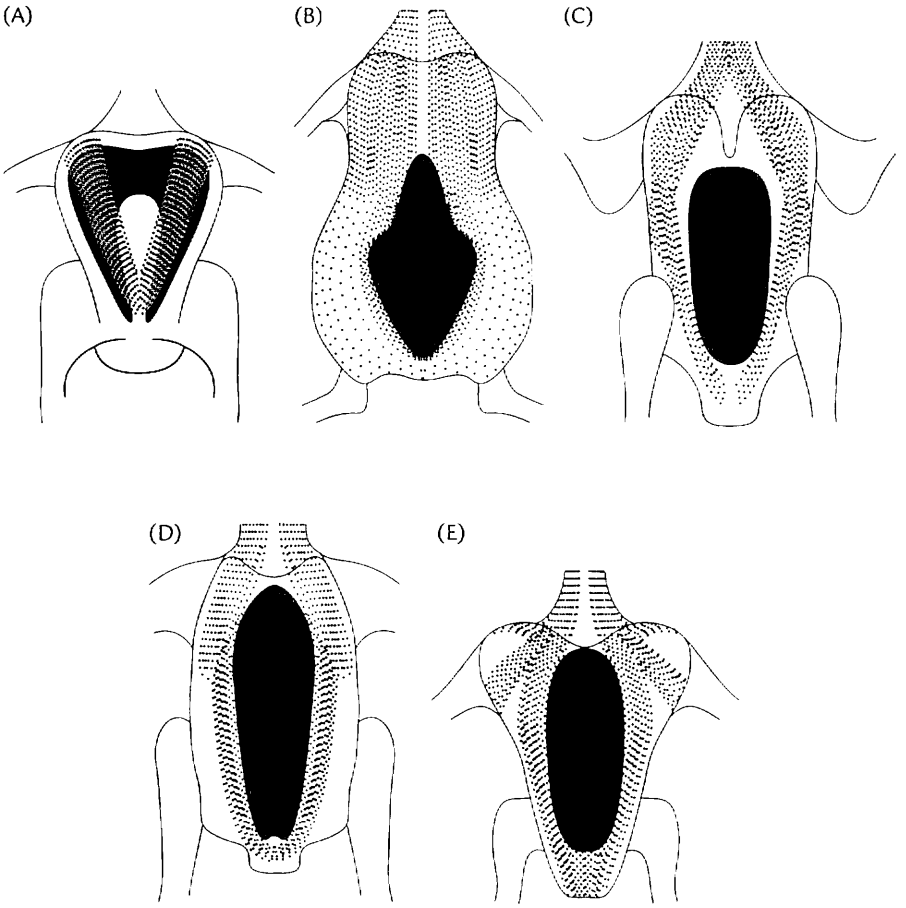


FIGURE 15–18 Incubation patches (in black) of (A) California Quail, (B) Red-necked Grebe, (C) White-crowned Sparrow, (D) Rook, and (E) Northern Harrier. Stippling indicates feather tracts. Clear areas indicate areas without feathers—called apteria. [*After Lea and Klandorf 2002*]

brooding. Pigeons and doves use a normally bare apterium, or featherless region (see Chapter 4).

The accumulation of fluids—edema—and the infiltration of white blood cells swell and soften the skin, allowing better contact between the surfaces of the incubation patch and the egg. The epidermis itself thickens into a callused surface that is not damaged by sustained contact or friction with the eggs. Finally, blood vessels, which deliver body heat to the eggs, proliferate throughout the patch. The arterioles in the network of blood vessels have well-developed musculature that directs the flow of warm blood to the skin surface during incubation and stops the flow when the parent is not actively incubating.

Incubation patches develop just before the incubation period under the direct control of the hormones estrogen and prolactin. The patches regress after hatching. If both parents incubate, then the patches develop in both sexes. If only one parent incubates, the other parent, regardless

of its sex, usually has the potential for developing a brood patch in case that parent should have to incubate for some unusual reason, such as its mate's death.

Prolactin or estrogen or both, depending on the species, stimulate defeathering and vascularization of the incubation patch. Progesterone stimulates the thickening and increased sensitivity of the epidermis. Most birds develop brood patches in response to experimental hormone treatment, except brood parasites, such as Brown-headed Cowbirds, which never incubate (Lea and Klandorf 2002).

Some birds lack incubation patches. For example, gannets and boobies, lacking brood patches, incubate with their feet instead. They grasp a single egg in their well-vascularized, webbed feet or even hold two eggs, one in each foot. Murres and penguins incubate their eggs on the top surfaces of their feet. Some penguins have a muscular pouch of belly skin that holds a single egg in this position.

Keeping Eggs Warm

The first priority of incubation is to keep the eggs close to the optimum temperature for development—that is, from 37° to 38°C. Internal egg temperatures are low at first, but they increase steadily owing both to parental incubation and to heat generated internally by the growing embryo's own metabolism (Figure 15–19).

Serious problems result if the embryo is exposed to temperatures outside the range of 35° to 40.5°C. Exposure to higher temperatures is lethal, and even a short exposure to lower temperatures between 26° and 35°C can disrupt normal development. Below 26°C, the development of young embryos simply stops. For these reasons, frequent or continuous warming is necessary unless ambient air temperatures are very high. Embryos in the later stages of development—of American White Pelicans, Ring-billed Gulls, and Herring Gulls—detect temperature changes of the egg within 1 minute and vocalize faster, signaling their need for heat (see also page 478). Parents then respond with increased incubation (Evans 1994; Brua 2002).

Incubating parents keep the internal temperatures of their eggs remarkably stable, despite the conflicts that incubation behavior itself presents. The natural incubation rhythm of a species (Figure 15–20) is geared directly to the maintenance of critical egg temperatures. At lower air temperatures, sessions on the eggs are longer and recesses for food and drink are shorter. Experimental heating of the nests of the Common Starling reduced the costs of incubation, including energy expenditure to keep the eggs at the temperature required for the development of the embryo (Reid et al. 2000). The parents reallocated the energy that they saved to later stages of that nesting attempt (feeding the young) and to a second nesting attempt. Compared with controls, starlings that were helped by the heating pad during their first brood incubation fledged more young from that brood and were more likely to hatch all the eggs in their next brood.

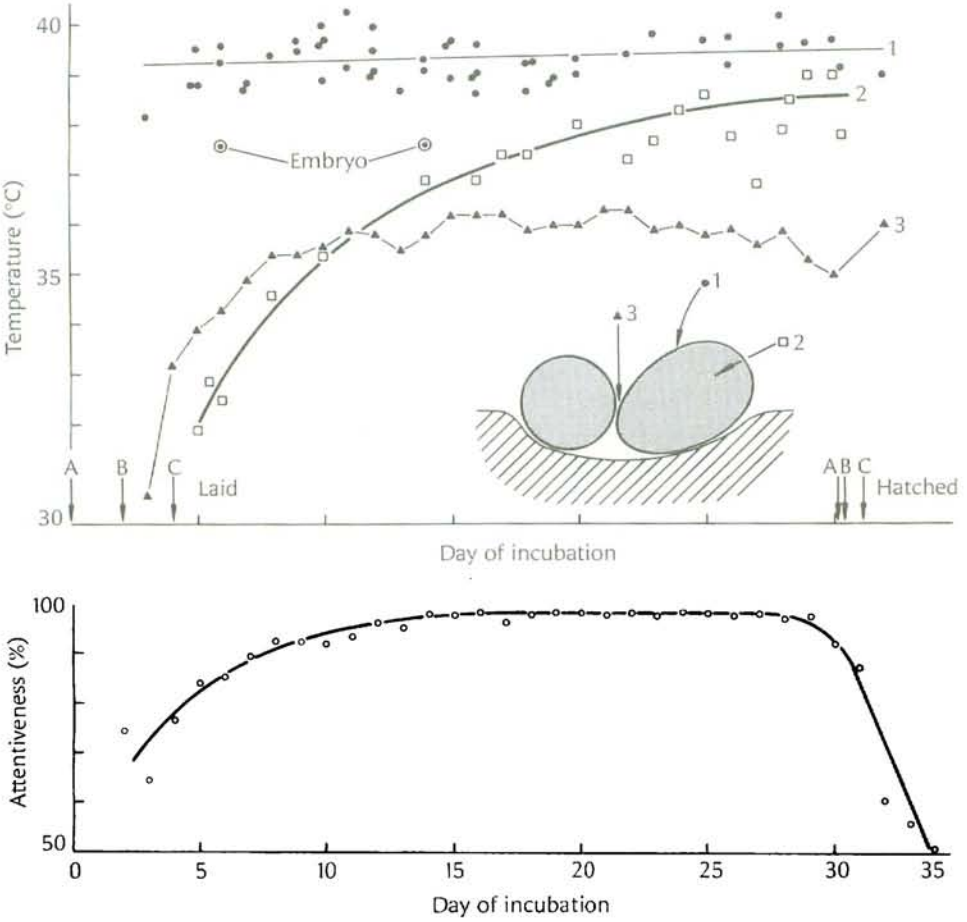


FIGURE 15–19 (*Top*) Egg temperatures during natural incubation by a Herring Gull. The three lines represent measurements taken at different sites: (1) the egg surface, (2) inside the egg, and (3) air between eggs A, B, and C. Points labeled "Embryo" indicate measurements taken inside the egg near the embryo on days 6 and 14. (*Bottom*) The constancy of incubation (attentiveness) of adults increased steadily in the first two weeks of incubation. [*After Drent 1975*]

Some, but not all, male Common Starlings help their mates incubate (Reid et al. 2002). Incubation time by the male supplements that of the female, leading to increased total nest attendance. Although they do not maintain the eggs at quite as high a temperature as do females, males rewarm cool clutches faster than females and thereby increase the pace of embryo development, leading to improved breeding success. This extra help leads to shorter incubation periods, greater hatching success, and larger nestlings.

Experiments with Crested Mynas and Common Starlings on Vancouver Island, British Columbia, demonstrated the effects of inadequate incubation behavior (Figure 15–21). Crested Mynas, a type of starling introduced to Vancouver from Hong Kong, persist with an incubation rhythm that is suitable for the tropical climate of their native Hong Kong

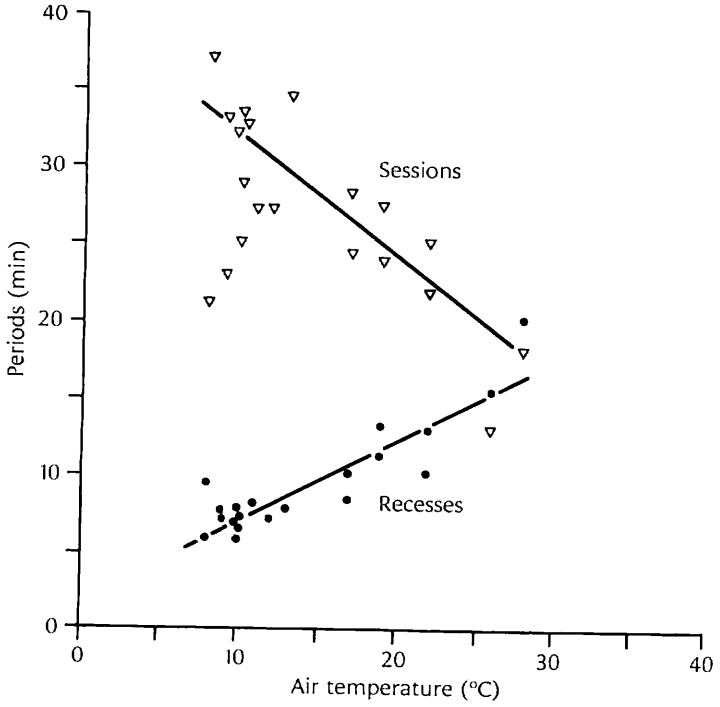


FIGURE 15–20 Incubation rhythms of the Great Tit are directly related to the air temperature in the nest box. Time on the eggs (sessions) decreases and time off the eggs (recesses) increases when the air is warmer. [*After Drent 1972; Kluijver 1950*]

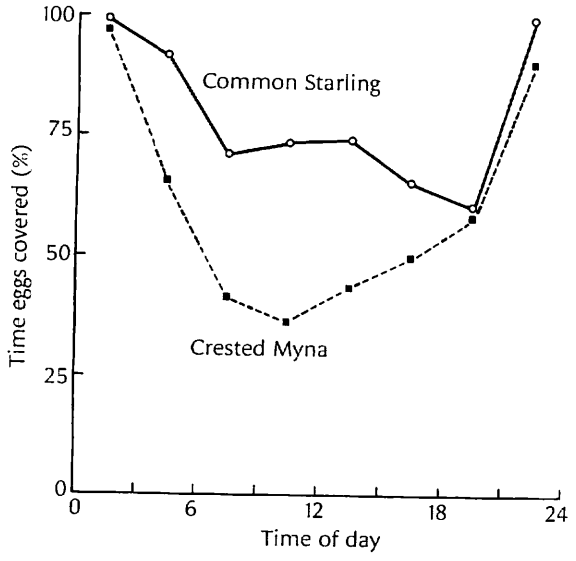


FIGURE 15–21 Differences in incubation behavior can have important consequences. On Vancouver Island, British Columbia, introduced Common Starlings are more attentive during incubation than are introduced Crested Mynas, which hatch fewer of their eggs in the cool climate there. This myna population is now extinct. The Common Starlings achieve greater fledging success. They have adapted to different climates throughout North America. [*After Drent 1972; Johnson 1971*]

but unsuitable for the cool Vancouver climate. They do not regulate incubation time by air temperature. Consequently, they hatch and fledge young from only 38 percent of their eggs. However, they hatch and fledge more young when their nest boxes are heated artificially. A low rate of reproduction is part of the reason for the failure of introduced Crested Mynas to maintain themselves in Vancouver. The related Common Starling, in contrast, expanded its range rapidly after its introduction to North America. This starling of north temperate zone climates is more attentive during incubation and therefore fledges more young (68 percent). Crested Myna eggs that are incubated by the Common Starlings usually hatch, showing that the normal incubation pattern of Crested Mynas, not the quality of their eggs, is at fault.

Keeping Eggs Cool

Birds that nest in hot places face the opposite challenge: keeping eggs cool. The temperatures of unprotected eggs quickly rise to lethal levels. Just leaving the nest to chase predatory gulls, for example, can cause the temperature of a Forster's Tern's egg to rise to 46°C in 10 minutes, and to 50°C during a 25-minute absence (Grant 1982). Shading the eggs, therefore, is a critical part of incubation behavior. Gray Gulls that nest in the extreme deserts of northern Chile incubate their eggs at night, when it is cold, but shade them during the day, when air temperatures reach from 38° to 39°C (Howell et al. 1974).

Conservationists, sightseers, and research scientists should be aware of the dangers of egg exposure. The unwitting disturbance of nesting colonies of island seabirds or vulnerable beach-nesting species such as the Piping Plover and Least Tern causes the parents to leave their nests and expose their eggs to the sun. Direct exposure to the hot sun, caused merely by brief disturbances, kills the sensitive embryos. At risk is the potential failure of entire nesting colonies. Human disturbance also increases the risk of predation or desertion (Götmark 1992).

Wetting the nest or eggs counteracts extreme heat with evaporative cooling. This practice is common among shorebirds, gulls, and terns. Killdeer, for example, cool their eggs by transferring water from wet belly feathers (Jackson and Jackson 2000). The Egyptian Plover, which nests on the hot sandbars of the Nile River, cools its eggs by covering them with a thin layer of sand and then sprinkling water on top of the sand. The nest temperature holds near 37.5°C as a result (Howell 1979).

Heat and water problems stress the parent itself while it tends its eggs in a hot environment. To protect eggs from the hot sun, the incubating parent must absorb and dissipate enormous amounts of radiant energy without overheating itself. Sooty Terns dissipate that heat by extending their legs fully, erecting their feathers, and panting (see Figure 6–11). The breeze removes the heat absorbed by their black backs. The more sunlight that incubating Herring Gulls absorb, the more they must pant. The stress on a bird's water balance is so great and the consequences of even temporary absences are so severe that gull mates must take turns to provide continuous egg coverage.

Turning Eggs

An incubating bird rises periodically to peer sharply down at its eggs. It then draws each egg backward with a sweeping motion of the bill, rearranging its clutch and turning the eggs. Parents rearrange their eggs so that those that have been on the outside of the clutch are moved to the center where the temperature is several degrees higher.

The turning of eggs is crucial for the normal embryonic development of most species. Regular turning of eggs in early incubation also prevents the chorioallantois from adhering prematurely to the inner shell membranes. Species differ in how often they turn their eggs: eggs rich in albumen get turned more often than yolk-rich eggs (Deeming 2002b). The turning of eggs optimizes the growth of the extra embryonic membranes and the fluid dynamics needed to absorb the albumen. Premature adhesion interferes with albumen uptake by the embryo and obstructs its ability to attain the tucking position essential for hatching.

Not all species turn their eggs. Palm swifts glue their eggs to palm fronds, where they remain fixed for the full period of incubation. Perhaps the movement of the palm frond prevents the adhesion of the membranes to the eggshell.

Successful incubation culminates in hatching, itself a challenging but sometimes cooperative and closely orchestrated event.

Hatching

Hatching—breaking the eggshell and emerging from it—is a physical challenge. In its final stages of development, the folded and compact chick fills the limited space inside the egg that was once occupied by yolk and albumen. The chick barely seems to fit inside the tight confines of the shell. By this time, the chicks communicate both with their siblings in the other eggs and with their parents. Calls by the developing embryo engage parents in the hatching process and help to synchronize hatching in precocial species (Brua 2002).

How exactly does a chick break out of the egg? The hatchling-to-be withdraws its head so that its bill passes between its body and its right wing. This so-called tucking position increases the efficiency of pipping, or breaking the eggshell, and therefore the chances of hatching successfully. To hatch, the chick first punctures the membrane that encloses the air chamber at the large blunt end of the egg. Then the chick pecks feebly but regularly at the shell while slowly rotating in a counterclockwise direction by pivoting its legs. After one to two days of "bumping," the chick leaves a circular series of fractures on the eggshell, and finally penetrates through the eggshell to the world outside (Figure 15–22). The power for the first pecks comes from the hatching muscle on the back of the neck (Figure 15–23). The hatching muscle withers when its task is done.

A special, calcified egg tooth on the tip of the bill helps the chick to break the shell. The hard, sharp-edged egg tooth is generally located just

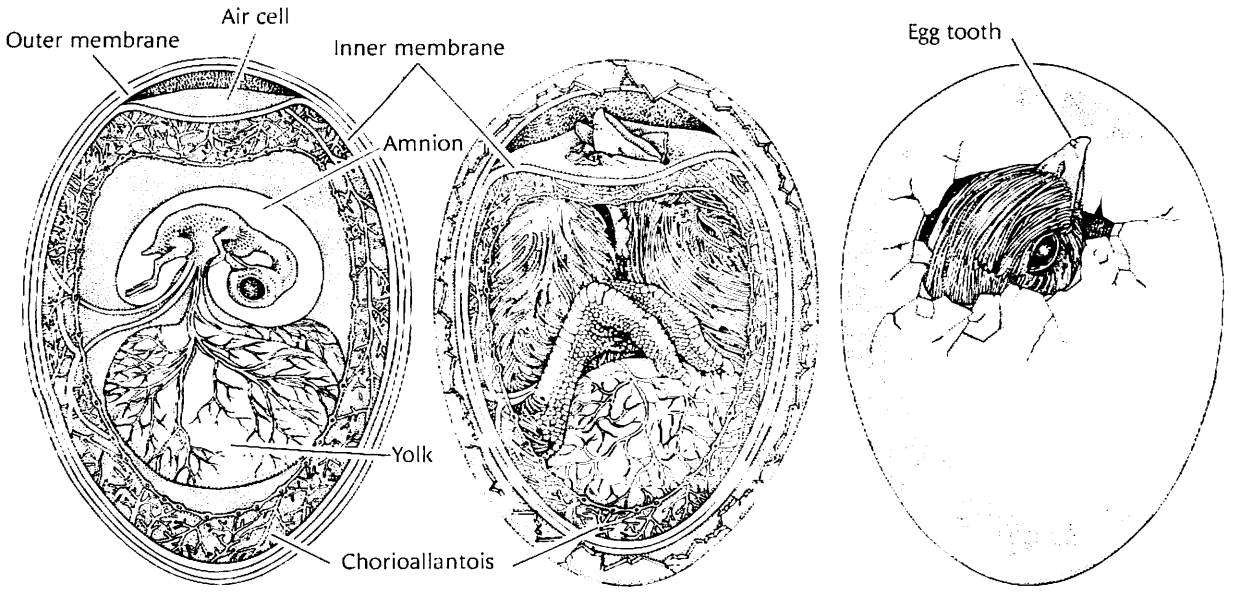


FIGURE 15–22 A chick's first breath. Shortly before hatching, the chick shifts into the tucking position, breaks into the air chamber with its beak (*middle*), and inflates its lungs for the first time. Before this event, the developing chick depends on oxygen exchanged through the capillary network of the chorioallantois (*left*). The chick chips its way through the eggshell with the aid of an egg tooth (*right*). [*After Rahn et al. 1979, with permission from Scientific American*]

before the bill tip where the tip curves downward. The sheath of the egg tooth includes the lower mandible in loons, rails, bustards, pigeons, shorebirds, auks, hornbills, and woodpeckers. Egg teeth drop off the bills of most baby birds soon after hatching: in one to three days in shorebirds and fowl and in as much as three weeks in petrels (Clark 1961). Songbirds gradually absorb the egg tooth.

Most birds chip a big hole out of the eggshell and finally shatter it with their body movements. Emerging woodcocks and Willets, however, split the eggshell longitudinally, ripping open a seam rather than breaking the eggshell into pieces (Wetherbee and Bartlett 1962). After hours or even days of struggling, ostrich chicks virtually explode from their thick-shelled eggs, shattering the shell into many pieces (Sauer and Sauer 1966). Sometimes, a parent ostrich will help crack the shell by pressing its breastbone down on the egg and then pulling the chick out by the head. A parent may also help its chick to hatch by enlarging the initial hole.

Prompt removal of eggshells after hatching protects the camouflage of a nest site. Parents may eat the shell, feed it to their chicks, or take it away from the nest for disposal. In a classic early experiment, Niko Tinbergen (1963) demonstrated that the removal of eggshells from the nests of Herring Gulls reduced predation by crows from 65 percent to only 22 percent.

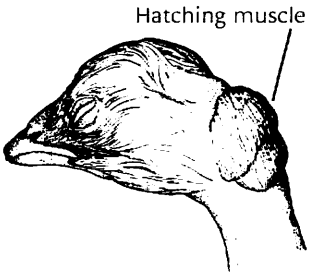


FIGURE 15–23 The hatching muscle is a short-lived feature of chick anatomy that helps the chick break out of the egg. [*From Bock and Hikida 1968*]

Eggs in a clutch may hatch almost synchronously or asynchronously at intervals that range from a few hours to more than a week. Staggered, asynchronous hatching is due to the onset of incubation before the clutch of eggs is complete. The first-hatched young often have an advantage over their younger siblings, which succumb first to shortages of food and sometimes to physical abuse (Stoleson and Beissinger 1995; see also Chapter 16). Different egg provisions (see page 407) can overcome some of these handicaps, as can different embryonic development rates for the two sexes. For example, even though female Common Kestrels are the larger sex by 20 percent, female embryos grow faster and have a shorter embryonic period than male embryos (Blanco et al. 2003). The female chicks hatch earlier than male chicks and assume higher ranks in the brood-size hierarchy.

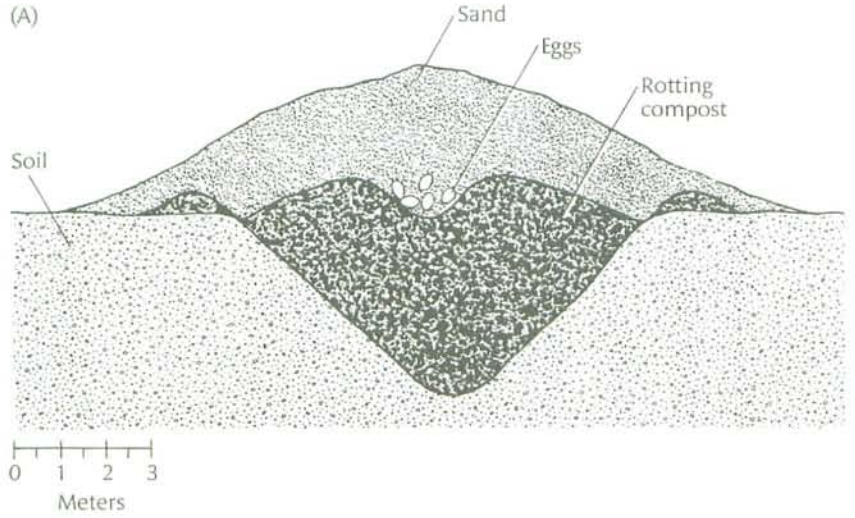
Highly synchronized hatching is characteristic of waterfowl and quails, which move their large broods from the nest to safer sites soon after hatching. For example, the 11 to 13 eggs in the clutch of a Mallard duck (see Figure 3–14B) all hatch within 2 hours, despite having been fertilized and laid over a two-week period. Differences in their rates of development bring early and late eggs closer together in the stages of embryo development.

Coordinated adjustments orchestrate the final synchrony of hatching. First, chicks inside the eggs communicate with each other. Older chicks that are ready to hatch "click" slowly (from 1.5 to 60 times per second), causing younger siblings to accelerate their hatching effort. Conversely, younger chicks unable to catch up click rapidly (more than 100 times per second), causing their older siblings to delay emergence as long as 33 hours (Brua 2002). The jarring of adjacent eggs by the first hatchling is the final signal, stimulating nest mates to make their final hatching moves and to break out together from 20 to 30 minutes later.

New hatchlings vary in their ability to run, thermoregulate, and feed. A species' mode of development frames the challenges that start for both parents and their offspring after the chicks hatch—sibling competition, parent versus offspring conflicts, and strategic brood reduction. The spectrum of modes of development from helpless (altricial) to mobile (precocial) is the central theme of Chapter 16. The extraordinary incubation and hatching feats of the extremely precocial moundbuilders, however, are a fitting climax for this chapter.

Moundbuilders

The megapodes, or moundbuilders, of Australasia are fowl-like birds that use heat from the sun, volcanic steam, or decomposing vegetation to incubate their eggs (Booth and Jones 2002; Figure 15–24). Reptilian as it may seem, this behavior evolved secondarily from normal avian incubation behavior. Regulation of the incubation temperature stems either from the thermal stability of the nesting site or from active manipulation by the birds. Two species, the Australian Brushturkey and the Malleefowl,



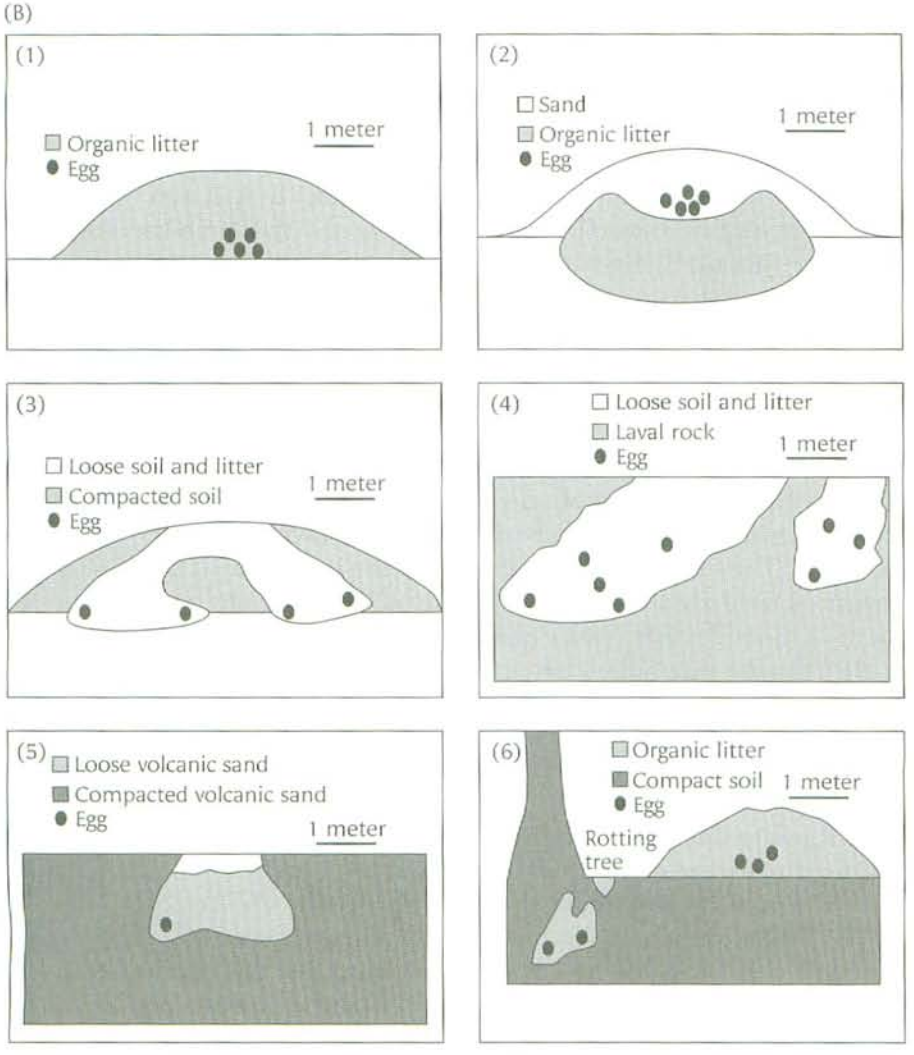


FIGURE 15–24 (A) Cross section of a Malleefowl incubation mound with eggs. Underneath the egg chamber is a pit full of decaying vegetation. Sandy soil covers the eggs. (B) Structures of megapode nests: (1) Australian Brushturkey—a mound of organic litter material raked together by parents is the most widespread system; (2) Malleefowl—the most sophisticated mound consists of a sand blanket atop a bed of decaying organic material; (3) Dusky Megapode—tunnels containing loose soil and litter inside a larger mound of compacted soil; (4) Tongan Megapode—tunnels filled with loose soil and organic material in solid, geothermally heated laval rock formations; (5) Maleo—simple pits in geothermally heated sand; (6) Philippine Megapode—tunnel dug between rotted tree roots and filled with loose soil and organic litter, as well as mounds of organic litter material as in the Australian Brushturkey structure (1). [*(A) After Frith 1959, with permission from Scientific American. (B) From Booth and Jones 2002*]

regulate the internal temperatures of their nest compost heaps with great sensitivity.

The great nest mound of the Australian Brushturkey weighs 6800 kilograms and maintains a stable equilibrium temperature of 33°C (Seymour and Bradford 1992; see Figure 15–24B1). The male brushturkey keeps the mound at this temperature by adding and removing litter and by making sure that there is enough water to keep the decay process going at the right level. The rate of heat production (200 watts) through microbial decay is 10 times that of a resting bird. It allows the megapodes to incubate many more eggs simultaneously than they could in the traditional way. Little maintenance is required after a large nest mound has been established with a critical mass of fresh litter (about 3000 kg), sufficient water content, and occasional mixing of the litter.

The "nest" of the Malleefowl is a large sandy mound, as large as 11 meters in diameter and 5 meters high, made of decaying vegetation and sand (see Figure 15–24B2). The hen inserts her large eggs deep into the nest at intervals throughout the nine month breeding season. Incubation temperatures inside the mound remain at 32° to 35°C as external air temperatures range from 0° to 38°C. The decomposition of litter placed under the eggs produces most of the incubation heat in the spring.

The male Malleefowl tends the mound alone. He spends 5 hours a day manipulating the amount of material covering the eggs to regulate heat loss or retention. He regularly checks the temperature inside the mound by testing the soil in his mouth. In the spring and summer, he cools the mound by opening it (to release accumulated heat) and by replacing hot sand with cooler sand. In the fall, when there is less sun and less decay, he manipulates the covering of a shallower pit that takes advantage of daytime solar heating. He spreads sand to warm it by day and then piles it over the eggs at night, adding extra insulation to seal in the heat.

Moundbuilder chicks hatch from their large eggs—from two to three times as large as the eggs of other birds of comparable size—and emerge from their incubation mounds after 42 to 99 days, the longest period of any bird. They do so unaided and ready for independent living without parents. David Booth and Darryl Jones (2002) provide an excellent review of moundbuilder chick biology and hatching.

Briefly, the moundbuilder embryo has an egg tooth early in its development but loses it by hatching time. Rather than pecking its way out of the egg, the hatchling kicks and shoulders its way out by causing the thin shell to shatter. Whereas most birds require from one to two days to switch from respiration through the chorioallantois membrane to breathing air, moundbuilder chicks do so in minutes. After they're hatched, they rest for an average of 16 hours, clearing their lungs before starting to dig their way upward and out of the nest. That work takes another 24 to 55 hours of effort, in which short bursts of digging alternate with longer rests. Residual yolk provides the energy required to fuel this effort. The chick first scratches out an air chamber around it and then scratches down the

ceiling above it, molding the loose material underneath it. Its plumage dries out as it climbs slowly upward, enabling it to thermoregulate when it finally reaches the surface. Finally, it emerges:

> Suddenly the back of its neck appears at the mound's surface. After the neck is free, the head quickly follows. The chick opens its eyes for the first time and rests briefly. Then it resumes its struggles, freeing one wing and then the other. Soon the whole body follows. Temporarily exhausted, the young Mallee-Fowl may lie exposed on the surface for some time, an easy prey to predators; but more often it tumbles down the side of the mound and staggers to the nearest bush to collapse in the shade, where it recuperates its strength after such prolonged exertion. Its recovery is swift: within an hour it can run firmly; after two hours it runs very swiftly and can flutter above the ground for thirty to forty feet. Twenty-four hours after its escape from the mound, it flies strongly. [Skutch 1976, p. 234]

Most other hatchlings enter a more dependent, temporary period of parental care, the topic of the next chapter.

Summary

Reproduction in birds requires the nurturing of eggs and young outside the body. Nests provide a cradle for eggs during incubation and for baby birds until they fledge. Nests vary in construction from simple accumulations of sticks or scrapes in the earth to major architectural achievements. Woven, pensile nests and the huge, apartmentlike compound nests of certain weavers represent the pinnacles of nest construction. Nest materials may include specific plants with pharmacological properties or feathers, hair, and spider webs. Particular methods of gathering nest materials and of constructing nests, which characterize each species, may have a genetic basis.

A nest has four primary purposes: protection from predators, the provision of a microclimate suitable for egg incubation, the provision of a cradle for dependent young, and the provision of a roosting chamber for adults tending their eggs and young. Camouflage, inaccessible locations, and fortresslike structures make nests less vulnerable to predators. Roofed nests and cavity nests have many protective advantages. Birds also nest near stinging insects for protection and are able to defend their nests or skillfully lure would-be predators away. The choice of safe nest sites may influence the evolution of other aspects of the morphology and behavior of a species.

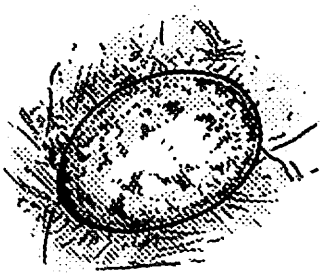
The thickness of insulation helps to govern a nest's microclimate, It also reduces the rate of egg cooling when an adult leaves the nest to feed.

Nest location with respect to sun, shade, prevailing breezes, or sheltering objects also affects incubation behavior. Burrows and cavity nests tend to buffer birds and their eggs from daily temperature cycles.

Precise incubation schedules keep egg contents within the narrow limits of embryo temperature tolerances. Most birds transfer body heat directly to their eggs through the bare, flaccid, and highly vascularized brood, or incubation, patch. Moundbuilders incubate their eggs by using the heat generated in heaps of decaying vegetation. In hot desert environments, the cooling of eggs by midday shading or wetting may be necessary. Incubation not only exposes parents to temperature stresses and predators, but also reduces the time that they have for feeding themselves. Male birds may relieve their mates by sharing incubation or by providing them with food. Patterns of nest attentiveness during incubation respond sensitively in the short run to the risks of predation.

A chick's first challenge is to break out of its shell. The egg tooth, a sharp-edged structure on the top of the bill, is a special feature for breaking the eggshell. Synchronized hatching in birds such as waterfowl and quail enables the young to leave the nest together soon after hatching. The hatchlings of many other birds remain in their nests longer.

CHAPTER 16



Parents and Their Offspring

Perhaps the single most striking feature of postnatal growth in birds is the dichotomy between precocial and altricial development.

[Ricklefs 1983a, p. 1]

The development of an individual bird begins with embryonic cell divisions and ends with the learning of the complex behavioral skills of a capable adult. Baby birds undergo part of their development inside the egg, then hatch from the egg, leave the nest, join flocks, and sometimes migrate to distant places. They learn to fly, to feed, and to sing. They distinguish predators from prey and potential mates from potential rivals.

Life-history theory tells us that the selfish interests of young birds will inevitably conflict with those of their parents (Trivers 1985). Parents should try to raise as many, equally vigorous young as possible. The conflict between the substantial time required for parental care and that required for self-maintenance is one of the key constraints on solo parenthood in birds. Chicks add another set of conflicts. They demand care that exposes their parents to increased predation risk and to physiological stress. In addition, chicks vie with one another for parental attention, protection, and extra portions of food.

This chapter follows the life of a bird from hatchling to fledgling and beyond. A central theme is the contrast between the altricial and the precocial modes of development. In these different modes, chicks hatch with very different degrees of physical maturity. First, we examine the major features of the physical growth and development of hatchlings. As the chicks grow, sibling rivalry and competition increase, sometimes leading to siblicide, especially when eggs hatch at different times, producing nest mates of different ages and abilities. Then, we examine the challenges and solutions of parenting in birds, which include favoritism. The chapter concludes with the fledging of young birds from their nest, followed by their behavioral growth, including the central process of imprinting.

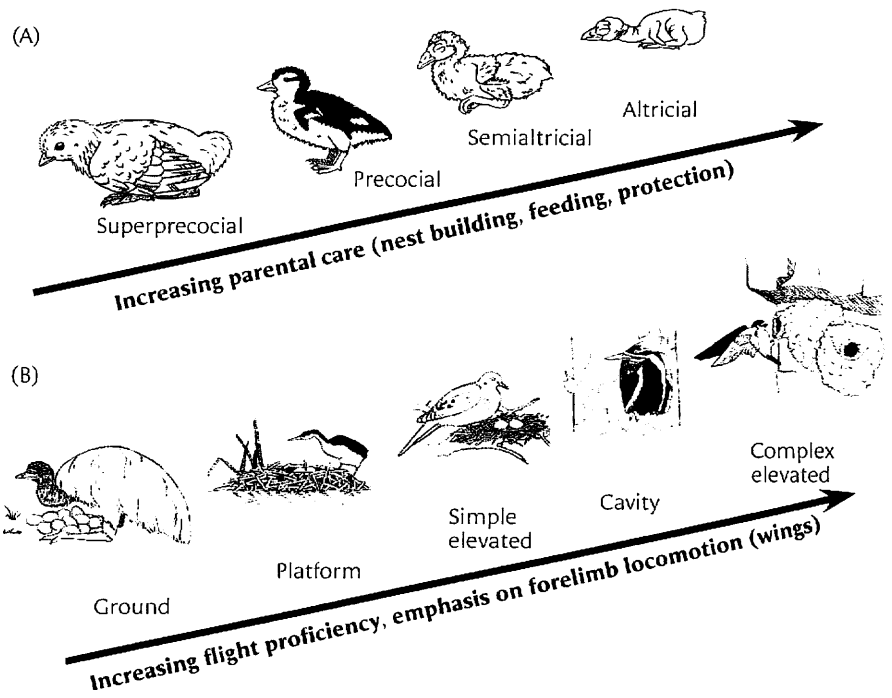


FIGURE 16–1 (A) A spectrum of developmental categories of hatchling birds, from independent (superprecocial) moundbuilders to helpless (altricial) songbirds that require the most parental care. (B) A spectrum of nest types, from simple ground nests to complex elevated nests, corresponds to birds' increasing flight proficiency, with reliance on wings (forelimbs) rather than legs for locomotion. The development of increased flight abilities requires increased parental care before dependent young master flight. *[From Dial 2003b]*

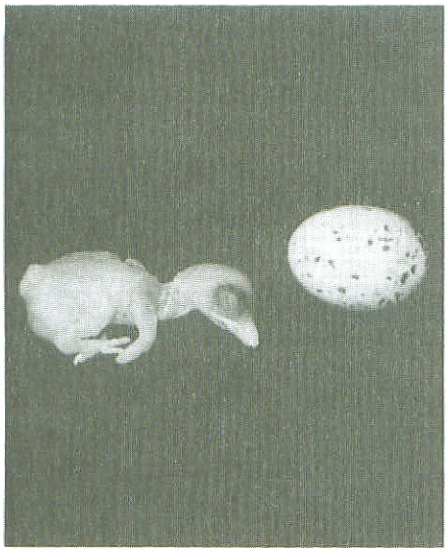
Altricial Compared with Precocial Modes of Development

Alternative modes of development start subtly with the yolk provisions of the egg, as described in Chapter 14 (see page 419), and emerge overtly when the chick hatches. The terms *altricial* and *precocial* refer to the states of physical maturity of the hatchling and its dependence on parental care (Figure 16–1 and Table 16–1). The different modes of development

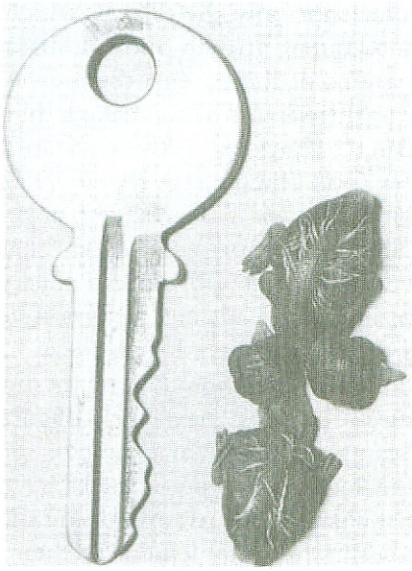
TABLE 16–1 Comparison of altricial and precocial modes of development

Character	Altricial	Precocial
Eyes at hatching	Closed	Open
Down	Absent or sparse	Present
Mobility	Immobile	Mobile
Parental care	Essential	Minimal
Nourishment	Parents	Self-feeding
Egg size	Small (4%–10%)[a]	Large (9%–21%)[a]
Egg yolks	Small	Large
Brain size	Small (3%)[a]	Large (4%–7%)[a]
Small intestine	Large (10.3%–14.5%)[a]	Small (6.5%–10.5%)[a]
Growth rate	Fast (3–4 times precocial rate)	Slow

[a] Percentage of adult weight.

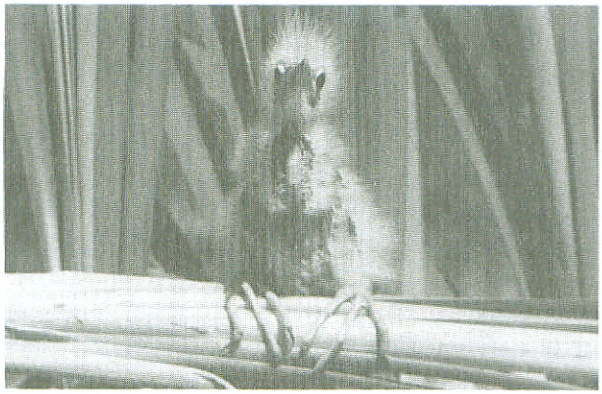


(A)



(B)

FIGURE 16–2 Baby birds and their state of development at hatching. (A) Cedar Waxwing, altricial; (B) Ruby-throated Hummingbird, altricial; (C and D) Least Bittern, semialtricial; (E) Leach's Storm Petrel, semiprecocial; (F) Whimbrel, precocial; note the egg tooth, the white structure at the tip of the bill, which the chick uses to break the eggshell. [*Courtesy of O. Pettingill, Jr./VIREO; A. Cruickshank/VIREO; W. Conway; D. Hosking*]



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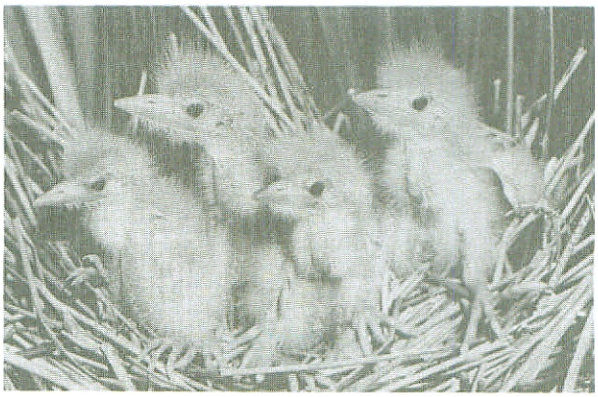

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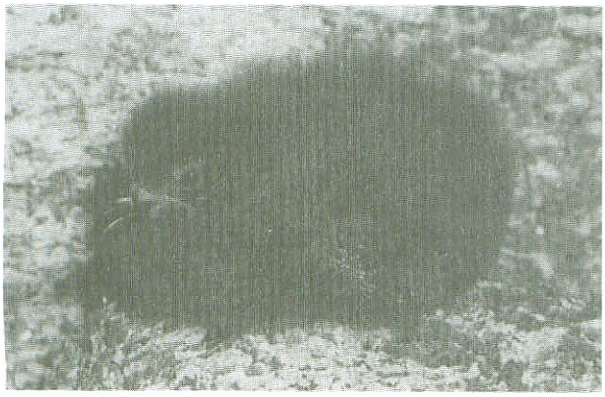


(E)

(F)

affect not only the way in which fledglings leave the nest, but also their subsequent growth and, ultimately, the patterns of care and the mating systems of the parents themselves.

Altricial birds are naked, blind, and virtually immobile when they hatch. They stay in the nest (are nidicolous) and depend on their parents for food (Figure 16–2A–D). The helpless, grublike nestlings of altricial birds look as if they have hatched prematurely. Altricial hatchlings have huge bellies and large viscera that support fast growth.

Compared with altricial chicks, precocial chicks hatch from larger eggs in a relatively advanced physical state and are soon mobile. Precocial chicks are usually covered with fuzzy natal down. They leave the nest (are nidifugous), run about, feed themselves, and regulate their body temperature soon after they hatch (Figure 16–2E and F). A three-day-old Lesser Scaup duckling, for example, can dive, catch a minnow, and return to the surface. Precocial chicks have large food stores to increase their initial chances of survival outside the egg. They absorb their substantial yolk reserves as a supplement to their feeding for several days after hatching.

Precocial development was probably the original mode among birds. It is typical of many basal groups of modern birds, including the ratites, waterfowl, and chickenlike birds. The ancient enantiornithine birds of the Mesozoic era also were precocial. A well-preserved avian embryo (in egg) from the Lower Cretaceous of China was distinctly feathered and precocial in its state of development (Zhou and Zhang 2004).

How did altricial development evolve? There is no simple evolutionary sequence from precocial to altricial. The altricial condition evolved independently in unrelated groups of birds. Although most birds are clearly precocial or altricial, intermediate categories also exist. The diversity of hatchling abilities sorts into at least six major categories of hatchlings based on classical criteria of mobility, open or closed eyes, the presence or absence of down, and the extent of parental care (Box 16–1 and Figure 16–3).

Condition		Down	Sight	Mobility	Parental nourishment	Parental attendance	Examples
Superprecocial		○	○	○	○	○	Moundbuilders
Precocial		○	○	○	○	●	Ducks, shorebirds, quail, grouse, murrelets
Subprecocial		○	○	○	◒	●	Grebes, rails, cranes, loons
Semiprecocial		○	○	◒	●	●	Gulls, terns, auks, petrels, penguins
Semialtricial	1	○	○	●	●	●	Herons, hawks
	2	○	●	●	●	●	Owls
Altricial		●	●	●	●	●	Songbirds, woodpeckers, parrots

○ **Precocial characters** ● **Altricial characters**

FIGURE 16–3 Development characteristics of baby birds at hatching, according to Margaret Nice's (1962) classification. Down: present or absent. Sight: open or closed eyes. Mobility: ambulatory or nestbound. Parental nourishment: no or yes. Parental attendance (for brooding or defense): absent or present. [*After Ricklefs 1983a*]

BOX 16–1

DEVELOPMENT CATEGORIES OF HATCHLINGS

Ornithologists recognize six development categories of hatchlings:

Superprecocial Wholly independent. Examples: moundbuilders and Black-headed Ducks

Precocial Hatchlings leave the nest immediately (nidifugous) and follow their parents; pick up their own food soon after hatching, although parents help to locate food. Examples: ducks and shorebirds; quail, grouse, and murrelets; also ostriches and kiwis

Subprecocial Hatchlings leave the nest immediately and follow their parents; are fed directly by their parents. Examples: rails, grebes, cranes, and loons; also guans and some pheasants

Semiprecocial Hatchlings are capable of body-temperature regulation; mobile but stay in the nest; fed by their parents. Examples: gulls, terns, auks, petrels, and penguins

Semialtricial Hatchlings stay in the nest (nidicolous), although physically able to leave the nest within a few hours or the first day; fed and brooded by parents. Examples: herons and hawks; also nightjars, albatrosses, and seriemas

Altricial Naked, blind, and helpless at hatching. Examples: songbirds, woodpeckers, hummingbirds, swifts, trogons, kingfishers, pigeons, and parrots

Semiprecocial chicks of gulls, terns, auks, and petrels are fed at the nest. The subprecocial chicks of grebes and loons cannot dive or chase prey skillfully. Their parents carry them on their backs, often under their wings, and so dive and feed relatively undisturbed. Semialtricial or semiprecocial modes of development evolved secondarily from altricial or precocial modes of development.

Rapid growth is a primary feature of altricial development and perhaps its driving evolutionary advantage. Altricial nestlings grow from three to four times as fast as precocial chicks. The evolution of such different growth rates is a major research topic. David Lack (1968) originally regarded growth rate as a balance between selection for rapid growth to escape predation and selection for slow growth to reduce food requirements. Although energetic efficiencies contribute to the fast growth rates of altricial birds, they cannot explain the difference in growth rates between altricial and precocial birds (Ricklefs 1983a).

Instead, growth-rate differences between precocial and altricial chicks may be related to the channeling of limited resources into either increased tissue mass or to the maturation of tissue functions required for survival (Ricklefs and Starck 1998b). The so-called tissue-allocation hypothesis suggests that the growth of tissue mass and the maturation of tissue functions (such as muscle contraction) are mutually exclusive. Altricial chicks grow fast by channeling resources efficiently into growth and by postponing tissue maturation. Fast growth rates enable them to pass quickly through the early, most vulnerable stages of development. A comparison of the altricial Common Starling, the semiprecocial Common Tern, and

the precocial Japanese Quail illustrates the interaction between the precocity of tissue maturation and the overall growth rate (Figure 16–4).

The different modes of development correspond to progressively mature functions of chicks at hatching (Starck and Ricklefs 1998). Increasing maturity is evident in the tissues of a hatchling as well as in its external appearance and behavior. The fraction of tissue that is fat free and dry, called its lean dry weight, increases as tissue matures. A low index of tissue maturity at hatching distinguishes altricial development from all other modes. Altricial hatchlings typically have an index of lean dry weight (Ip) less than 0.1, whereas all other categories of hatchlings have Ip values greater than 0.1. This result distinguishes the principal difference in growth rate between altricial and precocial chicks.

Also related to the tradeoff between tissue growth on one hand and maturity of function on the other hand is the increased reliance of altricial species on the wings, or forelimbs, for locomotion (Dial 2003b; see Figure 16–1). Precocial chicks have well-developed legs when they hatch, enabling them to leave the nest, start to find food for themselves, and hide from predators. Precocial species also emphasize bipedal locomotion

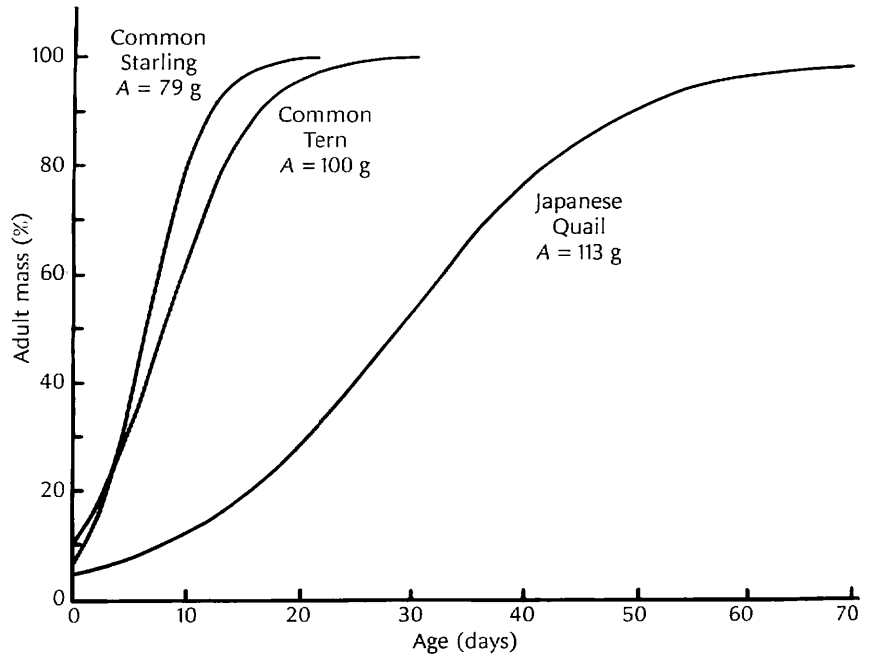


FIGURE 16–4 Growth curves for an altricial bird (Common Starling), a semiprecocial bird (Common Tern), and a precocial bird (Japanese Quail). *A* is the bird's mass at the top of the growth curve. Of these three species, the starling grows fastest, the tern grows nearly as fast as the starling, and the quail grows relatively slowly. The rapid maturation of the quail's large leg muscles, essential for precocial locomotion, detracts from the quail chick's potential growth rate. The tern's legs also develop rapidly, but the material and energy needed for the growth of its tiny legs are only minor investments relative to its overall growth. The starling puts energy into growth before tissue maturation. [*From Ricklefs 1979b*]

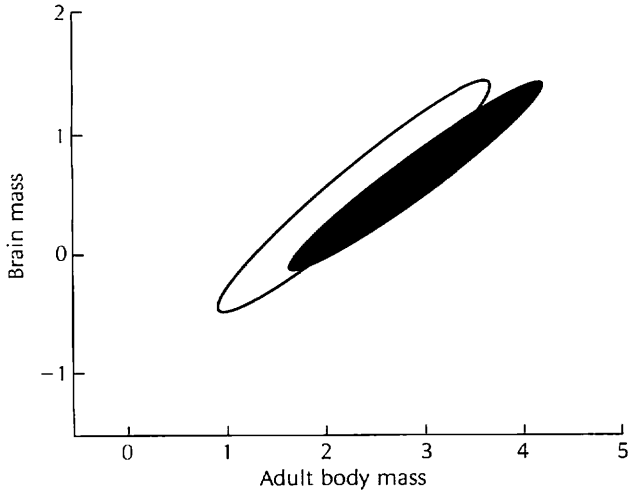


FIGURE 16–5 Logarithmic relation of brain size to adult body size. The brains of altricial species and semialtricial species (white oval) average larger than the brains of precocial bird species (black oval). [*From Ricklefs and Starck 1998b*]

as adults. In contrast, the initial dependence of immobile altricial hatchlings on their parents corresponds directly to these species' predominant use of their wings rather than their legs. Altricial chicks first delay the maturation of wings and flight muscles, and then they channel resources into their development. Swifts and hummingbirds, with their advanced flight abilities but diminutive legs and feet, represent the extreme of this shift of emphasis to forelimb locomotion.

Differences in brain development are another distinction between altricial and precocial bird species (Figure 16–5). In general, the brains of altricial birds are smaller (relative to body size) at hatching than are the brains of precocial birds. Parental care of altricial chicks substitutes for early functional differentiation of the brain. After hatching, the brains of altricial birds then undergo greater growth to an adult brain size that ultimately averages larger than that of precocial species of the same body size. This growth pattern allows the control functions of their enlarged forebrains to differentiate at a later stage than they do in the brains of precocial birds. Accordingly, altricial chicks learn active feeding skills and social skills at a later stage of development.

Temperature Regulation

Homeothermy—the ability to generate metabolic heat (endothermy) and to maintain a high, constant body temperature—is a major step of early development. Homeothermy releases a chick from its absolute dependence on parental brooding and enables it to tolerate exposure.

The process of hatching initiates the development of homeothermy as hatchlings undergo rapid changes in their metabolism and temperature responses (Mathiu et al. 1991). Pipping through the shell membranes gives a chick access to oxygen, which supports increased metabolism. Emergence

from the shell itself allows increased movement, as well as ventilation and shivering. Once out, the chick's down dries to form functional insulation. The stage is then set for the development of endothermy and the refinement of homeothermic thermoregulation through the maturation of muscular tissue and endocrine control systems. The advanced muscle development and natal down of hatchling precocial birds enhances their ability to thermoregulate. Precocial and semiprecocial chicks, such as those of quail, gulls, and terns, achieve 90 percent of their adult thermoregulatory capability within one week (Dawson and Whittow 2000).

Regulation of temperature by both precocial and altricial chicks improves in the course of development as they gain mass relative to surface area, increase metabolic heat production, and develop improved control by the nervous and endocrine systems. An altricial chick's ability to retain metabolic heat improves later as its feather coat thickens. Experimental shaving of nestling Great Tits and Eurasian Pied Flycatchers, for

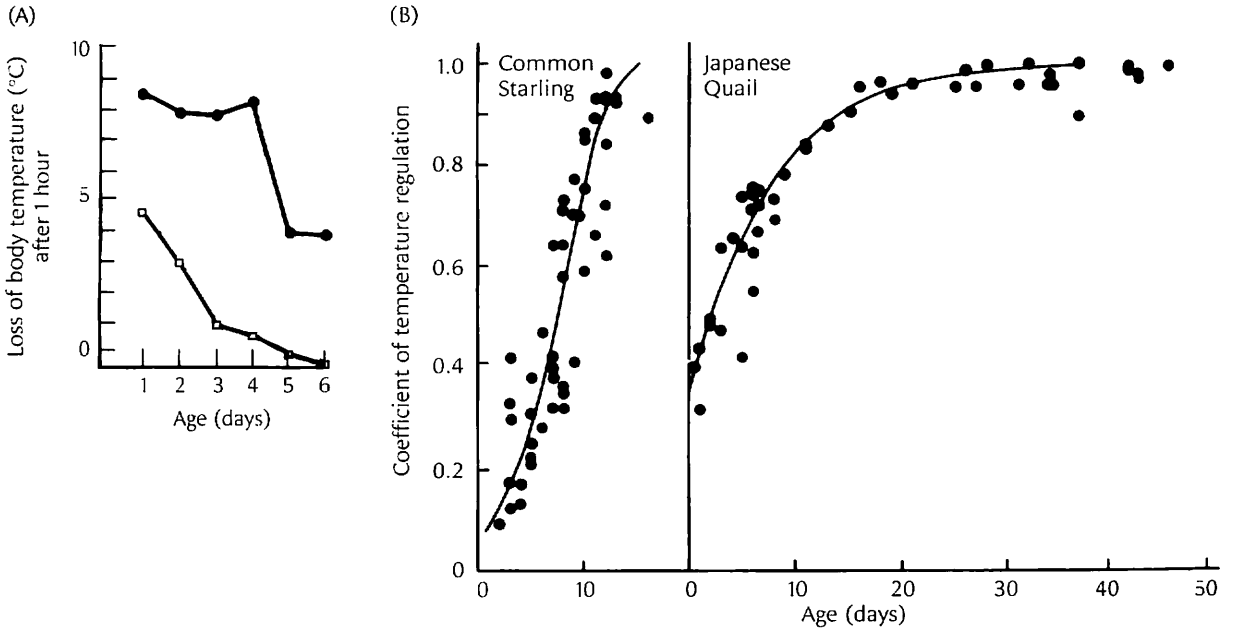


FIGURE 16–6 Development of homeothermy. (A) The ability of nestling Common Starlings to maintain a body temperature of 39°C increases with age and number of brood mates. The body temperature of a single nestling (black circles) from one to four days old drops between 8 and 9 degrees after 1 hour of exposure to an ambient temperature of 20°C, whereas the body temperature of a five-day-old nestling drops only 4 degrees under the same conditions. The presence of brood mates together (seven in this experiment; white squares) greatly reduces individual loss of body temperature. (B) Precocial chicks such as those of the Japanese Quail can maintain a high body temperature on hatching better than can Common Starlings; this ability improves with age in both species. The coefficient of temperature regulation is the percentage of the difference between adult body temperature and air temperature at 20°C that a chick maintains after 30 minutes. [*(A) After Clark 1983; (B) from Ricklefs 1979b*]

example, increases their oxygen consumption by 25 and 15 percent, respectively (Shilov 1973).

Skeletal muscle is the main source of heat production. The large leg muscles of a young precocial chick are of primary importance in early thermogenesis, followed by the pectoral muscles. Early development of large pectoral muscles in chicks of the Willow Ptarmigan and Leach's Storm Petrel facilitates their heat production (Aulie 1976; Ricklefs et al. 1980). Supporting their function in early thermogenesis, the pectoral muscles of nestling Leach's Storm Petrels mature by 2 weeks of age, even though the chicks do not fly for 9 to 10 weeks. The naked hatchlings of altricial songbirds with little skeletal muscle cannot regulate their body temperatures outside ambient temperatures of 35° to 40°C. They take a week to develop just the initial stages of thermogenesis by shivering.

Large broods need less parental care than do small broods, at least in cool climates. Decreased individual exposure, pooled metabolic heat, and the greater thermal inertia of their combined mass help the chicks in large broods to keep one another warm. The functional mass and thermal inertia of each chick in a brood increase with brood size. As a result, altricial chicks in large broods achieve homeothermy earlier than do those in small broods (Figure 16–6). Within a week or so, however, most young develop thermal independence and greater tolerance for exposure to the elements. Their growing independence allows single parents to gather the increasing amounts of food that the chicks require.

Energy and Nutrition

Baby birds require energy for maintenance, temperature regulation, activity, excretion, and growth. Growth itself accounts for a major fraction of total energy expenditures early in development. The energy channeled into growth constitutes from roughly 21 to 40 percent of a chick's energy budget for the entire developmental period. Total energy expenditures peak late in development. Important as it is, however, energy may be less important in determining rates and patterns of development than is nutrition. There are no fundamental distinctions between altricial and precocial species in this regard.

The production of new tissues requires nutrients such as certain amino acids that the body cannot manufacture. The sulfur-containing amino acids cysteine and methionine, for example, are essential for feather production. To provide the calcium for bone growth, parents feed their chicks fragments of teeth, bone, snail shells, and eggshells as dietary supplements. The bone growth of Lapland Longspurs, for example, requires more than the meager amount of calcium (0.1 percent by dry weight) in the crane flies and sawflies that they eat. Accordingly, their parents feed them lemming bones and teeth (Seastedt and Maclean 1977).

Chicks require lots of protein, especially in the early stages of their development. The parents of many species of songbirds supply mostly small, soft-bodied insects at first and then increase the proportion of fruits and seeds. Fruits do not usually provide an adequate diet for nestling growth

TABLE 16–2 Nutritional composition of avian esophageal fluids

Bird	Protein (%)	Lipid (%)	Carbohydrates (%)
Pigeon	23	10	0.0
Flamingo	8	18	0.2
Penguin	59	29	5.5

From Fisher 1972.

(Foster 1978). The chicks of Bearded Bellbirds and Oilbirds, which eat only fruits, grow half as fast as those of other tropical birds. The Resplendent Quetzal, a spectacular fruit eater, feeds its young only insects for the first 10 days and so they attain a more normal growth rate.

Pigeons, flamingos, and Emperor Penguins feed nutritious esophageal fluids to their young (Table 16–2). Pigeon milk, the best known of these fluids, is full of fat-laden cells sloughed off the epithelial lining of the parent's crop. Like the milk of marine mammals, this fluid is rich in protein (23 percent) and fat (10 percent). It also includes essential amino acids. Flamingo milk, the sole initial source of nutrition for the chicks of Greater Flamingos (see Figure 3–16A) has more fat and less protein than does pigeon milk. The esophageal fluid of the Emperor Penguin is rich in both fat and protein, and their chicks double their body weight in the first week of life.

Growth Rates

The growth of body mass of a baby bird during development follows an S-shaped, or sigmoid, curve (Figure 16–7). At first, the chick grows slowly; then the growth rate accelerates and mass increases rapidly. Finally, growth slows as the chick approaches its adult weight. The sigmoid curve allows a comparison of species that differ in size and growth strategies because it is defined mathematically by only a few variables: initial size, growth rate, and final maximum value.

There are two major exceptions to the typical shape of the growth curve. First, the mass of young ground-feeding birds, such as doves and Curve-billed Thrashers, levels off below adult mass. Chicks gradually achieve full size after fledging when their muscle and plumage development catches up with their skeletal development. Second, in aerial species such as swallows, swifts, and oceanic seabirds, the mass of a chick overshoots that of adults in the final stages of development. The mass of the oversized chick then declines as it metabolizes fat deposits and loses water from maturing tissues, especially in the skin and at the bases of the feathers. Some chicks near fledging temporarily outweigh adult birds.

Chicks of some bird species store excess energy as fat as insurance against poor food delivery by parents or as reserves for the days just after fledging when the chick learns to feed itself. Aerial passerines such as swallows deposit more fat than do other species, an adaptation to the irregularity of their food supply (O'Connor 1977). The accumulation of fat is

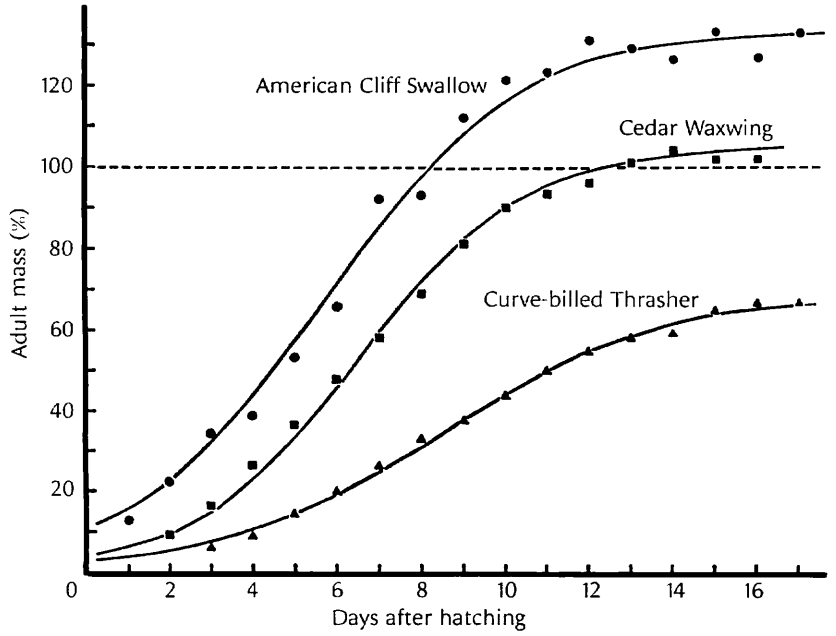


FIGURE 16–7 Sigmoid nestling growth curves of three altricial birds. Data are standardized to the maximum values of the growth curve to directly compare birds of different species size. [*After Ricklefs 1968*]

most striking in petrels. Their obese chicks reach masses twice those of the adults. Young Oilbirds, which are raised on the oily lipid-rich fruits of palms and other tropical trees, also accumulate large lipid stores. These stores are, in large part, excess energy that must be sidelined and stored in order for the chicks to extract adequate amounts of protein from their specialized, protein-poor and lipid-rich foods. Such excess lipid supplies also act as reserves for bad times.

The growth rates of chicks of different bird species vary 30-fold. More than half of the variation in growth rate relates directly to adult body weight: big birds grow more slowly than little birds. The growth rate decreases roughly as the cube root of adult body weight increases. The slow-growing Wandering Albatross (see Figure 17–3), one of the largest seabirds, has the longest known nestling period of any bird—as long as 303 days. In contrast, fast-growing small songbirds have short nestling periods of 10 to 12 days.

Different members of a species exhibit markedly different growth rates. Growth rates of individual birds in a species are affected by the quality and quantity of food, temporal pattern of feeding, and temperature, all of which vary according to locality, season, habitat, and weather. For example, the average fledging weights of Rhinoceros Auklets in British Columbia vary from 266 grams in bad years to 361 grams in good years (Gaston and Dechesne 1996). The effects of food supply on growth rate are perhaps best known in swifts and martins. The maturation of Common Swifts, for example, varies from 37 to 56 days, depending on feeding conditions. Chicks of these swifts can survive for as long as 21 days

of starvation by becoming hypothermic and ceasing to grow (Koskimies 1948).

The availability of food also affects the immune capacity of nestlings (Hoi-Leitner et al. 2001). Reduced immunocompetence owing to food shortage increases survival risk and reduces long-term breeding potential.

Begging for Food

Hungry nestling birds make their needs known through begging behavior, which includes both exaggerated body movements and loud calls. The young's begging cries stimulate parents to deliver food to the nest. Experimental changes in the volume and continuity of begging cries at the nest prompt greater activity. In a classic experiment, Lars von Haartman (1953) hid extra young Eurasian Pied Flycatchers behind the wall of a nest box. In response to their cries, the parents brought more food to the nest than was required for their nestlings. Recall also the simulation of host warbler calls by nestling cuckoos (see Chapter 13). Blue Tit parents immediately reduce their provisioning efforts when the chicks do not beg (Grieco 2001). After soliciting the silent nestlings to open their bills, the parents then spend more time away from the nest. As soon as the chicks resume their begging, the parents resume their normal provisioning effort.

As noted in Chapter 15, embryos in the egg call for increased parental attention when they are cold. After hatching, nestlings solicit care from their parents through the intensity and timing of their loud begging calls. Nestling Tree Swallows, for example, increase the rate and length of their begging calls when hungry and when cold (Leonard and Horn 2001).

Siblings coordinate their begging behavior to their own benefit. Nestling Common Black-headed Gulls, for example, extract more regurgitated food from their parents by begging together (Mathevon and Charrier 2004). Parent gulls react to the total intensity of begging rather than to the chick that is begging the loudest. Compared with single chicks, three siblings beg less often and not separately. They save their begging for an intense joint bout for a returning parent, which then dumps a full load of food on the ground in front of the chicks.

Birds at a nest, whether parents or young, risk discovery and death from predators. That risk increases with activity at the nest (see Chapter 15). Under discussion for years has been whether begging calls themselves attract predators to the nest. They do, at least for ground-nesting species (Figure 16–8). In a clever experiment, David Haskell (1994) monitored predation rates at artificial nests outfitted with miniature two-way radios that broadcast begging calls (of Western Bluebirds) or that were silent. Predators found most (75 percent) ground nests with begging calls within five days but found significantly fewer (23 percent) of the silent ground nests. In a second experiment, predators found significantly more of the ground nests that broadcast begging calls at a high rate compared with a low rate. Predation did not differ, however, between tree nests with and those without begging calls.

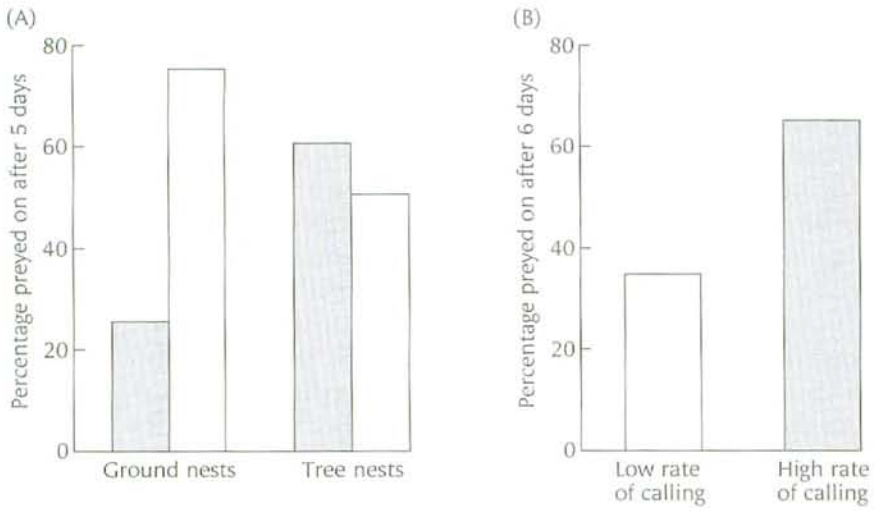


FIGURE 16–8 Begging calls by nestlings increase predation. (A) Predators found most ground nests with begging calls (white bars) within five days, but they found significantly fewer of the silent ground nests (gray bars). Tree nests with or without begging calls did not differ in the risk of predation. (B) Predators found significantly more of the ground nests that broadcast begging calls at a high rate compared with a low rate. [*After Haskell 1994*]

Counteracting the increased risk of predation owing to begging calls, many nestling birds scream loudly. These screams frighten an approaching predator, incite parents to come to the rescue, and stimulate nest mates to flee or hide (Roulin 2001). Strongly suggesting that screaming evolved as an antipredator strategy, nestlings of screaming species also have more conspicuous begging calls than do nestlings of nonscreaming species. Higher predation rates have favored the addition of screaming to their survival kit.

The gaping mouths of nestlings serve as visual stimuli that facilitate or, in some instances, allow food delivery by the parents. The chicks of some cavity-nesting species have brightly colored mouth markings that attract parental attention and serve as targets for food delivery. The mouth colors of nestling Great Tits, for example, make them easier for their parents to detect in dark nest cavities and hence affect the rate at which their parents feed them. Nestlings with (painted) yellow mouth gapes and side flanges are fed more frequently than are nest mates with (painted) red gapes and flanges, but only at low light intensities (Heeb et al. 2003). In well-illuminated nest cavities, there is no difference between red- and yellow-painted nestlings.

Sibling Rivalry

Growth rates of altricial nestlings tend to decrease as brood size increases. Large broods increase the differences in growth rate between older and younger siblings. The smallest chicks starve when food is insufficient.

These observations suggest that parents cannot deliver enough food to all nestlings to ensure the maximum growth and survival of all. For this reason, nest mates compete with one another for food. In its extreme form, competition among nest mates results in death or siblicide (cainism).

Vicious rivalry seems to be normal among the chicks of some birds, especially if the eggs hatch at staggered intervals. A small delay in hatching time places a younger chick at a competitive disadvantage with respect to its nest mates, particularly when food is in short supply (Box 16–2). Larger siblings tend to bully their nest mates to get the first choice of food delivered by their parents. For example, the younger of two South Polar Skua siblings has a good chance of surviving if it is nearly the same size as the older chick, but it has a poor chance of survival if it is only 8 grams (10 percent) lighter than its older nest mate (Procter 1975).

Different egg provisions can offset the disadvantages of being last to hatch when there are sibling rivalries (see page 407). In particular, mothers in some species add more testosterone (androgen) successively to later eggs of a clutch. The experimental addition of testosterone to eggs of Common Black-headed Gulls demonstrates this effect (Eising and Groothuis 2003). Chicks hatched from eggs with extra testosterone are initially more active and beg more frequently, thereby getting a larger share of the food than chicks from control eggs.

Siblicide is a standard practice in the nests of some eagles, skuas, herons, and boobies (Mock and Parker 1997). As a rule, parents react passively to the deeply rooted, destructive behavior of their offspring. In the well-

BOX 16–2

LAUGHING KOOKABURRAS: LAST TO HATCH LOSES

The Laughing Kookburra is the source of a famous laughing call heard in the background of many old movies. This large, terrestrial Australian kingfisher typically lays three eggs, but the third chick to hatch often doesn't survive to leave the nest (Legge 2002). Typically, its older two siblings kill it within a few days of hatching. They do so aggressively—tearing it apart with a specialized siblicide hook on their upper bills. Those that survive the physical abuse of their first days are then likely to starve to death in the weeks that follow as competition for food increases.

The probability of being torn apart by older brothers and sisters depends on the intensity of their own aggression toward one another. That intensity is greatest when the two older siblings are opposite sexes of similar size with the male hatching first. They fight with each other, hurting the third sibling in the process, especially if it is much smaller. Extra male helpers tend to reduce strife by increasing food deliveries to the nest. Their absence adds to what Sarah Legge has dubbed the "kookaburra siblicide syndrome." Getting rid of junior early has a significant effect on the growth and health of the senior brood mates. Those that kill their youngest nest mate attain higher final weight, larger skeletons, and better feather development than do those that let junior starve to death. These attributes lead to better survival and more likely recruitment into the breeding population in future years.

studied Verreaux's Eagle, for example, only once in 200 records did both siblings survive to the fledging stage. In most cases, the older sibling deliberately killed the younger eaglet (Gargett 1978).

Many raptors exhibit reversed sexual-size dimorphism; that is, males are smaller than females. Why should this reversal be so? The topic has been discussed without consensus. Keith Bildstein (1992) shifted the focus of discussions on the roles of adult raptors to the possible advantages of smaller-sized male nestlings. His "head start hypothesis" is based on observations of fledgling Northern Harriers, in which males develop faster and leave the nest earlier than their sisters. They gain flight and hunting experience ahead of their sisters and so hone skills that they will need as the primary provisioner of food to their mates and young. They are also less likely to overpower and injure their sisters by being smaller and leaving the nest early. The survival of sisters then adds to a young male's inclusive fitness.

Sibling rivalry is a way of life in some colonial herons (Mock 1984). Elder chicks of the Great Egret often kill their siblings, but siblicide is rare in the Great Blue Heron. Why should two such similar species differ in this way? The type of food brought by the parents to their nestlings is part of the answer. Great Egrets bring small fish, which are easily monopolized by an aggressive older sibling, whereas Great Blue Herons bring larger fish, which cannot be easily monopolized (Figure 16–9). When placed in Great Egret nests, young Great Blue Heron broods adopt the siblicidal tactics typical of the egret, in response, it seems, to the opportunities

FIGURE 16–9 Great Blue Heron. In this species, parents bring their chicks large fish, which are not easy for individual chicks to monopolize.

TABLE 16–3 Fate of the youngest chick in natural and experimental foster broods

Brood[a]	Number Alive by Day 25	Number of Siblicidal Deaths	Number of Other Deaths	Number of Broods Studied[b]
Great Egret chicks				
Natural	5	8	4	17
Foster	4	6	0	10
Great Blue Heron chicks				
Natural	8	1	10	19
Foster	1	6	2	9

[a]Natural broods were raised by parents of the same species. Foster broods were experimentally switched so that they were raised by parents of the other species; for example, foster Great Egret chicks were raised by Great Blue Heron parents.
[b]Typical brood size in all cases was three or four chicks.
From Mock 1984.

presented by the smaller food (Table 16–3). Surprisingly, the converse result does not take place. Great Egret broods cross-fostered in Great Blue Heron nests do not become more tolerant of their nest mates. Sibling aggression in the Great Egret is a deep-seated, obligatory behavior similar to that of raptors.

Location, location, location. A nestling's position in the (open-cup) nest affects whether the nestling is fed by its parents. The center of the nest is best (Ostreiher 2001). When deprived of food, first-hatched nestling Arabian Babblers take over and control that prime spot to preempt incoming food. Eliminating the central spot with a barrier evens the odds of feeding for all nestlings. When the parent babblers access the nest from only one direction, dictated by experimental fencing, the senior nestling takes over the prime (nearest) location and garners 52 percent of all feedings.

Rather than compete for food, Barn Owl chicks queue up and minimize competition by using begging calls to communicate with one another for position when their parents are away hunting for the next mouse (Roulin et al. 2000). One mouse for a chosen chick per visit is the routine. Chicks in small broods become more vocal after being fed, but, in larger broods, they quiet down in the absence of a parent. The hungriest chick then tunes up and gets first rights to the next mouse.

Parenting

In their first week of life, most baby birds need protection from cold air temperatures and from the hot sun. Thus, they impose two pressing demands on their parents: brooding and feeding. Parents routinely brood their young by sitting on them, usually in the nest. Brooding parents not only protect their young from the rain and predators, but also keep them warm. Parents of seabird chicks shade them from the hot sun (Figure 16–10).

Precocial chicks require more parental care than is usually recognized. Although they do not depend on their parents to deliver food, the precocial chicks of quail and waterfowl rely on their parents to locate food and to protect them. Quail chicks quickly learn what is and is not edible by pecking at objects shown to them by their parents. Parent ducks and geese also guide their chicks to food, with one exception: the Magpie Goose of Australia (see Figure 3-14B) transfers food from its bill tip to the chick's bill tip.

Protecting young from predators also is a demanding effort that requires constant parental vigilance. Males and females of four species of large plovers called lapwings, for example, face major time constraints while taking care of their mobile young. They alternate "tending" behavior in order to feed themselves (Walters 1982). Clapper Rails and other species regularly pick up chicks with their bills and move them to safety (Eddleman and Conway 1998).

Challenges

Parents should allocate their time and energy strategically, because raising young is one of the most energetically expensive periods of their annual cycle. Peak breeding activity, for example, increases total daily energy expenditures by as much as 50 percent. The fueling of this activity requires some combination of increased foraging time for food supplies, the use of accumulated reserves, or help by mates or fully grown offspring. For Fairy Penguins, the seasonal rearing of chicks consumes 31 percent of an adult's total annual expenditures of energy (Gales and Green 1990). Daily costs become extreme as the chicks reach full size, when the daily food consumption by hardworking parents exceeds 60 percent of their body mass.

Females of many bird species decline in body mass in the first days of the nestling period, revealing the tradeoff between parental care and self-maintenance (Chastel and Kersten 2002). The time spent by female House Sparrows in brooding their young nestlings decreases as brood size increases. Smaller broods produce less total heat and lose heat faster than larger broods do. As a result, females tending experimentally reduced broods experience a sharp drop in body condition when the young hatch and when brooding is most intensive. In contrast, females tending experimentally enlarged broods that don't require as much time lose weight only gradually during the nestling period. Males are not affected, because they spend much less time brooding (about one-third of that spent by females) and thus have ample time to take care of themselves.

The stresses of parental care also affect the immune systems of breeding birds, mediated by glucocorticosteroid stress hormones (see page 257). Recall that prolonged surges of stress hormones dampen a bird's immune response, making it more susceptible to disease and parasites. Increasing parental care by male Barn Swallows, by manipulating brood sizes, for example, reduces their immune response (Saino et al. 2002c). Highly ornamented male Barn Swallows, those with long tails favored by sexual selection, exhibit the strongest immune defenses, consistent

(A)

(B)

FIGURE 16–10
Thermoregulation of nestlings. (A) Gray Gull shading its young from the intense desert sun. (B) Laysan Albatross chicks can thermoregulate at an early age by dissipating excess heat from their large feet, which they expose to the breeze by leaning back on their ankles. Still, dehydration and poor thermoregulation are the primary causes of death among young Laysan Albatross chicks on Midway Island in the Pacific Ocean. [*(A) Courtesy of T. R. Howell; (B) courtesy of T. R. Howell and G. A. Bartholomew*]

with models of parasite-mediated sexual selection. They also have relatively low levels of stress hormones in their blood. They are either less exposed or less susceptible to the stresses of parental care than are males with shorter tails.

Solutions

A parent's options for adjusting its investments include choosing among rival nestlings, reducing risks of nest predation, favoring one sex over the other, and even sacrificing some of their young if necessary. Usually, the largest nestling or the biggest mouth seems to get most of the food (Box 16–3). Favoritism actually starts with different provisioning of the eggs (see page 407) and then extends to begging nestlings of different ages or at different stages of development (Lessells 2002).

Females of some species prefer to feed runt nestlings (Gottlander 1987). American Coots favor not only the smaller, late-hatched chicks in their broods, but also the chicks that are most colorful. In their natal plumage, these coot chicks sport bright orange, waxy-tipped filaments on the front half of the body, enhanced by brilliant red papillae of the skin around the eyes and base of the bill. Lacking the cryptic downy colorations of most precocial chicks, conspicuous coot chicks actually hide their heads when parents give alarm calls, doing their best to prevent detection by predators. Bruce Lyon and his colleagues (1994) trimmed back the orange plumes of some coot chicks and compared parental attention to them with that paid to control chicks in mixed broods. Parents favored the more

BOX 16–3

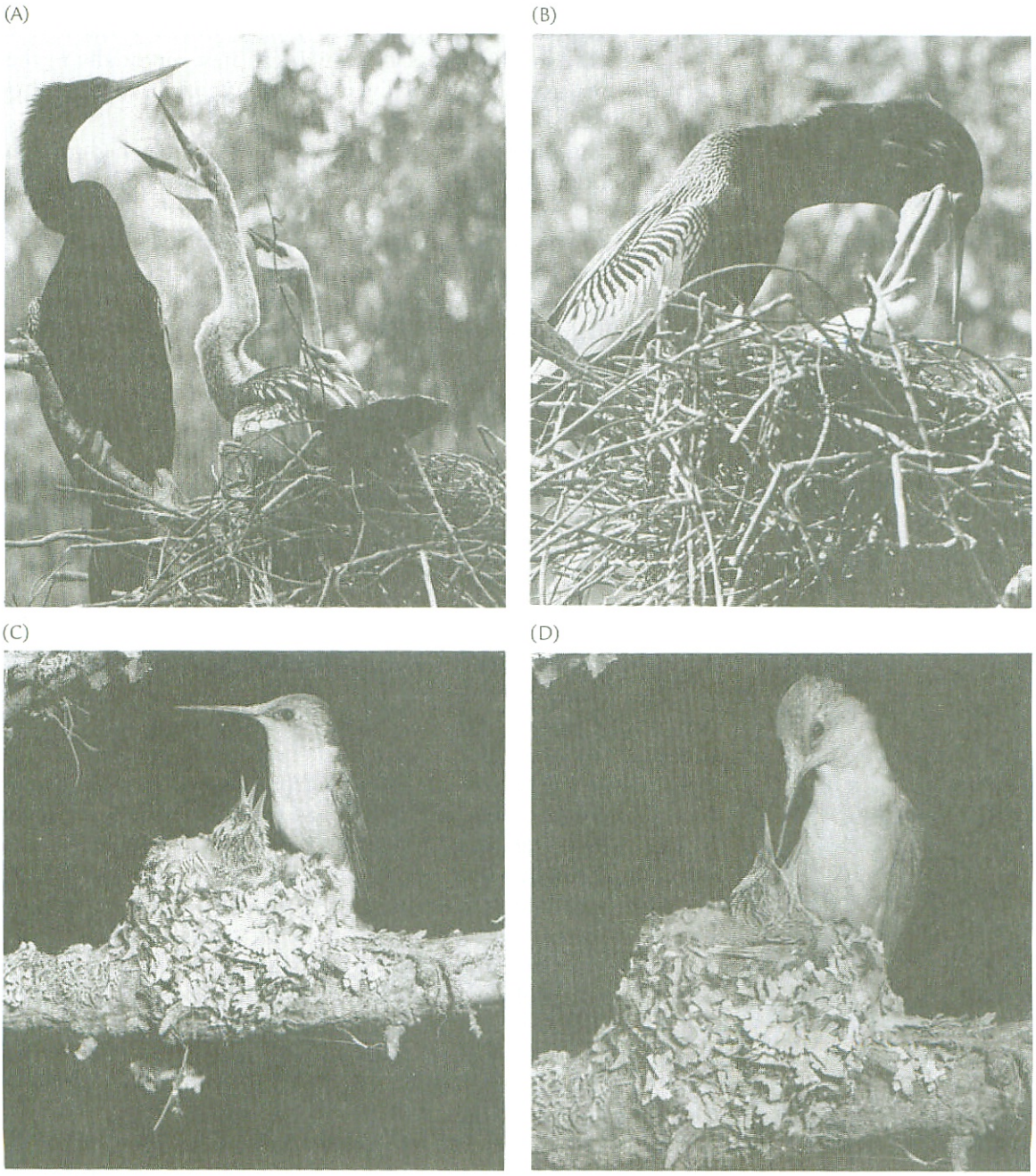
FEEDING NESTLINGS

How do nestlings get fed? Altricial nestlings receive food by direct insertion, sometimes deeply into the digestive tract. Young hummingbirds receive an injection of nectar and insects through their mother's long, hypodermic-like bill (see photographs). Commonly among seabirds, parents regurgitate a meal either directly into a nestling's mouth or onto the ground for the nestling to pick up. Young penguins and pelicans plunge their heads deeply into their parents' gullets. Spoonbills and albatrosses cross their large bills with those of their young, like two pairs of open scissors, so that the chicks' mouths are in position for food transfer.

How often do parents feed their nestlings? Food delivery rates to nestlings range from every second or third day for albatrosses to once or twice daily for seabirds, swifts, and large raptors to once per minute for some small land birds with large broods. Normal rates of food delivery by small and medium-sized land birds average from 4 to 12 times per hour. Trogons bring food to the nest once per hour, Bald Eagles 4 to 5 times per day, and Barn Owls 10 times a night. Recorded extremes of rapid food delivery to large broods include 990 trips per day by the Great Tit and 491 trips per day by the House Wren.

Food delivery rates vary according to the age of the young. Hatchlings require only small amounts of food but, as they develop, their appetites grow. The Eurasian Pied Flycatcher brings food to the nest every 2 minutes, making about 6200 feeding trips to nourish its young from

hatching to fledging. In general, parents must gather two to three times as much food as they need for themselves to cover the energy needs of their nestlings (Walsberg 1983). To meet such demands, the Common Swift of Europe flies 1000 kilometers a day, scooping insects from the sky.



Parent birds feeding young. (A) Anhinga young begging for food; (B) parent Anhinga feeding one of the young; (C) Ruby-throated Hummingbird nestlings begging for food; (D) parent hummingbird feeding one of the nestlings. [*Courtesy of A. Cruickshank/VIREO*]

brightly colored control chicks, which grew faster and survived better than their trimmed experimental brood mates.

What is best for a parent often conflicts with what is best for some of the offspring. First and foremost, parents should value their own survival over that of their offspring, particularly for species with high annual survival and few chicks per nest. That is, we would expect parental risk taking to be sensitive to life expectancy (Ghalambor and Martin 2001). We would expect long-lived species, which can nest repeatedly in the future, to take fewer risks than short-lived species, which have limited opportunities to nest.

Supporting this prediction are comparisions of matched pairs of species from Argentina (which have higher adult survival and a smaller clutch size) and from Arizona (which have lower adult survival and a larger clutch size). To assess risk to the nestlings, Ghalambor and Martin (2001) recorded the rate at which parents fed them in the presence of a model of a nest predator (jay). To assess risk to the parents themselves, they recorded the parents' own feeding rates in the presence of a hawk. As predicted, southern (Argentine) parents took less personal risk than northern (Arizona) parents, even if by taking less risk they sacrified their young. Conversely, northern (Arizona) parents assumed greater personal risk to increase the probability that their young would survive.

Underlying what may seem to be their spirited and cooperative parental effort, the sexes themselves may have different agendas and different best levels of investment of their time and energy. Males adjust their investment in relation to their own paternity. As in many species, extra-pair copulations are frequent in the Common Reed Bunting (Dixon et al. 1994). More than half of the young (55 percent) and nests (86 percent) of this species in Britain indicate that matings are with males other than a female's mate. Whereas female buntings are insensitive to the paternal identity of the young and feed them all in the same way, males provide more care to nests that contain higher proportions of young that they sired themselves. They can assess the probability of their paternity (by some unknown means) and then adjust their parental efforts accordingly.

The parental tactics of differently colored male House Finches correlate with alternative breeding strategies (Duckworth et al. 2003). Bright red males (with low prolactin levels) provide almost no parental care, whereas dull-colored males (with high prolactin levels) actively participate in the feeding of nestlings. By holding back on parental care, bright red males are less likely to die after the breeding season than are dull males. But the dull males achieve higher pairing success that compensates for their higher mortality. Apparently females prefer males that help, leaving males with the "choice" between being a good dad now or living longer and breeding more times.

Parents adjust their efforts in relation to their mates' efforts. Females can compensate for the loss of a mate—through death or desertion—by increasing their own efforts to full capacity (Osorno and Székely 2004). The deserted parent can choose to desert also, because it is unable to rear the young alone, or it can choose to continue with either the same effort or increased effort. Females may raise their young successfully as sin-

gle parents, but, in doing so, they incur costs affecting their long-term survival and productivity.

Even when sharing the costs of parental care with a mate, each partner must set the values of current efforts against the potential of future years. Tempering these costs and benefits is uncertainty about the amount of effort that a mate will invest, given that the mate faces similar strategic decisions. Shared parenting therefore becomes a kind of poker game, betting against one's partner's intentions while being careful not to cause the partner to desert (Whitfield 2002).

In general, the costs of parental care are less when rearing offspring of different ages than when raising offspring that are the same age. It's easier to raise children spaced apart at different ages than it is to raise twins or triplets. Nevertheless, female Blue Tits do better and survive better to the next breeding season when they care for same-age (hatched synchronously) broods of young than when they care for young of different ages, experimentally produced by hatching them asynchronously (Slagsvold et al. 1994; Figure 16–11).

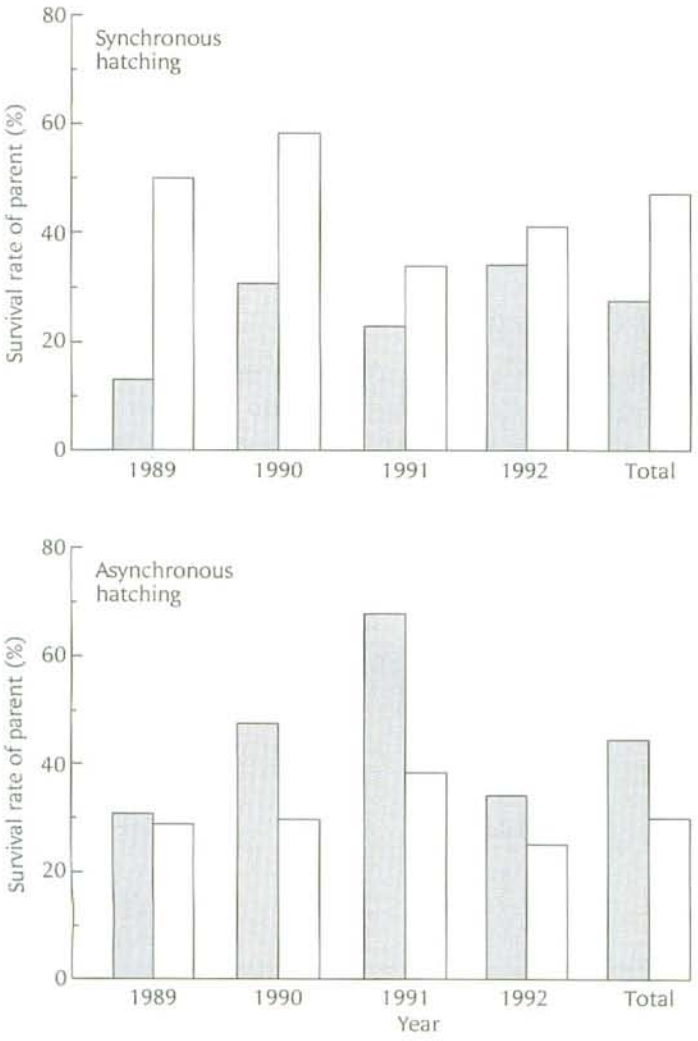


FIGURE 16–11 Survival rates of male (gray bars) and female (white bars) Blue Tit parents after rearing young with synchronous and asynchronous hatching. Females survive better when they raise synchronous broods because they get more help. [*After Slagsvold et al. 1994*]

Male Blue Tits fare oppositely. They survive better when parenting asynchronous broods than when parenting synchronous broods. The reason? Synchronous broods stimulate males to higher rates of provisioning effort at a cost to their survival. A female gains from this extra effort on the male's part by coasting a bit more and reducing her own effort, with the result that females survive better. Female Blue Tits usually win this contest in nature because they alone incubate the eggs. They don't start incubation until most of the eggs are laid and so will hatch them all at the same time.

Sexes of the Blue Tit on the island of Corsica also respond differently to their parental challenges—in this case, to infestations of blowflies that parasitize their nestlings (Hurtrez-Boussès et al. 2000; Banbura et al. 2001). In addition to feeding the young, females do almost all of the nest sanitation. They remove maggots, mend the nest, and remove fecal sacs (see page 447). The time spent by females on nest sanitation is higher in parasitized nests than in (experimentally) deparasitized ones. Males, however, just remove fecal sacs. Instead of spending time on nest sanitation, males concentrate instead on finding the best food for the nestlings—caterpillars. As a result, males deliver more and larger caterpillars than do females.

Caterpillars are a prime food for the development of nestling Blue Tits in other populations. They are also a source of carotenoid pigments responsible for the yellow plumage color of adults. How bright yellow an adult is indicates its ability to find caterpillars and thus how good a parent it will be. Experiments have supported this prediction. Cross-fostered nestlings fed by stepfathers having brighter yellow plumage developed best (Senar et al. 2002).

Sex Ratios of Offspring

Broods of nestlings don't always yield equal numbers of males and females. Many departures from a fifty-fifty ratio of males and females in broods of birds are due to differences in the survival of male and female hatchlings. Brood sex ratios of the Red-winged Blackbird, for example, depend on the age of the breeding female (Table 16–4). Young females fledge more daughters than sons, whereas old females fledge more sons than daughters. Although equal numbers of sons and daughters hatch in

TABLE 16–4 Surviving offspring of female Red-winged Blackbirds in three age classes

Age Class of Female Parent	Number of Surviving Offspring		
	Male	Female	Significant Difference
Young	28	50	Yes, more females
Middle-aged	53	66	No
Old	54	34	Yes, more males

From Blank and Nolan 1983.

the broods of young females, starvation is common and sons starve more often than daughters. Why? Young females lay poorly provisioned final eggs in the clutch, which causes the nestlings hatched from them to be most vulnerable to starvation. Young females also tend to lack the experience required to feed their nestlings adequately. A sex bias exists in the probability of starvation because male offspring need more food than their sisters do. They grow faster to a larger size and hence are more likely to starve. Older females, however, do not lay inferior final eggs, and they better provision their young. Hence, their large, fast-growing sons are less likely to starve.

The physical condition of both sexes and their ability to feed their young can bias the survival of the young according to their sex. Male chicks of the Lesser Black-backed Gull, for example, die more frequently when reared by parents in poor condition than when reared by parents in good condition (Nager et al. 2000). Female chicks, however, are not affected by the condition of their parents. The heightened mortality of male chicks is due to their greater sensitivity to poor egg quality and to the greater demands that they put on their parents in poor condition.

House Wrens in Wyoming provide another case study of the ways that females manipulate the sex of their offspring (Albrecht and Johnson 2002). The first female to mate with a polygynous male gets most of his help in raising her chicks. Second-mated females, which receive little assistance, fledge fewer and lower-quality young. Quality at fledging has a greater effect on the future reproductive success of male wrens than on that of female wrens. Conforming to prediction, second-mated females biased the sex ratios of their offspring toward females that could overcome a quality handicap. This result was not due to biased nestling mortality or biased feeding. Somehow, once again by unknown means, female wrens can control the sexual composition of their offspring in accord with theory.

Brood Reduction

One way that birds can cope with uncertainties about the number of young that they can raise in any particular year is to lay the number of eggs that should be successful in good years and then to sacrifice some of these eggs if necessary. Brood reduction protects parents against losing the entire brood should conditions for raising young be unpredictably poor. How is brood reduction accomplished? Starting incubation before the last egg is laid promotes asynchronous hatching, which in turn sets up options for brood reduction. Brood reduction itself ranges from overt siblicide, as in raptors and herons (see page 481), to more subtle, selective elimination of some members of a brood.

More optimistically, smaller last-hatched chicks serve as potential replacements or "insurance" should one of the older siblings fail. The Masked Booby, a large goose-sized, tropical seabird, lays one extra egg as insurance against the hatching failure of the first egg (Anderson 1989, 1990). Most gannets and boobies lay only a single egg and seem to be able to raise only one young. Asynchronous hatching of the two eggs

ensures predictable siblicide in the Masked Booby: the first chick pushes the smaller, second chick out of the nest shortly after it hatches. Asynchronous hatching followed by siblicide ensures that the peak food demands of two growing young never compromise the parents' ability to secure the survival of at least one chick. Laying an extra egg as insurance is an underappreciated parental strategy of birds (Forbes and Mock 2000). Alternatively, the last-hatched chick might supplement the parent's reproductive success by fledging successfully in good years, if it can overcome and reverse its initial handicaps.

Brood reduction is a standard practice in the Common Grackle, at least by some breeding females (Howe 1978). Some female grackles lay large clutches of five or six eggs, whereas others lay only two, three, or four eggs per clutch. Females that lay large clutches start incubation before they complete the clutch, but they rarely manage to raise the whole brood. The older siblings are fed first, grow faster, and are more likely to survive than are their younger siblings. Females that attempt large clutches put extra compensatory provisions of yolk and albumen into the last, larger eggs. These extra provisions, however, do not prevent the younger members of the brood from starving when food is scarce. The female grackles that lay only two, three, or four eggs in a clutch apportion their reproductive investment differently. They lay eggs of uniform size and equal provisions. They also wait until the last egg is laid before they begin incubation and thus hatch all the eggs at the same time. Females that breed conservatively in this way usually raise the whole brood.

Experiments with Lesser Black-backed Gulls demonstrate that the last-hatched, or so-called marginal, chick can overcome its initial handicap to fledge successfully (Royle 2000). These gulls typically lay three eggs, with probable loss of the third, last-hatched chick. The youngest chicks channel their initial food into mass rather than growth, buffering themselves against starvation, buying as much time as they can, and postponing the ultimate sacrifice of brood reduction as long as possible. Staying small initially compromises even further their ability to compete with their siblings and thus increases the chance that they will die in poor food years. Alternatively, in good food years, marginal surviving chicks then channel resources into accelerated skeletal growth and catch up with their siblings. The initial parental investment, hedging a parent's own bets, and a chick's growth options maximize success despite the unpredictability of food supplies.

Fledging

As a naked, blind hatchling transforms into a feathered juvenile, the young altricial bird approaches a pivotal event in its life—leaving the nest. Departure from the nest and then from parental care increases a chick's vulnerability to predators and the weather. Unable to fly well, baby birds are easy prey. The mortality rate during this period is high. After the first dangerous days have passed, however, the fledgling chick is safer than it would have been back in a vulnerable nest. Fledglings respond to the

warning calls of their parents by hiding or by staying still. Immobility combined with camouflaging plumage can render chicks extremely difficult to find.

Technically speaking, the nestling period is the interval between hatching and departure from the nest, and the fledging period is the interval between hatching and flight (Skutch 1976). The nestling and fledging periods may be the same for altricial birds, such as hummingbirds, but different for subprecocial and precocial birds, which have short nestling and long fledging periods. The moment of departure from the nest by altricial birds is commonly termed fledging even though the young birds may only flutter and scramble about for a few days before their first flight.

Long before they are ready to leave the nest or to fly, young birds develop essential strengths through exercise. Young pelicans jump up and down and flap their growing wings with increasingly effective strokes. Young hummingbirds grip nest fabric with their feet as they practice beating their new wings, anchoring themselves so as not to take off. When first airborne, some young birds respond to the new experience with astounding ability and control. Newly fledged and airborne Common Swifts spend their first night out of the nest on the wing (Tarburton and Kaiser 2001).

When a young Osprey launches itself on its first flight over a northern lake, it wobbles and flaps uncertainly, loses altitude, and seems certain to splash into the lake. In the last possible moments, it flaps more effectively and gains altitude, climbing steadily and safely high above the lake. It then glides in circles and practices steering and control. Successfully launched from the nest, the young Osprey migrates south for the winter (see Figure 10–2) and may someday become a breeding adult (Figure 16–12).

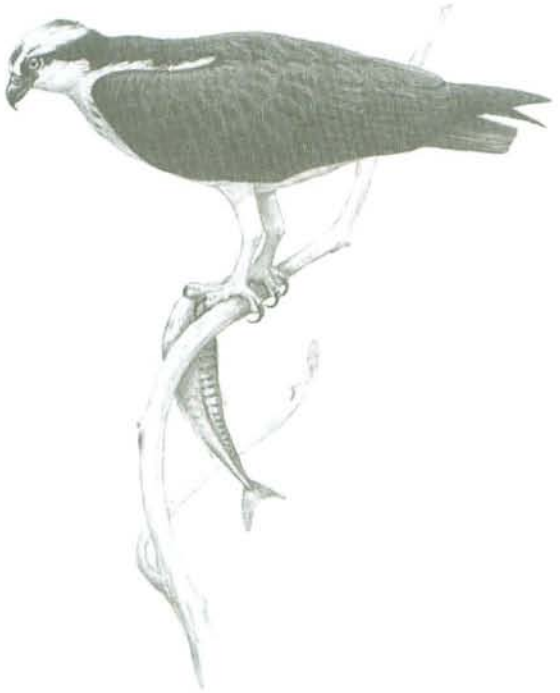


FIGURE 16–12 An Osprey. The young of this fish-eating species may make their first flight over water.

Mobile young birds move with their parents closer to good feeding grounds, a tactic that reduces the strain on the parents. The initial journey away from the nest is often a heroic one. One brood of Wood Ducks jumped 2 meters to the ground from their nest in a tree cavity and then followed their mother down a bluff and across a railroad track before swimming three-quarters of a mile across the Mississippi River to feeding grounds in good bottomland (Leopold 1951). More amazing still is the pair of Egyptian Geese that bred for several years on the roof of a three-story building in Johannesburg, South Africa. After the chicks hatched, the female herded them toward the roof's drain outlet and, after a little pushing and shoving, they fell three stories down the drain pipe to be shot out parallel to the ground by the curved end of the drain pipe (P. Ryan, pers. comm.).

Under more natural circumstances, precocial chicks that leave nests in tall trees or high cliffs must leap to the ground below, bouncing off soft earth if they are lucky or off jagged rocks if they are not. Torrent Ducks, for example, live in the dangerous waters of fast-flowing streams high in the South American Andes. To leave their nests in cliff crevices or holes above the streams, ducklings plunge as much as 20 meters into the turbulent water of the rocky streams below. Only rarely do they hurt themselves. Their light weight, buoyancy, and downy cushioning protect them from severe impact. Young seabirds that grow up on tiny cliff ledges overlooking the sea must leap into space, fall 150 meters, sometimes bouncing off jagged rocks, and then flutter to the water below.

Chicks of auks and their relatives (Family Alcidae) face a tradeoff between staying in their inaccessible, safe nests, often located on cliff ledges, and fledging to the ocean below, where growth rates are faster (Ydenberg 1989). At sea, parents do not have to commute long distances between feeding grounds and their hungry chicks. Better feeding rates at sea combined with reduced parental risk of predation favor early fledging. Young murrelets, for example, leave the nest shortly after hatching and swim rapidly out to sea. Chicks only two days old have been found 15 miles from land, carried in part by the local currents.

Mortality in the first few weeks out of the nest is typically high. A fledgling's chance of survival (measured by the number of future recaptures) increases in proportion to its mass at fledging (Figure 16–13). In general, a young bird's chances of survival increase with the state of its physical development when it leaves the nest. This more advanced development is one of the advantages of longer nestling periods and of faster growth in altricial nestlings. The availability of food, the quality of parental care, the number of siblings competing for that care, and the timing of departure from the nest all affect a fledgling's physical condition.

Yellow-eyed Junco nestlings and fledglings experience two early episodes of high mortality in the Chiricahua Mountains of southeastern Arizona (Sullivan 1999). Only 11 percent of banded nestlings reappear the following spring. Grown nestlings and fledglings incapable of extended flight easily succumb to predators, which take about 50 percent of the available young juncos in a nine-day risk period. Survival then improves

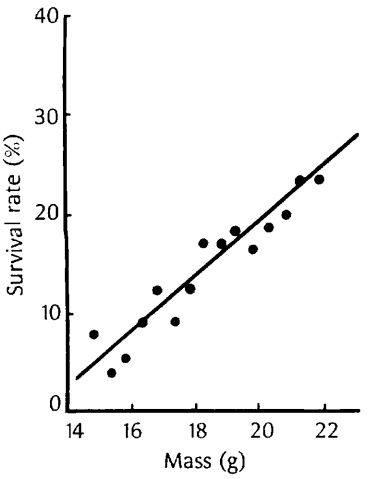


FIGURE 16–13 The probability of a young Great Tit's survival (and hence recapture by ornithologists) increases directly in relation to the mass attained by the bird before it leaves the nest. [*After Perrins 1980*]

for three weeks while parent juncos care for their mobile fledglings. With independence comes a second episode of high mortality due to starvation. Newly independent young find insects slowly and inefficiently and spend almost all day feeding. Approximately 51 percent of them die, most by starvation. These juveniles take about two weeks to develop adequate foraging skills.

Behavioral Growth and Development

Both heritage and experience affect the behavior of birds. Ended now are the intense debates of past decades about whether a particular behavior is innate or learned. The dichotomy was a false one. Instead, behavioral patterns of birds range continuously from those modified only slightly by experience to those derived entirely from experience. The embryonic growth patterns of the brain tied to length of the incubation period, for example, set the stage for later cognitive abilities required for foraging innovation and social interactions (Ricklefs 2004). Brief imprinting exposures and prolonged learning experiences both link a bird's genetic heritage of nerves, hormones, muscles, and bones to its social and ambient environments.

Innate responses to certain objects and color patterns guide a chick's solicitation of food from its parents. As soon as they are physically able, for example, hatchling Herring Gulls peck at the red spot on the bill tip of a parent to receive food (Tinbergen and Perdeck 1950). The apparently simple stimulus of red near the end of the bill is in reality quite complicated. It includes several ingredients such as shape and color contrast. Experiments with the use of color-patterned bill-like sticks with this species and with the Laughing Gull revealed that the most effective stimulus for eliciting pecking was a red or blue, 9-millimeter-wide, oblong rod, held vertically at a chick's eye level and moved horizontally 80 times a minute (Hailman 1967). Hatchling Herring Gulls react faster to a red

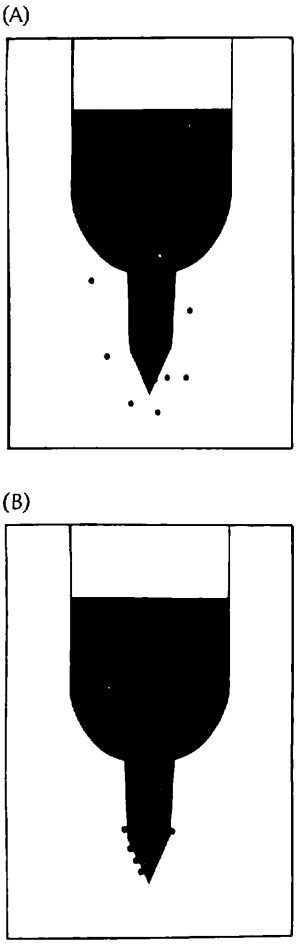


FIGURE 16–14 A Laughing Gull chick's pecking at an adult's bill becomes more accurate with age, as shown in an experiment using a painted card. Dots indicate pecks. The record of a chick (A) newly hatched and (B) two days later. [*From Hailman 1969, with permission from Scientific American*]

knitting needle with three white bands near the tip than they do to a parent's bill. The contrasting red and white borders of this stimulus enhance the most important stimulus features of a real bill.

All behavior shows some refinement with age. A Laughing Gull chick's accuracy in pecking increases with age as its depth perception, motor coordination, and ability to anticipate the parent's position improve. Older, more experienced chicks restrict their pecking to stimuli most similar to the head and bill of a real adult (Figure 16–14).

Predator Recognition

How do baby birds avoid danger? The natural and clearly beneficial escape responses of young birds to predators are both innate and learned. Baby domestic chickens innately avoid eating black and yellow prey, the warning coloration of many caterpillars. They then refine their choices with experience (Schuler and Hesse 1985). Similarly, hand-raised Turquoise-browed Motmots, for example, are frightened by sticks painted with black, red, and yellow bands to look like coral snakes (Smith 1975, 1977). Such a reaction is clearly adaptive—coral snakes are dangerous. Rather than having to learn to associate this color pattern with danger by direct experience, birds are genetically predisposed to avoid the risk, and then they learn refinements. Like other moundbuilders (see page 462), hatchling Australian Brushturkeys are independent as soon as they emerge from the compost mound. They respond innately to the alarm calls of Australian songbirds by becoming more alert (Göth 2001). They also react to real predators by crouching or running.

Learning about predators is important, too. Naive, young Great Tits fail to distinguish between a model of a predator and a model of a nonpredator, even though older, wild-caught juveniles and adults do so (Kullberg and Lind 2002). In part, young birds learn to recognize predators or to improve their recognition by observing the mobbing behavior of other birds. Adults scold and attack owls and snakes that they discover. Inexperienced birds quickly associate potential danger with this commotion. Eurasian Blackbirds will mob a harmless stuffed songbird or even a Clorox bottle if, in experiments, they have seen other birds appear to mob them (Curio et al. 1978).

Imprinting

The process of imprinting is fundamental to the development of behavior in many birds. Imprinting is a special kind of learning that takes place during a well-defined time period called the critical learning period, and it is irreversible. Something once learned during this period persists. Recall that passerine birds, for example, develop songs by using innate templates to filter experience during critical periods (see Chapter 8). Imprinting determines adult mate preferences and habitat preferences. Imprinting also determines the prey-impaling behavior of the Loggerhead Shrikes and the selection of nest materials and sites by adult Zebra Finches

(ten Cate et al. 1993). Successful captive propagation of endangered bird species requires careful attention to the early visual experiences of hand-reared chicks (Box 16–4).

An early sensitive period enables young precocial birds to establish the critical concept of "parent," on which their survival depends. The young of species that leave the nest shortly after hatching must learn to distinguish their parents from inanimate or inappropriate objects. Ducklings, for example, imprint most strongly on a moving and calling object when they are from 13 to 16 hours old. The objects that ducklings follow define their future acceptance of comrades and mates. They start with their parents.

Two particular stimuli help define a parent to ducklings: movement and short, repetitious call notes. Imprinting is enhanced when both stimuli are present, but movement alone is sufficient. Chicks, ducklings, and goslings will follow and imprint on a human, a moving box containing

BOX 16–4

ENDANGERED-SPECIES PROJECTS ACCOMMODATE THE SEXUAL PREFERENCES OF HAND-REARED BIRDS

When hand-raised by humans, captive baby birds tend to imprint on their human keepers and then to orient their adult sexual interests toward them. Disguises and models of parent birds are essential proxies for rearing California Condor chicks so that they will later exhibit proper species-recognition behavior (see photograph). Improper recognition behavior, however, sometimes has scientific advantages. Captive birds that have imprinted on their human keepers will ejaculate onto the keeper's hand, providing sperm for artificial insemination. This technique has been used for the captive propagation of endangered species, such as the Peregrine Falcon.

Feeding California Condor chicks. A model condor head serves as the surrogate parent for hand-raised California Condor chicks, preventing them from imprinting on their human keepers. [*Courtesy of the San Diego Zoological Society*]

a ticking alarm clock, or even a moving shadow on a wall. The strength of imprinting increases with the conspicuousness and variety of stimuli presented by the parent.

The next step in the behavioral development of a chick is to learn to distinguish its parents from other adults. The parents' visual appearance alone may be an important distinguishing factor. When exposed to different breeds of hens, baby chicks follow the one that looks most like their mother, on which they had imprinted initially (Collias 1952). Aggressive rebuffs by adults other than their parents may reinforce this process, quickly teaching chicks to avoid menacing adults of all kinds.

A baby bird may also imprint quickly on a parent's voice—one of the first sounds that it hears, perhaps even while it is in the egg. Common Murre chicks exchange calls with their parents before hatching and recognize their parents' voices on hatching (Ainley et al. 2002). Accurate parent–chick recognition is most important in birds that gather in large colonies and have chicks that require parental attention. In large colonies, young Sand Martins (also known as Bank Swallows) in large colonies, for example, are apt to wander into the wrong burrow and perish because they are not fed. The adult Sand Martins learn to recognize their own young by their distinctive individual calls and do not accept strange young (Beecher et al. 1986: Figure 16–15). In contrast, Northern Rough-winged Swallows, a related but solitary nesting species, do not discriminate between their own offspring and those of others placed in their nests. They feed whichever young occupy their nest.

Sexual Identity and Species Recognition

A chick's early visual experience with its parents typically affects its reaction to alternative color patterns, its social interactions and identity, and its eventual choice of a mate. Face- or head-color patterns, including skin colors of the face and bill, differ among related species. These patterns enable rapid identification by the birds themselves, as well as by bird watchers.

Sexual imprinting, as it is called, is widespread among birds. It has been documented in more than half of the orders of birds and in many families (ten Cate et al. 1993). The process starts with the specific signals of a parent, either visual or vocal, then generalizes more broadly, and, finally, adjusts to exclude the signals of other species (Figure 16–16). The process of sexual selection based on early imprinting experiences has likely played a major role in the evolution of distinctive plumage color patterns of bird species.

The white and dark "blue" color morphs of the Snow Goose of the Canadian Arctic provide an example that shows how sexual imprinting works (Mowbray et al. 2000). The different plumage colors of this species have a simple genetic basis. The dark morph results from a single dominant allele, and the white morph results from a pair of recessive alleles in homozygous condition. As a rule, white geese pair with other white geese, and dark geese also pair with each other, in what is called assortative mat-

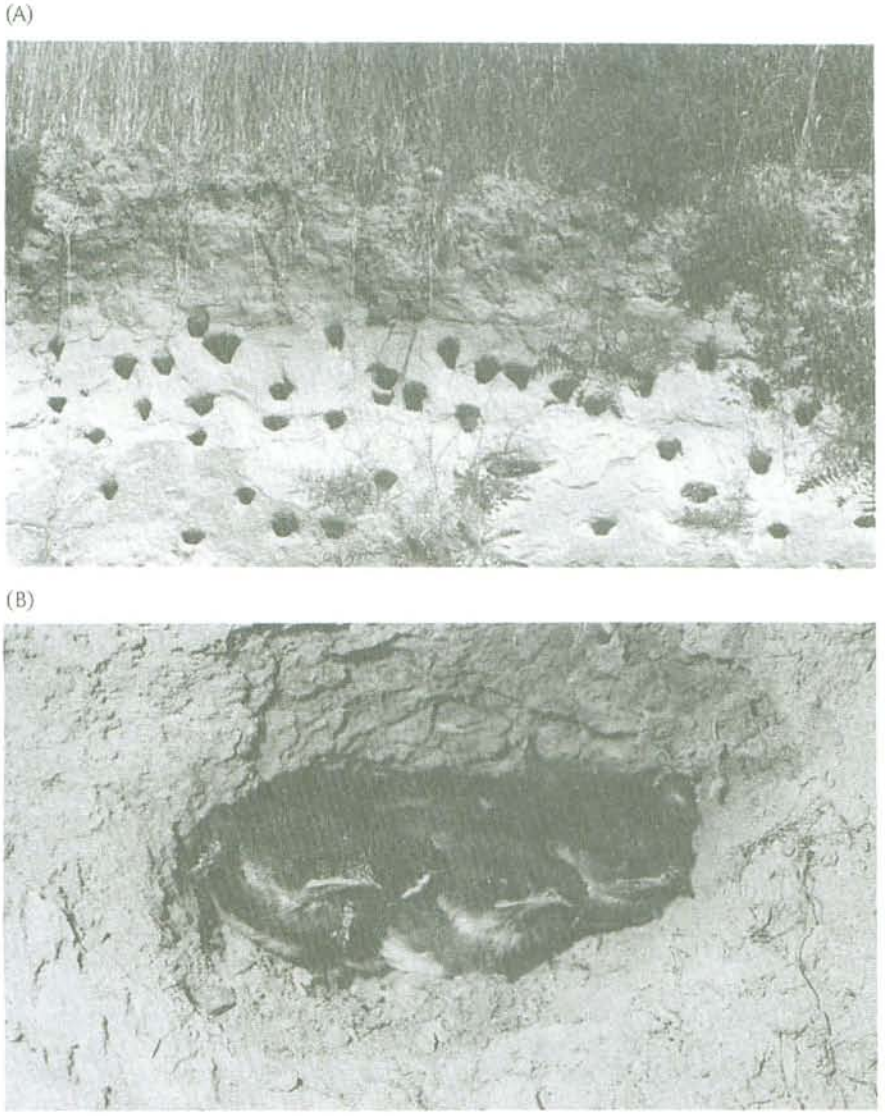


FIGURE 16–15 (A) Colonies of Sand Martins riddle dirt embankments with their nesting tunnels. (B) A brood of three young Sand Martins, almost ready to fledge, waits for food at an entrance. [*Courtesy of A. Cruickshank/VIREO*]

ing. At the La Pérouse Bay colony in northern Manitoba, mixed pairs are much less frequent than would expected in random pairings between color morphs.

Early visual imprinting on family color is the force behind these mating preferences. Young Snow Geese choose mates of the same color as that of their families, mainly that of their parents. Regardless of their own color morph, geese raised by white parents later choose white mates, and geese raised by dark parents choose dark mates. Geese raised by mixed pairs choose either white or dark mates. The color of siblings has a secondary effect, especially in mixed families with white-morph offspring

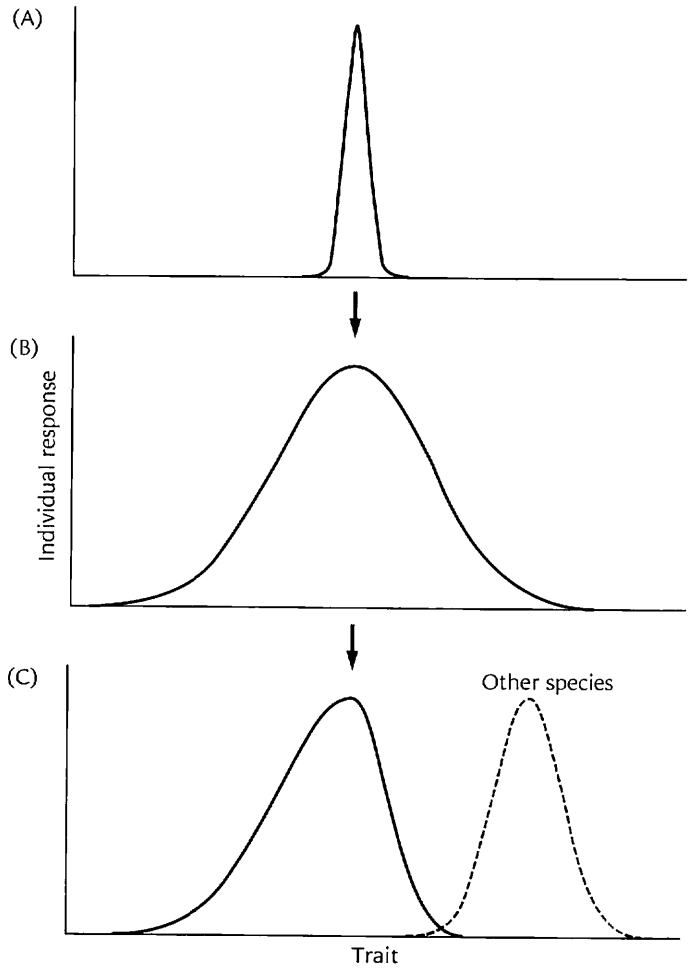


FIGURE 16–16 Model of the development of a female bird's mate preference throughout her life. (A) Distribution of signals that a chick associates with its parents. (B) A young bird's response curve generalizes outward from parental traits. (C) Experience with other species promotes changes in a female's responses. [*From Irwin and Price 1999*]

produced by heterozygous dark-morph parents. Young geese from such families occasionally choose mates unlike their parents.

Much more complex is the role played by imprinting in the early development of young obligate brood parasites, which are raised by host parents. Village Indigobirds imitate the songs of their host fathers, including dialect variation (see page 382). Host vocalizations enable female indigobirds to recognize potential mates with the same host heritage, as well as to lay eggs in the appropriate host nest. Host-specific lineages may then perpetuate themselves and evolve into separate species. Brood parasites still need to shift from social affinity with the host parents to social affinity with others of their own species. One possibility is that they use a species-specific "password" to do so (Box 16–5).

BOX 16–5

PASSWORD ACCESS TO COWBIRD SOCIETY

If sexual identity starts with a process of imprinting on parents and socializing with siblings, then how do brood parasites develop a sense of identity different from their host species? After fledging, young Brown-headed Cowbirds, for example, shift their affinities to other cowbird fledglings and to adults of their own species (Lowther 1993).

Mark Hauber and his colleagues (2001) discovered that one call, the "chatter," may serve as a kind of identity password for entry into cowbird society. The chatter is an innate, spontaneous, and invariant vocalization of young cowbirds. Its development requires no social experience. Nestling cowbirds are highly responsive to playback of this chatter. After they leave their host parents, fledglings and then later juveniles instinctively approach other chattering cowbirds or experimental broadcasts of the chatter. After they have reunited with others of their species, triggered by one or the other of the vocalizations, young cowbirds begin to have social experience with flock mates, learning and refining vocalizations, including dialects and other cultural traits, and ultimately their mating preferences.

Cross-fostering experiments, in which young are raised by parents of another species, illustrate the effects of early imprinting on a bird's sexual response to species-specific color patterns. Cross-fostering causes the sexual interests of many species to shift to the foster species. For example, male Zebra Finches raised by Bengalese finches (a domesticated form of the White-rumped Munia) prefer to court Bengalese finch females instead of Zebra Finches. When Zebra Finches are doubly imprinted on Zebra Finches and Bengalese finches, they prefer to court hybrids with visual features of both species (ten Cate 1987). Great Tits cross-fostered in the nests of Blue Tits survived well, but they behaved like their foster parents and siblings in many respects. As a result, they could not attract or accept a social mate of their own species (Slagsvold and Hansen 2001).

Two subtle aspects of the imprinting process in finches suggest how imprinting could promote speciation through sexual selection (ten Cate 1991; Irwin and Price 1999). First, males with artificially brightened or contrasting color patterns prove to be more attractive models to the young finches than are normally colored males. Second, young finches show a slight imprinting preference for novel or unfamiliar stimuli. Other studies also reveal that imprinting biases for the unfamiliar reduce the probability of inbreeding with siblings. If they proved to be general phenomena, imprinting biases for bright, unusual male color patterns would give those novelties an advantage and help to catalyze the process of sexual selection. This process would lead, initially, to increasingly different ornamentation and, ultimately, to the evolution of new species from small, isolated populations.

Learning Essential Skills

After chicks leave the nest, they enter a period of intense learning and practicing essential skills, including foraging and avoiding predators. They

depend, however, on their parents for several weeks or more for brooding, protection from predators, and learning to feed.

Fledglings of most small passerines stay with their parents for 2 to 3 weeks after they have left the nest. In the Tropics, where long apprenticeships also seem necessary to develop feeding skills, some young passerines stay with their parents for 10 to 23 weeks. Young boobies and terns depend on their parents for as long as six months after they have fledged—until they have mastered the art of plunging after fish. Young Tundra Swans stay with their parents for one to two years, through several long-distance migrations.

Fledglings should prolong this period of postfledging parental care as long as possible. Parents, however, should encourage independence of their young as soon as their investment is secure. The postfledging period, therefore, is a final period of parent–offspring conflict. In Montagu's Harriers, as the fledglings' flying and hunting skills improve, parents terminate the postfledging dependence by decreasing the amount of food that they provide (Arroyo et al. 2002). They hold back on food provisions despite increased and more aggressive solicitations. In years of low food availability and tougher hunting, the fledglings try even harder to extend parental care.

Prolonged learning and early imprinting exposures link an individual bird's genetic heritage to its social and ambient environments. Young birds must first develop their skills at finding food and capturing prey. Seemingly inept juvenile Royal Terns, for example, drop fish that they have caught almost 14 times as often as adults do (Buckley and Buckley 2002). Among fledgling Yellow-eyed Juncos, rates of pecking and feeding, as well as scanning for predators, increase dramatically with age, reaching adult levels of performance as the juveniles reach independence (Sullivan 1999).

In correlation with their inexperience, independent juveniles spend more time exposed to predators while foraging than adults do. Combined with greater risk of starvation when severe weather limits foraging time, inefficient foraging leads to increased mortality. By feeding together in flocks, newly independent juveniles increase their foraging time by sharing vigilance.

Other essential skills also develop with age and social experience. Orientation and navigation skills require calibration of compasses and definition of goals. Young songbirds acquire their vocal repertoire and learn to communicate through social interactions. The extraordinary Gray Parrot named Alex (see page 209) required social exchange with his tutor to learn words and concepts. He could not learn from a television video program (Pepperberg 1991). Social skills and dominance also improve with age. Mating status itself may require years of apprenticeship, as does successful parenting.

Some birds play. Young crows, ravens, jackdaws, and their relatives, for example, frequently play and even create elaborate social games similar to "king of the mountain" or "follow the leader." Stick balancing and manipulation or the exchange of sticks, sometimes while upside down,

and taking turns sliding down a smooth piece of wood in a cage, are among the many games that these intelligent birds play (Gwinner 1966).

Gulls provide another example. They often drop clams onto hard surfaces to break them open for food. Sometimes, they swoop down to catch them before they hit the ground, a game of "drop–catch" that looks like play behavior (Gamble and Cristol 2002). Detailed studies of drop–catch behavior in Herring Gulls rejected the alternative hypotheses that (1) a gull was testing the probability of theft by other gulls before actually letting the clam smash open or (2) the gull was trying to reposition the clam in its bill for a better drop (like a tennis player catching the ball to do a better serve). Most telling were observations that young birds played drop–catch more than older birds and often did so with objects other than clams. What looks like "play" is usually a form of practice for developing essential locomotory and social skills (Smith 1983).

Peregrine Falcons (see Figure 17–7) develop their hunting skills through playful practice and social interactions. After they fledge, young Peregrines depend on their parents for food for one to two months. They develop their flying and hunting skills through aerial interactions when playing with their siblings. In aerial dogfights, they chase and dive at each other, called stooping, and roll over to grapple each other's talons. As such acrobatic skills improve, they take food directly from their airborne parents by rolling over and snatching food from the parents' talons. When hungry, young Peregrines also try to chase their parents, which do their best to avoid the hassle by perching inconspicuously on tall city buildings (H. B. Tordoff, pers. comm.).

Programmed to chase, juvenile Peregrines can develop good hunting skills without much help from their parents. Initially, they chase anything large that flies nearby, including herons and vultures, as well as one another. After two or three weeks of this activity, they start to focus on smaller, potential prey in the right size range. Their first captures almost seem to be accidental, surprising contacts. Kills soon become more deliberate, usually directed initially at large easy-to-catch insects, such as butterflies and flying beetles, which they may eat on the wing. The adolescent Peregrines then graduate to taking birds as prey, killing them with increasing efficiency.

Summary

Most hatchlings fall into one of two categories, altricial or precocial. The former are helpless and completely dependent on parents, and the latter are mobile sooner and capable of greater independence. Ornithologists recognize the intermediate categories of semialtricial, semiprecocial, and subprecocial, as well as an extreme category of superprecocial for young that are wholly independent when they hatch.

The growth in mass of chicks follows a sigmoid (S-shaped) curve. There is a 30-fold variation in the growth rate of chicks of the various species. Growth rates relate directly to precocity of development and adult

body proportions. If growth of tissue mass and maturity of function are mutually exclusive, growth should slow as a bird matures. Growth rates of members of the same species also may vary considerably, owing to diet quality, food availability and reliability, and temperature. Older, larger chicks have a greater chance of survival than do smaller, younger siblings. Asynchronous hatching contributes to siblicide because it results in chicks of unequal size and strength. Food type also is a factor. Food that can be monopolized, such as small fish, promotes physical and sometimes mortal competition between siblings.

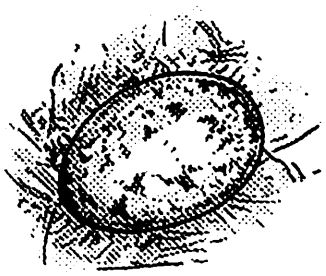
Parents face major challenges in the tradeoffs between raising their young and taking care of themselves. Peak breeding activity adds substantial daily energy costs, leading to loss of weight and increased hormonal stress. A parent's options for adjusting its investments include choosing among rivaling nestlings, reducing risks of nest predation, favoring one sex over the other, and even sacrificing some of their young if necessary. Favoritism actually starts with different provisioning of the eggs and then extends to responses to begging nestlings of different ages or at different stages of development.

A parent adjusts its effort in relation to its mate's effort. The options that are best for a male parent may conflict with those for a female parent, owing in part to the male's confidence in his paternity of the offspring. A female can compensate for the loss of a mate by increasing her own effort to full capacity. Parents can manipulate their investments into male or female offspring by provisioning eggs differently and by biasing their care and, hence, relative survival of the sexes. How females control the sex of the eggs that they ovulate is unknown, but several studies now indicate that they can do so.

Young birds show extraordinary skill and daring when they leave the nest. The flightless young of seabirds that nest on cliff ledges sometimes must leap great distances into turbulent waters below. How long young stay with their parents depends on the difficulty of skills that must be acquired.

Both genetic heritage and experience affect the behavior of birds. The nature of formative experiences varies from brief imprinting exposures during critical sensitive periods early in life to prolonged learning and cultural exchanges of information. Imprinting affects many aspects of avian behavior, from recognition of species to choice of nest sites and habitats. However, young birds must use experience to learn to find appropriate food efficiently and to avoid danger. Play behavior is an important way for young birds to practice the essential locomotory and social skills that they need to survive on their own.

CHAPTER 17



Lifetime Reproductive Success

In the end, an individual's lifetime reproductive success is what counts. [Charles Darwin in modern terms]

Each bird proceeds through a series of life-history stages from early development to the annual cycles of adults. Hormones guide, govern, and coordinate these stages (Jacobs and Wingfield 2000). Compounding the challenges of survival through each stage of the annual cycle are the tradeoffs between the short-term costs of reproductive effort and future breeding opportunities.

The rates of reproduction and annual survival of individual birds combine to measure an individual bird's lifetime reproductive success relative to that of its competitors—that is, its evolutionary performance. The reproductive successes of all individuals in a population together define the dynamics of that population's growth or decline. More broadly, the study of avian life histories integrates behavior, ecology, population biology, and evolution into a broad concept of the responses of birds to the environment (Ricklefs 2000b).

This chapter reviews the tradeoffs between survival and reproduction by birds. It starts with an overview of the main life-history patterns of birds and then introduces life-table analysis, which compiles the statistics, or demographics, of individual performance. The next sections of the chapter explore in detail the two central life-history traits, longevity and fecundity, to set the stage for a discussion of the tradeoffs between annual reproduction and age-specific survival. The final part of the chapter deals with the premier topic of avian life-history research—the evolution of optimal avian clutch sizes, or how many chicks a bird should attempt to raise at one time.

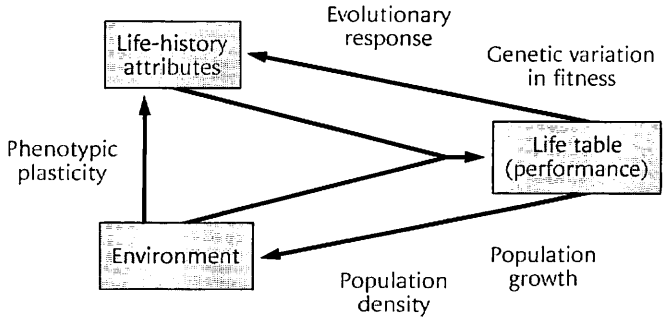


FIGURE 17–1 Influenced by the environment, the life-history attributes determine the lifetime reproductive success and relative performance of individual members of a population. Genetic variation in performance, called fitness, establishes an arena for natural selection and an evolutionary response in the population to variation in the environment. Variation in the environment also affects population growth and density-dependent feedback on individual attributes and performances. [*From Ricklefs 2000a*]

Life-History Patterns

Life histories are sets of evolved traits or attributes. Woven together, individual life-history attributes interact with environmental variables to determine the performance of an individual member of a population (Figure 17–1). In turn, each member's performance relative to that of others defines the selective advantage or disadvantage of that member's set of traits. In this way, the life-history attributes of a population evolve toward a particular optimum. Life-history attributes change population density and, as a result, affect the operating environment—positively or negatively. The diverse life-history patterns of birds are the products of this evolutionary process (Table 17–1).

Tradeoffs between longevity and fecundity are the traditional focus of life-history theory. The substantial tradeoffs between longevity and fecundity lead to different solutions or optimal balances for different species. Central to longevity is the probability of living to a particular age, called age-specific survivorship. As a whole, birds are long-lived, warm-blooded animals that age slowly. Besides increasing our understanding of their life-history strategies, investigations into the life spans of birds have potential application to the treatment of human aging and fertility (Holmes and Ottinger 2003).

TABLE 17–1 Extremes of avian life-history patterns

Species	Survival Before Breeding	Age of First Reproduction	Fecundity	Adult Mortality Rate
Albatrosses and eagles	Moderate (30%/year)	Late (8–10 years)	Low (0.2 young/year)	Low (5%/year)
Ducks and small passerines	Low (15%/year)	Early (1 year)	Moderate (3 young/year)	High (50%/year)

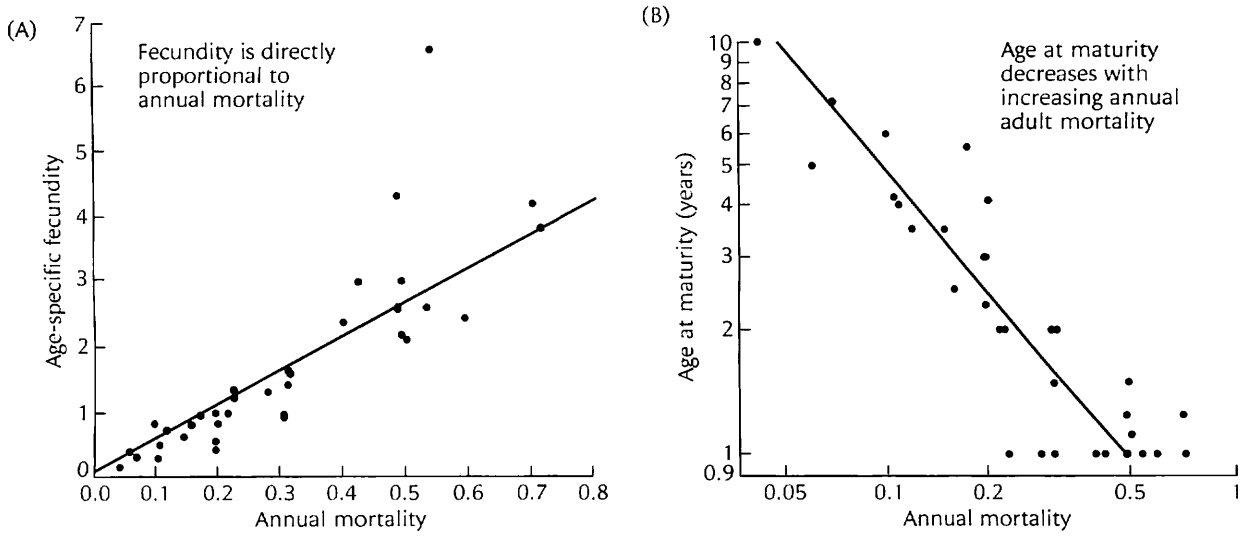


FIGURE 17–2 (A) Age-specific fecundity (number of fledglings per year) increases in short-lived species, graphed here as annual adult mortality (percent). (The greater the annual adult mortality, the more short-lived a species is.) (B) Age at maturity (first breeding) decreases in short-lived species, again graphed here as annual adult mortality (percent). [*After Ricklefs 2000a*]

Annual fecundity—the number of young successfully fledged in a year—increases directly with annual adult mortality. This relation is the central theme of avian life-history theory (Figure 17–2). Short-lived (high mortality) species, such as ducks and small songbirds, tend to have high fecundity. Long-lived (low mortality) species, such as albatrosses and eagles, tend to have low fecundity.

A Song Sparrow, for example, has a short life span, but it starts breeding without delay, after just one year. It then concentrates high annual output—from three to five nestlings twice a year—into a few consecutive years. At the other extreme is the Wandering Albatross, which takes a long time to start breeding—at 8 to 11 years of age—and reproduces slowly. It produces one chick every 2 years for as long as 50 years (Figure 17–3). A single axis spans the short and fast sparrow life history and the long and slow albatross life history. This "fast–slow" axis captures most of the variation in life histories among birds (Ricklefs 2000a).

Included in the sweep of life-history features tied to life span are behavioral traits of cognition and intelligence (Ricklefs 2004). Families of birds known for their intelligence and advanced social behaviors, such as crows, parrots, and woodpeckers, have large brains in relation to their body sizes (see Figure 7–10). Relative brain size is also linked to innovative foraging behaviors and, especially, play behavior (see Figure 7–14). Underlying this nexus of traits is the length of the incubation period: longer incubation periods enable the development of capacities for more advanced behavior.

Few avian life-histories depart from the tight correlation between annual fecundity and life span. No long-lived bird produces large numbers

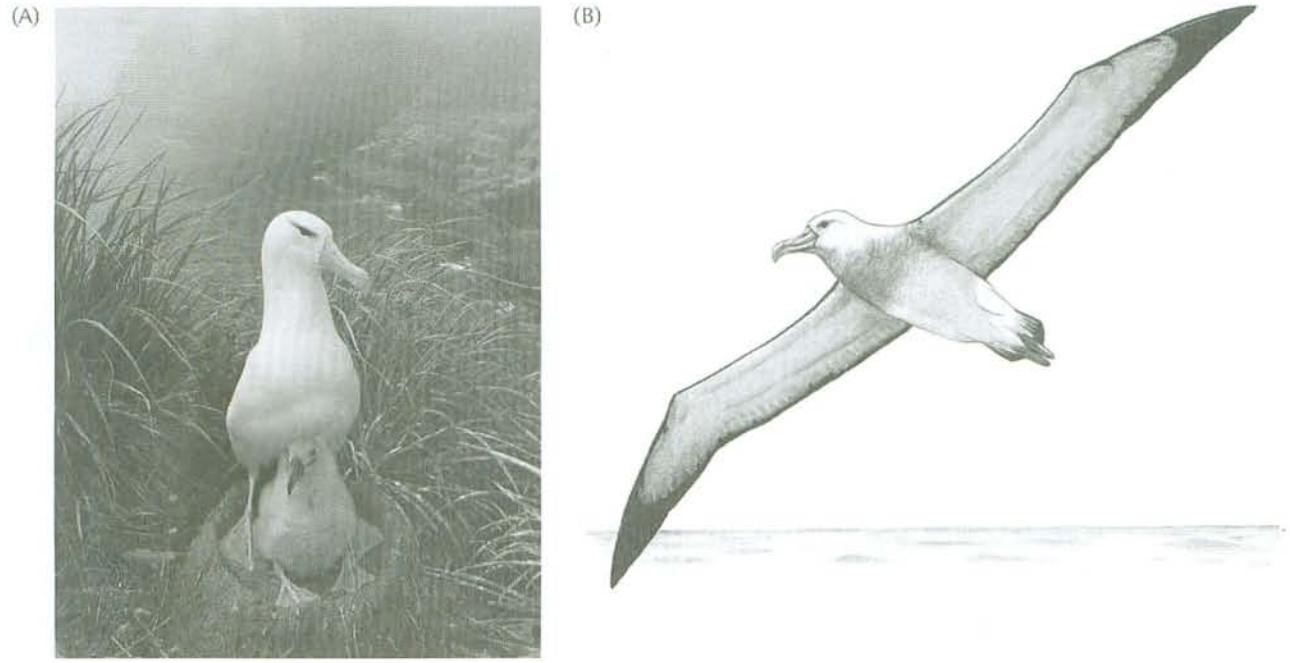


FIGURE 17–3 (A) The Black-browed Albatross and related species are long-lived birds that raise only one offspring at a time. (B) The Wandering Albatross produces one chick every 2 years for as long as 50 years. [*(A) Kevin Schafer/CORBIS*]

of young each year, as, for example, a maple tree produces seeds, or waits to the end of its life to produce lots of young, as a salmon does. Why would this be so? The evolution of avian life-cycle options may be constrained by the physiology of birds (Ricklefs and Wikelski 2002; Box 17–1). Endocrine control systems, in particular, must undergo delicate transitions between life-history stages, managing stress and the risk of alternative and incompatible behavior while minimizing damage from prolonged overdoses of hormones. In addition, early developmental patterns—particularly, long incubation periods—relate directly to long life spans in birds. Such correlations suggest a high level of evolutionary integration of life-history traits in birds from fledging to old age (Ricklefs 1993).

Life Tables

Life tables help us to project lifetime reproductive success and population trends from the primary life-history attributes. Survival and fecundity are primary life-history attributes. They change with age. For example, mortality rates are initially high among young birds less than one year old and then decline to nearly constant lower levels among adults. More broadly among species, age-specific mortality plays a major role in the evolution of life-history strategies. High adult mortality favors increased reproduc-

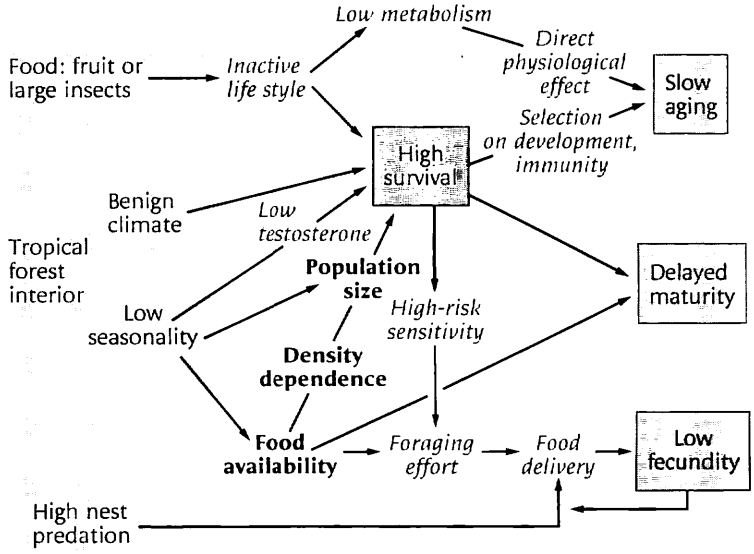
BOX 17–1

PHYSIOLOGICAL CONSTRAINTS SHAPE AVIAN LIFE-HISTORY TRAITS

The study of avian life histories includes physiological tradeoffs and constraints (Ricklefs and Wikelski 2002). These tradeoffs and constraints help us to understand the ways that selection pressures—such as food availability, seasonality, and predation—shape a species' life-history traits.

The diagram illustrates a model of the network of interactions that potentially connect environmental features of the tropical forest interior (shaded area) to the life-history traits (boxes in unshaded area) of a small tropical forest bird, such as a manakin. Shown are direct connections of behavior and physiology (in italics) as well as indirect connections of ecological feedbacks (in boldface).

Physiological responses such as metabolic rates and hormones, especially testosterone, mediate the interactions. Incompatible hormone controls of different behaviors and time-limited hormone responses to stress are likely to constrain fecundity, parental effort, and life span.



Model of the role of physiological processes (italics) and population processes (boldface) in the evolution of the life-history traits (boxes) of a bird species that lives in the interior of a tropical forest (shaded area). These species typically have long life spans, small clutch sizes, and delayed maturity. A manakin is such a species. [*After Ricklefs and Wikelski 2002*]

tive effort, whereas high juvenile mortality favors reduced reproductive effort. Fecundity or reproductive success also improve, at least initially, with age and experience.

Life tables, like those used in the insurance industry, summarize the vital statistics of age-specific survivorship and also age-specific fecundity

(Table 17–2). Four major attributes specify the performance of the average bird in a population: (1) the age at which a bird first reproduces; (2) its fecundity (the number of young that it fledges each year); (3) the survival of its young; and (4) its longevity, or life span, as an adult.

Life tables are usually based on the statistics of females because we can measure these statistics more reliably than we can those of males. Although also subject to error, the association of eggs in a nest with the female(s) that laid them is more pragmatic than that with the male or multiple males that might have fertilized them. From these measurements, we can project life expectancies and family sizes of other birds facing the same conditions. From the balance of survival and fecundity in life-table data, we can also project rates of net population growth and future population

TABLE 17–2 Time-specific life tables for female Eastern Screech Owls in either a suburban or a rural study area, 1976–1991

Age Classes[a]	S_x[b]	L_x[c]	Average Number of Fledglings per Individual	B_x[d]	LB_x[e]
		Suburban			
Fledglings	0.36	1.00	0.0	0.0	0.00
Adults					
1	0.49	0.49	1.6	0.8	0.39
2	0.58	0.18	2.6	1.3	0.23
3	0.61	0.10	3.1	1.5	0.15
4	0.67	0.06	3.2	1.6	0.10
5	0.75	0.04	2.7	1.3	0.05
6	0.75	0.03	2.7	1.3	0.04
7	0.75	0.02	2.7	1.3	0.03
8	0.75	0.02	2.7	1.3	0.03
9	0.75	0.01	2.7	1.3	0.00
10	0.75	0.01	2.7	1.3	0.00
		Rural			
Fledglings	0.30	1.00	0.0	0.0	0.00
Adults					
1	0.36	0.30	1.6	0.8	0.24
2	0.60	0.11	2.3	1.1	0.12
3	0.67	0.06	3.2	1.6	0.10
4	0.53	0.04	2.0	1.0	0.04
5	0.50	0.02	2.0	1.0	0.02

[a]All age classes present in each study area are included. Numbers in column represent age (in years) of adult.
[b]S_x, survivorship.
[c]L_x, probability of survival.
[d]B_x, number of female offspring per female subject, based on known 1:1 sex ratio.
[e]Summation of values in this column yields an R_0 (population replacement rate) = 1.01 for the suburban population and R_0 = 0.52 for the rural population.

From F. R. Gehlbach, unpublished data.

trends, whether up or down. The projection of population trends is critical to the sound conservation management of healthy, stable populations of birds.

The age at which a young bird first reproduces is a vital statistic in this regard. Theoretically, an early start has the greatest effect of all the variables on a bird's potential reproductive contribution to succeeding generations. The age at first breeding controls the interval between generations—or mean generation time (when children produce grandchildren)—which, in turn, drives the potential growth rate of a population. Consequently, age at first breeding dictates response time to natural selection or environmental change and thus the potential for speciation (Marzluff and Dial 1991). In addition, slow-maturing species, such as the California Condor and the Whooping Crane, are easily endangered and slow to recover from overhunting, accidental mortality, or outbreaks of disease because they are slow to replace reproductively active adults.

To create a life table for a particular bird population, ornithologists follow the annual progress of a class, technically called a "cohort," of individual birds from hatching until the last one dies. The proportion of the cohort that survives each year defines the annual survivorship, S_x. The probability of survival to a particular age, L_x, is the product of the preceding annual survival rates. The average number of young produced each year by an adult female in the cohort defines age-specific fecundity, B_x. The product L_xB_x specifies an individual bird's expected annual fecundity, which is to say, fecundity at a certain age discounted by the chance of dying before reaching that age (Figure 17–4).

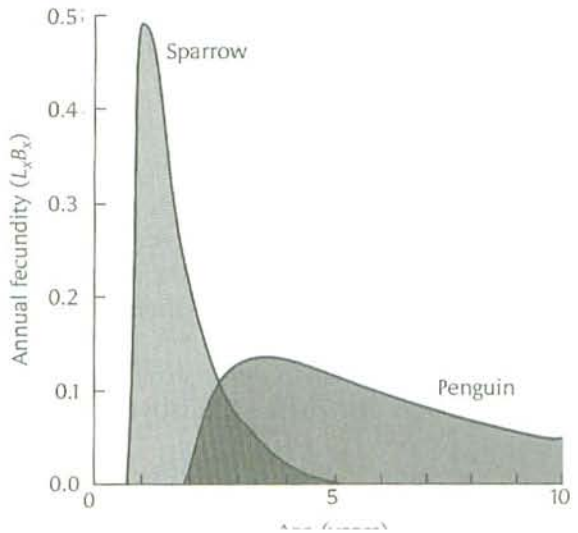


FIGURE 17–4 Reproductive efforts by a sparrow and a penguin, expressed in terms of expected annual fecundity, L_xB_x, where L_x is the probability of survival to a particular age and B_x is age-specific fecundity. The short-lived sparrow produces more young every year than does the long-lived penguin, but their total lifetime fecundities (areas under the curves) are roughly the same. [*After Ricklefs 1973*]

The values of L_xB_x for all age categories, x, sum to define R_0, which is the net reproductive rate. R_0 projects an individual bird's lifetime reproductive success and the expected rate of recruitment of new birds into the population. If one female replaces herself by a daughter during her lifetime, R_0 equals 1. A population composed of many such females should be stable in size. Larger values of R_0 are expected in growing populations, and smaller values are expected in declining populations. Thus, if R_0 = 1.5, the population will increase 50 percent in one generation. Conversely, a value of 0.8 indicates a declining population.

Consider the life tables compiled for Eastern Screech Owls (see Table 17–2). Fred Gehlbach (1994) compiled life-table statistics for two study populations in Texas, one in the suburbs and the other in rural woodlands. These small owls commonly nest in cavities in wooded habitats. They live between 7 and 13 years and produce one brood of two to three young each year.

In the suburbs, annual survivorship, S_x, of the screech owls increased with age to a maximum of 75 percent per year. Individual owls achieve full breeding potential by the age of 2 years, by which time each female produces an average of 1.3 female offspring each year, B_x. Actually, reproductive output varies greatly among females, and a minority (less than 25 percent) of long-lived females produced most of the fledglings. Adding the annual products of survivorship and fecundity L_xB_x, yields the net reproductive rate, R_0. In this case, R_0 is 1.01, a value indicating simple lifetime replacement of an average female by one daughter and thus a stable population size.

Screech owls, however, do not fare as well in the rural woodlands of central Texas. Both annual survival and fecundity are lower there, yielding a net reproductive rate of 0.5. That study population was declining.

Longevity and Life Span

Birds are remarkable for their longevity (Holmes and Ottinger 2003). Compared with mammals, they are long-lived both for their sizes and for their high metabolisms, which average from 1.5 to 2.5 times those of similar-sized mammals. Birds expend five times as much energy or more throughout their lifetimes as do mammals of the same size. The long lives of birds challenge current understanding of the aging process through cellular degeneration due to the oxidative by-products of metabolism (Box 17–2).

The life expectancy of most individual small birds that survive to independence is from 2 to 5 years. Individual members of large-bird species live an average of 20 years.

The maximum ages recorded in wild birds average between 10 and 20 years for songbirds and between 20 and 30 years for seabirds and raptors. Records of long-lived individual birds abound. Some birds live about as long as humans. Among the records are a female Northern Fulmar 50+ years of age, a 51-year-old Laysan Albatross, a 36-year-old Eurasian Oystercatcher, and a 34-year-old Great Frigatebird. One record holder is a

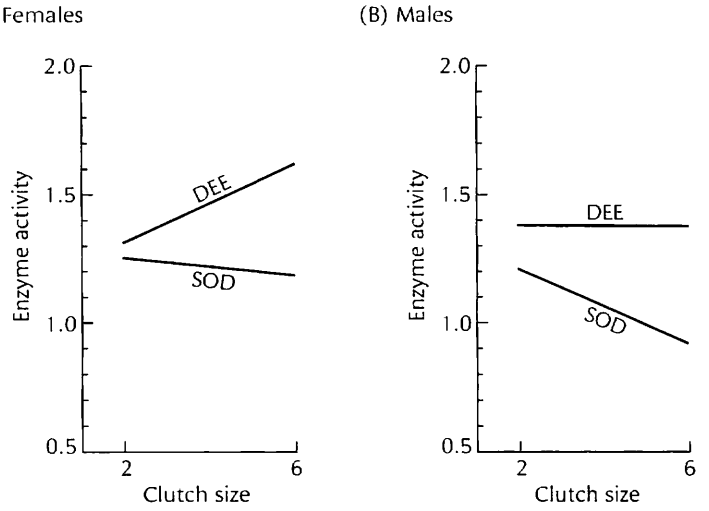
BOX 17-2

ANTI-AGING MECHANISMS IN BIRDS?

The long life spans of birds interest biogerontologists, the biologists who study the aging process (Holmes and Ottinger 2003). What is responsible for aging? Aerobic metabolism generates by-products known as reactive oxygen species (ROS) that damage cells, cell organelles (such as mitochondria), DNA, lipids, and proteins. Damage from ROS by-products is thought to be the major cause of aging, or senescence. For this reason, we get plenty of encouragement to include antioxidants in our diets by eating such foods as blueberries, Brussels sprouts, and tomato salsa.

High metabolic levels and reduced antioxidant activity increase ROS damage. Reproductive effort reduces antioxidant activity and thereby damages health and reduces longevity. Experimental doubling of the clutch sizes of Zebra Finches, for example, caused antioxidant activity to decrease by 24 to 28 percent in the male Zebra Finches, but not their mates (see illustration).

The long life spans of birds suggest that, despite their high metabolisms and major energy expenditures, they have interesting ways of prolonging life by reducing ROS damage through oxidative protection. The mechanisms responsible for slow aging may be linked to the evolution of flight, because bats show similar trends of life span and aging. However, we don't yet know exactly what these anti-aging mechanisms are or whether they directly increase the life spans of birds by neutralizing ROS activity (Ricklefs, pers. comm.).



Larger clutch sizes cause a reduction in the activity of the major antioxidant enzyme superoxide mismutase (SOD) in male Zebra Finches (B) but not significantly in female Zebra Finches (A). Daily energy expenditure (DEE) did not increase with the larger brood size in males, but females exerted additional effort. [*After Wiersma et al. 2004*]

female Royal Albatross named "Grandma," which was banded at her nest in New Zealand and then disappeared at age 53. Another record-holding seabird is a Manx Shearwater ringed on North Wales as an adult on May 22, 1957, and recaptured again 45 years later on April 3, 2002, having flown an estimated 800,000 kilometers on annual migrations

between Wales and South America, a distance equal to flying to the moon and back (Bhattacharya 2003).

Captive birds tend to live even longer than their wild relatives. Some parrots have lived to be 80 years old in captivity (Flower 1938).

Annual survival rates accrue to define life span. The survival rates of adult birds range from as low as 30 percent per year for Blue Tits and Song Sparrows to highs of more than 95 percent for Royal Albatrosses, Bald Eagles, and Atlantic Puffins. In general, large species survive better than small species, and seabirds survive better than land birds.

In North and South America, the survival rates of tropical and Southern Hemisphere songbirds trend higher than those of related north temperate zone birds (Martin et al. 2000; Martin 2004). Manakins on Trinidad, for example, live between 11 and 14 years with estimated annual survival rates of 89 percent (Snow and Lill 1974). Estimates of annual survival rates of the American Robin and related species *(Turdus)* increased from a low of 56 percent in temperate North American populations to 70 to 85 percent in subtropical and tropical populations (Ricklefs 1997).

The risk of death is strongly seasonal for most adult birds. Survival rates of songbirds strongly correlate with seasonal changes in average monthly temperatures, which indicate the harshness of the lean or winter season. Surviving the winter months of low temperatures and declining food is a challenge for resident species of northern latitudes, such as chickadees (see Chapter 18). Whether a seasonal environment is warm–cold or wet–dry, the shortage of food for several months in that environment increases mortality due to starvation. Population trends of some migrant European bird species are governed by overwinter survival in subsaharan Africa (Batten and Marchant 1977). Similarly, annual survivorship of American Redstarts corresponds in part to the quality of their winter habitats (Marra and Holmes 2001).

The severe winters of the northern latitudes increase adult mortality either directly or as a cost of migration. Migration itself brings substantial mortality in at least one species of wood warbler, and perhaps in many Neotropical migrants. Most field studies of the survival rates of migrants measure their returns to breeding or wintering territories each year and include both mortality on migration and mortality on the wintering grounds.

Approaching the question of mortality during migration more directly, Scott Sillett and Dick Holmes (2002) tracked seasonal survival in the Black-throated Blue Warbler. This handsome species migrates between wintering grounds in the Caribbean and breeding grounds in New England. Annual survival rates were estimated to be 51 percent for males and 40 percent for females. Month-to-month mortality, however, was negligible (for both males and females) from May to August in New England and from October to March in Jamaica. Instead, most of the annual mortality (85 percent) was during migration. Monthly mortality rates were at least 15 times as great during migration as during periods of residency on the breeding or wintering grounds. Chapter 18 examines the roles of demography and density dependence in population regulation throughout the annual cycle of the Black-throated Blue Warbler.

Age-Specific Mortality

Rates of annual survival change conspicuously with age in the first years of life and may also differ between the sexes. A young bird's annual chance of survival (from fledging to breeding) typically is about half that of an adult. Only 13 to 30 percent of fledgling Great Tits survive their first year, but 48 percent of adult females and 52 percent of males survive each year until the age of five years. After that age mortality rates increase (Cramp and Perrins 1993). Small land birds are especially vulnerable in their first year.

Revealing the high levels of predation on young birds are the metal bands, or "rings," that accumulated with songbird carcasses in the nests of Eurasian Sparrowhawks in Wytham Wood at Oxford, England (Perrins and Geer 1980). These raptors fed intensively on the marked research populations of Great Tits and Blue Tits. The sparrowhawks took 922 ringed tits in 1976, 759 in 1977, and 1220 in 1978. Most were juveniles. Each year, the sparrowhawks ate from 18 to 34 percent of all Great Tit juveniles in that population and from 18 to 27 percent of the Blue Tit juveniles in that population.

After birds have reached adulthood, their chances of survival increase and stay essentially constant. Survivorship in juvenile Florida Scrub Jays, for example, is extremely low during the first few months after they leave the nest (Woolfenden and Fitzpatrick 1996; Figure 17–5). Only

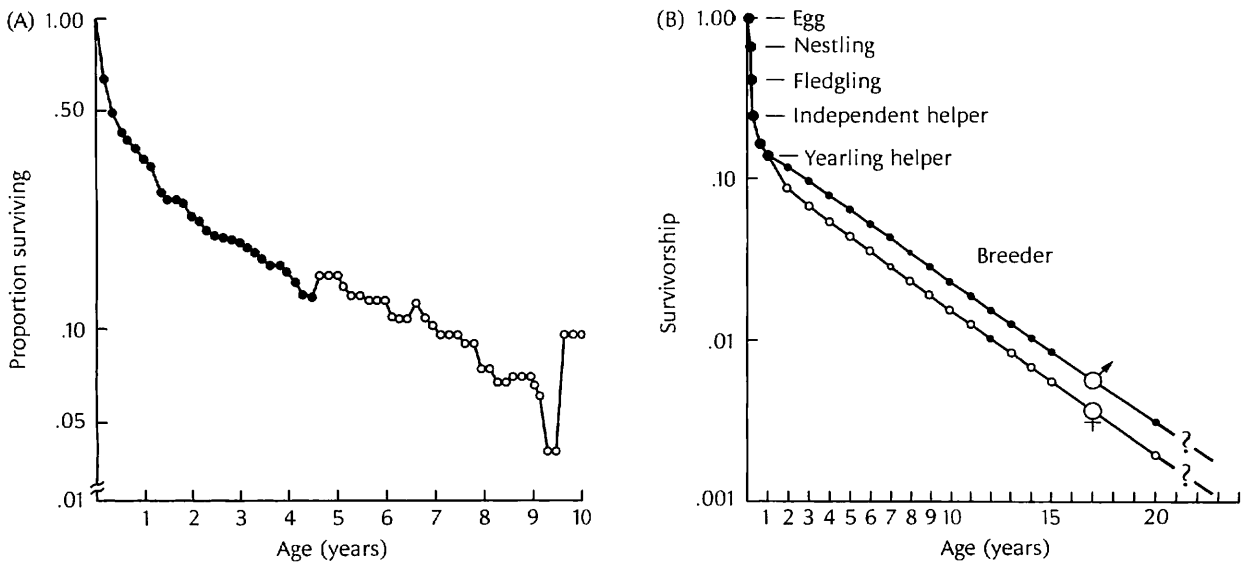


FIGURE 17–5 (A) Survivorship of Florida Scrub Jays (males and females combined) observed in a population in central Florida, from fledging through age 10 years. Black symbols indicate sample sizes of cohorts containing more than 100 potentially surviving birds. Data become more irregular and unreliable at the end because of small sample sizes. Note that the proportion surviving drops sharply in the first year of life to about 40 percent of the initial cohort. (B) A complete survivorship curve from beginning of incubation through possible age of senescence (question marks). Males (black circles) and females (white circles) diverge slightly after age one year because of the greater mortality of females, which disperse from their natal territory. Survivorship of breeders is identical between sexes. [*From Woolfenden and Fitzpatrick 1984*]

33 percent of Florida Scrub Jays survive their first year, after which they "graduate" to the higher survival rates of (breeding) adults, which average 78 percent a year.

A death rate that increases with age is called actuarial senescence. Until recently, there was little evidence that the death rate increases with age in birds, as it does in mammals, including humans. Now challenging the traditional view that mortality in adult birds is independent of age is evidence of senescence for at least 25 species including ducks, songbirds, and albatrosses (Holmes and Austad 1995; McDonald et al. 1996). A carefully controlled analysis of the life spans of adult Florida Scrub Jays revealed that their rate of mortality doubles in 6.4 years. Whether the increasing death rate in jays is due to the degenerative effects of their old age or other causes is not known (McDonald et al. 1996).

One potential cause—age-related declines in immune function—has been documented in wild populations of the Collared Flycatcher (Cichon et al. 2003). Older female flycatchers (5–6 years of age) produce fewer antibodies against a nonpathogenic vaccine of sheep red blood cells. They also produce smaller fledglings compared with young females (1 year old) and middle-aged females (3 years old). Recall that female birds transfer immunoglobulins to their young through the egg, which suggests that weakening immune capacities of older females could directly impair their young's health.

Fecundity

Fecundity—the number of young raised successfully—is a measure of an individual bird's reproductive success. Total lifetime reproductive success depends on the age at which a bird starts to breed, on how long it lives, and on the cumulative result of the bird's annual reproductive performance, both successes and failures. Annual fecundity, in turn, depends on the number of nesting attempts and the success of each attempt, the number of eggs laid each time (clutch size), and the age and experience of a breeding bird. Linked to these key elements of fecundity is a complex web of variables governing the relationships between parents and their offspring (Martin 2004).

Single and Multiple Broods Compared

The number of broods that a pair can raise depends, in general, on the length of the breeding season. Predation early in the cycle also can stimulate multiple renesting attempts. For these reasons, tropical birds generally attempt more broods than do temperate birds, owing, in part, to prolonged breeding seasons. In addition, because losses of nests and young to predators are higher in the Tropics than in temperate zones, renesting is often necessary to replace lost clutches. From two to six successive clutches are not unusual in the Tropics. The White-bearded Manakin, for example, typically lays from three to five clutches per season in Trinidad.

Long nesting cycles or restricted breeding seasons, such as those in Arctic latitudes (mid-June to July) tend to preclude extra broods. Hence, many temperate and Arctic birds—Pileated Woodpeckers, Ruffed Grouse, and Snowy Owls, for example—attempt only one brood. Short-lived species should try to attempt an extra brood or two each season if they can, given the uncertainty of surviving to the next breeding season. Experienced bluebirds, phoebes, and wrens raise two or more broods each season. Multiple broods in the same year significantly increase an individual bird's lifetime reproductive success.

Long-term studies of the breeding dynamics of Black-throated Blue Warblers at Hubbard Brook in New Hampshire revealed that about half (53 percent) of the females laid a second clutch of eggs after successfully fledging their first brood (Nagy and Holmes 2005a). These females nested on high-quality territories with more food (Figure 17–6). The proportion of females that laid second clutches also increased in other experiments in which supplementary food was provided and declined in experiments in which the availability of food was reduced (Nagy and Holmes 2005b). Both chicks and their double-brooded mothers benefitted from higher food availability. The young fledged at heavier body mass, which likely increased their survival after fledging. Double-brooded

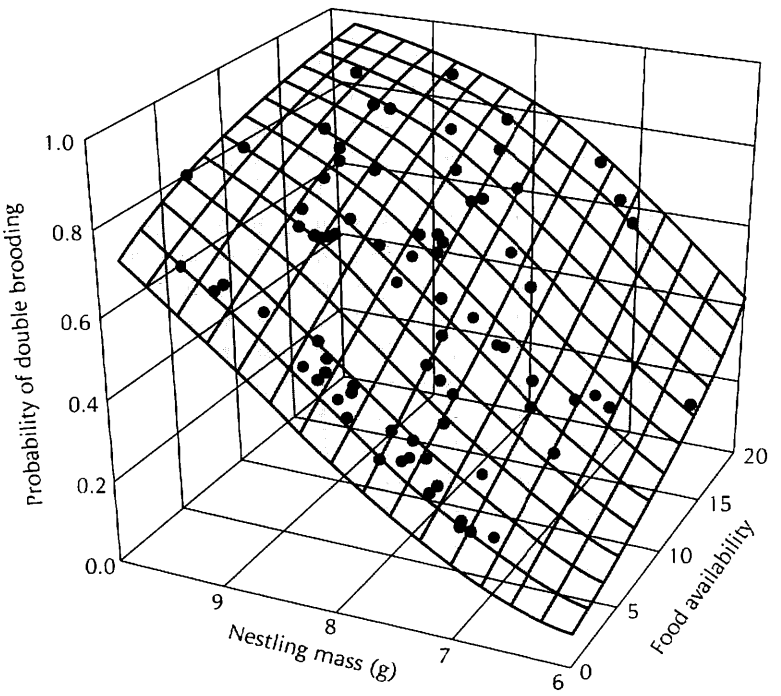


FIGURE 17–6 Food availability on territories of the Black-throated Blue Warbler affected both the mass of nestlings when they fledged and the probability that female Black-throated Blue Warblers would attempt a second brood. High-quality territories with the most food produced larger nestlings. Females on these food-rich territories were more likely to attempt a second brood. [*From Nagy and Holmes 2005a*]

females maintained their physical condition: they exhibited no extra costs of mortality the following winter. Annual survival of both was steady at 40 to 45 percent.

Some other bird species increase their seasonal productivity by overlapping successive clutches. Overlapping small clutches can be a better way of increasing fecundity than enlarging a single clutch, because it subdivides periods of peak parental care into smaller separate peaks. The male Goldcrest builds the second nest alone and then takes charge of the young in the first nest when the female shifts to incubate eggs in the second clutch. Then, challenged by the needs of two broods of young of differing ages, the male tends the older brood, for which the need is greatest. He shifts his attention to the second brood after the first has achieved independence.

Clutch Size

The number of eggs that a female bird lays in each nest, or clutch size, is an essential and heritable component of fecundity. Waterfowl, pheasants, rails, and many other precocial birds have clutch sizes of as many as 20 eggs. Passerines and other small land birds that feed their young lay clutches of 2 to 6 eggs, some as many as 19. The exact number varies among species. Within a species, it varies with latitude, climate, age, and quality of territory. Variation within a single species can be great. Northern Flickers lay from 4 to 14 eggs; Blue Tits lay from 8 to 19 eggs. Other birds have virtually invariant clutch sizes: precocial shorebirds typically lay 4 eggs, and oceanic birds lay only 1 egg. Hummingbirds and doves normally lay 2 eggs.

A simplified and traditional hypothesis is that nutritional requirements for egg formation limit the clutch sizes of precocial birds, whereas the abilities of parents to feed their young limit the clutch sizes of altricial birds. This classic explanation, however, opens rather than closes the discussion. For example, why should the Ruby-crowned Kinglet lay from 8 to 12 eggs, whereas the Yellow-rumped Warbler lays only 3 to 5 eggs (Martin 2004)? They are similar-sized species with similar life spans. They breed side by side in the boreal forests and eat similar insect foods. Food limitation cannot explain this difference. We will return to the question of food limitation and the evolution of clutch-size variations after first touching on some other aspects of fecundity.

Age and Experience

Birds that breed for the first time typically produce fewer eggs and raise fewer offspring than do older birds, primarily because competence and experience increase with age (Forslund and Pärt 1995). As yearlings, Peregrine Falcons are usually not good parents: they typically wait two to three years to breed (Figure 17–7). First-year pairs that try to breed usually fail (H. B. Tordoff, pers. comm.). One-year-old females, however, may nest successfully by pairing with an older mate. If they breed, young

FIGURE 17–7 A Peregrine Falcon. These raptors nest on cliff ledges. More recently, they also nest on tall buildings or bridges in urban areas.

males may kill their own young. For example, a one-year-old male in Milwaukee fertilized his mate's eggs and helped to fledge the young, but then he killed them by aggressively diving at them and accidentally breaking their wings. The next year, this male was less aggressive toward his offspring, which survived. In another case, a young female joined an experienced four-year-old male in Minnesota. She dropped her first egg into the nest box by accident while sitting on the front ledge and didn't know what do with it. She was unable to roll it from the edge of the box where it was lodged to the central nest scrape for incubation. The older male came to the rescue and promptly rolled it expertly from the edge of the box to the middle of the scrape. When the egg was in its proper place, thanks to the male, the female settled on it right away and laid the rest of the clutch in the scrape. In this case, incubation was successful, but often young females are inattentive and haphazard in their incubation behavior, causing their nests to fail.

Common Pigeons are prime prey for Peregrine Falcons. In addition to having a lowered risk of being caught, older Common Pigeons increase their reproductive output by overlapping sequential clutches of two eggs each. The extent of overlap of clutches increases with a mated pair's combined experience as parents and their ability to, together, handle the different stages of parental care at the same time (Burley 1980).

As a general rule, reproductive performance increases in the first years to a middle-age plateau and then declines in older birds. Improved foraging skills, better access to prime resources, and enhanced knowledge of predators all improve parental abilities. After their first year, for example, female Eurasian Sparrowhawks increase both the average number of eggs laid and the average number of young fledged per nest (Forslund and Pärt 1995; Figure 17–8). Seven- and eight-year-old females, however,

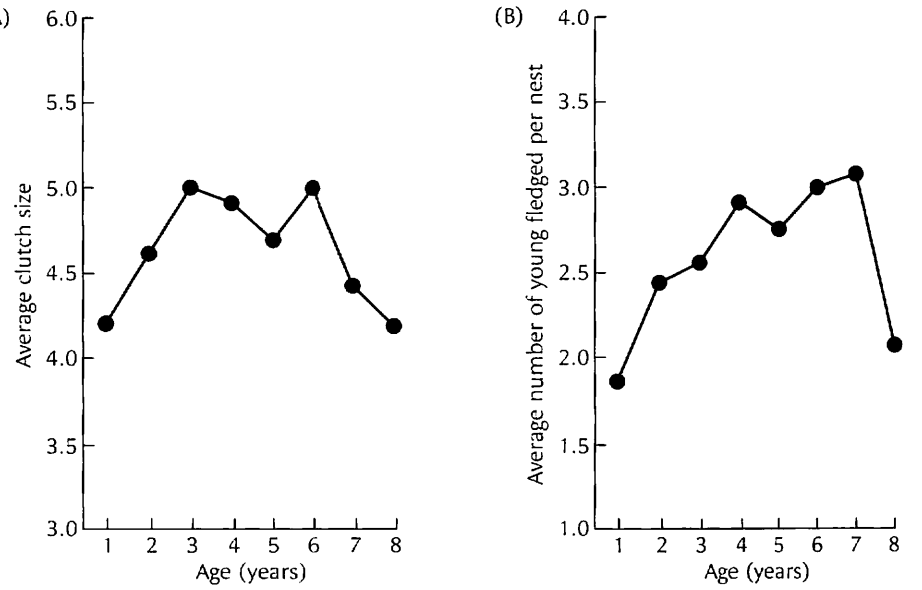


FIGURE 17–8 Age-specific fecundity in Eurasian Sparrowhawks. Both (A) clutch size and (B) the number of young fledged increase with age. Average clutch size grows to about five eggs in midlife but then declines in seven- to eight-year-old females. The average number of young fledged increases steadily with age and experience until age eight. [*After Forslund and Pärt 1995*]

exhibit reproductive senescence. Clutch size drops sharply at age seven, and the number of young that they fledge drops sharply at age eight.

In another example, older California Gulls produce more young than younger gulls (Pugesek 1983). The oldest gulls (12–18 years old) produce 1.5 young per year, whereas middle-aged gulls and the youngest gulls (3–5 years old) produce 0.8 young per year. Mature gulls feed their young more frequently, spend more time looking for food, and leave the nest unattended less often than do the younger members of the colony. This example is consistent with theory, which suggests that increased reproductive effort is expected of older birds with fewer years left to offset the costs of reproduction.

Delayed Maturity

Many birds wait a year or two or more to breed (Box 17–3). More generally, swifts breed at 2 years, parrots at 2 or 3 years, and raptors at 3 or more years. Water birds, except ducks, and seabirds generally take 4 or more years to breed for the first time, and large albatrosses and condors take from 8 to 12 years. Among the species with late maturity, age at first breeding correlates strongly with longevity (see Figure 17–2B).

In some species, the reduced prospects of reproduction in their first year disfavor investment in bright territorial signaling plumage, favoring instead more cryptic female plumages that help to reduce the risk of predation.

BOX 17–3

YOUNG FEMALE TREE SWALLOWS DELAY BREEDING

Floating populations of nonbreeding males, but not of females, are typical of birds. In an unusual case, many female Tree Swallows, especially yearlings, are unable to breed because of intense competition for nest holes. When they explore nest holes for vacancies, yearling females are subject to attacks by older residents, both males and females. Also counter to the general trend among birds, female, not male, Tree Swallows delay the acquisition of full adult breeding plumage for one year.

What might be the adaptive significance of these female swallows' delay in acquiring adult plumage? Ornithologists Bridget Stutchbury and Raleigh Robertson (1987) conducted experiments with models of yearlings and adults to test alternative hypotheses. They found that yearling females did not gain any reprieve from adult females, which attacked models with full breeding plumage or subadult plumages with equal intensity. Adult males, however, were always more aggressive toward the adult model. These ornithologists concluded that the subadult plumage of yearling females was advantageous because it signaled their inactive sexual status to resident males, not because it signaled their subordinate status to resident females.

Why should a bird delay breeding? Every extra year of nesting would seem to increase its chances of leaving some offspring. Birds that can breed in their first year should soon replace others that delay breeding for several years unless the costs of early reproduction are too severe. In long-lived birds, however, delayed maturity actually contributes to maximizing lifetime reproductive success. Delayed dispersal and cooperative breeding, for example, are a special case of delayed maturity (see Chapter 13).

The factors favoring delayed maturity are well documented in Adelie Penguins (Ainley et al. 1983). First, breeding entails greater risk than not breeding. The mortality of breeders (39 percent) is greater than the mortality of nonbreeders (22 percent). The greatest mortality is found the first time that young Adelie Penguins try to breed. An amazing 75 percent of 3-year-old females die in their first attempt to breed. The reason? They are less efficient at obtaining the food necessary to sustain the costly breeding effort. They may also be less wary or adept at escaping leopard seals lurking at the edge of the pack ice. Mortality then declines with age to 10 percent in 11-year-old breeding females.

Offsetting the risks of initial reproduction in Adelie Penguins are improved prospects for raising young in subsequent attempts. Adelie Penguins that breed for the first time at three to four years old (and survive that effort) are less likely to lose their eggs or young in subsequent nesting seasons than are those penguins that breed for the first time at a later age. Whether these early starters are inherently better breeders or the early start somehow enhances subsequent breeding success is not known.

Three to four years seems to be the minimum possible age for reproduction in small penguins such as the Adelie. Three main factors are responsible for this age requirement. First, studies of another species, the Yellow-eyed Penguin, suggest that two-year-old penguins are usually not

reproductively mature. Sixty-five percent of their eggs are infertile (Richdale 1957). Second, from two to three years of experience seem to be essential for young penguins to develop the foraging efficiency needed to accumulate the large energy reserves required for egg production and the long fasts while breeding. Third, at least one year of social experience is necessary to develop the behavioral skills required for successful pairing and the defense of nest, eggs, and young. Given the increased risks of mortality associated with breeding even when well prepared, there is a clear advantage to the three- to four-year delay typical of this penguin.

Males of some songbirds do not acquire full adult breeding plumage in their first breeding season, even though they are capable of breeding. Delayed plumage maturation reaches extremes, for example, in the lek-displaying Long-tailed Manakin, where young males wait eight years before reaching breeding status. Indeed, delayed maturation and the acquisition of adult features are widespread among birds (Lawton and Lawton 1986; Studd and Robertson 1985). Of the 105 sexually dimorphic passerines of North America, 31 (30 percent) do not attain full adult male plumage in their first year. Included in this number are Red-winged Blackbirds, Baltimore Orioles, Scarlet Tanagers, and American Redstarts.

Instead of the striking black-and-orange plumage of adult males, yearling or first-year male American Redstarts retain the olive-brown-and-yellow female plumage. They are sexually mature and establish territories (Sherry and Holmes 1997). But dominant older males force them out of optimal habitats into less desirable (conifer) habitats. More than half of the yearlings (57 percent) fail to reproduce, mainly because of a shortage of females. Only 25 percent of adult males don't find a mate, and some are even polygynous. In addition, the mates of yearling males on their inferior territories lay smaller and later clutches.

Annual Reproductive Effort

Increased investment into annual reproduction may take its toll on a parent's physical condition, on its reproductive potential the following year, and on its annual survival (see Chapter 16). The costs of breeding for young Adelie Penguins noted earlier are just one of many examples. Experiments with sea ducks called eiders show costs, too, specifically in reference to the effect of current effort on future fecundity. Sveinn Hanssen and his colleagues (2005) compared the costs of incubation for female Common Eiders by giving some females a three-egg clutch and others a six-egg clutch. Female eiders fast during incubation. The effort of incubating the larger clutch size increased the loss of mass in those females and reduced their immune functions. But the consequences did not become evident until the birds nested the following year and produced significantly fewer eggs.

Eastern Bluebirds also experience a future consequence of their annual reproductive effort (Siefferman and Hill 2005). The experimental enlargement of brood sizes prompts an increased feeding effort by the parents,

as compared with the efforts of parents with reduced broods. Males that fed reduced broods produced brighter plumage color the next year. Conversely, tending extra-large broods led to duller iridescence in the plumage of those males. The brighter-plumaged males that didn't overdo their effort the first year then mated with better females that laid eggs earlier in the next season.

The number of young fledged by Common Kestrels clearly affects their annual survival (Dijkstra et al. 1990; Figure 17–9). The reduction of brood size from the normal five chicks to just three increases the annual survival of both males and females. Increasing brood size from five chicks to six causes annual survival to drop sharply. Extrapolation of the curve fitted to these experimental data to even larger brood sizes suggested that trying to raise more chicks could be fatal. In fact, it is. Sixty percent of the kestrels that raised two extra nestlings were found dead before the end of the first winter, compared with only 29 percent of those that raised control or reduced broods (Daan et al. 1996).

A long-held and strongly supported doctrine is that females suffer greater mortality and thus have higher costs of reproduction than males do. This outcome, too, is evident in the kestrels: annual survival of females is 55 per cent compared with 70 percent of males, even when raising small broods. The better survival of male birds compared with females biases the sex ratio toward males in many bird populations, such as the American Redstart discussed earlier.

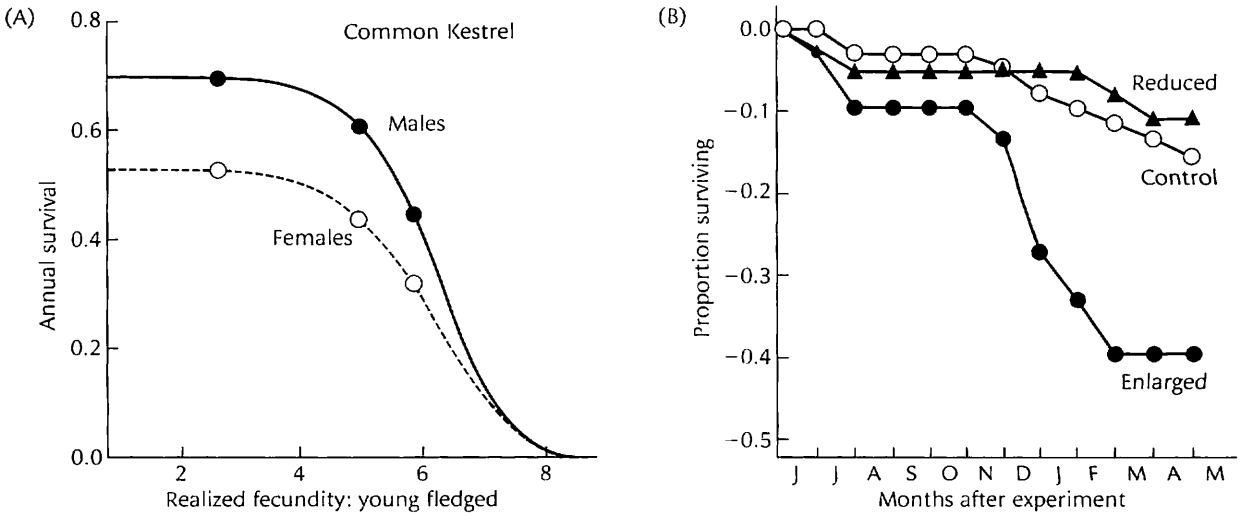


FIGURE 17–9 Tradeoff between reproductive effort and life span in the Common Kestrel. (A) Costs of reproduction are higher in females (white circles) than in males (black circles). Survival in both declined with experimental increases in brood size and in their realized fecundity (number of young actually fledged). (B) Enlarged brood sizes caused a major increase in mortality in the following year compared with control and reduced brood sizes. [*(A) After Ricklefs 2000a and Dijkstra et al. 1990. (B) After Daan et al. 1990*]

Does reproductive effort determine annual survival, as the short-term experiments with kestrels suggest, and perhaps a bird's full life span as well? Or is life span controlled by extrinsic factors: predation, winter or off-season starvation, or perhaps the risks of migration? Each of these factors could affect the number of lifetime breeding opportunities and therefore the appropriate level of annual investment. Increased reproductive effort can decrease the protective activity of major antioxidant enzymes (see Box 17–2).

The various life-history traits link together to define age-specific mortality, age-specific fecundity, and lifetime reproductive success. These complex linkages challenge us to resolve patterns of cause and effect.

Tom Martin (2004) asserts in his "new view of avian life-history evolution" that sources of age-specific mortality, such as nest predation and winter mortality, play a major role in determining the levels of reproductive effort of birds. He suggests that these sources of mortality can explain the differences in reproductive effort observed among species that occupy tropical versus temperate latitudes. In this view, the longer life spans of tropical and Southern Hemisphere birds, due to lower adult mortality, favor reduced annual reproductive efforts, including smaller clutch sizes. Local rates of nest predation (juvenile mortality) adjust reproductive effort within latitudes, and food availability then adjusts reproductive effort within species (Figure 17–10).

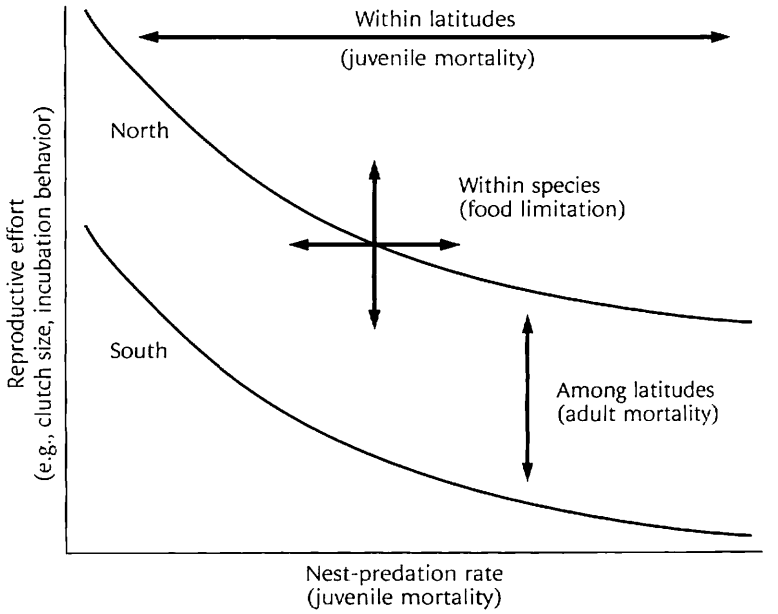


FIGURE 17–10 Major environmental influences on latitudinal variation in life histories. Martin's hypothesis proposes that age-specific mortality is of primary importance in explaining differences in birds' reproductive effort. Among latitudes, lower adult mortality in southern latitudes favors reduced reproductive effort. Within a particular latitude, lower nest (juvenile) mortality favors increased reproductive effort for a particular level of adult mortality. Food availability drives adjustments of reproductive effort within a species. [*From Martin 2004*]

Age-specific survivorship affects incubation behavior and, therefore, the length of the incubation period. It is well known that incubation periods within a species depend on the parents' attentiveness: More time actually incubating shortens the incubation period (see Chapter 15). Long-lived Argentine bird species are consistently less attentive than are their Arizona counterparts, even though predation risk is about the same in the two regions (Figure 17–11A). Recall the experiments demonstrating greater sensitivity to risks at the nest by Argentine species (see page 449). Another result of this study was that the species with low mortality as adults were less attentive to their nests, which increased the risk of losing their clutch to predators (Figure 17–11B). They opted instead for additional chances to breed in successive years.

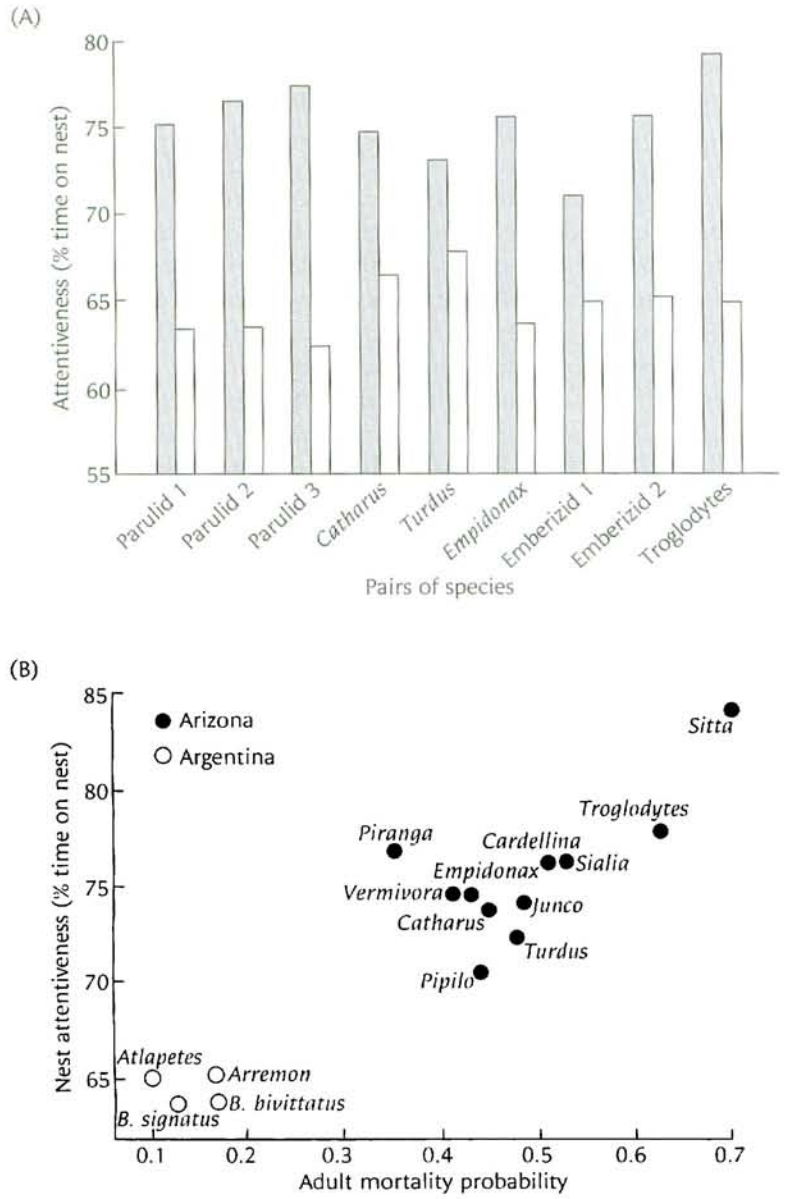


FIGURE 17–11
Attentiveness in Argentina versus Arizona. (A) Long-lived Argentine species (white bars) are consistently less attentive than are their shorter-lived matched equivalents in Arizona (gray bars). (B) Nest attentiveness increases with annual adult mortality. Black circles indicate Arizona taxa; white circles indicate Argentine taxa. Species with low adult mortality, especially those in Argentina, accept higher risks of nest loss by spending less time on the nest. [*From Martin 2002*]

Evolution of Clutch Size

No single topic has so occupied the attention of students of avian life-history patterns as has the evolution of clutch size. Clear patterns of clutch-size variation demand explanation. For example, average clutch sizes tend to be larger in the north temperate and in arid environments than those at lower, tropical latitudes and in wet environments. Why is this so?

The lively historical discussions about the reasons for such patterns continue, with increasing emphasis on nest predation and adult mortality. At work, however, are a host of factors ranging from phylogenetic history and constraints to age-specific tradeoffs between fecundity and life span. Clutch size is only one trait in a complex network of interacting traits that guide the evolution of diverse life histories in a population context. Now broadening the discussion is the integration of physiological constraints that govern avian life cycles with the dynamics of population ecology that affect an individual bird's lifetime reproductive success.

A formidable literature summarizes and interprets conspicuous patterns of clutch-size variation (Table 17–3). Clutch size is clearly an adaptation molded by selection over evolutionary time, but it is also sensitive to immediate environmental conditions. Some variations are due to genetic differences between individual birds, and others are due to a female's physiological condition (see Chapter 14). The inheritance of egg-laying ability is well known to poultry farmers, who increase egg production by artificial selection. What number of eggs maximizes short-term or lifetime reproductive success for a particular species?

Theoretically, an optimal clutch size—for each bird in an average year—produces the maximum number of young capable of surviving to sexual maturity. Theoretically again, an average optimal clutch size should prevail in local populations. Understanding the evolutionary forces responsible for the evolution of a particular clutch size, however, remains one of the most controversial and unresolved challenges for ornithologists, despite nearly a half-century of intense research. The debate about

TABLE 17–3 Conditions correlated with variations in average clutch sizes

Variable	Conditions Correlated with Small Clutches (2–3 Eggs)	Conditions Correlated with Large Clutches (4–6 Eggs)
Latitude	Tropics	Temperate/Arctic
Longitude	Eastern Europe	Western Europe
Altitude (temperate)	Lowlands	Highlands
Nest type	Vulnerable	Secure (cavity)
Body size	Large species	Small species
Habitat	Maritime, island, and wet Tropics	Continental, mainland, and arid Tropics
Feeding place	Pelagic seabirds	Inshore seabirds
Development mode	Altricial	Precocial

the evolution of clutch sizes among birds centers on applications and extensions of Lack's original food-limitation hypothesis.

Food Limitation

The avian clutch size is adjusted by natural selection to the maximum number of nestlings that the parents can feed and nourish. Food availability limits clutch size. This fundamental postulate, which was championed with great force by David Lack (1947, 1948), guided research for more than half a century (Ricklefs 2000b). The hypothesis assumes that individual birds will be disadvantaged by natural selection if they lay fewer eggs each year than they can raise.

The strongest support for Lack's hypothesis comes from observations of the relative success of various sizes of clutches and from experiments designed to test the ability of parents to feed extra young. Some of these experiments were discussed in preceding chapters. In now-classic work, Christopher Perrins and Dorian Moss (1975) experimentally increased and decreased the clutch sizes of Great Tits in Wytham Wood, near Oxford, England (Figure 17–12). Clutches of 10 to 12 eggs produced the most surviving young Great Tits. The probability of a chick's survival in a small brood was greater than in a large brood because the nestlings in a small brood are better fed and are heavier when they fledge, but the number of potential fledglings from small broods is, by definition, low. Above a brood size of 12, chicks tend to be underfed and to die, especially in "bad" years of poor food availability. In 6 of 13 consecutive years, the average natural brood size in the population was 10—that is, close to the most productive number—but the average brood size was slightly lower than predicted in other years, an outcome resulting in an overall average across years of 8.5.

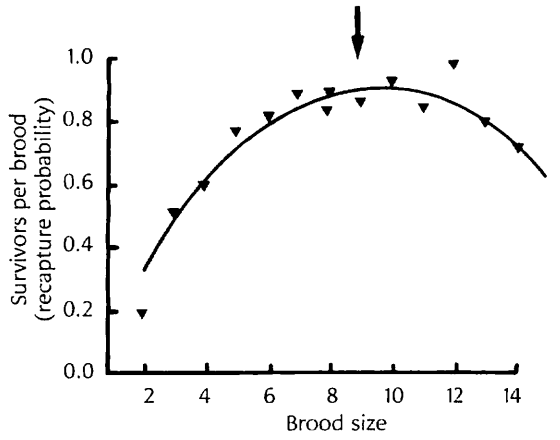


FIGURE 17–12 Lack's hypothesis of optimal clutch size projects a maximum number of surviving young as a result of the balance between the number of young hatched and their probability of survival. In the population of Great Tits in Wytham Wood, broods of 10 to 12 chicks are the most productive. The average clutch size in this species is 8.5 (arrow). [*From Perrins and Moss 1975*]

Thus, birds seem to err on the side of caution. The vulnerability of large clutches in bad years favors moderate clutch sizes in the long run (Boyce and Perrins 1987). Conversely, the practice of brood reduction gambles on the bonus of the occasional survival of an extra egg or chick (see Chapter 16).

The strengths and weaknesses of Lack's hypothesis can be seen in its application to the increases in clutch size with latitude. The average clutch sizes increase with latitude for many passerines, owls, hawks, herons, terns, gallinules, some fowl, and some grebes. Lack (1947) proposed that this increase was due to the longer day length at high latitudes. Birds nesting during the long high-latitude summer have more time to find food for their young and themselves.

The potentially positive effects of increasing day length, however, do not explain why clutch sizes increase with latitude for owls that feed at night and thus have less foraging time, not more. Clutch sizes also increase not with day length but with longitude from east to west in Europe, with altitude in the temperate zone but not in the Tropics, and on the mainland compared with adjacent islands. Different day lengths can't be the explanation for these trends. Finally, some species of birds can raise extra young that are added experimentally (Vander Werf 1992). Even some large seabirds, such as gannets, which normally lay only a single egg, can raise two young when an extra egg is added to the nest, without obvious short-term penalty (Nelson 1964). Thus, Lack's hypothesis, as stated above, cannot be fully generalized.

Seasonality and Density Dependence

Lack's hypothesis dominated the discussion of avian life histories for at least 20 years, from 1947 to 1967. In this period, two great ornithologists, Reginald Moreau and Alexander Skutch, led opposing, population-based viewpoints that emphasized the effect of population density on reproductive rate. They were, however, less forceful personalities than was David Lack (Ricklefs 2000b). As a result, their broader perspective did not prevail in their lifetimes. Their views were revitalized in a lucid challenge by Martin Cody (1966) and a series of new modeling approaches to population ecology.

From this work emerged the broader, modern population perspective of evolutionary ecology. This view recognizes the advantages of reducing the costs and risks of annual reproductive efforts to maximize lifetime reproductive success. The evolutionary ecology perspective also defined the effect of adult mortality, first, on population density and, then, on reproduction rates through density-dependent effects on food availability (Figure 17–13).

Seasonality of food is the key to these relationships. Birds of seasonal arid habitats in both Africa and Ecuador have larger clutches than do those in habitats that are humid year round at the same latitude. More generally, clutch sizes of birds relate directly to seasonal increases in food production rather than to absolute level of food production (Ashmole 1963b; Ricklefs 1980; Figure 17–14). This relationship exists because adult

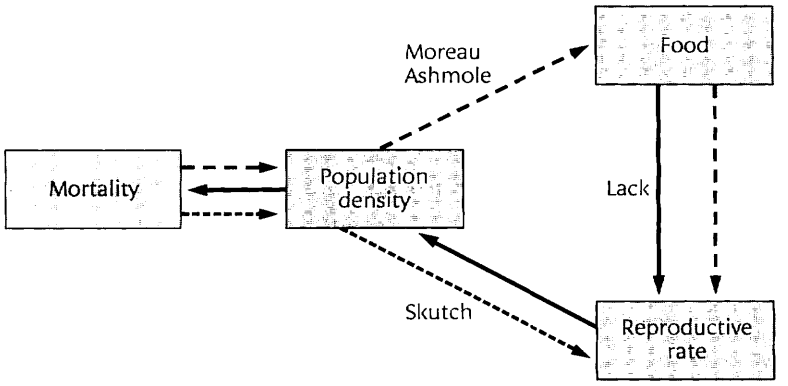


FIGURE 17–13 Different views of the relation between adult mortality and reproductive rate. Arrows indicate the direction of influence. David Lack (solid arrow) stressed the control of reproductive rate by food availability, and in turn, the control of population density and rates of mortality. Alexander Skutch, Reginald Moreau, and Phillip Ashmole favored broader views of evolutionary ecology that emphasized the effects of adult mortality on population density and then reproductive rate either directly (Skutch, dotted line) or indirectly through food availability (Ashmole and Moreau, dashed line). [*After Ricklefs 2000b*]

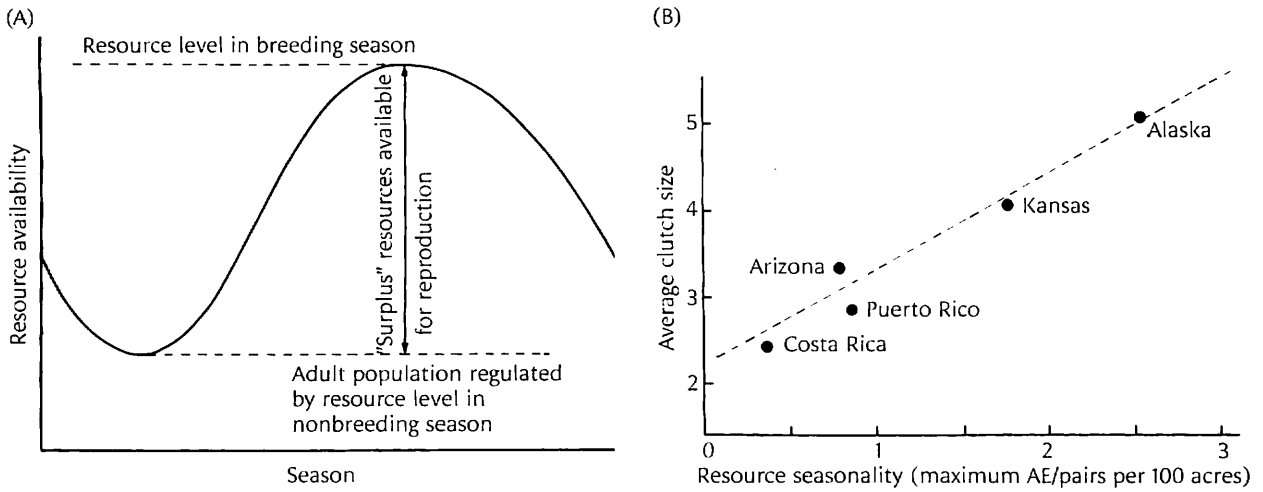


FIGURE 17–14 The seasonality hypothesis for geographical variation in clutch size. (A) Model of the seasonal increase in resources available for reproduction, measured in some months as the "surplus" above those resources that limit population size in the nonbreeding season. Clutch size varies in relation to the ratio of the breeding-season surplus to the adult population. Resources that are available during the breeding season depend on local demands by consumers, and these demands, in turn, depend on population density. The population densities of resident birds are regulated by low resource availability during the nonbreeding season. Seasonal increases above this baseline thus control the resources available for breeding on a per capita basis. (B) Clutch size increases with resource seasonality, measured as the ratio of maximum actual evapotranspiration (AE, an index of plant productivity) to the density of breeding pairs of birds. [*From Ricklefs 1980*]

mortality in the cold or dry season of lowest food availability determines population density and baseline levels of food consumption in a habitat. The survivors as well as seasonal visitors then can benefit from increased per capita food availability in the spring.

Through its control of adult mortality, variation in the seasonality of resources is the ultimate cause of geographical variations in clutch size, at least within a species. The pattern of clutch-size variation in the Northern Flicker, a widespread North American woodpecker, supports this "seasonality hypothesis" (Figure 17–15). Clutches of the flicker range from 3 to 12 eggs and increase by an average of 1 egg per 10 degrees of latitude. Variation in clutch size is directly correlated with the resources available to each breeding woodpecker. Walter Koenig (1984) estimated these resources as the ratio of local summer productivity (in terms of actual evapotranspiration, an index of plant productivity) to the breeding density of all woodpeckers. Local breeding densities of woodpeckers, in turn, are set by winter productivity, which determines how many woodpeckers survive until the breeding season.

Predation

Adult mortality is one of the principal population processes that shape avian life histories. Nest predation is another. Nest predation is a major force in the evolution of avian life-history traits ranging from nest construction and visitation (see Chapter 15) to clutch size and caring for young (Martin 2004).

In precocial birds, predation risk may limit clutch size by limiting the number of fledged young that parents can guard. Even though the par-

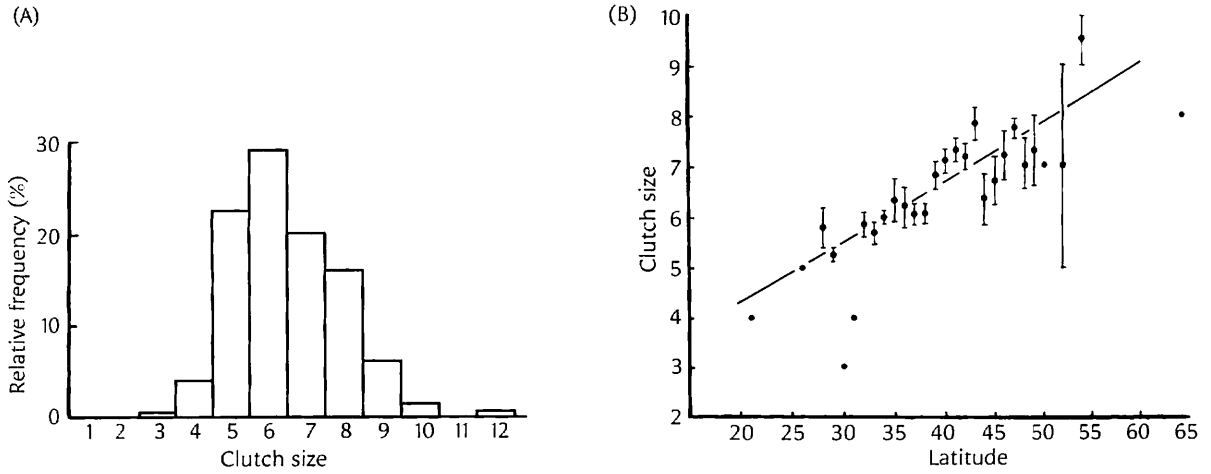


FIGURE 17–15 (A) The clutch sizes of Northern Flickers vary from 3 to 12 eggs. Relative frequency equals the percentage of total sample that had *x* number of eggs. (B) The increase in average clutch size with latitude supports the seasonality hypothesis. Vertical lines on the graph represent local variation in clutch size. [*From Koenig 1984*]

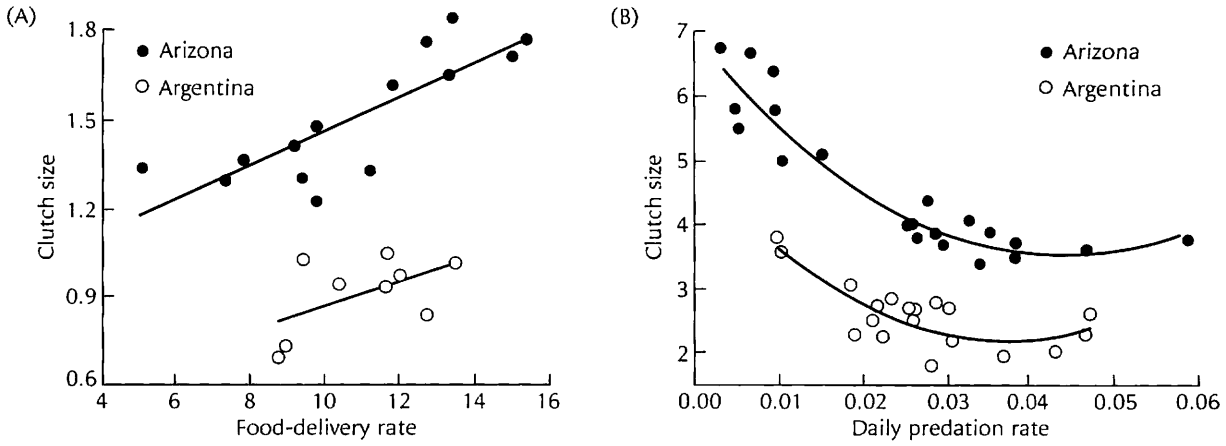


FIGURE 17–16 Predation selects for smaller clutch sizes through rates of parental visitation. (A) Larger clutches produce larger broods that require more frequent parental visitation for delivery of food. (B) Clutch sizes are negatively related to the nest-predation rate within each locality. Lower adult mortality in Argentina selects for smaller clutch sizes, and predation rates play a significant but secondary role. [*After Martin et al. 2000b*]

ents of many shorebirds do not feed their precocial young, for example, they brood and tend them actively and guard them from predators. Physical distance between parents and their mobile young increases with brood size and potentially sets an upper limit on brood size (Safriel 1975).

Nest predation may favor smaller clutches of songbirds in several ways. First, small clutches take fewer days to complete, reducing the daily risk of their being found. Second, smaller numbers of young in a nest make less noise that might attract predators (see Chapter 15). Third, and perhaps most germane, reduced visitation by parents to feed smaller broods reduces the risk that nestlings (and parents, too) will be found and eaten. Selection, therefore, favors risking fewer eggs at a time and renesting as frequently as possible in (tropical) habitats with high nest-predation rates.

Support for this hypothesis about clutch size and renesting comes, again, from comparisons of nesting pairs of matched bird species in Argentina and Arizona (Martin et al. 2000a; Figure 17–16). Reduced visitation rates in the face of different levels of nest predation explain the variation in clutch sizes among bird species within Arizona and Argentina but not between the two regions. Instead, the difference between regions is best explained by differences in adult mortality and adult attentiveness during the incubation period, as already mentioned.

Summary

Life histories are sets of evolved traits or attributes. Woven together, individual life-history attributes interact with environmental variables to determine an individual organism's performance. In particular, the study

of life-history patterns of birds explores the links between parental efforts and life span because, in the end, an individual bird's lifetime reproductive success is what counts. Compounding the challenges of survival through each stage of the annual cycle are the tradeoffs between the short-term costs and risks of reproductive effort and the opportunities for breeding in the future. The rates of reproduction and annual survival of individual birds also combine to establish the dynamics of their population's growth or decline.

A bird's lifetime reproductive output includes the age at which it first reproduces, the number of young that it fledges each year, the survival of those young, and its own longevity as an adult. Most small birds live from 2 to 5 years, whereas large birds may live from 20 to 40 years. Although many young birds die in their first year as a result of predation and starvation, the survival rates of adults are much higher and remain basically the same from one year to the next. Senescence has been demonstrated for several species of birds.

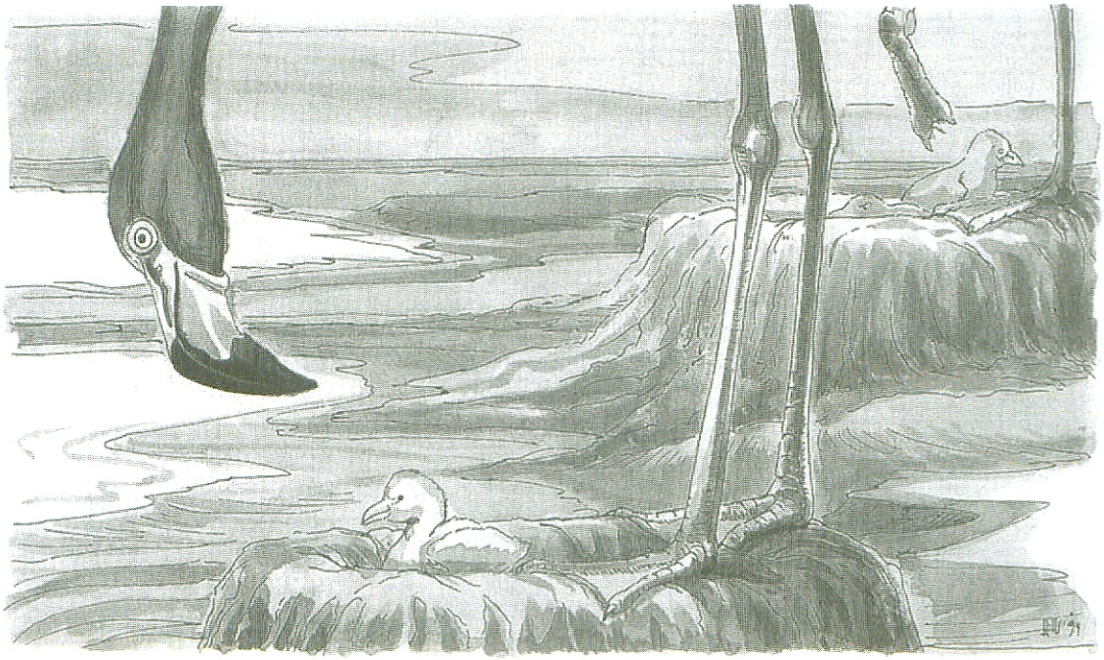
A fast–slow axis captures most of the variation among the diverse life-history patterns of birds. Life-table analyses compile the statistics, or demographics, of individual performance. In general, short-lived species usually breed when one year of age and produce many young each year. Long-lived species tend not to breed until they are several years old and to produce few young each year. Reproductive success and effort usually improve with age and experience. Delayed maturity is one way of maximizing lifetime reproduction. Birds also increase the number of young produced by raising several broods sequentially in a season and, in some cases, by overlapping successive broods.

Lack's original hypothesis that birds raise as many young as they can feed is now amplified and informed by the integration of the population-density effects of adult mortality, which affects food availability. High rates of nest predation favor smaller clutches.

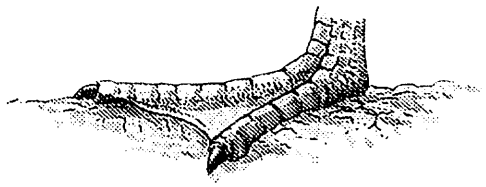
This chapter has reviewed individual life-history attributes as they evolve in response to the environment mediated by population processes such as adult mortality. Life-table statistics sum up the lifetime reproductive successes of individual members of a population to define whether the population is stable, growing, or declining. The dynamics of population trends themselves, including the nature of density-dependent regulation, are the subject of Chapter 18. The dynamics of bird populations based on the lifetime reproductive success of individual birds are also central to the themes of the final three chapters: the evolution of new species (Chapter 19); the coexistence of species in communities (Chapter 20); and the future viability of species, the heart of conservation of biodiversity (Chapter 21).

PART 6

POPULATION DYNAMICS AND CONSERVATION



CHAPTER 18



Populations

The successful conservation of any threatened species requires knowledge of both its population biology and its ecological requirements. [Bourliere 1991, p. v]

Bird populations fluctuate dynamically in their sizes and their distributions. Dramatic rebounds may follow worrisome declines, climate-induced bottlenecks, or local wipeouts due to disease or predation. Fluctuations in population size, whether short term or long term, affect the genetic diversity of a population, the process of local selection, and the potential for speciation—the topics of Chapter 19.

The fluctuations in bird populations are the summed successes and failures of individual survivorship and fecundity, outlined in Chapter 17. Small-bird species with short generation times have high growth potential. They are able to respond opportunistically to environmental changes, including human-dominated landscapes. Large-bird species with long generation times, however, do not rebound easily from their population setbacks.

This chapter on populations is based on the principle that populations are dynamic, not stable or static, in their sizes and distributions. We first consider the growth potential of populations and the factors that control or limit that growth. The next topic, population regulation, concerns the effects of density-dependent forces within populations, including social interactions. The final sections of this chapter summarize the value of long-term trends of bird populations as indicators of environmental quality. The population dynamics of a species are fully intertwined with their viability and their conservation needs, previewed here and then explored further in Chapter 21.

Growth

Bird populations fluctuate dramatically in size from year to year. Major storms or unpredictable climate shifts can affect local bird populations in

BOX 18–1

REBOUND OF THE SHORT-TAILED ALBATROSS

Although small populations of birds are vulnerable, they can be resilient. Most small populations have an intrinsic potential to rebound from severe reductions. A legendary case is that of the Short-tailed Albatross. It once nested in abundance in the western Pacific and congregated at the entrance to San Francisco Bay when whale slaughtering produced abundant food there.

By 1929, feather hunters reduced this species to one population of 1400 birds that bred at Toroshima, an island refuge off southeastern Japan. Eruptions of the island's volcano in 1939 and 1941 destroyed this remaining albatross colony. The species was declared extinct when no birds returned to the island to breed from 1946 to 1949.

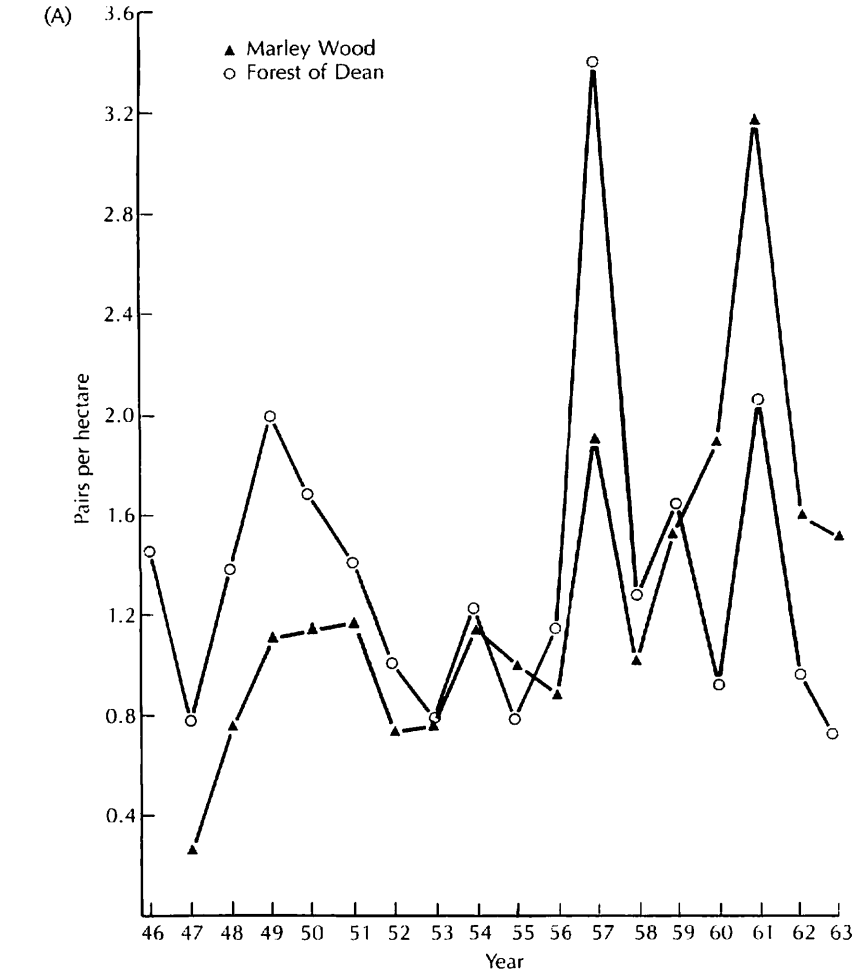
Remaining, however, were some young birds that had been at sea. (Albatrosses wait 10 or more years before starting to breed.) In 1954, six pairs of these young survivors returned to Toroshima and produced a total of three young. Today, despite their low fecundity and delayed maturity, Short-tailed Albatrosses are recovering. The world population increased to 1840 birds in 2005 and continues to rebound.

the short term. Healthy populations, however, typically rebound from their short-term setbacks (Box 18–1).

Bird populations also change slowly with the passage of time. Great Tit populations throughout Holland and England, for example, have grown in average size since about 1950, whereas local densities fluctuate fourfold from year to year (Figure 18–1A). Gradual warming of the European climate aided their widespread increase, and winter food fluctuations caused the changes from year to year. Conversely, Texas quail populations, both Scaled and Northern Bobwhite quail, are declining steadily (Figure 18–1B). Widespread degradation of habitat is the reason. Populations of both species, but especially those of the Scaled Quail, increase with rains and decline in dry years.

Bird populations have great growth potential. The 120 Common Starlings that were introduced into Central Park in New York City in 1890 multiplied into more than 200 million birds continent-wide in a century (Cabe 1993). More recently, but with similarities, the eastern population of the House Finch started when a few caged birds were released on Long Island in 1940. The population grew rapidly in number, roughly 21 percent per year from 1965 to 1979 (Hill 1993; Figure 18–2). Expanded geographical distributions accompanied this rapid population growth. The range of the population expanded from Long Island throughout the eastern United States and Canada. Continuing to expand westward to the midwestern states, this population made contact in Kansas 25 years later (early 1990s) with the well-established western populations of House Finches.

Some life-history traits, particularly short generation times (early age at first reproduction combined with short life span), foster the evolutionary and geographical success of species through their effects on population



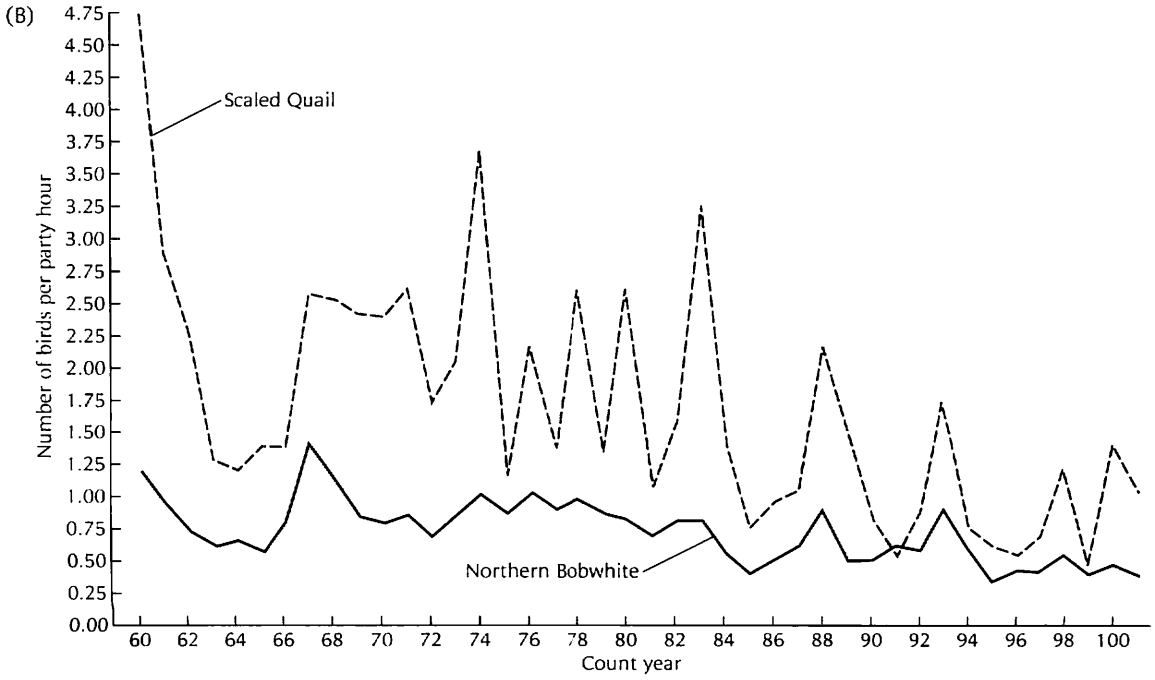


FIGURE 18–1 (A) Annual fluctuations in the density of breeding pairs of the Great Tit in two British forests, Marley Wood and the Forest of Dean. (B) Annual fluctuations and long-term population trends in Texas quail. A count-year number is assigned to the years in which the a bird count started and ended. For example, the number 60 refers to the years 1959–1960 and the number 100 refers to the years 1999–2000. The total counts each year are standardized with respect to effort in terms of "party hour," or, specifically, the average of the numbers of individual birds of a species per party-hour values for each count circle in the region. [*(A) After Lack 1966. (B) From National Audubon Society 2002*]

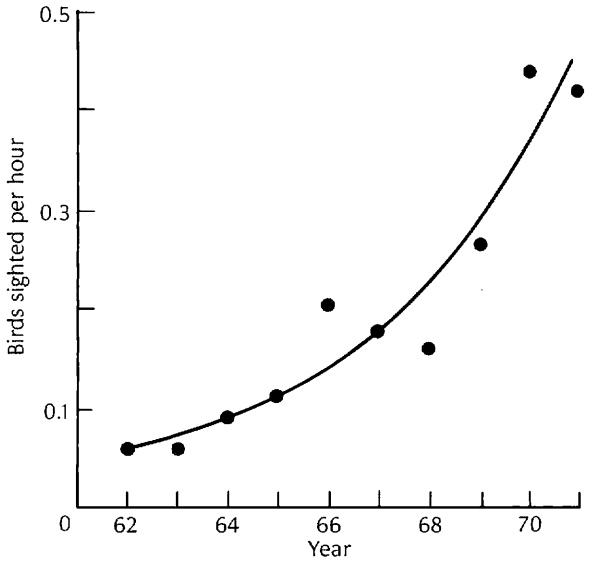


FIGURE 18–2 Exponential population growth of House Finches introduced east of the Mississippi. [*After Bock and Lepthien 1976b*]

growth rates. Short generation times greatly accelerate the rates of population growth. The reproductive success of individual birds in the first generations quickly compounds itself, compared with species that take years to mature and have few young at a time. Short generation time explains why bacteria and insects multiply so fast. In both birds and mobile mammals such as bats, short generation times also promote the ability to colonize, to speciate, and to diversify (Marzluff and Dial 1991).

In general, large-bodied species with low reproductive rates have annual growth potentials ranging from 10 to 30 percent. Small-bodied species with large brood sizes and high reproductive potentials have an annual growth potential ranging from 50 to 100 percent in favorable years (Ricklefs 1973).

A thriving population in a new environment grows in size in an S-shaped, or sigmoid, growth pattern on a graph. The rate of growth increases slowly at first, then accelerates, and later declines because of negative feedbacks that lower reproduction and survival. As the size of a growing population approaches the maximum supportable by the environment, called the environment's carrying capacity, the population growth rate slows down as its needs for resources begin to exceed their availability. The growing population also becomes increasingly vulnerable to predation and disease. The population then fluctuates in size about an equilibrium value that an environment can support in a typical, or average, year.

The two key phases of the S-shaped growth curve are the period of maximum growth and the final period of reduced growth ending with the stabilization of average annual population size. The changing population growth rates derive from the demographic parameters of survival

and fecundity reviewed in Chapter 17. Recall that, when values of per capita replacement, R_0, are greater than 1, they correspond to a growing population, and values less than 1 correspond to a declining population. The instantaneous growth rate, r, of the population is the logarithmic form of R_0. In the phase of accelerating growth, the rate of change in the number of birds with time—dN/dt, from differential calculus—is the product of the instantaneous growth rate r and the population size N at time t. This relation is expressed mathematically as

$$dN/dt = rN$$

Bird populations have tremendous growth-rate potential in the acceleration phase. Newly established North American populations of the Cattle Egret, for example, grew exponentially. Native to Africa, the Cattle Egret colonized North America (from South America) in the early 1950s and then increased dramatically from 1956 to 1971 (Telfair 1994). The calculated value of r was 0.21 for the 16-year period from 1956 to 1971 (Bock and Lepthien 1976a), but, owing to immigration as well as reproduction, was as high as 0.84 during the initial 5 years of this expansion. After 1971, the growth rate of the Cattle Egret population in North America slowed down as the population stabilized and fluctuated about its upper level (Figure 18–3). The species then declined in northern states.

The recruitment of young birds into a local population every year drives the growth of a local population. Local recruitment includes the

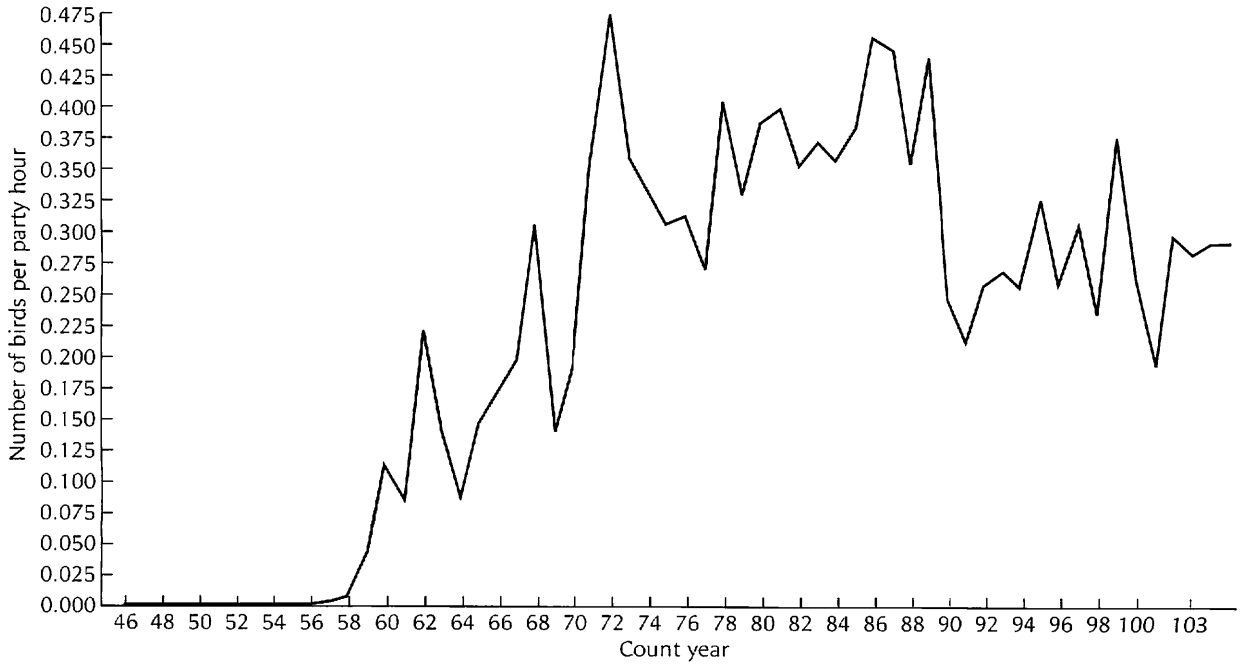


FIGURE 18–3 Population growth of Cattle Egrets that colonized North America in about 1950. Count-year number 46 refers to the years 1945–1946; number 103 refers to the years 2002–2003. [*From National Audubon Society 2002*]

number of young produced in the breeding season and, particularly, the proportion that survive their first six months of life. In addition to those produced locally, recruits include young from other places. Immigrants from elsewhere contributed to the initial growth of the Cattle Egret populations in North America (Telfair 1994). Immigrants also contributed significantly to the growth of the population of Atlantic Puffins on the Isle of May, off eastern Scotland. The number of puffins there increased by 19 percent a year from 1973 to 1981 (Harris and Wanless 1991). Recruitment of immigrating young birds from a population on the Farne Islands 80 kilometers away accounted for 3 percent, whereas local production accounted for 16 percent.

Control

Inevitably, critical resources such as winter food stop or limit continued population growth. In regard to the puffins on the Isle of May, the survival of both adults and immatures declined after 1981 as a result of widespread declines in winter food in the North Sea. The lower survival rates halted the growth of the population, which stabilized in size.

Ecologists distinguish between the terms "limitation" and "regulation" of population sizes. Limitation refers to any ceiling on population growth. Habitat, food, climate, disease, and predation are the primary forces that limit the sizes of bird populations.

Regulation refers to the effects of population density on population size. Density-dependent changes in birth rates and death rates buffer the short-term fluctuations in populations. Both mean clutch size and number of fledglings of the Great Tit, for example, depend on local population density. Great Tits lay fewer eggs when population density is high than when it is low. Sixty percent of the variation in annual mean clutch size is directly related to population density. Success in rearing nestlings also decreases as population density increases, because of increased predation and because fewer females attempt second broods (Figure 18–4).

Long-term studies of the demography of the Snow Goose nesting colony at La Pérouse Bay, Manitoba, illustrate the negative consequences of increasing population density. These studies documented a steady growth of the population followed by a decrease in its growth rate due to the damage inflicted by the geese on their own Arctic marsh feeding grounds (Cooch and Cooke 1991). This Snow Goose population increased steadily in size by approximately 8 percent per year after 1973 because fecundity routinely exceeded mortality. The growing population, however, damaged the quality and availability of the nutritious tundra grass required by breeding geese and their goslings. Repeated degradation of the tundra caused gosling weight at fledging and subsequent adult weight to decline 11 percent from 1973 to 1981. First-year survival declined from 50 to 35 percent. These changes caused population growth to slow down, consistent with the operation of density-dependent processes.

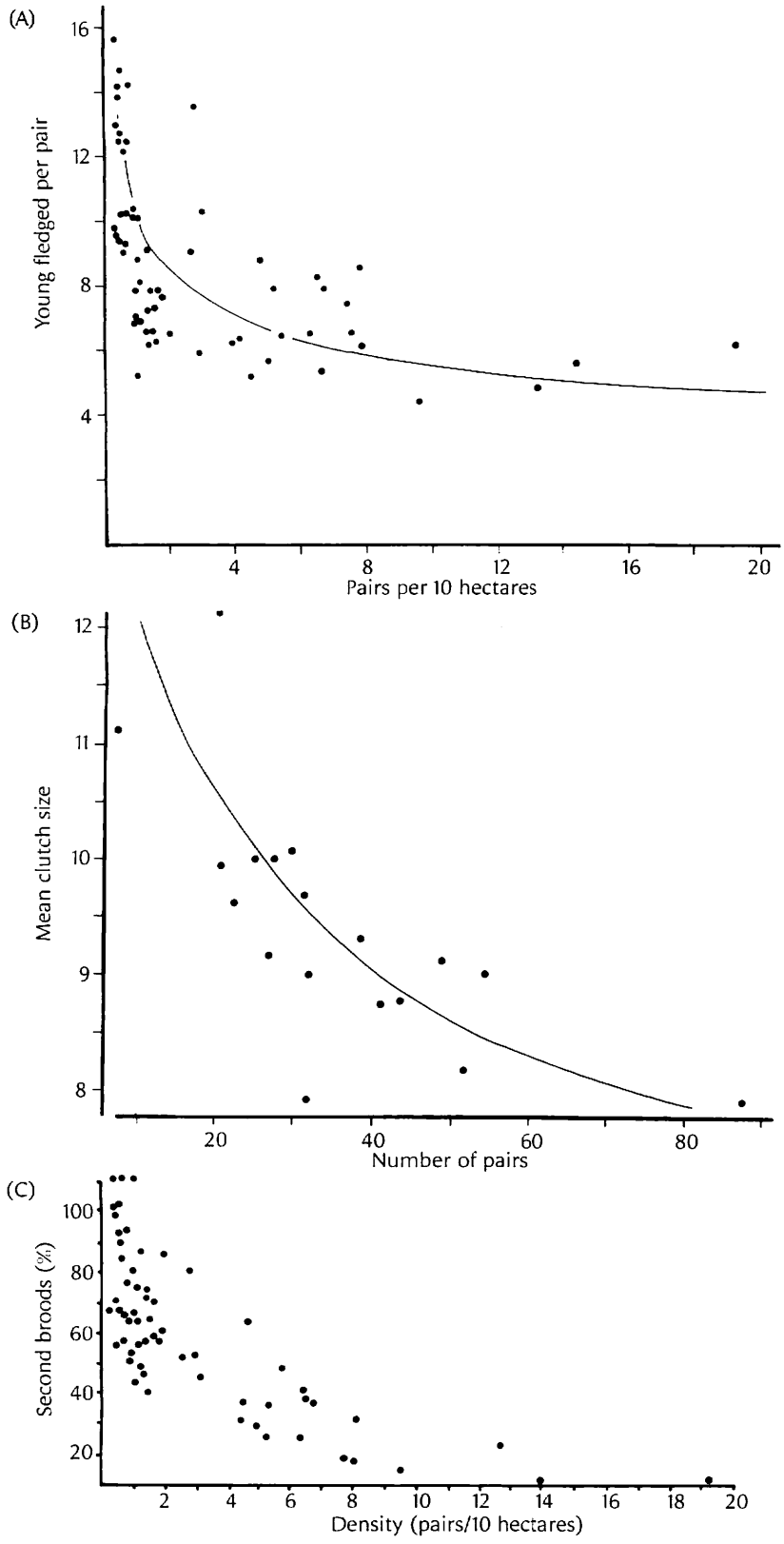


FIGURE 18–4 (A) Reduced fecundity at higher densities in the Great Tit is due to (B) smaller clutches at high population densities and (C) less frequent attempts to raise second broods. [*After Klomp 1980; Kluijver 1951*]

The distinction between "limitation" and "regulation" can be challenging. Food supply, for example, can limit numbers in either a density-dependent way or in a density-independent way. The proportion of birds that starve would be independent of population density if mass starvation were due to a major ice storm that eliminated critical food supplies. On the other hand, the proportion of birds that starve may depend on the number of birds that vie for declining winter food supplies that can potentially support 50 birds but not 100 birds.

The life-history parameters of fecundity or survival may be subject to density-dependent influences, but they still may not limit population sizes. Density-dependent clutch sizes or adult survival, for example, might not limit population size if, instead, hurricanes kill most of the juveniles each year, limiting recruitment into the breeding population no matter how many chicks fledge. In a more specific example, density-dependent fecundity and survival in the breeding season have only a minor effect on the population sizes of Great Tits. Instead, the availability of winter food regulates population size through the density-dependent survival of juveniles during the winter season. Habitat limitation, territorial behavior, and dispersal also play mediating roles.

The next sections first consider the ecological forces that limit population sizes. Then follow the ways in which population density and social forces can interact with ecological forces to regulate population sizes.

Limitation

The sizes of populations are limited by the available habitat and food supplies. They are also limited by the prevalence of natural enemies, including predators, parasites, and diseases.

Habitat

More than any other factor, habitat availability determines population size. Many endangered species, such as Red-cockaded Woodpeckers and Kirtland's Warblers, are extreme habitat specialists with limited and local distributions that correspond to their particular needs. The Red-cockaded Woodpecker, for example, is intimately tied to old-growth southern pine forests. Unlike most woodpeckers, Red-cockaded Woodpeckers excavate their nest cavities in living rather than dead pine trees. They require a highly limiting resource—namely, pine trees that are 80 to 100 years old and have been infected by the red heart fungus. The fungus rots the old pine tree's heart wood just enough to allow the woodpeckers to excavate. This excavation, however, requires a major investment of time and energy. Not surprisingly, clans of this cooperatively breeding woodpecker reuse the same cavities for years.

Major reductions in primary habitats reduce bird populations accordingly. Like Red-cockaded Woodpeckers, Spotted Owls depend on the remnant old-growth forests in the Pacific Northwest. These forests now

cover less than 10 percent of their original extent. Rails, bitterns, and waterfowl populations generally declined throughout the United States as wetlands were drained for agricultural, industrial, and suburban development. Less than 10 percent of the original wetlands of California remain. In recognition of the loss of habitat, many conservation efforts have shifted their emphasis in recent years from species protection to the preservation of critical habitats.

Many species occupy assorted habitats that vary in quality. Local population densities of Great Tits, for example, vary predictably with habitat quality. Deciduous hardwood (oak and beech) forests, for example, support 10 times as many breeding pairs as do pine forests. Mixed hardwood–pine forests support intermediate population densities. The density of tits increases as the composition of trees in a local forest shifts from pine to oak and beech (Figure 18–5). Less food in pine forests than in oak-and-beech forests leads to larger territories and more starvation of nestlings. The amplitude of annual population fluctuations also is greater in thinly populated pine habitats than in densely populated oak-and-beech woodland. The pine forest is a secondary, or suboptimal, habitat occupied by the overflow of Great Tits that are excluded from deciduous woods. Conversely, individual birds from pine-forest habitats quickly fill vacancies in the hardwood forest.

The essential resources provided by a particular habitat range from food to nest sites. For some birds, the availability of nest holes limits population size. Woodpeckers can dig their own nest holes, but other birds must either use abandoned woodpecker holes or dig their own in soft dead wood. Dead trees and branches are routinely removed from the managed forests of Britain and other parts of Europe. The resulting shortage of nest sites caused the extirpation of the White-backed Woodpecker and clearly

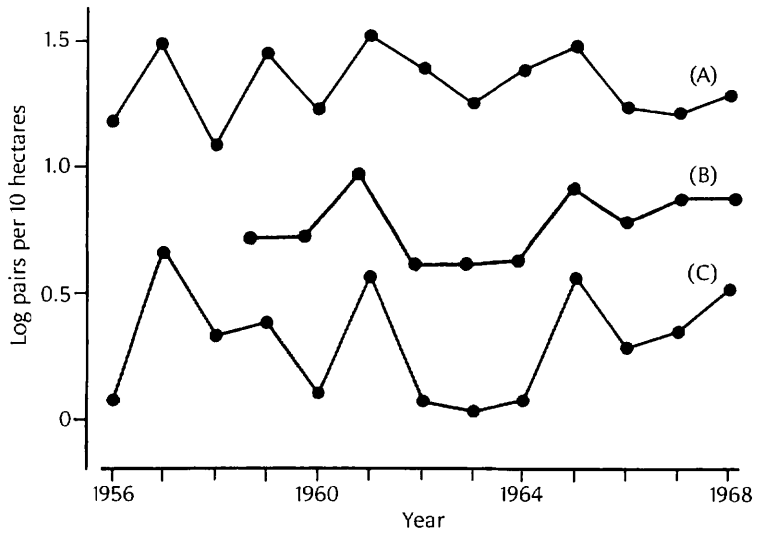


FIGURE 18–5 Densities of Great Tits breeding in (A) oak forests are higher than those in (B) mixed oak–pine forests and much higher than those in (C) pine forests. [*After Klomp 1980*]

limits the population densities of species such as the Great Tit and the Eurasian Pied Flycatcher. In lieu of natural nest sites, these species readily adopt nest boxes, which increase local population densities. Similarly, populations of the Eastern Bluebird of North America rebounded from their widespread decline with the installation of bluebird nest-box trails (see Chapter 21).

Widespread deforestation favors species that inhabit open country but hurts species tied to large timber. Now-familiar birds of cleared and second-growth habitats, such as the Chestnut-sided Warbler, the American Robin, and the Indigo Bunting, were once scarce.

Changes in the forest understory also affect bird populations in forests. Grazing cattle destroyed the undergrowth of forests in Finland, causing local losses of species such as Eurasian Blackcaps and Dunnocks that depended on the undergrowth. Both species increased in abundance after 1956 with the removal of the cattle from the forests. Similar destruction of forest undergrowth is now a result of the population explosion of the white-tailed deer in eastern North America. This large browsing mammal changes the normal vegetation structure of a maturing forest by eating and killing young plants that provide the low cover and shrub layers required by many ground-nesting forest birds.

Because of their high densities on tropical wintering grounds, migrant birds are especially vulnerable to the destruction of natural habitats (Terborgh 1980). Clearing 1 hectare of forest in Mexico eliminates the same number of warblers as clearing from 5 to 8 hectares of breeding habitat does in the United States. Many migrants congregate to winter in the prime agricultural lands of tropical highlands. Conservation of these tropical habitats will be essential to maintain viable populations of Neotropical migrants.

On a positive note, birds respond quickly to the availability of good habitat. Restored riparian woodlands, well-managed grasslands, and forest regrowth all attract appropriate bird species, which grow robust local populations.

Food

Food supply, which often depends on climate, limits population growth and influences population size, most conspicuously in the form of their year-to-year fluctuations.

Most of the evidence of starvation among temperate-zone birds comes from density-independent losses of songbirds, waterfowl, and waders during hard winters. The very cold winter of 1981–1982, for example, was hard on British birds (O'Connor and Cawthorne 1982). During that winter, mortality rates in several species were 2 to 10 times the normal rate. Common Redshanks were unable to feed, because shrimplike amphipods—their main food—remained deep in their burrows when intertidal areas froze. White Wagtails, searching for insects along frozen shorelines, could no longer find one every 4 seconds, the average rate needed for their subsistence.

Detailed local studies documented the correlation between food abundance and size of island populations of Darwin's finches (Grant 1986). For example, Daphne Major, one of the small islands in the Galápagos archipelago, suffered severe drought in 1977, resulting in a critical shortage of the seeds that sustain the resident ground finches. When seed abundance plunged sharply in both number and volume, finch abundance declined by a similar order of magnitude in both number and total biomass (Table 18–1; see also Figure 1–14, which illustrates the effect of this event on average bill sizes in the population).

Seabird populations also are limited by their food supplies (Cairns 1992). Millions of Peruvian seabirds starve when their main food—the anchovy, a small fish—disappears over short time periods as a result of changes in surface-water temperatures due to El Niño. The total population of cormorants, pelicans, and other seabirds dropped from 27 million to 6 million birds in 1957 and 1958, increased to 17 million as food supplies returned, and then plummeted again to 4.3 million birds in 1965 (Idyll 1973). In recent years, the maximum number of seabirds in good years has declined owing to the overfishing of the anchovy populations. Seabird populations throughout the world face similar challenges.

Widespread food shortages cause irruptions, or mass evacuations, of populations, especially of birds from the arctic and subarctic regions. The periodic southward invasions by Snowy Owls are a classic spectacle coinciding with the cyclic abundance of lemmings of the tundra (Parmelee 1992). More than 14,000 Snowy Owls were counted in southeastern Canada and New England during the great Snowy Owl invasion of 1945 to 1946. Because they were away from their usual habitat and food supplies, many of the owls died of starvation.

Other northern owls move south in search of food when populations of their vole prey drop, especially after a summer of good owl reproductive success. In the summer of 2004, the populations of red-backed voles and other rodents crashed throughout the boreal forests of Canada. Manitoba vole populations dropped to their lowest levels in 12 years. Experts expected a southward movement of owls the following winter. Beyond all expectation came thousands of owls. Unprecedented numbers invaded the fields and backyards of Minnesota in the winter of 2005. Local experts

TABLE 18–1 Effects of seed availability on ground-finch abundance on Daphne Major in the Galápagos

	Seeds		Finches	
Year	Total Number per Square Meter	Total Volume (cm^3/m^2)	Total Number	Biomass (kg)
1973 (wet)	4821	15	1640	26
1977 (dry)	295	5	300	6

From Grant and Grant 1980.

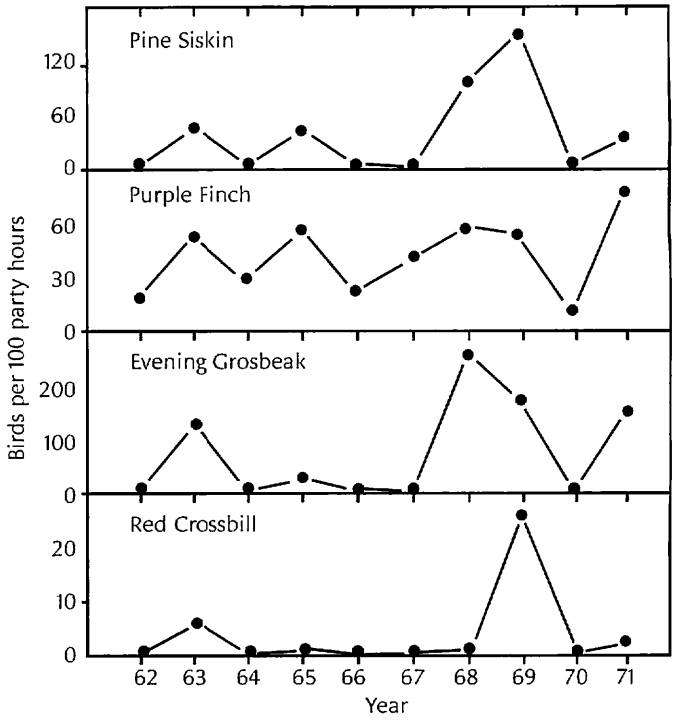


FIGURE 18–6 Annual variations in the winter abundance of four northern finches in the Chesapeake Bay region. Curves are based on annual Christmas counts. [*After Bock 1980*]

estimated that more than 5000 owls crossed the border into Minnesota. Most of them were Great Gray Owls, along with hundreds each of Northern Hawk-Owls and Boreal Owls.

Irruptive invasions of the seed-eating birds of northern coniferous forests also create dramatic population events (Bock and Lepthien 1976c). Invasion years, which are often the same in the New and Old Worlds, correspond to years of poor boreal forest seed production. During these invasion years, flocks of northern finches appear along roadsides and at backyard feeders. Eight North American species—the Pine Siskin, the Red-breasted Nuthatch, Red Crossbill, Two-barred (also known as White-winged) Crossbill, Purple Finch, Pine Grosbeak, Evening Grosbeak, and Common Redpoll—tend to invade in the same years (Figure 18–6).

Natural Enemies

Predators, parasites, and diseases are natural enemies that zero in on prosperous species and cause local densities to drop or distributions to contract. If the effect is occasional or short term, the local populations fluctuate in annual size. If the negative forces are chronic or severe, some local populations become extinct, especially if they cannot recruit dispersing birds from other populations.

Natural predators are a major source of annual mortality among birds, especially nestlings, incubating females, and young birds in their first year. Relentless predation is a driving force of natural selection for escape behaviors, camouflage plumage, and social behavior. With some conspicuous exceptions, however, predators don't limit or regulate the bird populations on which they prey (Newton 1998). Instead, they take weak, sick, and young birds, many of which are part of the surplus that exceeds locally limiting food supplies.

As a rule, predators are opportunistic. They take what is most available and switch to more common prey species when numbers of another decline. Hawks and owls eat many of the same prey eaten by mammalian predators such as foxes and weasels, and they compensate for one another in their functional response to the numbers of available prey. Some populations of grouse go through regular cycles of growth and decline that correspond to the intensity of predation. The populations of the Ruffed Grouse of Alaska, Canada, and the Great Lakes states cycle at intervals of 8 to 11 years in concert with population cycles of the snowshoe hare (Rusch et al. 2000). Predators, especially Northern Goshawks and Great Horned Owls, switch to grouse as the hares decline, causing the numbers of grouse to decline also, with a slight lag. More generally, by increasing their takes when prey populations are on the increase, predators—as well as intensive hunting by humans—may dampen the population cycles of prey species.

The endangerment and extinction of island birds by introduced predators is a conspicuous exception to the statement that predators don't limit bird populations. Most (119, or 92 percent) of the 129 bird species that have become officially extinct in the past 500 years are island species. Roughly half of these species were exterminated by introduced predators and diseases. The rest were driven to extinction by direct human exploitation and habitat destruction (BirdLife International 2000).

Ducks and upland game birds are another major exception to the rule that predators don't limit prey populations. Predation on duck nests by mid-sized predators, such as raccoons and red foxes, is a primary source of mortality of hen ducks. Mid-sized predators can also limit annual production and hence recruitment the following year, especially when good nest cover is limited. Mid-sized predators also limit the annual breeding success of game-bird species such as Northern Bobwhite in North America and Red Grouse (a subspecies of the Willow Ptarmigan) in Scotland (see page 556).

Ironically, high rates of predation on game-bird nests tend to be our own doing. They are due to the removal of top predators, such as coyotes, wolves, and mountain lions. These animals once ate the mid-sized predators but did not severely prey on nests.

Parasite infections and diseases can devastate bird populations. They can also have severe effects on their ecology, life histories, and evolution (Loye and Carroll 1995). Among the many consequences, increased exposure to parasites spurs birds to invest more into immune defense (Lindström et al. 2004). In that way and others, parasite loads bias mate choice,

drain energy required for reproduction, and favor traits, such as plumage quality and display endurance, that signal male health (Hamilton and Zuk 1982; see page 339).

The parasites of birds range from parasitic worms and blood parasites to ticks, mites, bedbugs, and blowflies. Grebes host at least 249 species of parasitic (helminth) worms (Figure 18–7). More than 100 of these species are grebe specialists (Storer 2000). Colonial bird species generally host substantial loads and a high diversity of kinds (taxa) of blood parasites, or hematozoa (Tella 2002). Maggots of blowflies and botflies infect a high proportion of the nests of many temperate-zone species as well as tropical songbird species (Figure 18–8). The maggots weaken and kill the nestlings by draining substantial quantities of blood and other fluids.

Parasites can pose a major conservation threat to island species. Maggots of parasitic botflies, for example, threaten an endangered parrot, the Puerto Rican Amazon (Snyder et al. 1987). Pearly-eyed Thrashers, whose nestlings are heavily infected with botflies, transport the botfly maggots with them as they follow new roadcuts into the forest refuges of the Puerto Rican Amazon.

Similarly, parasitic blowflies accidentally introduced into the Galápagos Islands in 1997 now infect most of the nests of Darwin's well-known finches, including the endangered Mangrove Finch (Fessl and Tebbich 2002). The larvae feed on the blood of the nestlings at night and sometimes burrow deep into their bodies, including their brains. On the island of Santa Cruz, the average little finch nestling had 23 maggots on it. One quarter of the nestlings surveyed were dying as a result of the infection. Death rates of finch juveniles also are rising.

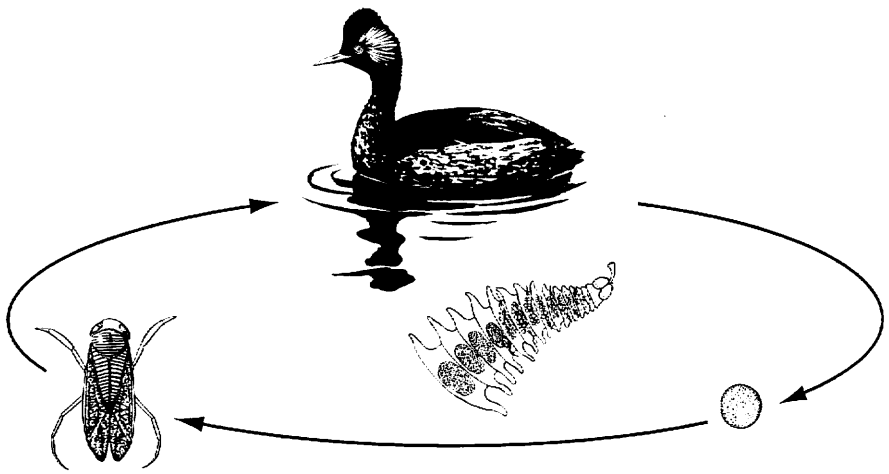


FIGURE 18–7 Life cycle of a common cestode parasite *(Tatria biremis)* of grebes of the Northern Hemisphere. All but one of the 29 species in the family Amabiliidae are grebe specialists. Individual Black-necked Grebes (also known as the Eared Grebe), the definitive host shown here, carry an average of 2794 worms apiece. Worm eggs passed from the grebe's intestine are picked up by the intermediate host, a corixid bug, which the grebes later eat and complete the cycle. [*From Storer 2000*]

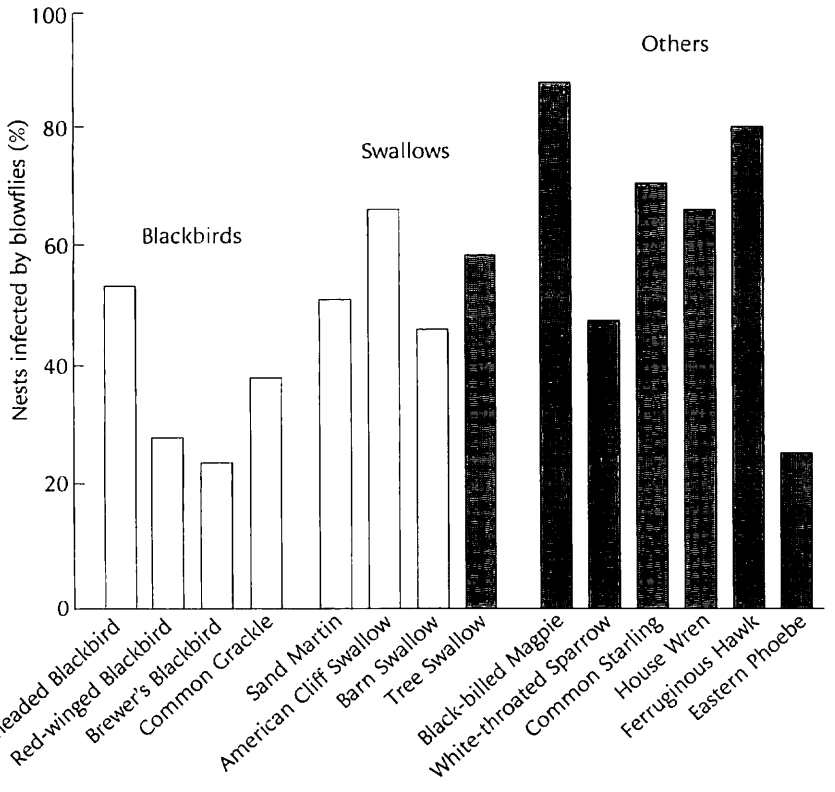


FIGURE 18–8 Frequencies of nest infection by blowflies. White bars represent colonial nesting species. Dark gray bars represent solitary nesting species. The Barn Swallow (light gray bar) nests both solitarily and colonially. [*From Loye and Carroll 1995*]

Local outbreaks of diseases, both bacterial and viral, occur regularly in bird populations worldwide and are now making headlines in the news as threats to human health, too (Box 18–2). Summer outbreaks of botulism kill hundreds and sometimes thousands of waterfowl locally each year. An outbreak of avian cholera killed 4000 seabirds, mostly cormorants, in two weeks in one seabird colony in South Africa in January 2004. But these outbreaks are mostly temporary setbacks.

Island bird populations are particularly vulnerable to disease because they lose their resistance to mainland diseases. For example, lowland populations of the Hawaiian honeycreepers that survived the early deforestation of the islands were destroyed by diseases. Captain Cook and his successors accidentally introduced mosquitos to the islands in the early 1800s. The mosquitos carried bird pox and malaria, which eliminated native birds at low altitudes (Warner 1968; Olsen 1992). The potential spread of other diseases such as that caused by the West Nile virus (WNV), for example, into small and island populations of endangered species, including the endangered Hawaiian honeycreepers, is now a major concern.

The arrival of the West Nile arbovirus on the East Coast of the United States in the summer of 1999 drew both public and professional attention

BOX 18–2

AVIAN FLU

The global success of modern Euro-Caucasian societies traces to the origins of agriculture and the domestication of animals thousands of years ago. New diseases transferred from domesticated livestock and poultry, however, were one of the costs of the agricultural revolution (Diamond 1999). Smallpox, for example, came originally from swine. Now, animals carry and transmit 863 of the 1415 microbes that cause diseases in humans. Cats and dogs transmit 43 percent of those human-disease-causing microbes, livestock 39 percent, and rodents 23 percent. Birds transmit just 10 percent (Rosenwald 2006).

Outbreaks of viral diseases occur regularly in bird populations. Arboviral and other mosquito-borne diseases, including West Nile, are just one category of them. Their levels of transmission to humans are typically low.

Waterfowl carry many genetically distinct strains of avian influenza viruses, which are occasionally transmitted to domestic poultry and humans, sometimes with deadly results. The "Russian flu" spread from Central Asia to Russia, Europe, and North America in 1889–1990 and killed about 1 million people. The "Spanish flu" of 1918–1919 killed at least 40 million people. Subsequent epidemics have been less deadly owing in part to the widespread recent use of flu vaccines.

Influenza viruses come in three primary forms. Bird flu is caused by the most virulent of the three forms. A deadly H5N1 strain of avian flu emerged in the chicken farms of Asia, first in China and then in South Korea. It is spreading to wild bird populations as well as throughout the poultry industries of Asia, Europe, and Africa.

The virus causes high levels of mortality in wild birds (Birdlife International 2006). Between 5 and 10 percent of the world population of the Bar-headed Goose perished in the outbreak at Lake Qinghai in China in the spring of 2005. The virus was also isolated from the Red-breasted Goose in Greece. Most of the world population of 88,000 is confined to just five roosts in Romania and Bulgaria, both affected countries.

What should be done—or not done? From a human health perspective, H5N1 is not yet a major threat, pending critical mutations of the virus that would enable human-to-human transmission. The mandatory destruction of domestic poultry has major economic and social costs. As to the wild birds themselves, the evidence for the role of wild birds spreading the disease remains weak. Illegal traffic of infected poultry is responsible for the rapid spread of the disease. Further, the World Health Organization, the Food and Agriculture Organization, and the World Organization for Animal Health (OIE) agree that the control of avian influenza in wild birds by culling is not feasible. They point out that attempts at culling would spread the virus more widely as survivors disperse to new places and healthy birds become stressed and more prone to infection.

to the potential consequences of diseases in native bird populations. The uncontrolled WNV spread across the country from New York to California in just five years. The *Culex* mosquitos that spread the disease feed primarily on birds in May and June. American Robins are one of their preferred sources of a blood meal in early summer. Heavy summer rainfalls caused major local increases in arboviruses transmitted by burgeoning mosquito populations. Where the mosquito populations increased in the United States, the WNV hurt local populations of American Crows,

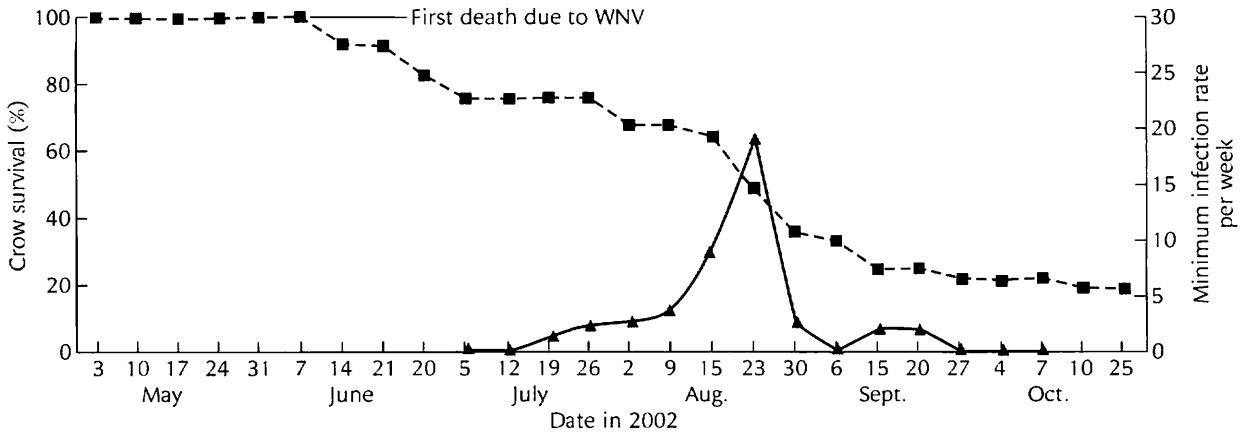


FIGURE 18–9 Effect of West Nile virus (WNV) on a radio-tagged American Crow population in Illinois. The survival curve (dashed line) illustrates the loss of 31 of 39 crows relative to WNV minimum infection rates (solid line) of mosquitos collected weekly at crow roost sites in east-central Illinois in 2002. [*After Yaremych et al. 2004*]

raptors such as Great Horned Owls and Red-tailed Hawks, and a variety of songbirds, including Black-capped Chickadees (Caffrey and Peterson 2003; Bonter and Hochachka 2003; Figure 18–9).

Illinois was especially hard hit when the disease arrived in 2002. The WNV promptly killed 19 of 28 marked crows in Champaign-Urbana (Yaremych et al. 2004). When the WNV first reached Stillwater, Oklahoma, that same year, it killed at least 39 of 120 marked birds in a local study population of American Crows (Caffrey et al. 2005). The following year, the WNV killed 51 (65 percent) of 78 marked crows, including 82 percent of the juveniles.

Such intense effects, however, tend to be local in nature. Widely distributed, abundant species, such as crows, rebuild local populations in a few years by recruiting young crows from other populations. With time also, resistant birds prevail by virtue of natural selection.

One of the best documented examples of the decline of a bird species caused by bacterial disease is that of the introduced and rapidly expanding population of House Finches in eastern North America, mentioned earlier in this chapter. A new infectious disease reversed their growth into a significant density-dependent decline (Hochachka and Dhondt 2000). The first cases of conjunctivitis, caused by a novel strain of the poultry disease pathogen *Mycoplasma gallisepticum* and manifest as conspicuous swellings of the eye, were reported from Washington, D.C., in the winter of 1993–1994. The pathogen typically kills an infected bird within two to four weeks. Arrival of the disease in different places consistently causes the local House Finch populations to decline and to stabilize at a lower level (Figure 18–10). Also documented by this study for the very first time was the geographical spread, or epizootic, of a novel strain of disease-causing bacteria in wild bird populations.

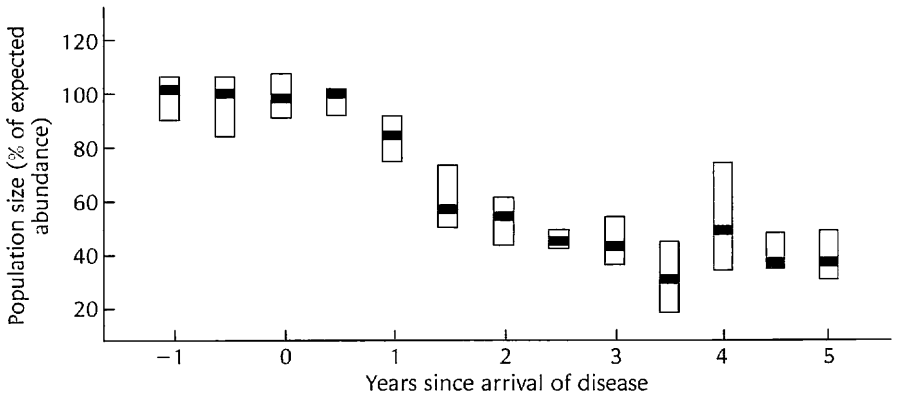


FIGURE 18–10 Effect of conjunctivitis eye disease on local House Finch populations. Changes in abundance of House Finches after the arrival of the disease are expressed as a percentage of the abundance that would be expected in the absence of this disease. Thick horizontal bands indicate median values; boxes span values from 25 to 75 percent of the sample. [*After Hochachka and Dhondt 2000*]

Regulation

Population sizes are said to be regulated whenever birth rates, reproductive success, or death rates vary with population density. Mentioned earlier were density-dependent clutch sizes and number of young that Great Tits fledge. We will return to the population dynamics of Great Tits later in this section. First, we examine the ways in which social forces mediate the availability of habitat and, therefore, local population size in density-dependent ways.

Social Forces

Territorial behavior spaces individual birds according to the available resources. Competition for the best territories can be intense and density dependent. The intensity of competition affects the size of a territory that can be defended effectively and thus the number of birds that can nest in the available habitat. The spacing of territorial individual birds in primary habitat excludes some birds from the breeding population or forces them to occupy secondary habitats where nesting is less successful and the risk of mortality is greater.

The occupation of available habitat has three stages (Figure 18–11). First, primary habitat fills up. Then, unable to find vacancies in primary habitat, surplus birds move to suboptimal habitat and wait for vacancies in better habitat. Finally, as suboptimal habitats are filled, remaining birds must simply wait, usually as floaters, for vacancies in either habitat. Defined as nonterritorial birds whose movements exceed those of territorial birds (Winker 1998), floaters live singly on home ranges that overlap the breeding territories of established pairs. They also may form flocks in areas that are not occupied by territorial breeders. In effect, floaters indi-

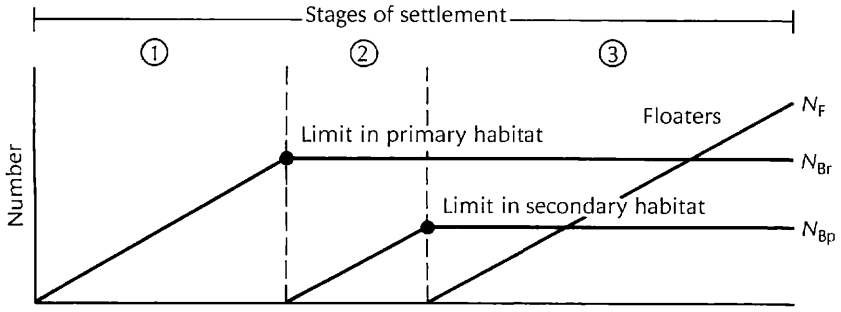


FIGURE 18–11 Stages of settlement in a local population of breeding birds. The first breeding birds to arrive in an area occupy primary habitat (stage 1). Birds unable to establish territories in primary habitat settle in secondary—or poorer—habitat (stage 2). Floaters are birds unable to establish territories because they arrive after all the breeding habitat is filled (stage 3). Abbreviations: N_F, number of floaters; N_{Br}, number breeding in primary habitat; N_{Bp}, number breeding in secondary habitat. [*After Brown 1969*]

cate that the size of the breeding population is limited by the (saturated) habitat available.

These stages are evident in the use by Great Tits of oak and then pine forests, as discussed earlier. The occupation by male Black-headed Grosbeaks of territories differing in quality provides another example. This species exhibits delayed plumage maturation. Young males have duller breeding plumages than those of old males. Geoffrey Hill (1988) found that the breeding territories defended by males varied in vegetation structure and in the abundance of the grosbeaks' principal nest predators, Western Scrub Jays and Steller's Jays. Males that were three or more years old defended territories with mixed vegetation and few jays. These males achieved the highest reproductive success. Yearling and two-year-old males settled on territories with denser vegetation and more jays. These males suffered more nest predation. Among these young males and irrespective of their age, the more brightly colored birds occupied territories of slightly better quality than did the dull-colored birds. Each year, the males shifted to better-quality territories that became available.

Large numbers of birds may be floaters by necessity. Nonterritorial floaters constitute about 50 percent of a population of the Rufous-collared Sparrow (Figure 18–12) (Smith 1978). This tropical bunting, which is closely related to the White-crowned Sparrow of North America, defends territories and breeds throughout the year. Floaters, or members of the "underworld," live in well-defined, small home ranges. The ranges of young females are restricted to a single pair's territory, whereas the ranges of young males encompass from three to four established territories. Males and females of the underworld with overlapping home ranges have well-defined, intrasexual dominance hierarchies. The dominant birds of the appropriate sex fill new vacancies. Floaters quickly replace established males that disappear or that are experimentally removed.

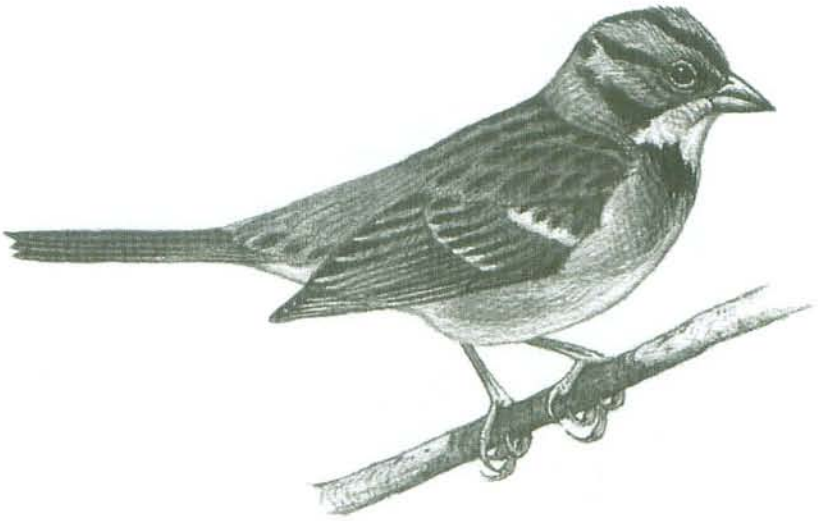


FIGURE 18–12 Rufous-collared Sparrow, a species with a well-developed "underground" of birds waiting for a breeding opportunity.

The dynamics of control and attempted takeover of limited territorial spaces are illustrated by Susan Smith's description of what happened when a territorial male Rufous-collared Sparrow (color banded RO) disappeared for nine days after capture and banding on August 10:

> Less than one hour after his capture, two banded underworld males were courting his mate, GY, but she actively chased both throughout the day. Also, at least four neighbor male owners invaded the territory repeatedly and were driven out by GY. By August 15 one of these, YO, had formed a stable pair with GY, and two other underworld males . . . had established small territories at each end of YO's former territory. Both actively courted YO's former mate, RRO, who, unlike GY, readily associated with both. On August 17 I saw RRO copulating with the one that sang more, RBO, and by August 18 they were established as a pair in her territory. Yet less than 24 hours later RO had returned and regained his territory and mate, and YO had reclaimed most of his old territory with RBO, holding a small corner, forming a trio of one female (RRO) and two males (YO and RBO). Five weeks later YO had regained all his territory, and RBO rejoined the underworld. [Smith 1978, p. 577]

Social interactions between neighbors also govern the density-dependent regulation of Black-throated Blue Warblers on their breeding grounds in New England—specifically, the number of young that they fledge and the quality of those young (Sillett and Holmes 2004). This smartly plumaged wood warbler winters in the Caribbean and summers in the

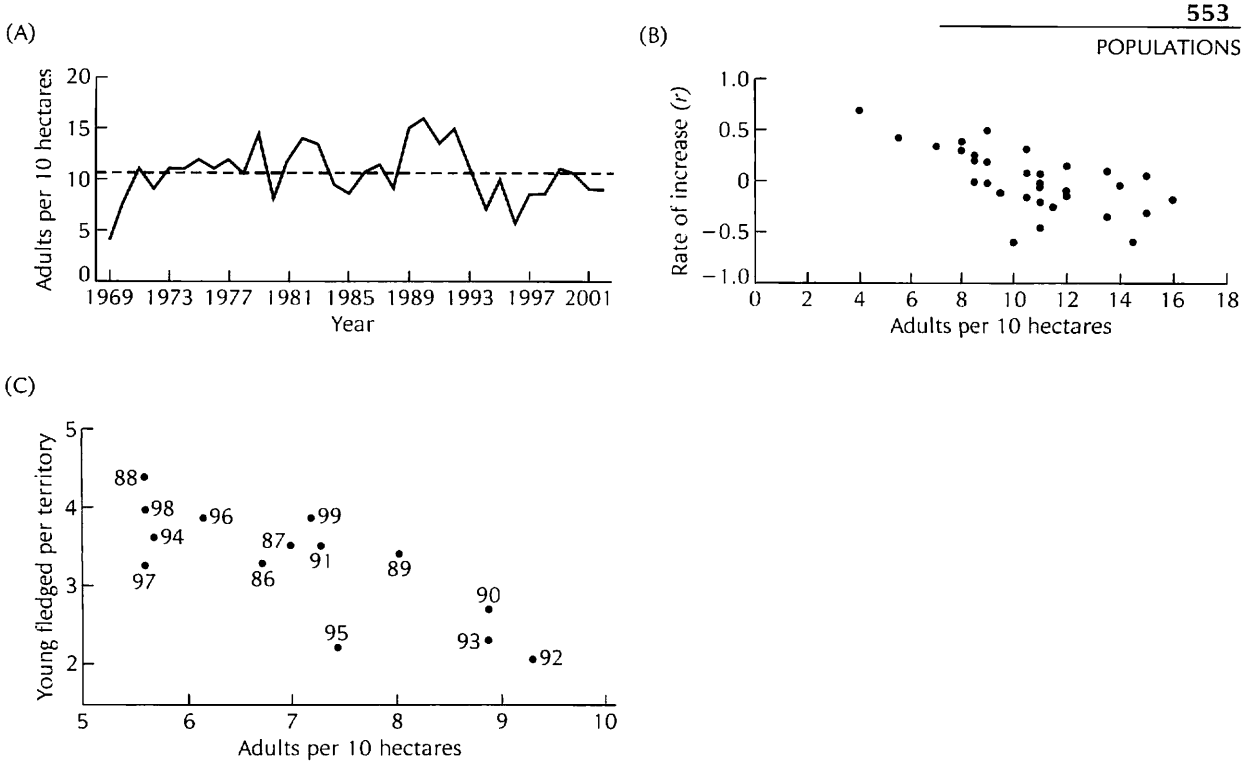


FIGURE 18–13 Density-dependent population regulation in the Black-throated Blue Warbler. Population trends are from plots at Hubbard Brook Experimental Forest in New Hampshire. (A) The number of adults was stable for 30 years with minor fluctuations about an average of 10 per 10 hectares. (B) Population growth rate was negatively correlated with population density each year, causing decreases in abundance after years of high density and increases in abundance after years of low density. (C) Annual fecundity declined as the density of breeding adults increased on a 64-hectare plot. Numbers next to the black circles are years. [*From Rodenhouse et al. 2003*]

north woods of eastern North America. Recall that adults suffer most of their annual mortality during migration between their seasonal residences (see Chapter 17).

Density-dependent factors on the breeding grounds stabilized local populations of Black-throated Blue Warblers (Figure 18–13A). How does this regulation work? As population density of the warblers increased, individual annual fecundity (number of young fledged, average mass of fledglings) declined; so did the the annual growth rate of the population (Figure 18–13B and C). Females in denser populations also attempted fewer second broods.

Conversely, the number of young fledged and their quality, as well as the number of second broods, increased at low densities. The experimental removal of neighbors confirmed this dynamic: the number of young fledged on the remaining territories increased (Rodenhouse et al. 2003; Figure 18–14). These density-dependent effects caused low population densities to rebound and high population densities to reduce themselves.

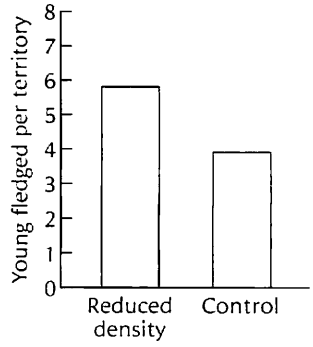


FIGURE 18–14 Black-throated Blue Warblers: Experimental removal of neighbors reduces density and increases fecundity (number of young fledged per territory). [*From Rodenhouse et al. 2003*]

Consequently, the population density regulated itself at a long-term stable average of 10 adults per 10 hectares (see Figure 18–13A).

The density-dependent changes in fecundity in Black-throated Blue Warblers stemmed from increased competition between neighbors breeding at high densities, particularly in years of low food availability (Sillett et al. 2004). When the removal of neighbors reduced crowding, territorial males spent less time fighting and more time foraging for food. Their territory sizes increased and, consequently, so did the foraging area available to them. As a result, the parents were able to feed their young more often. The heavier fledglings were more likely to return the following year, increasing population density and perpetuating the process of density-dependent regulation.

Great Tit Populations

Ornithologists have monitored populations of the Great Tit in Holland since 1912 and in England, especially in Wytham Wood, near Oxford, since 1947. This species is quite sedentary and nests readily in boxes, especially in managed woodlands where natural cavities are scarce. Inspection of the nest boxes yields accurate censuses of breeding pairs, clutch sizes, and young raised. Deciphering the dynamics of population regulation has been a primary goal of this research (Perrins 1979; McCleery and Perrins 1991).

The main finding is that Great Tit populations are density dependent (Figure 18–15). The patterns of population regulation seen in the Great Tit have broad application to other birds. As a rule, bird populations seem to be limited by food scarcity during the nonbreeding season.

Great Tit populations undergo substantial seasonal changes influenced by reproduction, mortality, and local migration. Each year, the population increases rapidly when the breeding adults produce fledglings. This rapid population growth, however, is short-lived. The heavy mortality of young birds and the loss of some adults then cause a steady decline. Although substantial, the losses to Eurasian Sparrowhawks, mentioned in Chapter 17, have little final effect on the population as a whole (McCleery and Perrins 1991).

The survival of both juvenile and adult Great Tits is density dependent. An average of only 22 percent of the juveniles survive their first year. Recoveries of banded birds throughout Britain showed that females are less likely to survive in a high-density-population year than in a low-density-population year.

Most telling were pioneering experiments by Hans Kluijver (1966) in a population on an isolated Dutch island in the North Sea. He removed 60 percent of the eggs and nestlings in some years but not in other years. Both juvenile and adult survival doubled in the years when he removed eggs and nestlings, owing to decreased density and reduced competition among the remaining birds. Juvenile survival rose from 11 to 20 percent and the survival of adults rose from 26 to 54 percent. Immigration and emigration did not affect these experimental results, because migrations

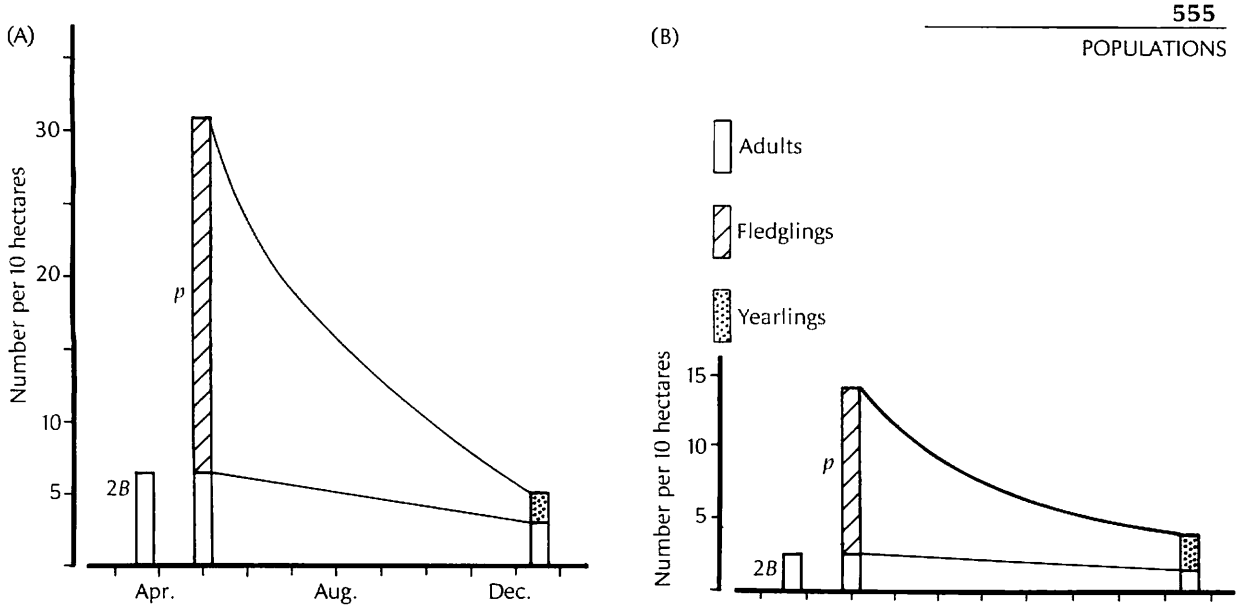


FIGURE 18–15 Great Tit production, *p*, and survival to the winter in years with (A) high and (B) low breeding densities in a model population. Nesting in the spring adds many young birds to the population, but most of them die by winter. Averages of 3.5 and 6 fledglings are produced per breeding pair, 2*B*, in high- and low-density years, respectively. [*After Klomp 1980*]

did not occur on the tiny island. In other experiments, the survival rate of juveniles in autumn and winter was positively correlated with the percentage of breeding birds removed in the summer.

Although annual variations in reproductive success, adult survival, and juvenile survival all potentially influence the density of the population during the breeding season, survival outside the breeding season actually controls population size the following year (Klomp 1980). The survival of juveniles in particular is the key controlling variable. Winter food supplies, especially the seeds of beech trees, control juvenile survival in both Oxford and Holland. Young Great Tits in Holland, for example, depend on beechnuts from November to late February when other foods are scarce. Beechnut crops vary greatly from year to year, and this essential reserve food supply is easily exhausted in poor crop years.

The survival of juvenile Great Tits in a year of beechnut scarcity has a major effect on recruitment levels the following year and, hence, on population size. In one study on an island off the coast of Holland, local recruits averaged about 20 percent of the breeding population each year.

Recruitment also varies in relation to adult mortality over the winter (Van Balen 1980; Figure 18–16). The recruitment of young birds into the breeding population dropped when winter food was provided at bird feeders, starting in 1966, decreasing adult mortality and, consequently, the number of vacancies available. Such observations demonstrate once again that the density of established adults influences dispersal and recruitment patterns.

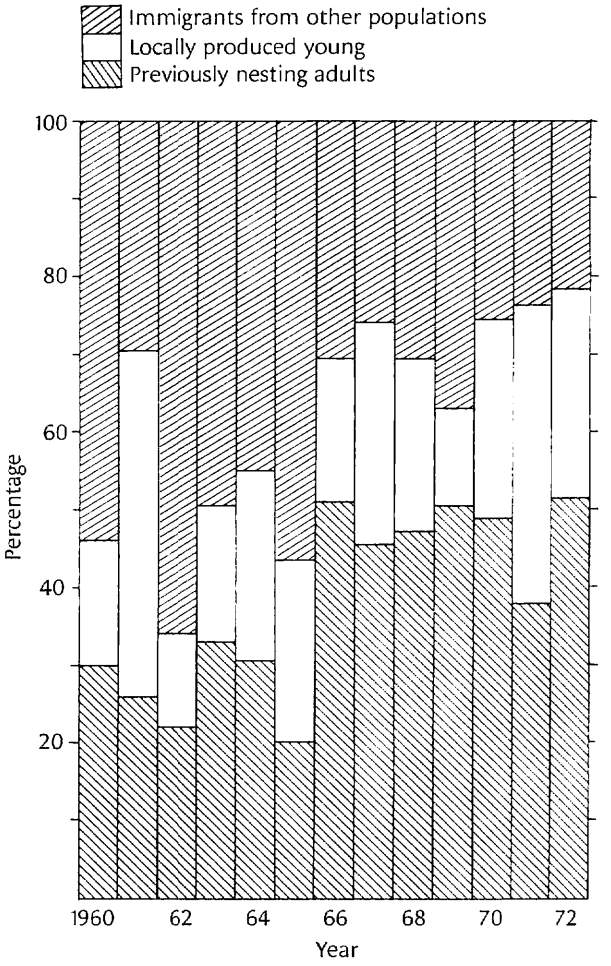


FIGURE 18–16 Composition of a population of Great Tits breeding on the island of Vlieland off the coast of Holland. Opportunities for immigration and the recruitment of Great Tits from other populations depend on the overwinter mortality of the resident adults. [*After Van Balen 1980*]

Dispersal itself increases with population density. In one well-studied case, young male Great Tits dispersed as little as 354 meters (median) in years of low population density and as much as 1017 meters (median) in years of high population density (Greenwood et al. 1979). Young male Great Tits disperse farther in populous years to find unoccupied territories, which are scarce because so many established males survive. Young that fledge late in the season usually disperse farther because young fledged earlier in the season occupy the nearest territorial openings.

Red Grouse Population Cycles

Complex mixtures of density-dependent social behavior, parasite loads, and predation regulate the population cycles of the Red Grouse, a popular and strongly managed game species of the moorlands of Scotland. "Red Grouse" is the long-used name for this distinctive subspecies of the

Willow Ptarmigan. The populations of the Red Grouse undergo both long-term declines and short-term cycles (Thirgood et al. 2000). Most local populations of Red Grouse in Scotland have four- to eight-year cycles (Figure 18–17). Grouse numbers increase from lows of 30 birds per square kilometer to highs of 120 birds per square kilometer.

The population cycles of the Red Grouse partly relate to food availability and predation. Also contributing in a major way to the regulation of these cycles are an intestinal parasite (a nematode worm named *Trichostrongylus tenuis*) and the intensity of aggressive social interactions. We will consider the worm first.

The experimental cleansing of worms from local grouse populations through the application of a specific drug to 20 percent or more of the grouse in the population eliminates or sharply reduces the highs and lows of the population cycle (Hudson et al. 1998). This worm burrows into the soft walls of the intestinal ceca, causing local damage, internal bleeding, decreased absorption, and mortality in the Red Grouse. Infection levels of individual grouse can be severe: this worm was responsible for "grouse disease," which devastated the Red Grouse populations in the nineteenth century. The nematodes reduce the rate of weight gain in females before incubation, as well as clutch size, hatching success, and chick survival. They also affect adult survival. Secondarily, the parasites may increase vulnerability to predation by reducing the ability of the grouse to control scent emission from the intestinal ceca. Both hunting dogs and foxes use these odors to locate grouse. The effects of the parasites on breeding production and survival are density dependent. The effects intensify with population density, ultimately causing short-term population declines.

Social interactions—specifically, density-dependent territorial behavior and spacing—also govern the population cycles of Red Grouse. Early studies showed that the advantage of aggressive males increases with the density of grouse and causes an exodus of less aggressive birds. This aggressiveness leads to low recruitment and thus the downturn of the cycle

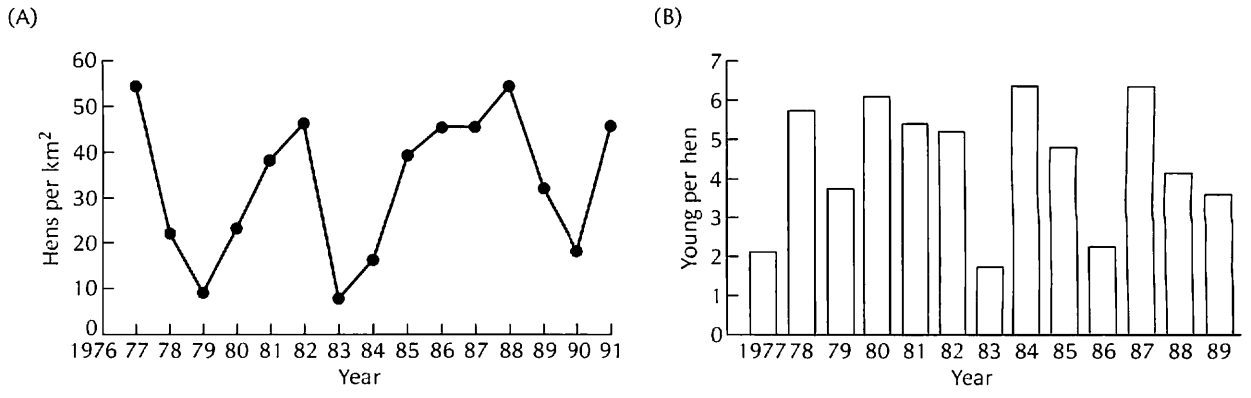


FIGURE 18–17 Changes in (A) size of the breeding population (number of hens) and (B) breeding success (young per hen) of Red Grouse in one study area in Scotland. [*From Hudson et al. 1992*]

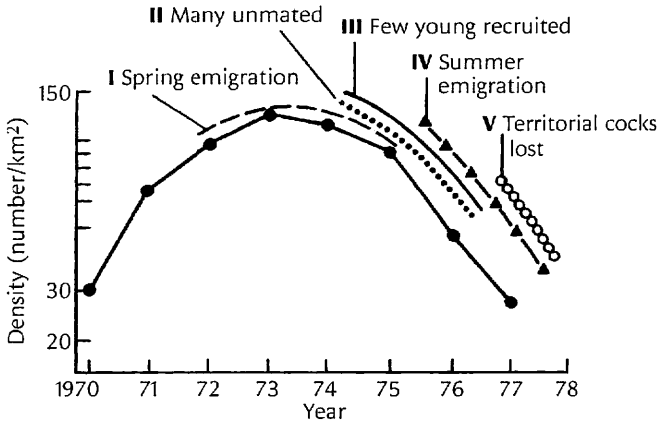


FIGURE 18–18 Social forces driving the population cycle of the Red Grouse. The density of Red Grouse cocks holding breeding territories cycles from lows of 30 birds per square kilometer to more than 100 birds. The solid line shows the density of cocks in the spring. The decline at high population densities is due partly to the control of large territories by increasingly aggressive males, which reduces the recruitment of young, promotes emigration by less aggressive males, and the loss of vulnerable territorial males themselves. [*After Watson and Moss 1980*]

(Figure 18–18). François Mougeot and his colleagues (2003) caused increasing populations to decline just by adding testosterone implants that increased the aggressiveness of territorial males. Testosterone implants reduced both fall male density and the recruitment of breeding males and females the following spring by 50 percent.

Long-Term Population Trends

Established populations may be stable, like that of the Black-throated Blue Warblers in New Hampshire. Alternatively, they may gradually increase or decline over decades. Beyond the short-term cycles of their local populations, numbers of Red Grouse have declined by 50 percent in the twentieth century owing to the loss of quality moorland habitat. The leaves of heathers are the primary food of this grouse. The grouse select nutritious leaves, and, in the spring, leaf quality affects maternal nutrition, egg quality, brood size, chick survival, and adult summer survival.

What happened? Increased grazing of sheep favored rough grassland instead of heather moorland, reducing the quality of both food and the cover that the grouse use to hide from predators. The conversion of the moorlands into rough grasslands also favored population increases of pipits and voles. They, in turn, attracted more predators—specifically, Northern Harriers (also known as Hen Harriers). Increased predation by harriers, especially on grouse chicks in the summer and young grouse in the fall, increased mortality rates. High densities of harriers suppressed local population cycles of the Red Grouse.

Standardized schemes for monitoring the numbers of game birds, such as the Red Grouse, guide decisions for managing populations that can

sustain annual hunting by sportsmen. The management of waterfowl populations is a major enterprise in this regard. Many species of North American ducks declined severely in the early 1960s to lows of roughly 20 million breeding pairs (Figure 18–19). The number of Northern Pintails alone dropped from historical highs of 10 million pairs to record lows of 1.8 million pairs. Agencies in Canada, the United States, and Mexico then formulated the North American Waterfowl Management Plan

(A)

(B)

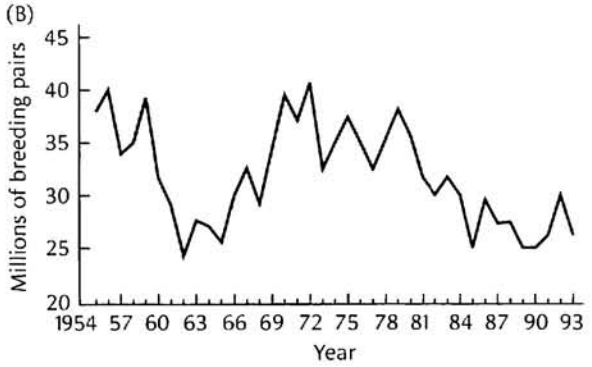
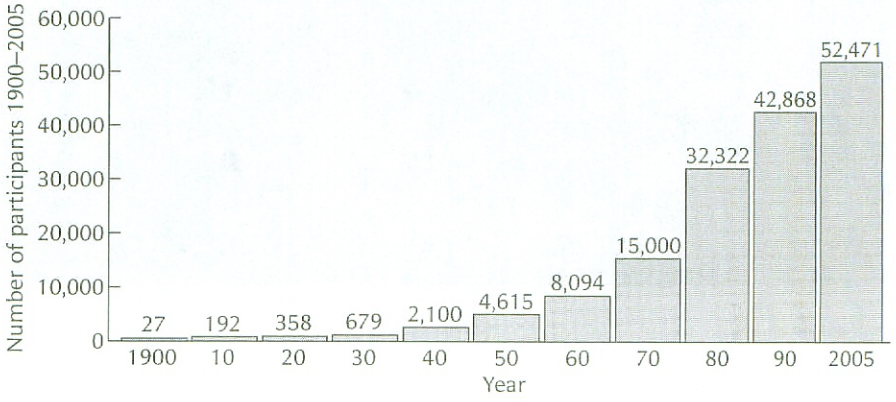


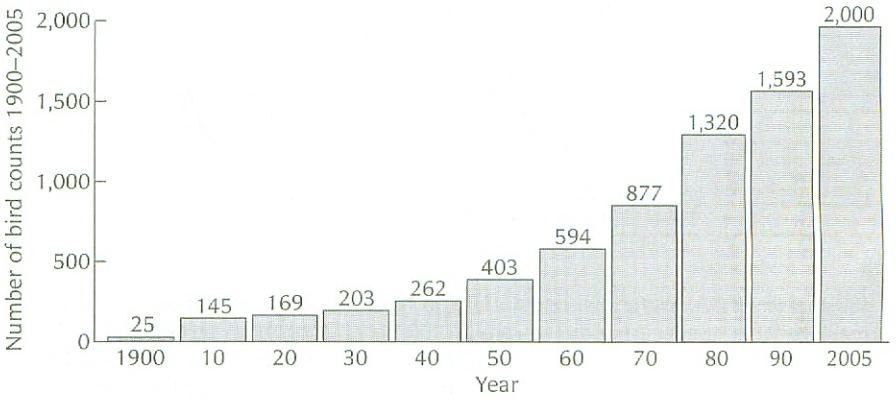
FIGURE 18–19 (A) Waterfowl populations in North America depend on wetlands, a habitat that is disappearing at the rate of 300 hectares or more per day. (B) Population fluctuations and long-term decline of North American duck populations from 1954 to 1993. Numbers expressed as millions of breeding pairs. [*(A) Courtesy of A. Cruickshank/VIREO. (B) From U.S. Fish and Wildlife Service 1993*]

FIGURE 18–20 Audubon Christmas Bird Count. (A) Map of count circles, 2000 in all. (B) Growth of citizen scientist participation. [*(A) and (B) From National Audubon Society 2002*]

(A)

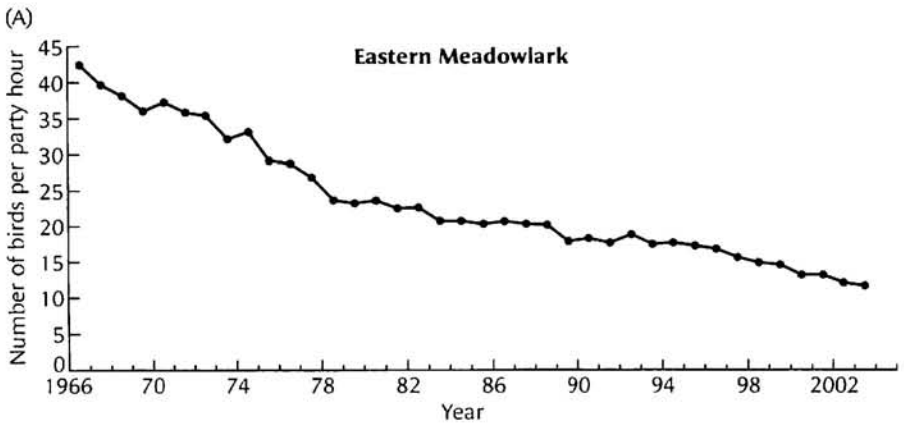
(B)





(NAWMP), which set population-growth targets for each species, accompanied by close regulation of annual harvests and close monitoring of annual nesting productivity. The stabilization, recovery, and rebuilding of the North American duck populations is well underway.

Nationwide programs also monitor the long-term population trends of non-game-bird species in both North America and Europe. Based on the participation and expertise of large numbers of volunteer citizen scientists, the Audubon Christmas Bird Count (CBC), for example, documents the changing early-winter distributions of North American birds (Figure 18–20). The original 27 Christmas Bird Counts in 1900 tallied a total of 18,500 individual birds of 90 species in all the counts combined. Now, more than a century later, more than 60,000 volunteer birders tally millions (70,000,000 in 2005; 193,000,000 in 2006) of individual birds of 652 species north of Mexico and 1544 additional species internationally each winter. More than 2000 count circles engage dedicated compilers throughout North America and elsewhere throughout the world. The computerized data, available online (http://www.audubon.org/bird/cbc/index.html), document population trends of North American bird species (Figure 18–21).



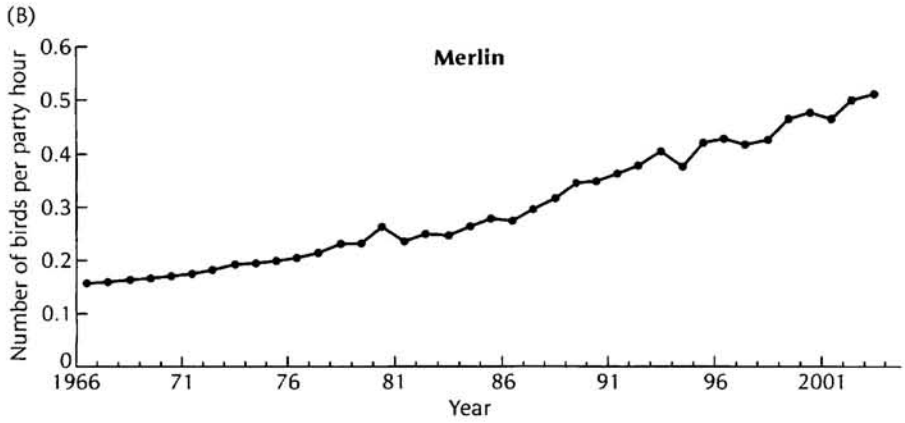


FIGURE 18–21
Computerized data from Christmas Bird Counts document (A) the decline of the Eastern Meadowlark, one of many grassland bird species in trouble, and (B) the growth of Merlin populations. [*Photo, A. Morris/VIREO; graphs, from National Audubon Society 2002*]

BOX 18–3

THE BREEDING BIRD SURVEY

Complementing the Christmas Bird Count and based on a more formal protocol of counting birds is the government-sponsored Breeding Bird Survey (BBS). It documents distributions and population trends of breeding bird species in June and July each year. Like the Christmas Bird Count, the BBS relies on the time given by thousands of skilled volunteer birders, or citizen scientists, and their early-morning efforts.

Data produced by the BBS survey sounded the alarm on behalf of the Neotropical migrants undergoing broad-scale decline (Robbins et al. 1989). The alarm, based on scientific trend analysis, rallied a conservation coalition of government agencies and nonprofit organizations under the umbrella alliance Partners in Flight. Modern non-game-bird conservation initiatives grew from this platform of broad-scale, coordinated participation, striving to apply the lessons and successes of the North American Waterfowl Management plan to the future vitality of species such as the Cerulean Warbler and Henslow's Sparrow. Here is a brief summary of its history:

> During the 1960s, Chandler Robbins and his associates at the Migratory Bird Population Station (now the Patuxent Wildlife Research Center) in Laurel, Maryland, developed the concept of a continental monitoring program for all breeding birds. The roadside survey methodology was field tested during 1965, and the North American Breeding Bird Survey (BBS) was formally launched in 1966 when approximately 600 surveys were conducted in the U.S. and Canada east of the Mississippi River. The survey spread to the Great Plains states and prairie provinces in 1967. By 1968, approximately 2000 routes were established across southern Canada and the contiguous 48 states, with more than 1000 routes surveyed annually. . . . During the 1980s, the BBS expanded into the Yukon and Northwest Territories of Canada, and Alaska. Today there are approximately 3700 active BBS routes across the continental U.S. and Canada, of which nearly 2900 are surveyed annually. . . . BBS data can be used to produce continental-scale relative abundance maps. When viewed at continental or regional scales, these maps provide a reasonably good indication of the relative abundances of species that are well sampled by the BBS. [From Sauer et al. 1997]

The Breeding Bird Survey, sponsored by the U.S. government, has been tracking the trends of breeding species since 1960 (Sauer et al. 2005; Box 18–3). The population dynamics and trends of healthy bird populations are not uniform over such large geographical areas as North America. Instead, some local populations of a particular species increase while others elsewhere decline over the same time period. Trend data, therefore, are best analyzed in regional and local segments. The resulting maps of the population trends of a species portray a topography of areas of increase, or sources, and areas of decrease, or sinks (Figure 18–22).

Bird Population Trends As Bellwethers

Biologists and politicians both recognize that birds are sensitive indicators of environmental health. Ever since the proverbial use of a canary in a

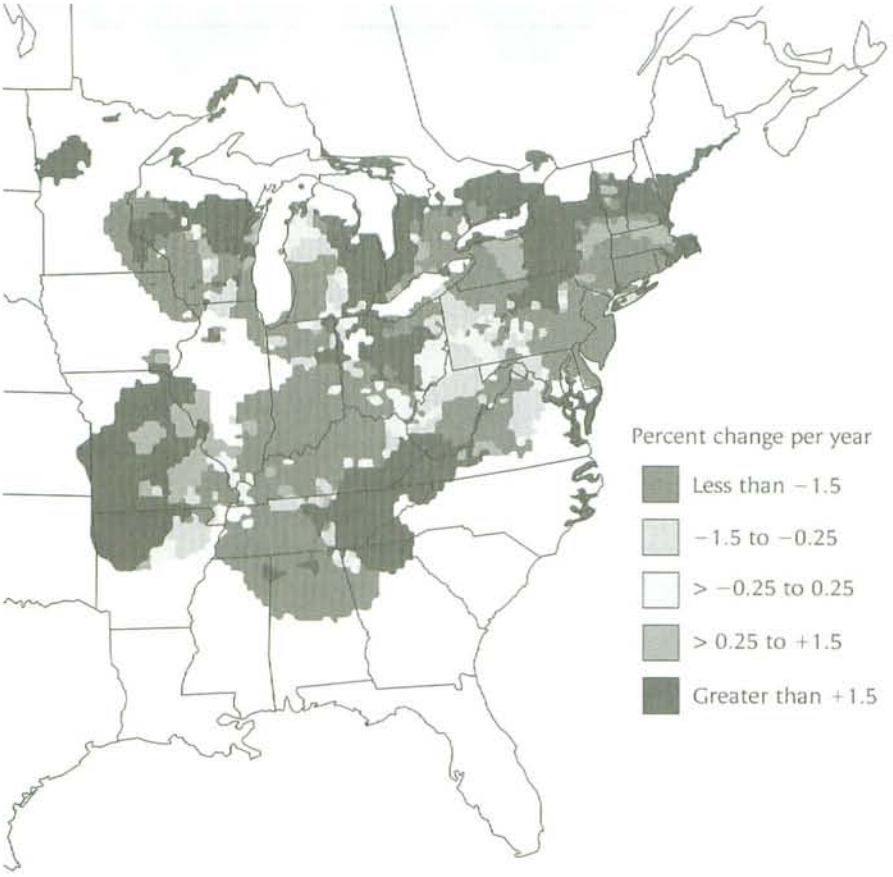


FIGURE 18–22 Geographical mosaic of population trends of the Blue-winged Warbler throughout its breeding range. Average annual changes in local population density since 1960 correspond to shifts in the population and the loss of suitable old-field habitats. [*From Sauer et al. 2005*]

mine shaft, birds have served humanity as bellwethers of the state of the environment. Sensitive to toxic coal-mine gases, canaries would succumb long before such gases reached levels dangerous to miners, forewarning them with ample time to get out of the mine. Outside the mine shaft, birds not only forage in vast numbers across the hemisphere, but their interactions as predators, prey, pollinators, and seed dispersers make them pivotal players in ecosystem dynamics. As a result, bird populations become excellent indicators of biodiversity and barometers of ecosystem health (Box 18–4).

The visible deaths and reproductive failures of raptors and songbirds alike in the 1950s sounded the alarm about the overuse of persistent organochloride pesticides, which were quietly taking their toll on human health as well. Accumulated pesticides, particularly DDT, not only kill birds directly but also interfere with eggshell production and thus cause nesting failure (Risebrough 1986). Pesticide poisoning nearly exterminated Peregrine Falcons (see Figure 17–7) and Ospreys (see Figure 16–12)

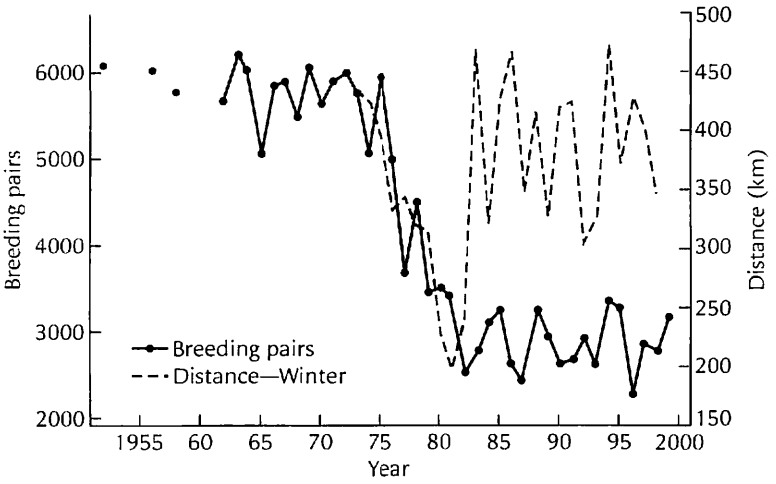
BOX 18–4

GLOBAL WARMING AND SEABIRDS

Seabird populations now warn us of the effect of global warming on the world oceans as well as the consequences of overfishing. Species that live in the polar regions, both Arctic and Antarctic, are among the first to be challenged by the warming of the oceans. Seabirds of the North Sea had their worst breeding season on record in 2004. The reason? Increases in water temperature due to global warming destroyed plankton populations at the base of the food chain and the small fish populations that depend on plankton. Both seabirds and commercial fisheries at the top of the food chain lost their critical food supplies.

Seabird populations in Antarctica are sensitive to the extent of the sea ice pack there, which is breaking up owing to global warming (Croxall et al. 2002). Populations of the Emperor Penguin, for example, declined 50 percent from the mid-1970s to 1982 (see the graph below). Global warming is breaking up the ice too early in the penguins' annual cycle and causing an increase in the mortality of molting adults and juveniles, with a special twist. After breeding, Emperor Penguins must haul themselves onto intact pack ice and stay put there while they molt for three to four weeks. Molting penguins die if they have to swim far in prematurely open water.

Countering this mortality and helping to stabilize their populations is a positive effect of global warming. Open-water feeding areas, called polynyas, are larger and closer to the (winter) breeding colonies. Breeding success and adult survival during this demanding period of the annual cycle are increasing as a result.



Size trend of the breeding population of Emperor Penguins at Pointe Geologie, Adelie Land, Antarctica, in relation to distance between the colony and the northern limit of the pack ice in winter. The greater this distance, the fewer the breeding pairs. [*After Croxall et al. 2002*]

in the eastern United States and Eurasian Sparrowhawks in Britain. Together, these raptors served as indicator species because, as predators at the top of the food chain, they concentrate toxins in their bodies.

Similarly, the Bald Eagle, the national bird of the United States, became a national equivalent of the canary. Its population was in steep de-

cline. The reproduction of Bald Eagles in northwestern Ontario, for example, declined from an average of 1.26 young per nest in 1966 to a record low of 0.46 in 1974. Their reproduction increased to an average of 1.12 young per nest after DDT was banned (Grier 1982; Figure 18–23).

Paralleling the case of the Bald Eagles is that of the Brown Pelican, one of the most familiar and abundant birds of the Gulf and West Coasts of North America (Figure 18–24). This species faced extinction in the 1960s because of widespread reproductive failure (Schreiber 1980b). Hydrocarbon pesticides in the marine food webs of coastal California, coastal Louisiana, and nearby Texas interfered with the production of normal eggshells, and the pelicans typically laid eggs with very thin or no shells. The fragile eggs were easily broken under the weight of an incubating parent. The lack of reproduction in Brown Pelicans in California,

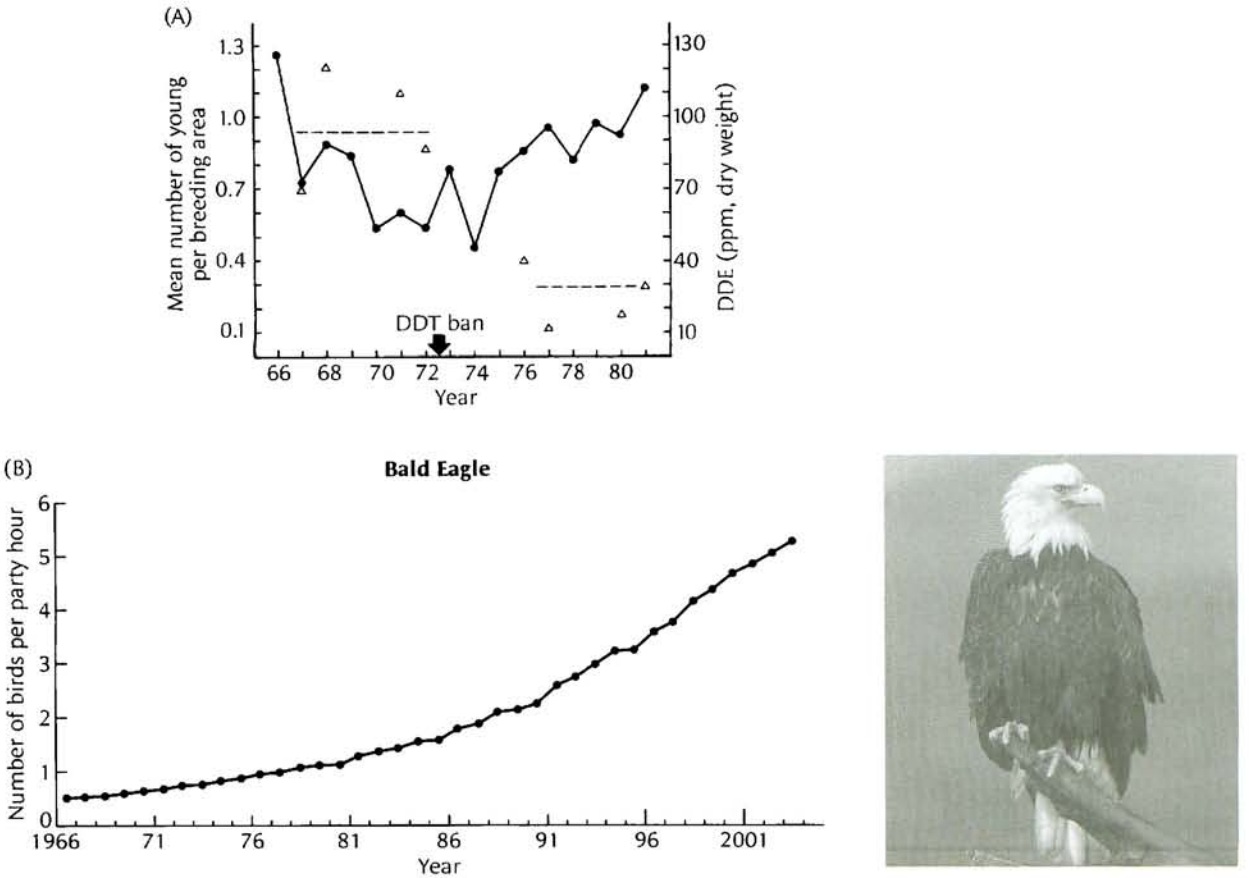


FIGURE 18–23 Return of the Bald Eagle. (A) Reproduction in Bald Eagles (solid line) improved after the use of the pesticide DDT (arrow) was banned. The ban resulted in a drop in chemical residues (DDE) in eggs (triangles). Dashed lines represent weighted mean concentrations of DDE before and after the ban. (B) Population recovery of Bald Eagles in Wisconsin based on Christmas Bird Count data. [*(A) From Grier 1982, copyright 1981 by the AAAS. (B) Graph from National Audubon Society 2002; photo, T. Vezo/VIREO*]

FIGURE 18–24 The Brown Pelican underwent reduced reproduction and severe population declines owing to the thinning of eggshells by DDT. The pelican populations are now increasing on both the East and the West Coasts of North America.

where eggshell thinning was most severe, and the alarming disappearance of pelicans from Louisiana and Texas, placed this bird on the endangered species list in 1973.

In each case, especially the high-profile plight of the Bald Eagle, conservationists identified the cause of the problems with bird populations. Governments banned the pesticides that were responsible, and users from home owners to farmers restricted their applications of the toxins. Under close scrutiny, Bald Eagles, Ospreys, Peregrine Falcons, and Brown Pelicans recovered. No longer endangered, Brown Pelican populations are now expanding rapidly in California and on both the Gulf and the Atlantic coasts. Bald Eagles are now quite common in most of their original range.

Population Crashes and Bottlenecks

The conservation future of a population depends in part on its size and its genetic structure. Small populations have less genetic diversity than do large populations. Severe declines in population size, often called population "crashes," reduce genetic variability and increase inbreeding among

the survivors. Students of population genetics refer to these temporary reductions in population size and reduced genetic diversity as "bottlenecks."

The survivors that remain after a population crash are subject to increased inbreeding, and its negative effects can limit recovery. The failure of eggs to hatch is one of the predictable negative effects of inbreeding, due to the effect of deleterious genes on embryological development. Hatching failure of 10 percent is the norm for outbred species. Higher failure rates indicate problems (Briskie and Mackintosh 2004). For example, half of the eggs of the endangered Kakapo, a flightless parrot, in New Zealand fail to hatch. Many other bird species of New Zealand have undergone severe population bottlenecks, either from historical endangerment or from the small numbers of birds of exotic species introduced onto the islands. A broad comparative survey of these species revealed that hatching failure increased with the severity of the population bottlenecks in both native and introduced species (Figure 18–25). Hatching failure increased in both groups when the bottleneck population sizes fell below 150 birds.

Population crashes of Song Sparrows studied on Mandarte Island off the coast of British Columbia favored individual birds with little past inbreeding in their pedigrees. This color-marked population crashed severely in 1979–1980 and again in 1988–1989 owing to severe winter weather (Keller et al. 1994). Eighteen percent (18 males, 9 females))

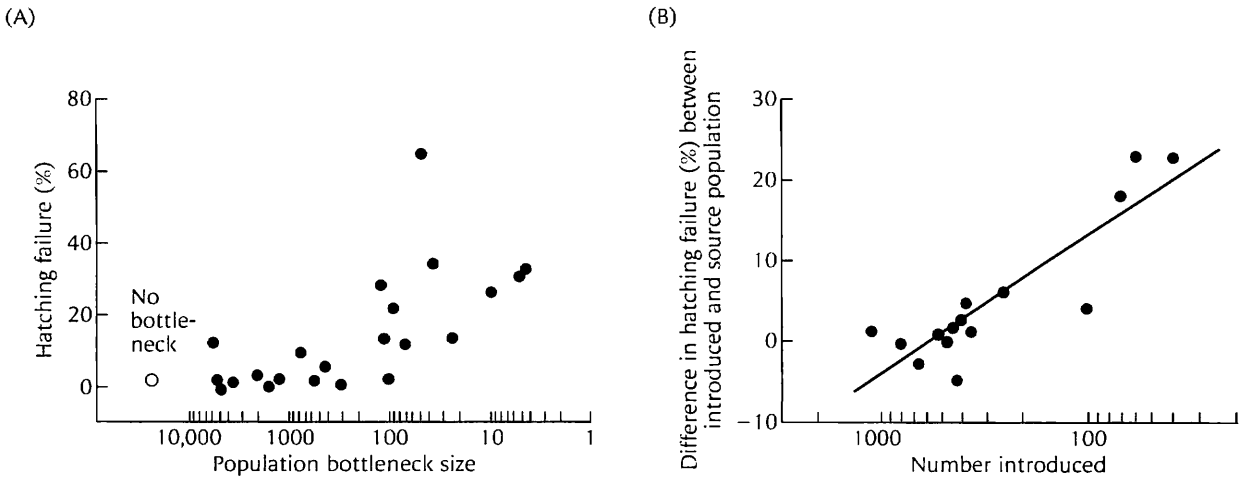


FIGURE 18–25 Hatching failure rates increase with the severity of bottlenecks in bird populations in New Zealand. (A) Hatching failure in native species, many of which are endangered or recovering from endangerment. The smaller the population bottleneck, the greater the hatching failure. (B) Hatching failure rates of species introduced in small to modest numbers. The hatching failure rates are expressed as the difference between the rate observed in the population after it was introduced to New Zealand and the hatching failure rate observed in the population that was the source of the introduced birds. The smaller the number of introduced birds, the greater the difference in hatching failure in comparison with the source population. [*After Briskie and Mackintosh 2004*]

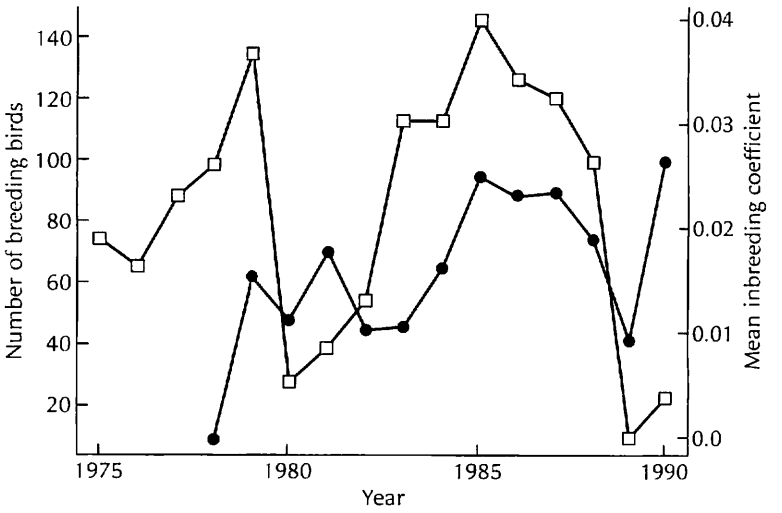


FIGURE 18–26 Changes in size of the population (line with squares) affect the average level of inbreeding (calculated genetic relationship to its grandparents) that prevails in a population of Song Sparrows on Mandarte Island in British Columbia. Levels of inbreeding (line with circles) increase during periods of population growth and the retention of multiple generations in the population. Population crashes, as in 1979–1980 and 1988–1989, culled the most highly inbred sparrows from the population, sharply reducing the average inbreeding coefficient. [*From Keller et al. 1994*]

survived the 1979 crash, and 11% (7 males, 4 females) survived the 1988 crash. The survivors had a significantly lower average inbreeding coefficient than did the population before the crash (Figure 18–26). This result is a rare demonstration that inbreeding can depress survival through an environmental challenge.

Island populations in particular tend to be small and to have lower genetic variability than is typical of related species on the mainland. Originally, the Mauritius Kestrel, found only on the same island as that of the fabled Dodo, exhibited about two-thirds of the genetic heterozygosity found in mainland kestrels (Groombridge et al. 2000). Then, from 1940 to 1960, pesticides exterminated most of this island kestrel population, reducing it to fewer than 50 birds and, in the end, to just one breeding pair. The population crash reduced allelic diversity by 55 percent (from 3.1 to 1.4 alleles per locus) and genetic heterozygosity by 57 percent (from 0.23 to 0.10). Conservation efforts rebuilt the population to 200 pairs from just one breeding pair. This replacement population is increasing in genetic variability by accumulating new mutations at a rate predicted for such a small population.

Summary

Bird populations range in size from hundreds of millions of birds to just a handful of survivors. In general, population sizes fluctuate dynamically from year to year as a result of changes in breeding success and mortality.

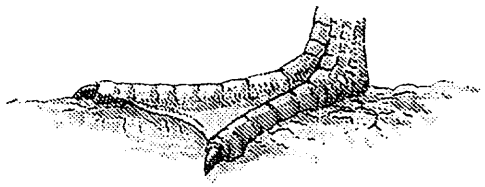
The growth of a population in a new environment usually follows a pattern of a slow initial rate of increase, followed by accelerated growth rates, and finally, a decline in growth rates in response to factors that lower reproduction and survival. Established populations tend to stay close to a long-range average size.

Habitat loss and pesticide poisoning of the food chain severely affect some populations. Some bird species, especially those that require cleared or shrubby habitats, benefit from human expansion. Major ecological forces—habitat, food, climate, predation, and disease—set upper limits on population growth. Diseases and parasites probably play a more substantial role in limiting bird populations than has been understood until recently. At high densities, social forces and density-dependent changes in fecundity or survival regulate populations about an average size. Surplus birds of territorial species stay in the background as "floaters" while they wait for an opening. Population sizes depend on the balance between rates of dispersal and recruitment, which, in turn, are often density dependent. Detailed studies of Great Tit populations in Holland and England and of Black-throated Blue Warblers in New Hampshire illustrate the nature of density-dependent regulation of population size.

Extrinsic forces, such as numbers of vole prey, drive cyclic changes in population size in some species such as owls. In game birds, such as ptarmigan of the tundra, density-dependent aggression and parasite infections drive these cycles. Long-term declines correspond to changes in habitat and increased predation. Long-term trends in bird populations, documented especially by large numbers of citizen scientists, serve as bellwethers of the quality of the environment as well as changes in climate.

This chapter started with the point that bird populations are dynamic, fluctuating in size from large to small and back to large again. Population sizes may change dramatically in size over periods of several years, owing to annual variations in survival and fecundity. In general, most local populations probably undergo periods of small size. Some rebound, others become extinct. Such periodic bottlenecks reduce genetic variability in local populations and, more importantly, provide the principal theaters for evolutionary change and speciation, the topic of the next chapter.

CHAPTER 19



Species

The origin and nature of species remains utterly mysterious.
[Bateson 1922, p. 55]

The first bird species of the Mesozoic era 150 million years ago diversified many times. Repeated speciation—the separation of one species into two or more derived species—multiplied their numbers and enriched the biodiversity on Earth.

The process of speciation is no longer mysterious. New species of birds evolve through sexual selection and ecological adaptation in isolated populations. The process of speciation starts with visual or vocal differences based on minor genetic changes or, sometimes, cultural experience. Continued genetic divergence leads to reproductive incompatibility. Unlike insects, however, birds retain their reproductive compatibility long after they achieve behavioral isolation.

This chapter begins with an introduction to species concepts and how birds speciate, a topic initiated in Chapter 3. Then follow the patterns of geographical variation and genetic structure of bird populations, including clinal variation—gradients of changing character states such as darkening feather color—and examples of genetic differences between local populations. Cases of hybridization figure prominently in studies of avian speciation in part because they provide tests of reproductive compatibility. In addition, the details of hybridization help to reveal the social and genetic architectures of species differences. The final section of the chapter summarizes the behavioral aspects of speciation from imprinting to social and sexual selection. Studies of Darwin's finches on the Galápagos Islands capture some of our best perspectives and insights into the process of speciation in birds.

What Is a Species?

Species are the primary units for describing and analyzing biological diversity. Each species has a characteristic size, shape, color, behavior, ecological niche, and geographical range.

The number of officially recognized bird species changes with increasing knowledge. In the early stages of avian taxonomy, ornithologists described slightly different populations as distinct species. Knowledge of geographical variation was limited then. Sometimes, our predecessors classified differently plumaged sexes or age classes as different species. As a result, the number of known species climbed to about 19,000 in the early 1900s.

Combining, or "lumping," species on the initial lists followed, as an understanding of age, sex, and geographical variations increased. Many so-called species were reclassified instead as distinct populations, or "subspecies." Adding to the mergers of species on the initial lists was the adoption in the 1940s of a broader species concept—the polytypic species concept, which allows a species to contain two or more variant forms. It embraced the potential reproductive compatibility of variable populations. Changing practices in the first half of the twentieth century reduced the number of species that were officially recognized to 8600 (Mayr and Amadon 1951). More recently, the taxonomic pendulum started to swing back to a middle position with the recognition of more distinct, isolated populations as species. Current lists of the birds of the world recognize about 10,000 species (Dickinson 2003; Gill and Wright 2006).

How best to define species as the fundamental units of biology has been the topic of a perennial debate that dates to Darwin himself (Zink 1996; Avise and Wollenberg 1997). Competing species concepts range from the practical to the philosophical (O'Hara 1993). The Phylogenetic Species Concept, which is attracting practitioners, is described later in this chapter. However, the species concept that prevails generally and in this textbook is the Biological Species Concept, or BSC (Mayr 1970; Coyne and Orr 2004). So defined, "Species are groups of freely interbreeding natural populations that are reproductively isolated from other such groups."

The reproductive compatibility of individual organisms—ranging from mate choice to the viability and fertility of offspring—serves as the ultimate criterion for inclusion in a biological species. Sexual reproduction links males, females, and their offspring into cohesive populations, sometimes in surprising ways (Box 19–1). Mating of like individuals with each other, called assortative mating, isolates some sets of those cohesive populations from other sets of similarly cohesive populations. Thus, White-crowned Sparrows mate with each other, but they do not interbreed with Song Sparrows that nest nearby. American White Ibises mate with each other, but they do not interbreed with the Glossy Ibises that nest in the same colonies.

Assortative mating may go unrecognized. Until 1965, for example, ornithologists recognized just one species of large black-and-white grebe (genus *Aechmophorus*) of western North America, called the Western Grebe (see Figure 3–16B). This grebe, which is best known for its elaborate "rushing" courtship display, has two color forms. The light-phase bird has a pale back and an orange yellow bill and is white above its ruby red eyes, whereas the dark-phase bird has a yellow green bill, with black extending below the red eyes.

BOX 19–1

POPULATION COHESION OF CUCKOOS

Separate populations of Common Cuckoos, a specialized brood parasite (see Figure 13–5), seem to defy the concept of reproductive cohesion. Recall that females of the brood-parasitic Common Cuckoos sort into sets of individual birds that lay different-color eggs. Their eggs mimic the eggs of their specific hosts. Sets of females that lay similar eggs are called *gentes*. Are the *gentes* different species even though females are not distinct in other ways? What about the males?

The solution to this puzzle is found in the sex chromosomes (Gibbs et al. 2000). Females segregate into genetically distinct sets of birds that carry the same *(gente)* genes for egg color. These genes are located on the W sex chromosome. Recall that females have one W and one Z sex chromosome.

Males have two Z sex chromosomes and are not genetically subdivided into matching *gentes*. They also do not discriminate among females from different *gentes*. Instead, they interbreed nondiscriminately with these host-specific females. Thus, the males provide the genetic cohesion of just one species.

While studying the courtship behavior of these handsome water birds, Robert Storer (1965) tallied the compositions of mated pairs in northern Utah and discovered that light-phase grebes paired preferentially with each other. So did dark-phase birds. Censuses of large grebe populations in Utah, Oregon, and California proved that mixed pairs of light-phase and dark-phase grebes are rare, constituting less than 3 percent of all pairs. Subsequent study revealed differences in their advertising call, which they use to locate their mates, plus differences in foraging behavior, size, and DNA (Storer and Nuechterlein 1992).

The discovery of assortative mating indicated reproductive isolation between coexisting, or sympatric, populations. Consequently, the light and dark color phases are now dubbed separate species, called Clark's Grebes and Western Grebes, respectively.

No accepted or specific genetic distances currently define species of birds. Imagine, however, being able to identify any species of bird from a short, standardized DNA sequence that might be embossed as a microdot on a museum label or readily available from a feather. This vision of a DNA bar may be as possible as it is ambitious, prescribing bar codes not just for birds but also for all organisms (Marshall 2005).

A successful pilot test on birds breathes life into the concept (Hebert et al. 2004). DNA sequences of the mitochondrial DNA gene encoding cytochrome *c* oxidase I *(CO1)* clearly distinguished 260 species of North American birds (Figure 19–1). Closely related species in the same genus averaged 7.9 percent divergence of these sequences, compared with an average of 0.4 percent for different individual birds of the same species. With just a few exceptions, differences among species exceeded 1.25 percent. Unusually low divergences characterized the Herring Gull and its close relatives, which speciated in the past 10,000 years, as well as species

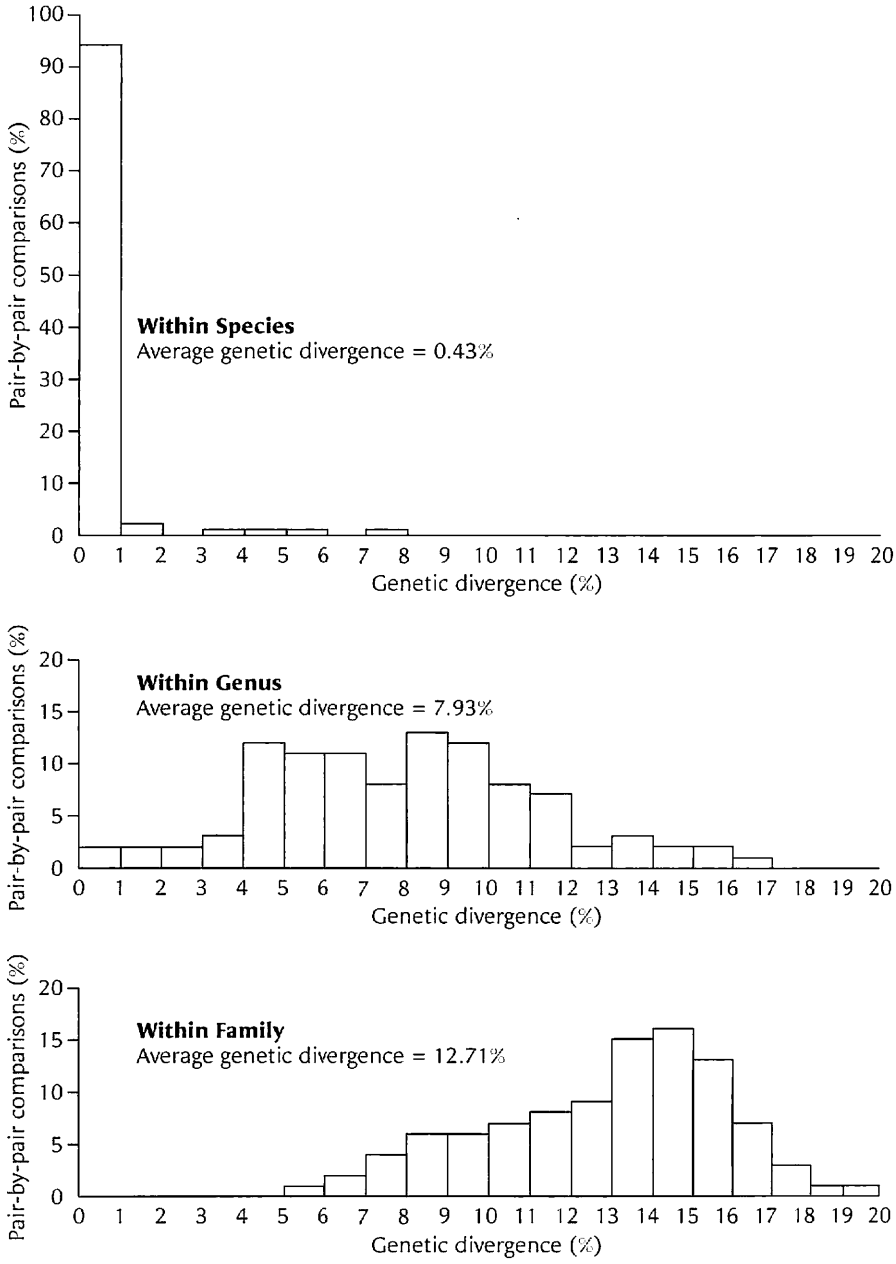


FIGURE 19–1 The mitochondrial gene *CO1* reliably distinguishes currently recognized bird species from one another. Genetic divergences averaged 0.4 percent within species, compared with 7.9 percent between species within various genera. Species in different families averaged 12.7 percent with much variation. The results are based on pair-by-pair comparisons of the nucleotide-sequence differences found in 437 North American bird species. [*After Hebert et al. 2004*]

of oystercatchers, crows (American compared with Northwestern), and two ducks (Mallard compared with American Black Duck).

In addition to suggesting that one gene could serve as a systematic bar code for birds, this pilot survey revealed surprisingly deep genetic differences within four species: Eastern Meadowlark, Warbling Vireo, Marsh Wren, and Solitary Sandpiper. Each of the first three species is known to comprise two populations that might merit recognition as distinct species. A hidden, potentially new species of Solitary Sandpiper, however, emerges as a complete surprise.

Allopatric Speciation

Most species of birds evolve in geographical isolation, called allopatry, under conditions of minimal gene exchange with sister populations (Figure 19–2). The allopatric speciation model explains the origin of most species of birds. Comparisons of the different mockingbirds isolated on different Galápagos islands, for example, led Darwin to formulate his insights about the origin of species and the importance of geographical isolation. Isolated islands of habitats on continents set a similar stage for speciation of the bird populations that occupy them.

Sister populations separated and isolated in geographical space diverge from each other. Sometimes, divergence is slow and, sometimes, it is rapid. Conspicuous patterns of geographical variation among populations are a result of this divergence.

One-third of the species of North American birds show conspicuous geographical variation among distinct regional populations, or subspecies. The 51 described subspecies of Song Sparrows, for example, range from sooty in the Pacific Northwest to pale brown in the deserts of California and from medium-sized in Ohio to large, thrush-sized birds in the Aleutian Islands. Geographical variation can evolve, sometimes rapidly, because different environments favor different attributes (Parker 1987). The crests of Steller's Jays in the western United States vary in length in relation to the openness of the vegetation in their habitats and to their effectiveness as social signals (see Figure 11–10). The different bill dimensions of Fox Sparrows in the western United States correspond to differences in their diets (Zink 1986; Figure 19–3). Geographical differences in size or color may be due directly to environmental differences rather than evolved genetic differences among populations (Box 19–2).

Divergence may be a random process, it may follow adaptation to different habitats, or it may result from sexual selection. The enhancement of plumage ornamentation, size, and song traits through sexual

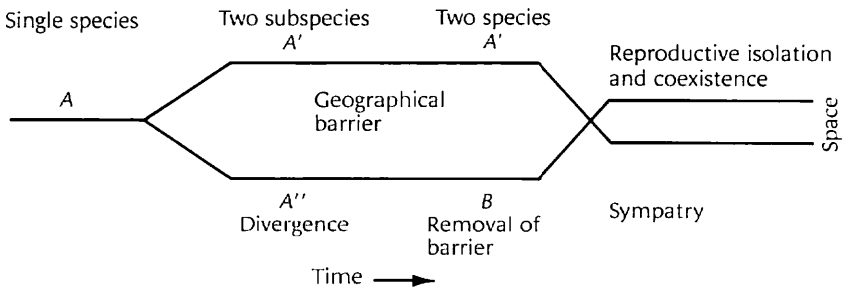


FIGURE 19–2 Geographical speciation proceeds through the divergence of populations in space and time. Letters designate genetically discrete populations. The separation of a population facilitates genetic divergence (*A* yields *A'* and *A''*). The reproductive incompatibility of populations (*A'* and *B*) can result from sustained isolation. A reversal of geographical isolation and range expansions can lead to coexistence as separate species.

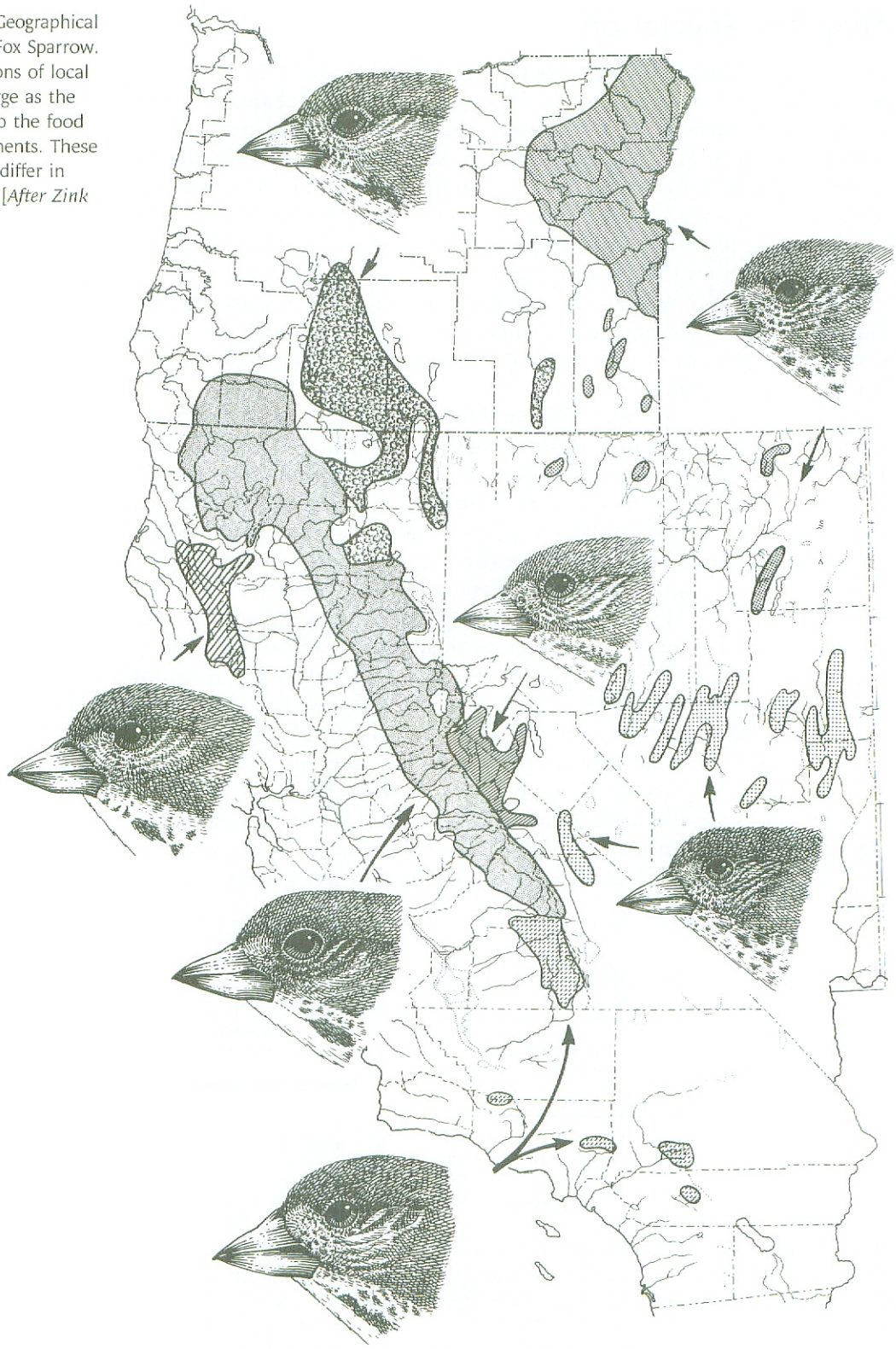


FIGURE 19–3 Geographical variation in the Fox Sparrow. The bill dimensions of local populations diverge as the sparrows adapt to the food in local environments. These populations also differ in body coloration. [*After Zink 1986*]

BOX 19–2

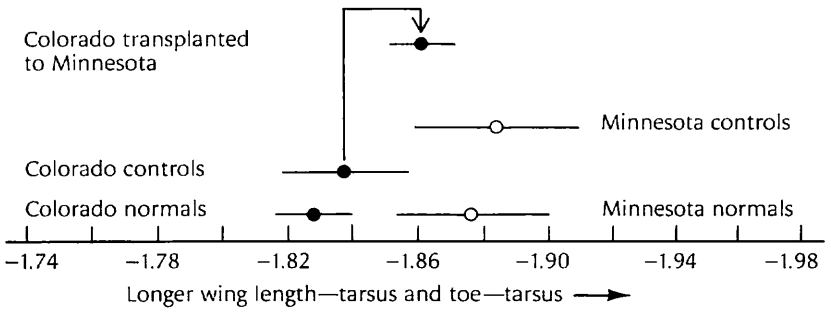
CHARACTER HERITABILITY

We tend to assume that size and color variation are genetically controlled and that they are not directly affected by the environment. This assumption is reasonable, but it is not certain.

In her pioneering study, Frances James (1983) demonstrated the effects of local environments on size features of Red-winged Blackbirds. Both their bill shapes and their wing lengths vary geographically. Some of this variation can be attributed directly to the environment.

When James transplanted eggs from the nests of one population to nests of another morphologically distinct population, the dimensions of fostered chicks grew to resemble those of their foster parents. Red-winged Blackbirds transplanted from the Everglades to Tallahassee, Florida, grew shorter, thicker bills, similar to those of the Red-wings in Tallahassee. Red-wings from Colorado transplanted to Minnesota developed longer wings and toes (see illustration). Thus, these young acquired some of the attributes of the host population. The incompleteness of morphological shifts by transplanted birds, however, revealed a significant degree of genetic control or heritability.

The heritability, H, of a character is the proportion of total observed variability that is controlled by the genes rather than by the environment. From one-half to most of the size variation observed in bird species has a genetic basis. Body masses of chickens are moderately heritable ($H = 0.53$). In contrast, feathering traits, breast angle, body depth, keel length, and shank pigmentation have lower heritabilities: $H = 0.25–0.40$ (Kinney 1969). Studies of character heritability in wild birds, often difficult exercises in quantitative genetics, indicate moderate to high heritabilities: 0.43 to 0.95 (Boag and Noordwijk 1987). Such heritabilities expose characters to long-term genetic change by natural selection and to short-term environmental modifications (because H is less than 1.0).



Environmental influence on the dimensions of nestling Red-winged Blackbirds. When transplanted to nests in Minnesota, eggs from nests in Colorado yielded nestlings that were shaped more like Red-wings in Minnesota than were the controls in Colorado. Nestling shape is here defined in terms of a discriminant function that relates wing length to size of the legs and feet. [*From James 1983*]

selection is especially important to the early divergences of sister populations (Price 1996). The divergence of ornaments or song then leads to reproductive isolation through assortative mating. Continued divergence leads to genetic incompatibility that reduces the viability or fertility of hybrid offspring.

The interactions of divergent sister taxa—if and when they come back into contact, called secondary contact—test their reproductive, ecological, and behavioral compatibility. Species in secondary contact encounter new opportunities to mate with dissimilar birds. They may coexist without interbreeding but compete for quality territories. Of particular relevance to the speciation process, hybridization may be limited at first in its frequency of occurrence or the species may practice strict assortative mating that leads to reproductive isolation and, thus, conformity to the definition of biological species.

Alternatively, divergent taxa in secondary contact might hybridize and blend with each other, depending on the extent of the their divergence. Quite possibly, hybridization is responsible for the modern characteristics of some modern bird species. The Gilded Flicker of the southwestern United States, for example, may be of hybrid origin (Short 1965). Some local populations of towhees in Mexico consist only of hybrids with characteristics of both the Spotted Towhee and the Collared Towhee (Greenlaw 1996).

Darwin's Finches

Peter and Rosemary Grant (1997) and their colleagues studied the details of the process of speciation by Darwin's finches for more than 30 years. Their findings helped to define the rules of the speciation process (Box 19–3).

BOX 19–3

SEVEN RULES OF SPECIATION IN BIRDS

Seven primary rules summarize the essential features of the speciation process in birds (After Grant and Grant 1996):

1. Speciation starts with divergence in geographical isolation, or allopatry.

2. Divergence in allopatry through ecological adaptation or sexual selection precedes sympatry (coexistence in overlapping geographical areas without interbreeding).

3. Premating isolating mechanisms evolve in allopatry before postmating isolating mechanisms evolve in either allopatry or sympatry.

4. Premating mechanisms include the effects of learning and cultural processes such as sexual imprinting.

5. Postzygotic incompatibilities arise first in females (the sex with two different sex chromosomes), in accord with Haldane's rule. (Haldane's rule says that both male and female hybrids may be sterile, but the sex with two different sex chromosomes—male fruit flies and mammals, female birds—tends to be sterile more often than the sex with two of the same sex chromosomes.)

6. Genetic mechanisms differ for the control of premating mechanisms (additive polygenes) and for the control of postmating mechanisms (*non*-additive effects of dominance and epistasis, which is an interaction between nonallelic genes, especially one in which one gene suppresses the expression of another).

7. Divergent bird species retain genetic compatibility and the potential for viable F_1 (first generation) hybrids longer than do mammals and for millions of years after speciation.

They concluded that the multiplication of species of Darwin's finches, 15 total, followed three basic steps, repeated over and over again (Figure 19–4). First was the original colonization of the Galápagos Islands by the ancestor from mainland South America, probably a grassquit of the genus *Tiaris* (Sato et al. 2001). Second was the colonization of other islands by dispersal from the first island. Speciation of these finches took place when small colonizing founder populations underwent rapid but simple genetic changes followed by population growth and adaptive divergence. Third, derived and divergent populations recolonized the original, or "first," islands. Secondary contact and coexistence with their sister populations or species completed the speciation process. Some of Darwin's finches now have moderately large populations on several islands united by gene flow.

Hybridization, though rare, occurs between some pairings of all six species of ground finches as well as with other Darwin finches—namely, the tree finches and cactus finches. First-generation (F_1) hybrids are viable and fertile, as are later backcross hybrids. The current species retain substantial genetic compatibility with little sign of postmating isolating mechanisms. These mechanisms will develop slowly as a result of continued divergence of species that are effectively isolated reproductively by their species-recognition behavior (see page 599).

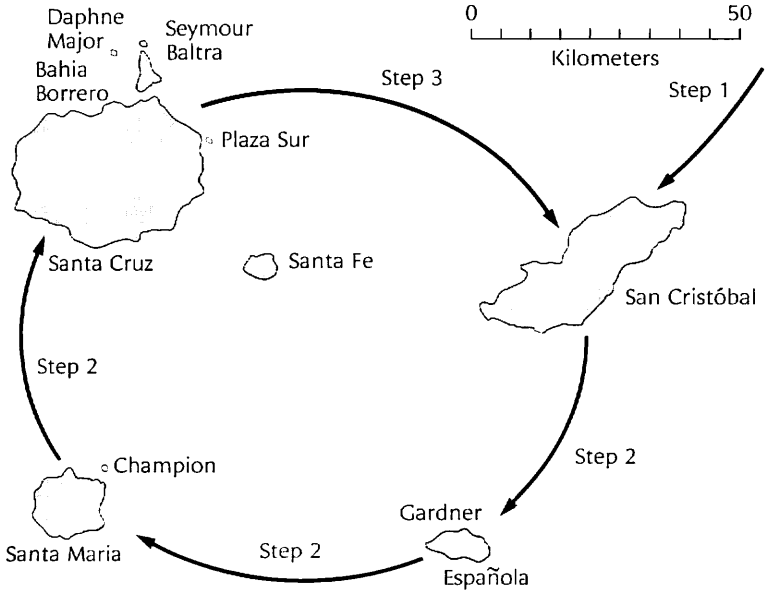
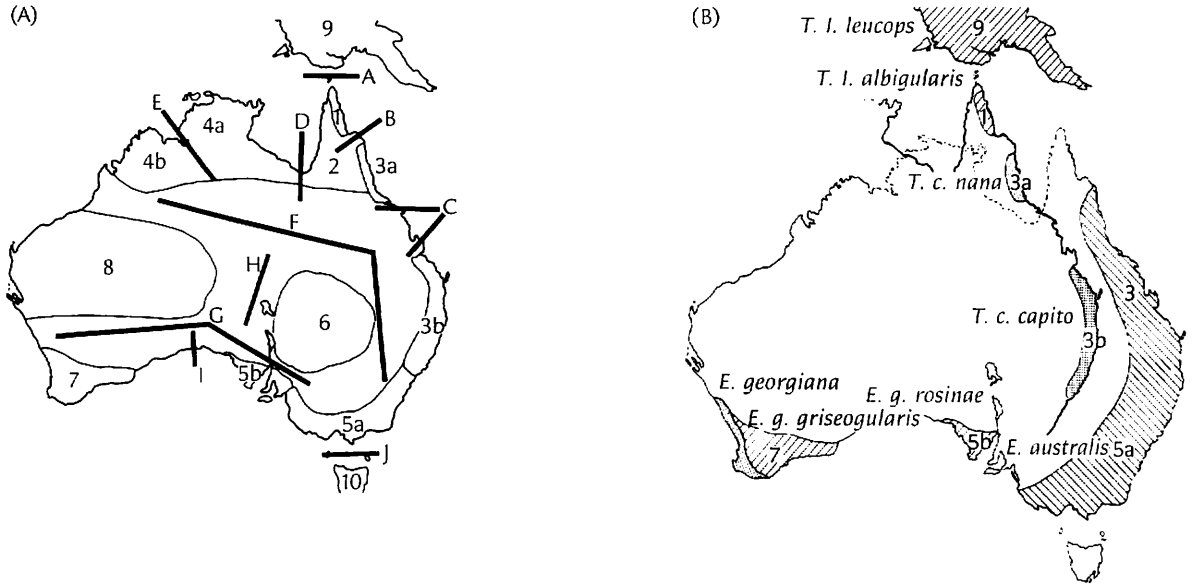


FIGURE 19–4 A model of allopatric speciation in Darwin's finches of the Galápagos Islands. First, their mainland ancestor, a grassquit, colonized one of the islands (step 1). Its descendants dispersed and colonized additional islands (step 2), starting new isolated populations that diverged from one another. In the final step (3), members of a divergent population established themselves on the original island and coexisted there—in sympatry—without interbreeding with the descendants of a parent population. [*After Grant and Grant 1997*]

Geographical Isolation on Continents

The isolation of bird populations on remote oceanic islands is easy to envision. Isolation on the mainland is less so. In overview, changing climates and their effects on habitats isolate bird populations on continental landscapes. For example, wet–dry cycles fragmented the habitats and isolated bird populations from one another in Australia, Africa, and South America (see Figure 3–2). Fractured sets of sister populations, or vicariants, then evolve into different species.

The history of the modern Australian birds featured 10 specific fractures (Figure 19–5). Among them was a major separation of the birds of the northern and eastern part of the continent from the birds of the central and southern regions. The birds that occupied wet habitats on the southern edge of Australia also split from those of the central arid region. Later, the birds of the central arid region and the birds of the southern moist region split again. The deterioration of climates during the Pleis-



E. australis = Eastern Yellow Robin (areas 5a and 3)
E. g. griseogularis and *E. g. rosinae* = Western Yellow Robin (areas 7 and 5b)
E. georgiana = White-breasted Robin (dotted area at bottom left)
T. c. nana and *T. c. capito* = Pale-yellow Robin (areas 3a and 3b)
T. l. leucops and *T. l. albigularis* = White-faced Robin (areas 9 and 1)

FIGURE 19–5 Fragmentation of Australian habitats was responsible for the geographical speciation patterns on that continent. (A) Ten primary ecological barriers (A–J) separate the geographical regions of endemism (areas of restricted distribution) of Australian birds (1–10). (B) Distributions of Australian robins *(Eopsaltria* and *Tregellasia)* in relation to the major areas of endemism of Australian birds. The eastern coast is enlarged at the right so as to show the different distributions of the two species found together there. [*From Cracraft 1982a*]

tocene epoch caused the birds of the two northern regions to split repeatedly at different sites. Sister taxa diverged with these separations, producing, for example, the current assemblage of species and subspecies of Australasian robins. These sister taxa came back into contact when their ranges expanded during favorable climatic periods.

DNA comparisons can help to define how long ago populations were separated. Generally speaking, species exhibit nucleotide divergences in roughly 2 to 8 percent of their mitochondrial DNA (mtDNA). Bird species in tropical South America exhibit more genetic divergence than do temperate-zone species (Capparella 1991). On the basis of the critical assumption that DNA diverges at a rate of roughly 2 percent each million years, many species originated in the Pliocene (3.5 to 7 mya) and some are older still (Klicka and Zink 1997; F. B. Gill et al. 2005).

Winter Wrens, for another example, underwent repeated fragmentation, or vicariant events, of their populations throughout the Northern Hemisphere dating to the Miocene (Drovetski et al. 2004; see the geologic time scale in Table 2–1). This widespread tiny songbird is found throughout northern North America and Eurasia. Slight differences in plumage colorations of different populations contributed to the description of as many as 43 subspecies (Hejls et al. 2002). Analysis of their mtDNA *(ND2)* revealed the main features of their evolutionary history that were not evident from external comparisons.

The expansion of Winter Wrens started from their original populations in North America. They spread widely throughout the Northern Hemisphere roughly 13 million years ago in the middle Miocene (Drovetski et al. 2004). Much later, the glaciations of the early to mid-Pleistocene split the wren populations sequentially into six evolutionarily significant units with species-level genetic divergences (3 to 8.8 percent).

Pleistocene climate changes played a major role in defining modern birds of the northern continents. Through numerous extinctions, the glaciers pruned the species assemblages that had prospered in the gentler preceding climates of the Tertiary. Losses accrued with the habitat fragmentation that was a regular consequence of the repeated advances and retreats of the glaciers. Those bird populations that survived the effects of changing climates on major habitats shrank in size and became fragmented in their distribution. When the glaciers retreated, the bird populations followed and engaged in new confrontations with one another.

In some cases, postglacial expansions of populations throughout the northern United States and Canada have been too recent to allow substantial genetic divergence (Ball and Avise 1992). For example, widespread North American bird species, including Red-winged Blackbirds, Downy Woodpeckers, Mourning Doves (Figure 19–6), and Black-capped Chickadees, have nearly the same mtDNA genotypes from one side of the continent to another.

The Yellow-rumped Warbler provides an example of populations that diverged while fragmented by the glaciers. Now considered one large polytypic species, the Yellow-rumped Warbler includes four distinct

FIGURE 19–6 Mourning Doves are a common sight (and sound, with their mournful coo) throughout much of the United States. Their populations there have expanded too recently to allow substantial genetic divergence in mtDNA.

subspecies. Two of them are sedentary populations in Mexico (*nigrifrons*) and Guatemala (*goldmani*). They are distinct forms in both plumage color and genetics, with a long history of isolation. The migratory populations that breed in North America diverged from the sedentary populations in the early Pleistocene and then split again into eastern (*coronata*) and western (*auduboni*) forms owing to the Wisconsin glaciation of the late Pleistocene. The eastern and western populations diverged into the distinctive subspecies of the Yellow-rumped Warbler—the Myrtle Warbler and Audubon's Warbler, respectively (Figure 19–7). Although they differ in plumage coloration, they exhibit few genetic differences.

Myrtle Warblers and Audubon's Warblers now interbreed in the narrow mountain passes of the Canadian Rockies. These divergent populations came back into contact about 7500 years ago, when the glaciers retreated and the forests reunited. Westward movement of Myrtle Warbler genes and eastward movement of Audubon's Warbler genes have extended the zone of intergradation, or hybrid zone, beyond the mountain passes to create a zone of intergradation 150 kilometers wide. Whether Myrtle and Audubon's Warblers meet the criterion of "freely interbreeding" required for species status is under discussion, with a strong proposal to recognize all four subspecies of the Yellow-rumped Warbler (Mila et al. 2005).

Ring Species

Ornithologists have long predicted that divergence among populations linked in a series or chain over a large continental area could lead to the

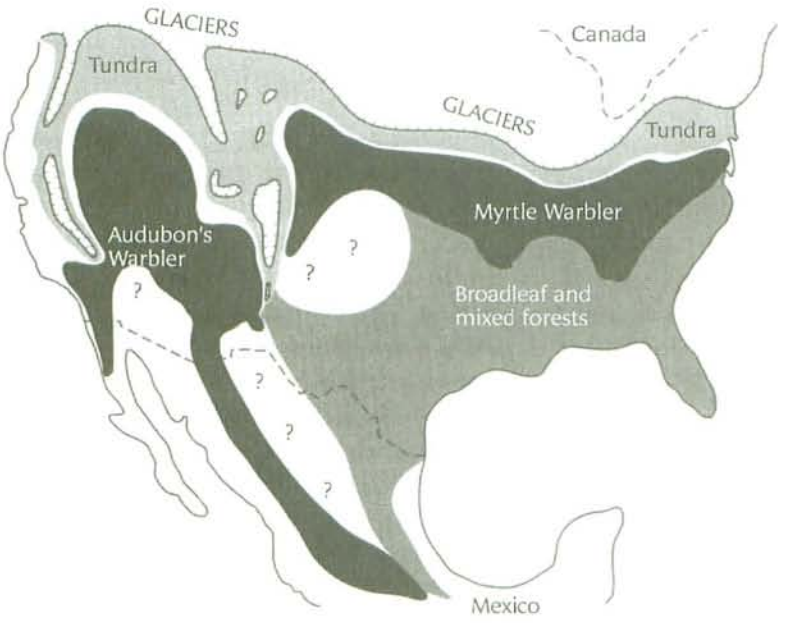


FIGURE 19–7 Model of the distributions of the eastern subspecies of the Yellow-rumped Warbler, or Myrtle Warbler, and the principal western subspecies, or Audubon's Warbler. They became separated during the Pleistocene epoch (Wisconsin glaciation), when they diverged from a common ancestor. Question marks indicate regions for which the habitat type at that time is unknown. [*From Hubbard 1969*]

reproductive isolation of the populations at the ends of the chain. The discovery of such so-called ring species—two reproductively isolated forms connected through a chain of interbreeding populations—would support this prediction, but few such discoveries have materialized. Now, after many years of searching, we have a viable and intriguing example of an avian ring species—namely, the Greenish Warblers of central Siberia (Irwin et al. 2005; Box 19–4).

The Phylogenetic Species Concept

Concerns about the practical application of the Biological Species Concept prompt some ornithologists to prefer instead the Phylogenetic Species Concept (PSC). For example, unlike Myrtle Warblers and Audubon's Warblers, the vast majority of isolated and divergent populations do not come into contact. Distinctly different, geographically separated, or allopatric, populations therefore force ornithologists to make an educated guess in regard to what might happen should contact be established in the future.

According to the PSC, a species is the smallest aggregation of populations that can be diagnosed by a unique combination of character states in comparable individual organisms (Nixon and Wheeler 1990). Each historically fragmented population with distinct characteristics serves as the

BOX 19–4

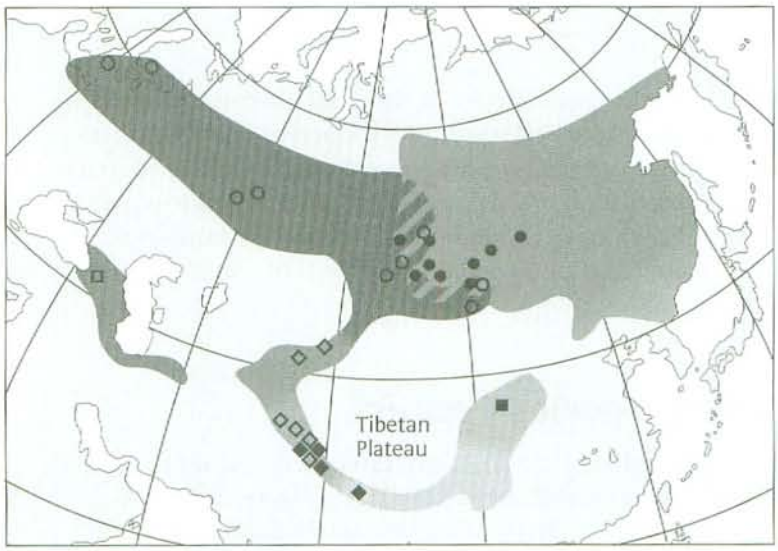
A RING SPECIES IN SIBERIA

The Greenish Warbler ranks high on the list of truly nondescript birds of the world. Nevertheless, it invites our attention as the best example of an avian ring species in which intergrading populations connect two reproductively isolated populations (Irwin et al. 2005).

The Greenish Warbler breeds in a narrow band of tree-line habitat in Siberia and the Himalaya. The band of that tree-line habitat encircles the high-altitude deserts of the Tibetan Plateau, forming a geographical ring of connected populations (see map). The one gap in the ring in northern China is due to recent habitat destruction.

Classical studies of size and plumage coloration, what there is of it, defined a series of intergrading subspecies, or closely related species, throughout this ring. Genetic comparisons by Darren Irwin and his colleagues confirm the continuous intergradation between adjacent populations, except for the two most northern ones, which coexist without interbreeding in central Siberia. They are reproductively isolated, terminal populations of increasingly divergent, interbreeding populations.

Historically, Greenish Warblers expanded on two fronts into Siberia as the climate warmed. Rapid adaptation to the northern forests and the migration distances required to reach them, which favor longer wings, caused the populations to diverge on the two fronts and to be reproductively isolated as biological species when the two northernmost populations came into secondary contact.



Ring populations of the Greenish Warbler in Siberia. Different shades represent different morphological subspecies that intergrade with each other. The two widespread northern subspecies *Phylloscopus trochiloides nitidus* (west) and *Phylloscopus trochiloides plumbeitarus* (east) coexist without hybridization (hatched area) in central Siberia. Habitat destruction in northern China has recently interrupted the continuity of the ring of populations. Symbols for localities sampled indicate major clades (groups related by evolutionary descent from a common ancestor) based on mitochondrial DNA. Open symbols represent western clades; solid symbols represent eastern clades. The genetic distance between individual birds within and between clades increases with geographical distance around the southern chain of populations. [*After Irwin et al. 2005*]

working unit of the PSC. Rather than combine geographically distinct, but potentially interbreeding, populations with distinct evolutionary histories into one larger, variable, or polytypic, species, the PSC distinguishes each one as a separate evolutionary species unit.

This approach gives greater weight to the evolutionary histories of the isolated populations than it does to the fact that they might interbreed where and when they achieve sympatry. For example, the four populations of Yellow-rumped Warbler and the six genetic groups of Winter Wrens merit attention as significant evolutionary lineages and status as phylogenetic species. Full application of the PSC to the birds of the world would roughly double the number of species recognized.

Population Size and Structure

Population sizes and structures guide the evolution of geographical variation. In particular, the movement of young birds from the sites where they hatched to the sites where they breed, called natal dispersal, determines population structure (Figure 19–8). Colonial seabirds, such as albatrosses, gulls, and terns, usually return to their natal island colonies. Songbirds such as the House Wren, Great Tit, the Eurasian Pied Flycatcher, and the Song Sparrow stay within a few kilometers of their natal territories. Only a few individual birds of such species disperse widely.

Large natal dispersal distances unite populations. Small natal dispersal distances enhance genetic isolation. In general, dispersal also promotes outbreeding (Greenwood 1987). The tendency to stay near one's birthplace, called philopatry, increases the probability of breeding with near relatives, even siblings, and thus increases the risks and costs of inbreeding (see Chapter 18).

Effective Population Size

The average dispersal distance of a species defines the size of a local, reproductively cohesive population, or deme, in which gene exchange is theoretically a random process. Small demes are more likely to evolve faster and in directions more likely dictated by chance than are large ones.

The number of birds in a deme is called the effective population size, which decreases with shorter dispersal distances of juveniles. The effective sizes of bird populations also decrease when small groups of colonists start new populations, when populations fragment into small isolates with limited dispersal, when populations are confined to isolated colonies on long, narrow coastlines, or when just a few birds dominate nonmonogamous breeding systems, as do lekking manakins or grouse (see Chapter 13).

Ornithologists estimate that noncolonial passerine birds disperse 1 kilometer per year (Barrowclough 1980). This distance indicates that the effective population sizes of such birds are quite large—from roughly 175 to 7700 birds—and that evolutionary change tends to be slow and adaptive. It follows, also, that bird speciation usually results from slow,

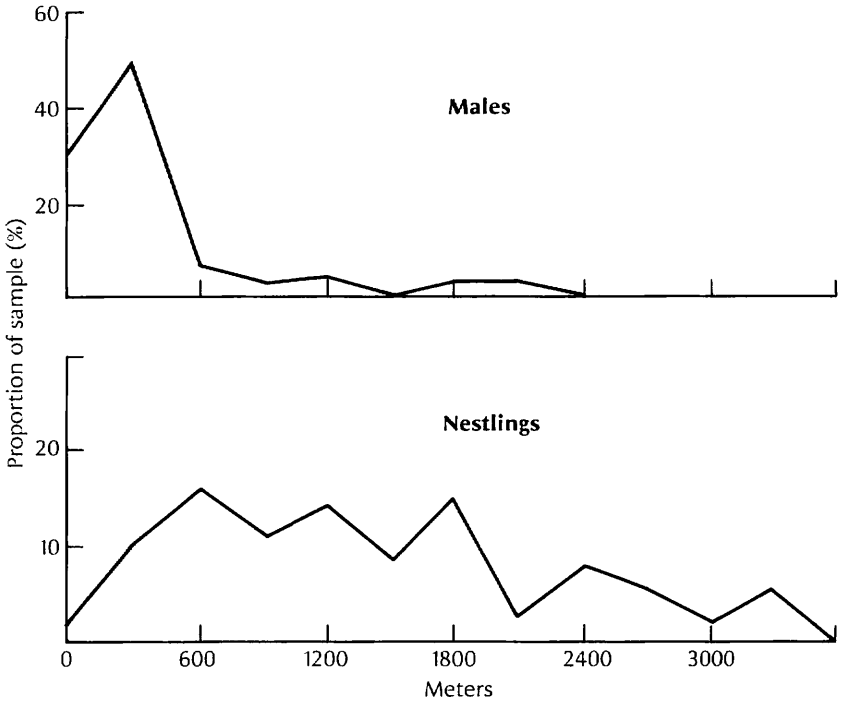


FIGURE 19–8 Dispersal of adult male (*top*) and nestling (*bottom*) House Wrens. Most adult males disperse over a small area, whereas young wrens disperse more widely. [*After Barrowclough 1978*]

adaptive divergence of large, fragmented populations or from rapid genetic change in small, founder populations (Barrowclough 1983).

For example, populations of Common Mynas introduced to Australia, New Zealand, Hawaii, Fiji, and South Africa from India differ genetically more from one another than do populations in Asia. Most of these introduced populations started as small founder populations. Subsequent reductions in population size and random changes in gene compositions in the past 100 to 120 years have promoted genetic shifts comparable to those between different subspecies of other birds (Baker and Moeed 1987).

Clines and Local Evolution

The evolution of geographical differences among bird populations depends on the relative strength of two opposing forces: natural selection and gene flow. Natural selection—the differential propagation of genotypes—promotes divergence by favoring one genetic attribute over another. Gene flow—the movement and incorporation of alleles among local populations due to dispersal—opposes divergence by blending the differences among adjacent populations.

Clines are gradients of changing character states, such as (increasing) body size or (darkening) feather color. How much the character changes

from site to site along the gradient depends on the relative intensities of divergent selection and gene flow due to dispersal.

Clines are especially conspicuous in birds that have simple (Mendelian) genetic color morphs. The proportions of red (actually bright rufous) versus gray Eastern Screech Owls, for example, change systematically with locality. Local populations change from mostly red owls in Tennessee to mostly gray owls in Maine and Florida (Figure 19–9). The advantages of color alternatives derive from protective coloration or exposure to predators such as the Great Horned Owl. As the type of forests changes from rich brown hardwoods in the center of their range to grayish conifers in the north and to pinelands in the far south, the concealing coloration changes from reddish to gray.

Clines may be either static or dynamic. In static clines, the equilibrium between selection and gene flow is stable: the composition of the populations will stay the same. Dynamic clines change with time as a result of an ongoing diffusion of neutral traits due to gene flow or as a result of an advantage of one trait over its alternatives.

Bananaquits provide one example of a dynamic cline (Wunderle 1983). These small, tropical, warblerlike, nectar- and fruit-eating birds are abundant

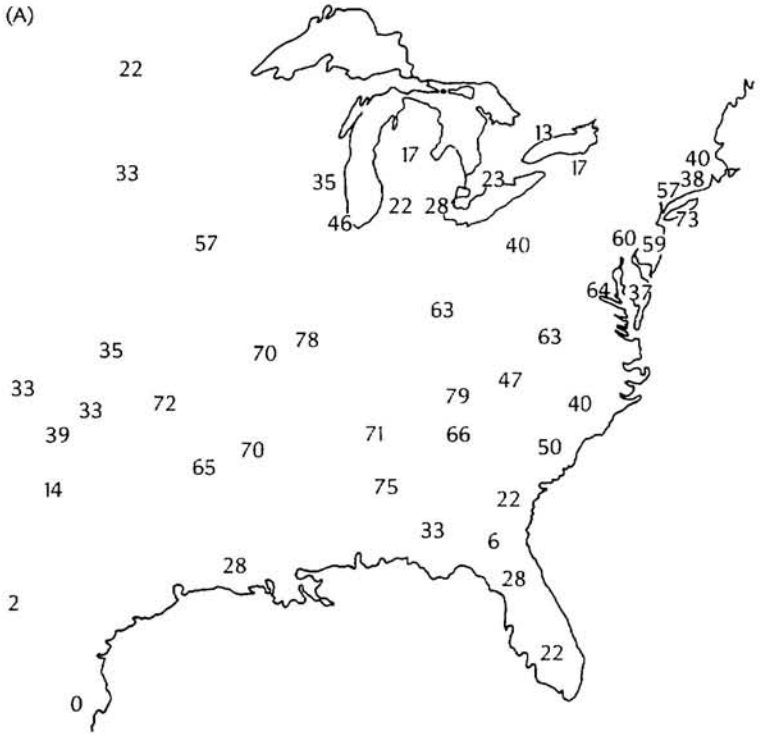


FIGURE 19–9 The proportions of red-phase Eastern Screech Owls found in local populations (A) decline from high values of 70 to 80 percent in the center of the range of this species to 30 percent or less at the edges of the range. (B) Eastern Screech Owl. [*(A) From Owen 1963. (B) R. & A. Simpson/VIREO*]

on islands of the Caribbean. The yellow-and-black color form of Bananaquits prevails throughout most of the Caribbean. An all-black form of this species, determined by a single dominant mutant allele, inhabits the island of Grenada (Theron et al. 2001).

Yellow-and-black Bananaquits from adjacent islands colonized the arid southwestern corner of Grenada in the early 1900s. They replaced the black form in their initial foothold on the island and then expanded progressively to the north and east. Exhibiting a 17 percent selective advantage, yellow-and-black Bananaquits advanced eastward at a rate of roughly 400 meters per year, mixing with and then replacing black forms. As a result, the proportions of the remaining black form increased clinally to the north and east. The replacement continued dynamically for 21 years and then stopped when droughts limited continued population growth and expansion of yellow-and-black Bananaquits (MacColl and Stevenson 2003). The dynamic cline stopped and stabilized as a static cline (Figure 19–10).

Sometimes, bird populations evolve differences on an extremely local scale. Two examples illustrate this phenomenon. First is the striking geographical divergence among populations of a species of white-eyes *(Zosterops)* within the confines of a small island in the Indian Ocean. Second are detailed studies of genetic population structure of the Great Tit on Vlieland island off the coast of Holland. These studies refocus our attention on the potential scale of microevolution (evolutionary change between local populations) in birds.

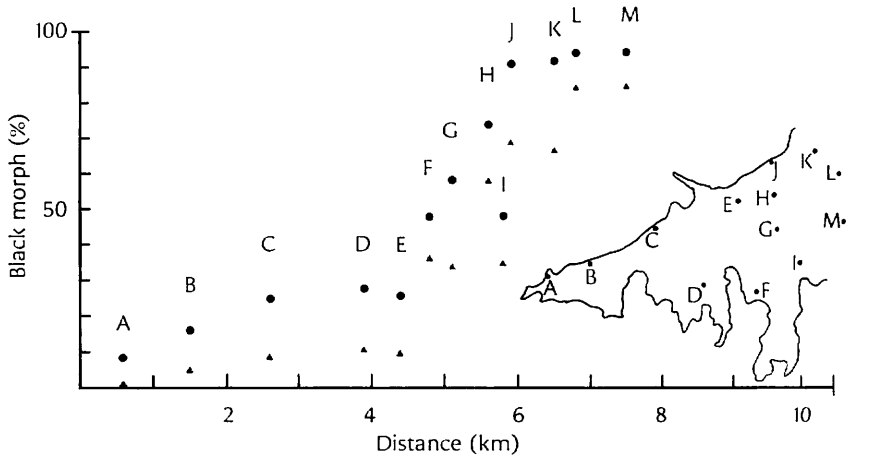


FIGURE 19–10 Yellow-and-black Bananaquits are common only in southwestern Grenada, the region of their recent colonization of this island. All-black birds (black morphs) occupy the rest of the island. Shown here are the proportions of the black morph (black circles) at sampling sites (A through M) for the interval 1974–1978, graphed in regard to distance from the westernmost point of the island. Triangles indicate the results of resampling the localities in 1981 and show how proportions of the black morph have declined. [*From Wunderle 1983*]

White-eyes are Old World ecological equivalents of the Bananaquit (Figure 19–11A). One species lives only on the small, rugged island of La Réunion in the western Indian Ocean. Like Eastern Screech Owls, the Reunion Gray White-eye has gray and rufous brown color morphs, which change in proportion rapidly over distances of only a few kilometers on steep mountainsides (Gill 1973). Proportions of gray white-eyes in local populations increase clinally with altitude from none in coastal populations to more than 90 percent in populations above 2000 meters. Gray white-eyes predominate through some strong advantage in the gray heath vegetation of high altitudes. Conversely, brown white-eyes are favored by selection in the hardwood forests of lower altitudes. The advantages of "browns" downslope and of "grays" upslope establish a steep clinal gradient.

Independent of the proportions of the two color morphs, brown white-eyes vary strikingly in color and size at different locations on La Réunion. Three distinct populations, each with altitudinal clines in size

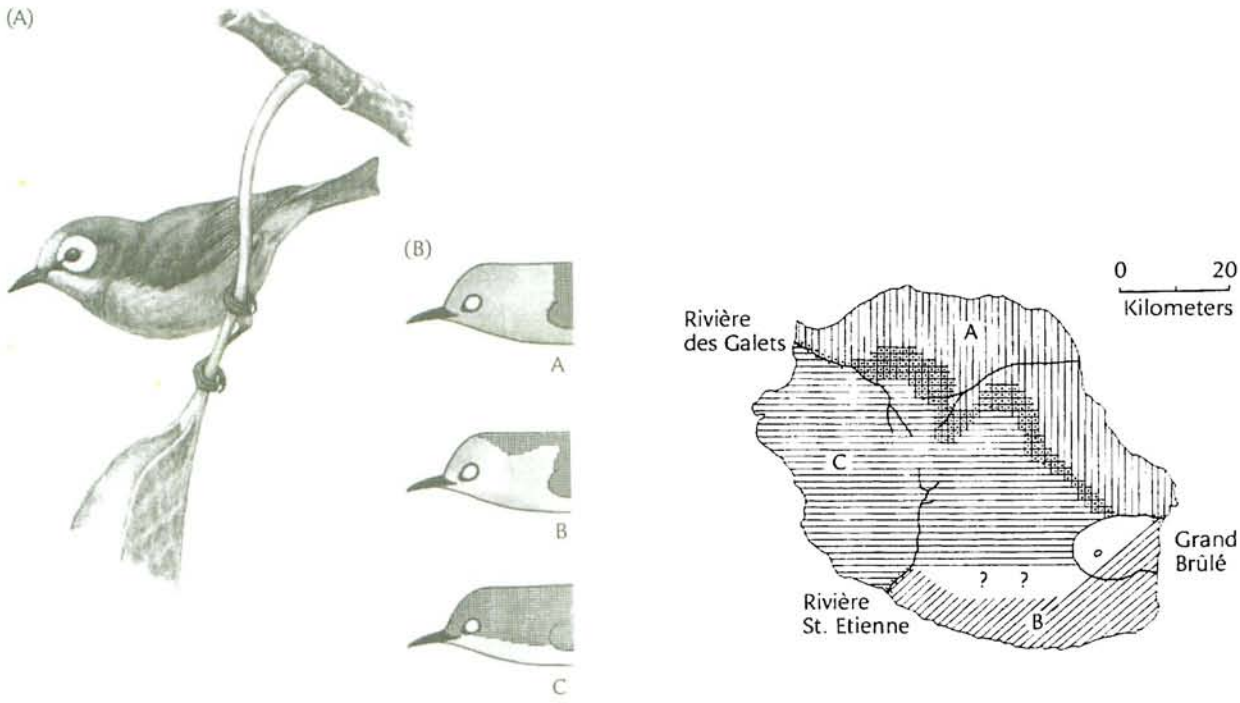


FIGURE 19–11 (A) White-eyes (Zosteropidae) are highly opportunistic songbirds of the Old World Tropics and successful colonists of remote oceanic islands. (B) Three distinct populations of the Reunion Gray White-eye evolved on the island of La Réunion in the Indian Ocean. Zones of contact and hybridization are indicated by dots (in darker area). Population B is isolated along the coast, separated from the other two populations by the Rivière St. Etienne and lava flows of Grand Brûlé. It probably originated as a result of hybridization between populations A and C. The contact between populations B and C, indicated by question marks (?), remains unknown. [*From Gill 1973*]

and pigmentation, occupy the coastal regions (Figure 19–11B). A gray-headed form, a brown-headed form, and a gray-crowned, brown-naped form evolved as small, isolated populations on different sides of the island before the arrival of humans. After widespread cutting of the forests, we speculate, the ranges of each color form expanded and now abut one another at major riverbeds and at a lava flow, thus remaining partly isolated.

Much smaller than La Réunion is the tiny 4022-hectare island of Vlieland on the coast of the Netherlands. Vlieland is home to two genetically distinct populations of Great Tits. A remarkable 30-year study documented the movements and genetics of the Great Tits and quantified the microevolutionary interaction between selection and gene flow (Postma and Noordwijk 2005). Different levels of immigration and gene flow from the mainland sustain a genetic difference between the two populations.

Specifically, female Great Tits on the western part of the island consistently lay on average 1.15 more eggs in a clutch than do female Great Tits on the eastern part of the island only a few kilometers away. This difference in clutch size has a strong genetic component: females that move eastward or westward within the island continue to lay the clutch sizes that are consistent with their place of origin. The root cause of the difference between sites lies curiously in the rates of immigration and settlement by tits from the mainland.

Selection on Vlieland as a whole favors females that live twice as long as the mainland tits and produce smaller clutch sizes. But each year, females from the mainland, which are genetically predisposed to lay larger clutches, migrate to Vlieland. They migrate mostly to the west side of the island. Immigrants account for 43 percent of the annual recruitment to the west side compared with only 13 percent to the east side. The local selection for small-clutch females can override the 13 percent influx in the east but not the 43 percent influx in the west.

Hybrids

Much early thinking about speciation in birds emphasized hybrids. This emphasis was based on direct but, we now realize, inappropriate applications of fruit fly *(Drosophila)* genetics to birds (Grant and Grant 1997). Small genetic changes tend to cause male sterility in fruit flies but not in birds. Instead, with some exceptions, birds retain the potential for successful hybridization through surprisingly high levels of genetic divergence. Consequently, successful hybridization among birds is not limited to closely related or sister species (Zink 1996). Unlikely parents sometimes hybridize successfully because of their retained genomic compatibility. Intergeneric hybrids between species of wood warblers, ducks, and pheasants, among the many examples, testify to this compatibility.

More than 10 percent of bird species are known to hybridize (Grant and Grant 1992). The word "hybrid" itself grabs our attention. It evokes

the powerful concepts of novelty, strength, sterility, inferiority, and superiority (Gill 1998). Hybrid birds both challenge and fascinate ornithologists. Each year ornithologists report new novelties due to hybridization. Deciphering their parentage can be a wonderful ornithological puzzle.

Descriptions of the first "Brewster's" and "Lawrence's" Warblers collected in Massachusetts in 1874, for example, provoked much debate. They finally proved to be hybrids between Blue-winged Warblers and Golden-winged Warblers (Gill 2004; see page 596). In another case, at the beginning of North American ornithology, Audubon himself described the enigmatic "Cincinnati Warbler." A century and half later, Gary Graves (1988) determined it to be a hybrid between a Kentucky Warbler *(Oporornis)* and a Blue-winged Warbler *(Vermivora)*.

Hybrid Inferiority

Hybrid inferiority may first be evident in intermediate plumage or displays. They can render the hybrid less effective in courtship. Hybrid crosses of Anna's Hummingbirds and Costa's Hummingbirds, for example, are intermediate in many details of plumage as well as in the circular courtship flight displays characteristic of these species (Wells et al. 1978). Similarly, a hybrid male of a cross between the Sharp-tailed Grouse and the Greater Prairie Chicken was unable to perform bobs, bows, and foot stomps correctly and mated infrequently as a result (Evans 1966).

Some bird hybrids exhibit sterility or substantial inferiority. Like mules—the hybrids of female horses and male donkeys—almost all the hybrids of the Eastern Meadowlark and the Western Meadowlark are sterile (Lanyon 1979). The hybrids appear normal and healthy, but they produce infertile eggs when paired in captivity with an Eastern Meadowlark or a Western Meadowlark. Because there is no gene flow between them, the two meadowlarks remain distinct biological species, in contrast, say, with Myrtle and Audubon's Warblers.

Both male and female hybrids may be sterile, but the sex with two different sex chromosomes—male fruit flies and mammals, female birds—tends to be sterile more often than the sex with two of the same sex chromosomes (see Box 19–3). Data from vertebrates and invertebrates broadly support this expectation—known as Haldane's rule because it was stated first by J. B. S. Haldane (1922). Studies of hybridization between Eurasian Pied Flycatchers and Collared Flycatchers support the predictions of Haldane's rule (Gelter et al. 1992). From 15 to 20 percent of the breeding pairs in their hybrid zone in northern Europe are mixed-species pairs. Female hybrids are typically sterile, but male hybrids are fertile.

Hybrids may produce viable sperm or fertile eggs, but the test of their fertility comes later in the development of the zygotes produced by them. Blocks of genes of one parental species recombine with the genes of the other species for the first time in meiosis and gamete formation in the first-generation (F_1) hybrid. Incompatible gene combinations may then disrupt the delicate process of embryo development in

the second-generation (F_2) offspring. This phenomenon is called F_2 breakdown. For example, female F_1 hybrids between different species of junglefowl (wild chickens) lay fertile eggs, but few of them hatch (Morejohn 1968). The embryos perish before hatching as a result of developmental failure caused by incompatible sets of genes.

Hybrid Zones

Hybrid zones offer ways to study the genetic and social architectures of speciation (Harrison 1993). But hybrid zones vary greatly. Some shift location in response to changes in selection or dispersal. Some are old, narrow, and continuing sinks of hybrid inferiority. Others are stable zones of hybrid superiority. Still others are new contacts in the early test phases of genetic and social confrontation that may be resolved through natural selection.

The proportions of hybrid and parental phenotypes in a zone of overlap serve as criteria for judging whether two populations are the same species. Evidence of free interbreeding or lack thereof is the principal criterion for deciding whether populations are different species. The conservative decision is that the two populations belong to the same biological species when hybrids are abundant and blending freely with parental types in a zone of overlap (American Ornithologists' Union 1998).

Conversely, separate species status is warranted if no hybrids are present and complete reproductive isolation is manifest. Species status also is warranted if hybrids appear in low frequencies, if interspecific pairings are infrequent, if hybrids are less viable than the parental forms, or if the hybrid zone is narrow and stable.

A variety of bird species found throughout eastern North America are replaced by populations of similar or closely related taxa in the western part of the continent. In the Great Plains alone, 11 of 14 such pairs of taxa engage in hybridization (Rising 1983), including eastern and western populations of the Northern Flicker—the Yellow-shafted Flicker and the Red-shafted Flicker, respectively—and two orioles—the Baltimore Oriole and the Bullock's Oriole (Figure 19–12). Farther north are additional cases of replacement with hybridization.

To assess the extent, dynamics, and consequences of hybridization, ornithologists obtain samples of individual birds from a series of localities throughout the zone of overlap. In the procession from east to west through the zones of contact between these taxa, the first samples of flickers and orioles include only the eastern representative of the pair. The samples from the hybrid zone consist of intermediate and variable phenotypes. Most birds at certain localities in the hybrid zone are intermediate in appearance, a finding that indicates that they freely interbreed. In accord with the Biological Species Concept, the eastern and western counterpart populations of the flickers are currently lumped into single species. Then continuing to sample west of the hybrid zone, the composition switches to include only the western representatives.

FIGURE 19–12 The eastern Baltimore Oriole and the western Bullock's Oriole interbreed in a narrow zone of overlap in the Great Plains. The lighter gray indicates the extent of infiltration of Bullock's characters eastward and of Baltimore characters westward. These two oriole species were once lumped together as the Northern Oriole, but later study revealed that they are not closely related sister species. [*From Rising 1983*]

The pendulum of species taxonomy has swung back and forth in regard to the eastern Baltimore Oriole and the western Bullock's Oriole (Rising and Williams 1999). Initial studies of the hybrid zone suggested extensive interbreeding. Consequently, in 1983, the Committee on Classification and Nomenclature of the American Ornithologists' Union (AOU) lumped the two species into a single species, the "Northern Oriole." Additional studies of the hybrid zone revealed that it was narrow and stable in some areas and that hybridization decreased with continued contact in other areas. In addition, phylogenetic studies revealed that Baltimore and Bullocks's Orioles were not closely related sister species after all. Consequently, the AOU Checklist committee reversed its original decision and, in 1995, restored the two orioles to full species status, to the delight of the residents of Maryland.

Stable Hybrid Zones

Hybridization in zones of secondary contact often persists and continues unabated for centuries. The narrow hybrid zone between the Hooded Crow and the Carrion Crow of Europe has not changed in width for at least 500 years. Hybrids between the all-black Carrion Crow and the black-and-gray Hooded Crow are easily recognized by their variable color patterns (Figure 19–13). At least some of the hybrid zones in the Great Plains region of North America, including that of the Northern Flicker, are of ancient origin, dating to the expansion of isolated populations after the retreat of the glaciers 10,000 years ago.

Two theoretical models explain the stability of such hybrid zones. The bounded superiority model of Moore (1977) proposes that hybrid zones

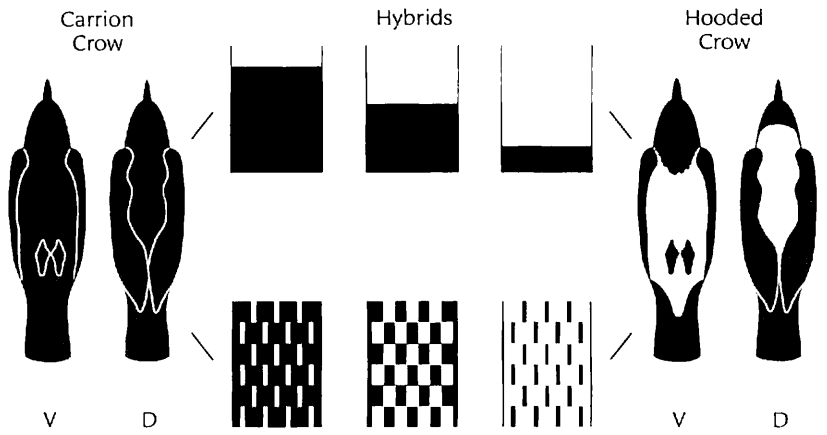


FIGURE 19–13 Color patterns of hybrid crows. Two main series of continuous variation in the distribution of black pigmentation characterize hybrid phenotypes. Boxes schematically represent the body. V, ventral view; D, dorsal view. The same amount of black pigmentation may be either uniformly scattered over gray parts of the "pure" Hooded Crow phenotype (*lower series*) or may be concentrated toward the rear of the body (*upper series*). [*From Saino and Villa 1992*]

coincide with intermediate ecological or climatic conditions where hybrids are equally or better adapted than their parents. The model best explains the stable hybrid zones of both the crows in Europe and the flickers in North America. The stable hybrid zone of Hooded and Carrion Crows coincides with an ecological interface between alpine valleys and the intensively cultivated plains, where hybrid and nonhybrid crows are equally fit (Saino and Villa 1992). The hybrid zone between the western (red-shafted) and the eastern (yellow-shafted) populations of the Northern Flicker has not changed in width or location for at least 100 years and probably much longer (Moore and Buchanan 1985). The continued free interbreeding between the flickers suggests no disadvantages and perhaps some advantages of hybrids in the zone of their contact.

The dynamic equilibrium model of Nicholas Barton and Godfrey Hewitt (1985) proposes that a stable hybrid zone is a population sink of inferior hybrids produced relentlessly by immigrants from the adjacent, large, pure populations. Sharp boundaries between the hybridizing species are a result. This model applies well to zones of hybridization by grasshoppers and perhaps, with a twist, to Townsend's and Hermit Warblers in the Pacific Northwest, described in the next section.

Transient Hybridization

Hybridization sometimes occurs just upon the initial contact of two species and then stops as reinforcement of correct species recognition sets in. For example, the Silvereye of Australia colonized Norfolk Island in the South Pacific east of Australia at least three times, most recently in 1904 (Gill 1970). Shortly after the third invasion, some of the Silvereyes hybridized with the descendants of the preceding invasion, which in the interim had evolved into the larger Slender-billed White-eye. But hybridization did not continue, and the two white-eyes now coexist as distinct species on Norfolk Island without interbreeding.

Two species in secondary contact are not always equal. Competitive interactions between species cause hybrid zones to change location. Sometimes, new competitive interactions cause the local extinction or replacement of one species by another (Rhymer and Simblerloff 1996).

The Townsend's Warblers and Hermit Warblers of the great forests of the Pacific Northwest of North America provide a prime example of replacement following transient hybridization (Rohwer et al. 2001; Figure 19–14). Of the two, Townsend's Warbler is the competitively superior, aggressively dominant species. By virtue of their behavioral advantages, Townsend's Warblers are steadily replacing Hermit Warblers. Townsend's Warblers have been winning for thousands of years. The hybrid zone between the Townsend's Warblers and the Hermit Warblers stays narrow owing to selection against the hybrids, which don't compete successfully for quality territories. The location of the hybrid zone, however, is moving steadily southward into the remaining Hermit Warbler populations.

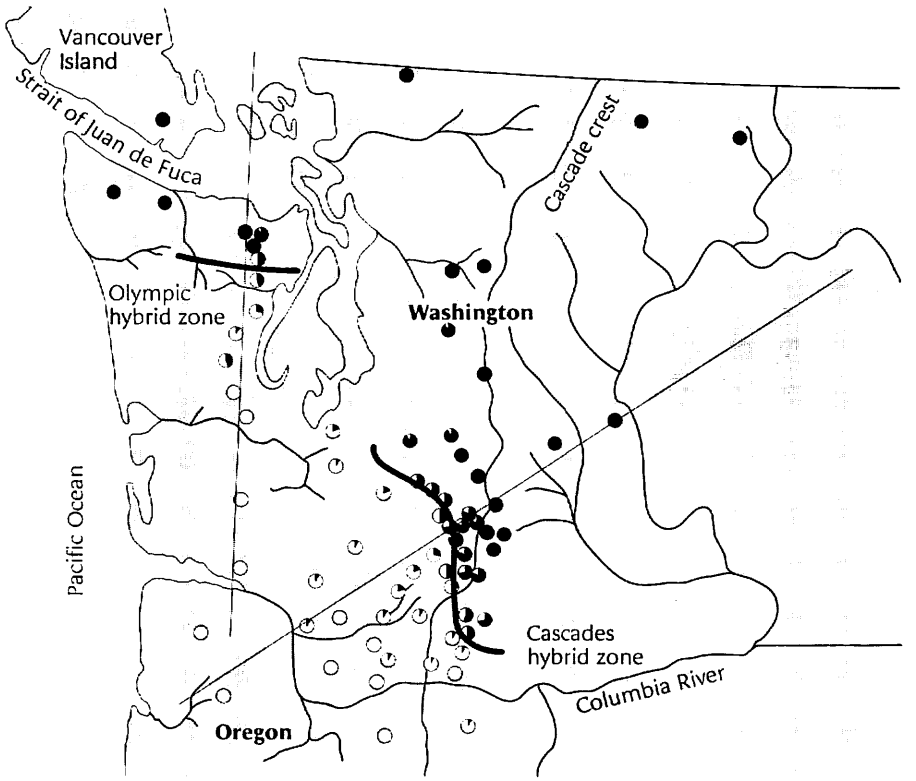


FIGURE 19–14 Location of two hybrid zones (Olympic and Cascades) of Townsend's Warblers and Hermit Warblers in Washington State. Black circles indicate pure Townsend's Warbler populations, and white circles indicate pure Hermit Warbler populations. Samples from mixed populations show proportions of the two phenotypes. Heavy lines indicate midpoints of phenotype transitions. Thin straight lines indicate transects sampled through zone used to analyze changes in characters. [*From Rohwer et al. 2001*]

The distinct, but neutral, mitochondrial DNAs of the two species move reciprocally and symmetrically in opposite populations. Recall that mtDNA is a small circle of DNA that undergoes maternal inheritance. Female birds pass it to their chicks in the cytoplasm of the ovum of the egg. But, because Townsend's Warblers replace Hermit Warblers as the hybrid zone moves forward, a substantial genetic footprint of Hermit Warbler mtDNA remains behind in the replacement Townsend's Warbler populations. The markers persist as a "ghost" image of the original Hermit Warbler range that once extended into southern Alaska.

Blue-winged Warblers and Golden-winged Warblers further illustrate the dynamics at work in transient hybridization (Gill 2004). Blue-winged Warblers generally replace Golden-winged Warblers, their sister species, within 50 years of local contact. The Golden-winged Warbler is declining throughout most of its original range and in some places it is endangered.

Among their plumage-color differences, the color patterns of these two species of wood warbler are strikingly different (Figure 19–15). The difference in face patterns is controlled by a single pair of alleles with dominance. First-generation hybrids, called "Brewster's Warblers," produce viable offspring when they mate with either Blue-wings, Golden-wings.

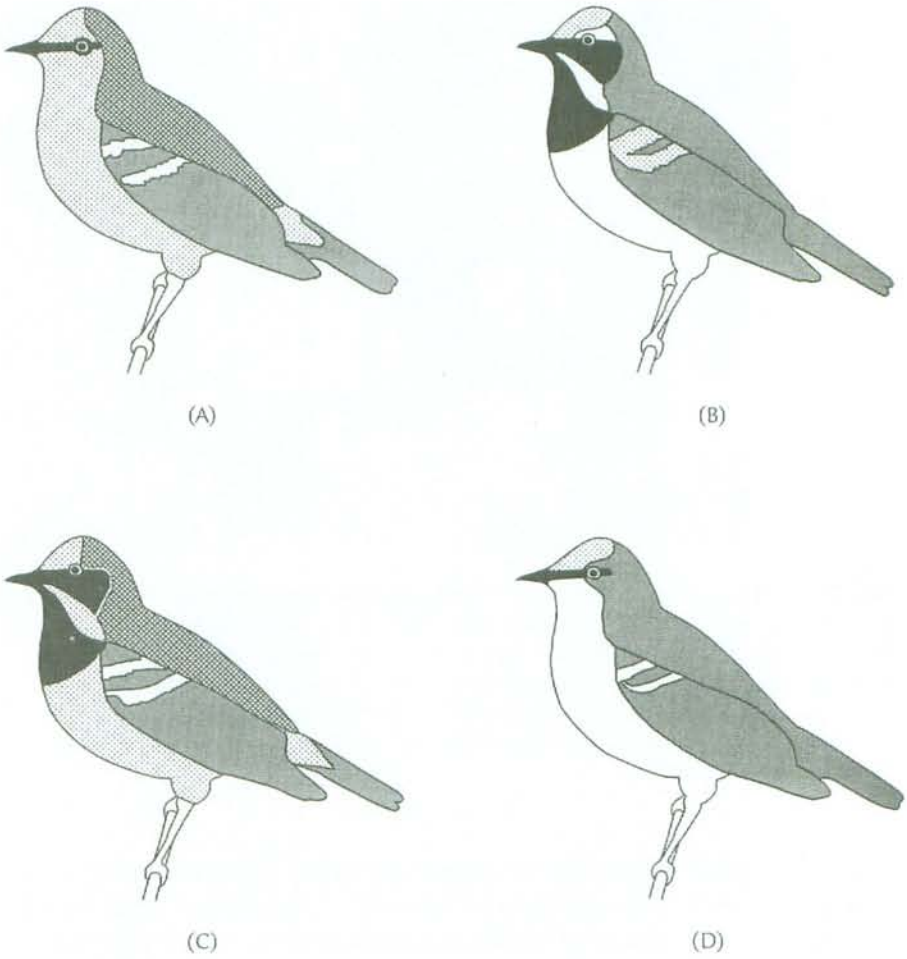


FIGURE 19–15 Two species and two hybrids of warblers: (A) Blue-winged Warbler; (B) Golden-winged Warbler; (C) Lawrence's hybrid; (D) Brewster's hybrid. Stippling represents bright yellow; dark hatching represents olive. Gray, black, and white are as shown in the drawing. Blue-winged Warblers are bright yellow and olive with white wing bars and a narrow black line through the eye. Golden-winged Warblers are gray above, white below, with yellow wing bars and crown, and bold black patches on the throat and the eyes. The contrasting facial color patterns of the two species have a simple genetic basis, like the color phases of other species. The plain throat and narrow black eye line of the Blue-winged Warbler are dominant to the black throat and black eye patch of the Golden-winged Warbler. Other plumage-color characteristics are controlled by several genes that supplement one another. The Brewster's Warbler resembles a Golden-winged Warbler with the face pattern of a Blue-winged Warbler. The Lawrence's hybrid resembles a Blue-winged Warbler with the face pattern of a Golden-winged Warbler. [*After Ficken and Ficken 1968*]

or other hybrids. The blending of plumage colors coupled to the alternative facial color patterns produces a variety of hybrid types, including "Lawrence's Warbler." Male "Brewster's" hybrids are disadvantaged with respect to obtaining mates and tend to be excluded from optimal territories (Confer and Tupper 2000). There is no evidence that female "Brewster's" hybrids exhibit the negative effects of hybridization predicted by Haldane's rule (see page 591).

The Blue-winged Warbler was once an uncommon species of the South Central United States. The Golden-winged Warbler nested farther north and at higher altitudes in the Appalachians. The clearing of forests in the mid-1800s and the increases in second-growth vegetation throughout the northeastern United States benefited both species. The Blue-winged Warbler expanded northward into the range of the Golden-winged Warbler. Hybridization and replacements followed.

The replacement of Golden-winged by Blue-winged Warblers proceeds through a predictable shift in the composition of local assemblages of these warblers. At first Golden-winged Warblers prevail locally in the heart of their original range, with perhaps an occasional pioneering Blue-winged Warbler or odd hybrid form. Increases in immigrant Blue-winged Warblers balance the proportions of the two species. In addition, an assortment of intermediate hybrids backcross to both parental species. Finally, only Blue-winged Warblers remain, perhaps with remnant Golden-winged genes (Shapiro et al. 2004). The pace, pattern, and genetic details of replacement vary substantially among localities.

Behavior and Speciation

This chapter and preceding chapters emphasized the power of social recognition in birds. The power of social recognition is key to understanding the evolution of new species of birds. It explains why bird species in general hybridize so rarely despite their genetic compatibility (Gill 1998).

The behavior of birds, particularly their capacity for new behavior and its cultural transmission, can drive their speciation (Wyles et al. 1983; West-Eberhard 1983). Broad correlations among brain size, taxonomic diversity, and rates of molecular genetic change suggest that enhanced brain capacities and behavioral innovations catalyze speciation and taxonomic diversification in both primates and songbirds.

Behavior, rather than the environment, can be the driving force of evolutionary change when individuals exploit the environment in new ways. New habits then spread rapidly through the population by cultural transmission, followed by the evolution of anatomical traits that enhance the effectiveness of individuals practicing the new habit. New behaviors that ultimately spawn anatomical change are more likely to arise in populations of individuals that have the intelligence to develop such behavior.

The evolution of premating isolating mechanisms in allopatry stands out as the first step in the speciation of birds. This first step entails only

minor genetic change (Grant and Grant 1997). Preferential pairing of like types, or positive assortative mating, maintains the cohesion of populations and the separation of coexisting species. Substantial genetic divergence then follows changes in mate-choice practices.

Behavioral changes in social recognition and in mate choice need not be entirely genetic. Instead, cultural learning of paternal songs can drive mate choice. Early imprinting starts a process of social preference that segregates coexisting birds into distinct clusters. Assortative pairing follows, with rare mistakes. Recall that early imprinting by Snow Goose goslings on the color of their parents determines later mate preferences and leads to assortative mating (see Chapter 16).

Speciation in birds, therefore, can be a cultural process as well as a genetic process. Cultural speciation based on sexual imprinting of parental characters and behaviors is potentially a significant part of the speciation process in birds (Grant and Grant 1996; Vaneechoutte 1997; Irwin and Price 1999; Ten Cate and Vos 1999). The brood parasitic indigobirds are the classic, though specialized, example of this process in the wild (Chapter 13). Cross-fostering young birds with other species also illustrates the power of sexual imprinting (Chapter 16).

How, then, do a young precocial bird and young of other species without parental care develop a sense of social identity? Recall the megapodes, or moundbuilders, that leave the compost nest independently upon hatching, running off on their exceptionally strong young legs (Chapters 15 and 16). They provide valuable insights into early social recognition. Experiments using robotic chicks of the Australian Brushturkey revealed that the young megapodes gather naturally with other young of their own species. They do so by responding innately to a series of visual cues, both behavioral and morphological (Göth and Evans 2004). In particular, the strong ultraviolet (UV) and other short wave-length reflectance of the legs of their kin evokes a strong innate social response. The chicks approach robots with the right UV leg color. So the color of their powerful little legs, which are not readily seen by hawks from above, serves as a natural club membership card. No one, however, knows how these initial social responses lead to their choice of mates when they grow up.

Social Selection

Social selection favors new signals or communication of identity that can drive the speciation process (West-Eberhard 1983). Charles Darwin (1871) recognized the importance of social selection long ago. Signals of communication enable individuals to compete successfully for mates, space, or access to food.

Sexual selection (see Chapter 12) is one kind of social selection that promotes, for example, the extravagant display plumages of male birds-of-paradise. Songs also are subject to elaboration through vocal contests and cultural change. Through social ritualization these same attributes enable pair formation, species recognition, and initial reproductive isolation.

The development of song differences between Marsh Wrens of eastern and western North America illustrates the role of social selection in speciation. Recall that western Marsh Wrens have innate brain capacities for larger song repertoires than do eastern Marsh Wrens (Chapter 8). Male Marsh Wrens duel vocally with one another to win the best territories and the most females. The larger repertoires and brain capacities of the western Marsh Wrens reflect intense competition for females in restricted pothole cattail marshes. Specifically, sexual selection and the behavior of countersinging have led to the elaboration of the brain nuclei that control singing behavior, associated differences in song-learning abilities, and mating preferences. Generally separated by a 100-kilometer gap, eastern and western Marsh Wrens coexist and pair assortatively in some marshes in the northern Great Plains (Kroodsma et al. 1997). Divergence has proceeded far past the initial stages of premating isolation through song divergence. The two Marsh Wrens also exhibit substantial divergence in the base pair sequence of the cytochrome oxidase I gene of their mitochondrial DNA (Hebert et al. 2004).

Speciation in Darwin's Finches

Early in this chapter we examined the basic steps and seven rules of speciation in Darwin's finches. Most significantly, the long-term field studies of these birds by Peter and Rosemary Grant have revealed the importance of behavior, especially learned songs, in the speciation process.

Darwin's finches are prime examples of adaptive radiation of bill sizes, feeding habits, and behavioral innovations (Grant 1999; see also Chapters 1 and 7). Periodic and stringent sorting of individuals with new behaviors and new anatomical features promote the evolution of new species of finches.

The evolutionary history of Darwin's finches has been marked by episodes of strong selection for changes in bill morphology. The direction and intensity of selection, however, are unpredictable. They change dramatically on the time scale of decades (Grant and Grant 2002). The drought of 1976, for example, resulted in a shift of bill sizes to those that enabled the finches to feed efficiently on the seeds that were available (Chapter 1). Similar steps contribute to speciation of birds generally.

Changes in bill size and feeding behavior lead to premating isolation, because Darwin's finches use bill morphology to recognize their own species. Experiments with finches in their natural habitat demonstrated that bill size, shape, and color are primary visual cues that determine mate choice. Laurie Ratcliffe and Peter Grant (1983) tested the responses of several pairs of sympatric species of ground finches *(Geospiza)* to taxidermy mounts of different species. Males and females both discriminate between their own species and other species based on visual cues of bill morphology.

The use of visual cues starts when young finches imprint on the appearance of their parents. Later they use those visual cues, and also song, to choose their mates. In this way, bill size and shape serve as a premating

isolating mechanism. Visual differences in bill size also channel early social interactions to other individuals of the same species.

In addition to bill morphology, song differences acquired through vocal imprinting play a significant role in species recognition and mate choice by Darwin's finches (Grant and Grant 1997). The songs of Darwin's finches diverge between populations due to errors of chance or copying as well as extinction of local songs. Like many songbirds (Chapter 16), young finches imprint on their father's song, a cultural trait, as well as morphology, a genetic trait.

Territorial males discriminate between songs of their own and other species in carefully controlled playback experiments. Song also tends to be a primary cue for mate choice. With rare exceptions, females avoid mating with males that sing another species' song. They also avoid mating with males with songs that closely match the songs of their father, which reduces the risk of inbreeding.

The process of imprinting on the father's song, however, is not perfect. On the island of Daphne Major, occasionally a young male Cactus Finch learns the song of the Medium Ground Finch. Such a mistake leads further to mistakes in mate choice and thus to hybridization. In one case, a female Medium Ground Finch mistakenly mated with the male Cactus Finch that wrongly sang her species' song. Their hybrid offspring then backcrossed without serious penalty to other Medium Ground Finches (which sing like their father).

Summary

Species are the primary units of systematic biology, serving as the basis for describing and analyzing biological diversity. Of the many competing species concepts and definitions, the one that prevails in ornithology is the Biological Species Concept (BSC). It states that a species comprises a set of populations that are capable of freely interbreeding under natural conditions. An alternative concept, the Phylogenetic Species Concept (PSC), stresses historical patterns of divergence and would recognize more distinct local populations than does the Biological Species Concept.

Birds on continents speciate through vicariant events such as division of large populations of North America by glaciations or of South America and Australia by wet–dry climate cycles. Secondary contact—the reuniting of previously isolated populations—tests the ability of populations to interbreed. Once considered separate species, the Audubon's Warbler and the Myrtle Warbler appeared to interbreed freely where they come into contact in the Canadian Rockies. On the basis of this evidence they were lumped together and are treated as populations of the same biological species, the Yellow-rumped Warbler.

Birds retain their genetic compatibility and potential for hybridization long after they achieve behavioral isolation based on visual or vocal differences arising from minor genetic changes or sometimes cultural experience. Hybrids of genetically divergent species may be unable to produce

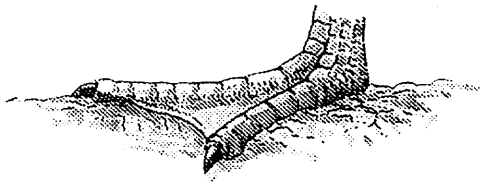
viable sperm and eggs. Incompatible blocks of genes also may disrupt early embryo development.

The evolution of geographical differences among natural bird populations depends on the relative strengths of two opposing forces: the intensity of natural selection favoring one genetic attribute over another and the rate of genetic blending as a result of interbreeding of individuals from different locations—gene flow. Clinal variation of simple genetic color phases track the opposing strengths of these two forces.

New species of birds evolve via premating isolating mechanisms that arise through sexual selection or ecological adaptation in isolated populations. Darwin's finches on the Galápagos Islands provide examples and insights into this process. The capacities of birds to develop new, learned behaviors may contribute to the process of speciation. Behavior, rather than the environment, can be the driving force of evolutionary change if a new behavior is followed by the evolution of new anatomical traits that support the behavior. Sexual imprinting contributes to a process of cultural speciation in some, but not all, birds.

This chapter stressed the process of divergence and speciation of birds, particularly some of the genetic and behavioral features of that process. Ecological changes feature strongly in the completion of the speciation process. Coexistence of reproductively isolated species in sympatry requires resolution of competitive interactions for food, for nest cavities, or other limiting resources. Ultimately these interactions define the community of species that coexist in a particular habitat or locale. The next chapter examines the formation and richness of ecological communities of birds.

CHAPTER 20



Communities

The wet tropical lowlands are rich in diversity of species, in diversity of structure, and in their general aspect of luxuriance.
[MacArthur 1972, p. 199]

Resources, such as food and nest holes, determine not only the local population size for a species but also how many species can coexist locally in one habitat. Coexisting groups of species are called communities.

This chapter emphasizes the dynamic nature of bird communities, including those on islands where the patterns of losses and gains of species are best documented. Whether the numbers of species reach an equilibrium helps to define positions in the continuum of community structures. At one end of the continuum are "open" assemblages determined largely by geographical history with room for additional species. At the other end of the continuum are "closed" communities organized by interspecific competition for limited resources and resistant to invasion by additional species.

After a review of the general patterns of species diversity in space and time, this chapter looks at the role of competition in structuring bird communities. Patterns of ecological segregation and geographical replacement among similar species point to a role for competition in community structure. But rigorous documentation of actual competition is difficult. The role of interspecific competition as a dominant force that controls the composition of communities is hotly debated. In one situation, the effects of competition among European tit species on their reproduction and foraging illustrate the costs of coexistence for ecologically similar and closely related species. The local compositions of species, however, also relate to larger playing fields of geography and history.

The Dynamics of Communities

Whether it's a question of tallying the numbers of individual birds of different species while birding or doing a formal census, the result is the

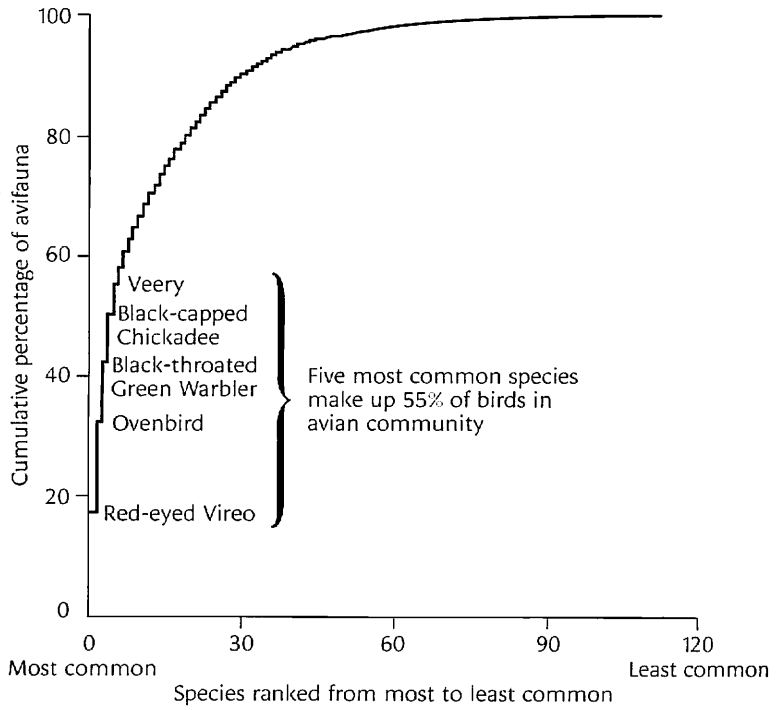


FIGURE 20–1 Most species are rare, and a few are abundant. The distributions of species abundance typically compile to a log normal distribution, with a long skewed tail to the right, such as the one shown here. Data that are intrinsically geometric or multiplicative rather than additive produce log normal distributions. Populations multiply. So, in principal, the distribution of their abundances should be log normal. [*Graph after Temple 2004*]

same. Most species are rare or present in small numbers, and a few are common or abundant (Figure 20–1). Their distributions correspond to the dynamic nature of bird species, which multiply, prosper, and fail. They expand and contract. They generalize and specialize. Local and assemblages of species therefore correspond to their combined histories and prosperities. Competition for limited resources also may determine which particular species coexist and in what numbers.

Evolution and the availability of resources both play major roles in forming communities. The local compositions of species change from epoch to epoch in accordance with evolutionary history and from season to season in accordance with resource availability. Reflecting regional history, avifaunas (the birds of a particular region or time period) are the grand result of millions of years of evolution, adaptive radiation, immigration, dispersal, and extinction of bird taxa. Invasions and fusions of species from other regions supplement adaptive radiations of ecological types within a region. Owing to the availability of resources as well as to their histories, local bird communities increase dramatically in both size and diversity in tropical forests, in comparison with local communities in northern temperate forests.

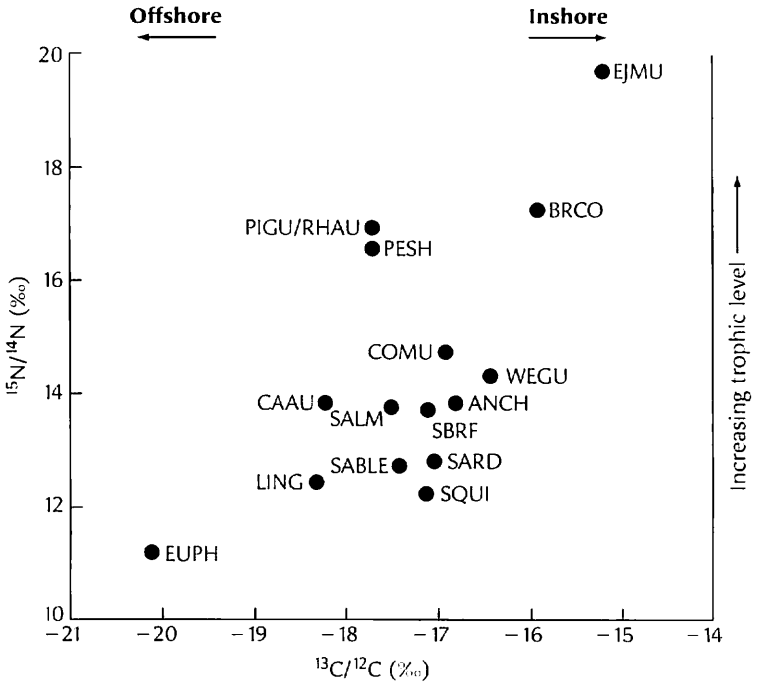
The species in a community can occupy different trophic levels, or feeding levels, and range from insect-eating warblers to the hawks that eat them and from plankton feeders to fish eaters (Box 20–1). Each species

BOX 20–1

STABLE ISOTOPES CLARIFY SEABIRD FOOD WEBS

Stable isotope analysis (SIA) helps ornithologists to decipher food webs, especially marine systems that are hard to study directly. The ratio of two isotopes of nitrogen ($^{15}N/^{14}N$) in animal tissues, for example, increases from zooplankton (krill) to krill-eating fish or birds to fish-eating birds (cormorants) and sea lions at the top of the food chain (Sydeman et al.1997; see graph). This ratio increases with each step in the food chain because the metabolic synthesis of new protein from food consumes more of the lighter isotope ^{14}N, leaving more (3 percent) ^{15}N in the predators' tissues. The marine-system food web off the coast of California, for example, includes five levels, with seabirds occupying the upper levels, from three to five.

The ratio of stable isotopes of carbon ($^{13}C/^{12}C$) in tissues reveals where seabirds feed, on the basis of the kinds of prey that they eat, and whether they change feeding habits at different stages of the breeding cycle. Feeding on fish near the coast leaves a different signature of carbon isotopes in the tissues from that left by feeding on krill in the open ocean. SIA of the egg albumen of California seabirds, for example, revealed that Cassin's Auklets and Common Murres use krill to produce their eggs. Common Murres then shift to fish to feed their young, as do most of the other seabirds. Rhinoceros Auklets and Pigeon Guillemots rely on fish throughout the breeding cycle, including egg production.



Trophic structure of a community of seabirds and their prey on the coast of California based on analyses of stable nitrogen and carbon isotopes, expressed in parts per thousand (‰). (The formula for calculating these values in standard delta notation produces a negative number for carbon.) Nitrogen isotopes change with trophic level in the community. Birds and sea lions occupy higher trophic positions than fish, squid, and krill. Carbon isotopes vary with inshore versus offshore feeding habits. Abbreviations: EUPH (krill, or euphausids), LING (lingcod), SQUI (squid), SABLE (sablefish), SARD (sardine), SALM (salmon), SBRF (short-bellied rockfish), CAAU (Cassin's Auklet), ANCH (anchovy), WEGU (Western Gull), COMU (Common Murre), PIGU (Pigeon Guillemot), RHAU (Rhinoceros Auklet), PESH (Pelagic Shag), BRCO (Brandt's Cormorant), EJMU (northern sea lion). [*From Sydeman et al. 1997*]

has specific requirements, called its fundamental ecological niche (Grinnell 1917). For example, we expect to find Pileated Woodpeckers in forests with large trees full of carpenter ants. Pileated Woodpeckers occupy a wide variety of forests with big, ant-ridden trees, but the Red-cockaded Woodpecker of the southeastern United States has a different and highly specialized niche. It requires old pine forests with trees from 80 to 100 years old that have been infected by the red heart fungus.

Woodpeckers play a central role in the larger community. They and their dead trees are a resource that supports a healthy diversity of vertebrate and invertebrate species that depend on one another. The foraging and nest-excavation activities of woodpeckers determine how dead trees actually decay and become available for use by other species (Farris et al. 2004). For example, more than 50 percent of the woodpeckers sampled in the ponderosa pine forests of northern California carried fungal spores on their bills. They transport these spores from tree to tree, causing new trees to decay and to become suitable for excavation of their new nest holes. Many species of hole-nesting birds and small mammals use the diversity of nest holes that result, building guilds (sets of ecologically similar species) of interdependent nest-cavity species (see Figure 15–5).

Resource availability and evolutionary history shape communities, and, together, they give rise to competition—the interactions among species through which one species may directly or indirectly preclude the presence of another. Competition itself can play a major role in forming communities. From a larger pool of potential candidates for a community, competition selects those species best able to coexist (Figure 20–2). Competition typically constrains a species' habitat or feeding opportunities and thus narrows that species' realized ecological niche. This outcome is more likely than the exclusion of one species by another.

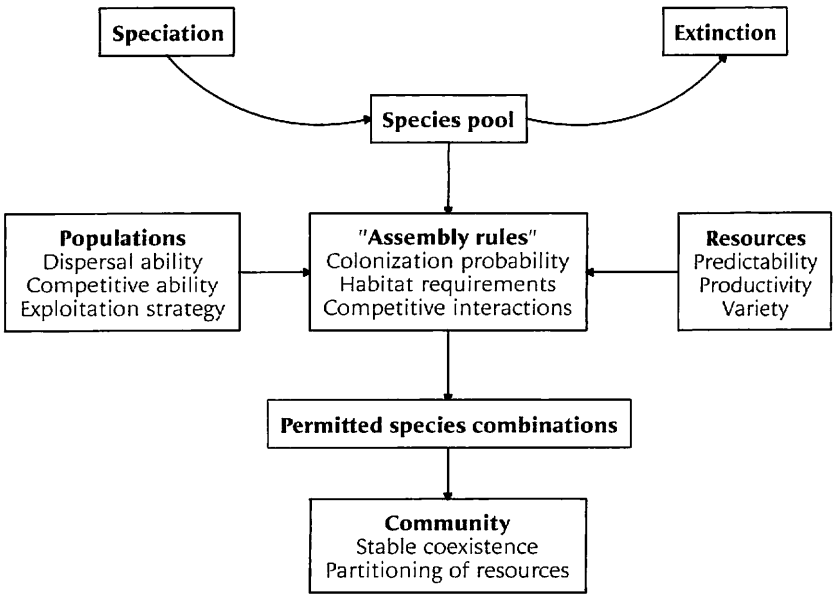


FIGURE 20–2 According to some ecologists, stable communities of coexisting bird species derive from a larger pool of species through the dynamics of population dispersal, through colonization in relation to habitat or other resources, and sometimes by competitive resolution of unstable species combinations. [*After Wiens 1983*]

Ecologists debate the relative importance of these three forces—evolutionary history, resource availability, and competition—in community ecology. Competition has long been assumed to be the main force in structuring bird communities, but irregular seasonal changes keep many communities in a state of dynamic flux. Habitat disturbance, fluctuating resources, ongoing colonizations, and local extinctions impose short-term changes on avian communities. In addition, deforestation and the rotation of farmlands transform woodland habitats and their communities of bird species into patchworks of chronically unstable and unsaturated habitats. New or unstable habitats invite opportunistic use by birds and invasion by exotic or introduced species. Some communities, therefore, lack predictable structure and, instead, may be fortuitous or historical collections of species (Hubbell 2001; but see McGill 2003).

Islands

Because islands are such discrete places, island birds provide many of our clearest examples of community dynamics as well as the process of speciation (see Chapter 19). We can deduce and sometimes actually document the arrivals of new colonists and their subsequent adaptations, expansions of distribution, and disappearances in time.

The active dispersal from and colonization of isolated places are trademarks of bird behavior. The dynamics of colonization are most apparent

BOX 20–2

CHARACTER DISPLACEMENT EVOLVED RAPIDLY IN SUPERTRAMPS

Between the large, exotic islands of New Guinea and New Britain in the South Pacific lie several small islands, the Long group. On these little-known islands, Jared Diamond and his colleagues (1989) discovered an example of the rapid evolution of character displacement between two species of small, nectar-feeding honeyeaters (genus *Myzomela*).

The Long group's volcanic caldera collapsed 300 years ago in one of the largest known volcanic explosions. It undoubtedly eliminated all bird life. The current avifauna consists mostly of small island specialists, or supertramps, that have recolonized the island. Among the now established supertramps are two similar honeyeaters, the Ebony Myzomela from the northern Bismarck Archipelago and the Scarlet-bibbed Myzomela from the southern Bismarck Archipelago. The two honeyeaters are present abundantly together all over the Long islands and often feed in the same flowering trees.

These honeyeaters are the only two bird populations on the Long islands in which the birds have evolved to different sizes since colonization. The Ebony Myzomela is now larger than the birds of its ancestral populations, and the Scarlet-bibbed Myzomela is now smaller. The difference in size between the birds of the two colonizing populations has increased from 24 to 43 percent on the Bismarck Archipelago to 52 percent on the Long islands. Elsewhere, closely related species of honeyeaters coexist only if they differ in size by 50 percent or more.

Diamond and his colleagues concluded that the changes in size in the two honeyeaters on the Long islands represent character displacement in response to each other's presence during the few centuries since the Long group's devastating eruption.

on oceanic islands, such as the West Indies, which receive periodic arrivals of new visitors dispersing over water from larger source areas. Water barriers favor colonization by highly mobile species that travel in small groups. Bananaquits in the West Indies and white-eyes in the Indian and Pacific Oceans are superb island colonists—or "supertramps" (Diamond 1974). Their extraordinary dispersal abilities enable them to be the most predictable first colonists on newly formed islands (Box 20–2). Successful colonization of one island may be followed by the colonization of adjacent islands and continued spread throughout a region.

A colonist's ecological flexibility and its competitive ability to fit into the local community increase its chances of establishing a population on a new island. Bananaquits and white-eyes are generalized opportunists, able to take advantage of local situations. They breed readily and repeatedly. After they are established, their populations thrive and grow rapidly in an environment with few enemies—specialized predators, competitors, diseases, or parasites.

Population growth under such conditions of so-called ecological release leads to large, dense populations and to the use of a wider variety of habitats than is the case on the mainland. Resident birds of the Pearl islands off western Panama, for example, achieve densities from 20 to 40 percent higher than those reached on the adjacent mainland. They also forage over a greater vertical range and use more habitats than do their mainland counterparts (MacArthur et al. 1972). Both the average number of habitats used by a species and the density of each species in a particular habitat may double on small islands with few species, such as St. Lucia and St. Kitts of the Caribbean (Table 20–1).

Populations on different islands diverge from one another as they adapt to local niches. The divergence of allopatric populations was discussed as

TABLE 20–1 Relative abundance and habitat distribution of birds in five tropical localities[a]

Locality	Number of Species Observed (Regional Diversity)	Average Number of Species per Habitat (Local Diversity)	Habitats per Species	Relative Abundance per Species per Habitat[b] (Density)	Relative Abundance per Species[b]	Relative Abundance of all Species[b]
Panama	135	30.2	2.01	2.95	5.93	800
Trinidad	108	28.2	2.35	3.31	7.78	840
Jamaica	56	21.4	3.43	4.97	17.05	955
St. Lucia	33	15.2	4.15	5.77	23.95	790
St. Kitts	20	11.9	5.35	5.88	31.45	629

[a]Based on 10 counting periods in each of nine habitats in each locality.
[b]The relative abundance of each species in each habitat is the number of counting periods in which the species was seen (maximum 10); this number times number of habitats gives relative abundance per species; this relative abundance times number of species gives relative abundance of all species together.

From Cox and Ricklefs 1977.

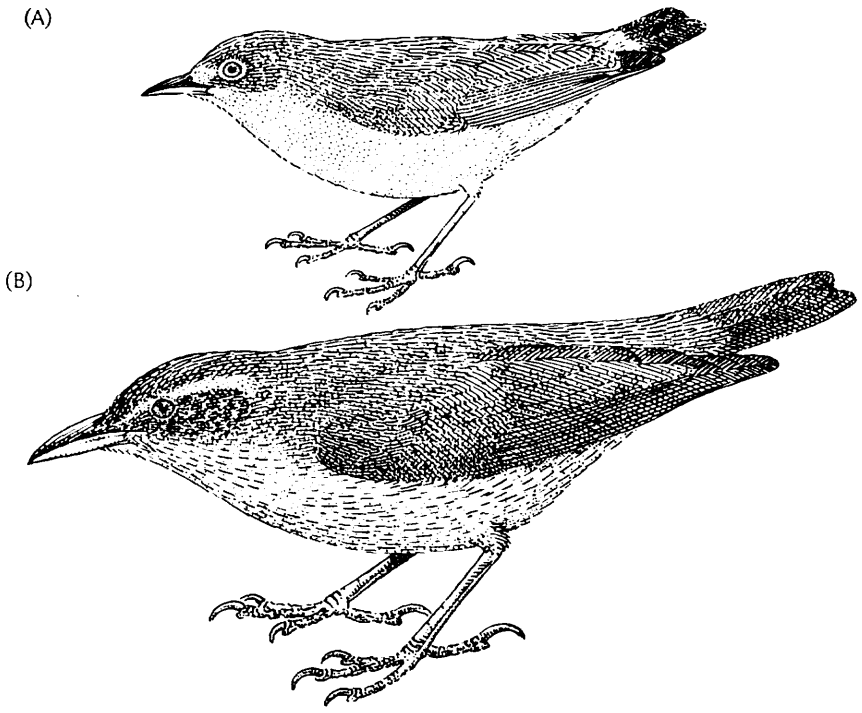


FIGURE 20–3 White-eyes are excellent island colonists that often occupy unfilled niches on remote islands that have few other birds. Shown here are (A) a typical species, the Bridled White-eye, and (B) a large, thrushlike species, the Giant White-eye. These species are found together on Belau (Palau) in the Caroline Islands. [*From Lack 1971*]

part of the speciation process for Darwin's finches (see Chapter 19). Generalized colonists, such as white-eyes, may take over the specialized niches of species that are missing from island communities. The increased specialization of the first colonists then contributes to their ability, as well as to that of their descendants, to coexist with later arrivals. On La Réunion in the Indian Ocean, where there is no nectar-feeding sunbird, the Reunion Olive White-eye has become a specialized nectar-feeding species in both bill morphology and behavior (Gill 1971). It coexists there with a second, generalized white-eye, the Reunion Gray White-eye (see Chapter 19). In the tropical Pacific, unusually large species of white-eyes have evolved independently on 12 small islands that have few other species. These large white-eyes often coexist with one or more other, smaller species of white-eyes (Figure 20–3).

Turnover

Turnover—the addition and loss of species—causes the composition of avifaunas to change with the passage of time. The time scales range from the long-term, gradual replacements of ancient taxa by more recently evolved taxa to short-term, yearly changes. The number of species may

or may not reach an equilibrium where new additions through colonization or speciation balance extinctions.

The number of species present in northern Scandinavian bird communities, for example, fluctuates by 15 percent from year to year (Järvinen 1980). Farther south, in the rich deciduous forests of Birdsong Valley, Sweden, annual turnover is about 10 percent. In both regions, the repeated extinction and immigration of small numbers of rare species (from one to two pairs total) are the primary causes of annual variations in community richness. Higher turnover in the north is caused by the greater unpredictability of weather during the breeding season and the greater proportion of rare species, which in turn are more likely to become extirpated or locally extinct.

The local turnover of species is a fundamental concept of geographical ecology. Both island and mainland avifaunas are subject to conspicuous species turnover. Turnover rates of 1 to 20 percent of species a year prevail on small, offshore islands, such as the Channel islands off the coast of California (Diamond 1980). Annual censuses of birds on a small British island, Calf of Man, revealed that Northern Wheatears and Eurasian Stonechats repeatedly became extinct on the island, only to be replaced within a short time by new immigrants of the same species. In this way, regular immigrations may obscure regular extirpations until the population establishes itself (Figure 20–4).

Like human civilizations, bird populations undergo long-term cycles. The expansion of their numbers and their geographical range is followed by diversification, speciation, specialization, and then decline, local extirpation, and the replacement by younger species (Ricklefs 2005). The bird population cycles themselves span long intervals of roughly 1 million years, which allows plenty of time for new traits to evolve.

Initially formulated to explain the deployment of ants on the islands of the South Pacific (Wilson 1961), these so-called taxon cycles capture the concept of dynamic changes in the composition and structure of bird communities on islands and most likely on continents, too. Current data

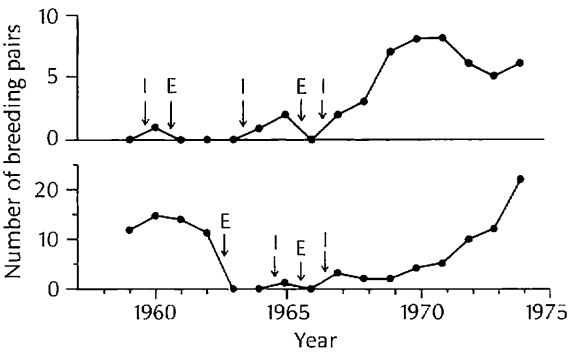


FIGURE 20–4 Turnover of Northern Wheatears (*top*) and Eurasian Stonechats (*bottom*) as indicated by annual breeding bird censuses on the Calf of Man, a small British island. Regular extinctions and replacements of small populations take place. Abbreviations: I, immigration; E, extinction. [*From Diamond 1980*]

suggest that the cycles of different species are largely independent and not coordinated, for example, by climate cycles.

What really triggers the expansions in birds' population size and range? We don't know. A principal hypothesis favors escape from burdens of enemies—parasites, diseases, or predators—by virtue of a new mutation or behavioral trait.

Conversely, reproductive success and population size tend to decline as a result of increased susceptibility to enemies—namely, parasites and predators. Aggressive new colonists or competitors also force previously established residents to retreat into a subset of the available habitats. Declining population sizes increase the probability that some populations will become extinct. Local extinctions then fragment the distribution of the species. The House Wren, for example, was once widespread on islands of the Lesser Antilles of the eastern Caribbean. It then disappeared for no apparent reason from Guadeloupe and Martinique and is close to extinction on St. Vincent.

What may appear to be the direct, competitive replacement of older endemic species on islands by new colonists may only be coincidence. For example, Mourning Doves replaced the endemic Socorro Dove on Socorro Island, off Baja California, in the 1970s. The extinction of the Socorro Dove and the colonization by the Mourning Dove turn out to have been independent events related to the establishment of a garrison of the Mexican army. The army's cats ate the tame endemic doves. Its new wells provided the drinking water required by the colonizing Mourning Doves (Jehl and Parkes 1983).

Biochemical analyses of ages and relationships among island bird populations confirm complex patterns of expansion, specialization, and the fragmentation of distributions. The oldest of the 57 lineages of small land birds occupying the Lesser Antilles dates back roughly 10 million years (Ricklefs 2005). Expansions and recolonizations by derived species produced a complex mosaic of communities of species on different islands. For example, two lineages of mimic thrushes (Mimidae), the West Indian thrashers and tremblers, date back roughly 4 million years. Their history features at least 16 chapters of island colonizations and divergences of subspecies or species (Hunt et al. 2001). The three modern-species groups of tremblers derive from splits at the beginning of the Pleistocene 2 million years ago.

Island Biogeography

Although island avifaunas may change regularly in the composition of their species, the number of species present theoretically reaches a balance between gains due to immigration and losses due to extinction (MacArthur and Wilson 1967). The predictable balance between gains and losses is known as the equilibrium theory of island biogeography. By this theory, the point of intersection between the immigration curve and the extinction curve defines an equilibrium species number (Figure 20–5). The rate of extinction increases with the number of species on an island because there are more species with competition-reduced population sizes.

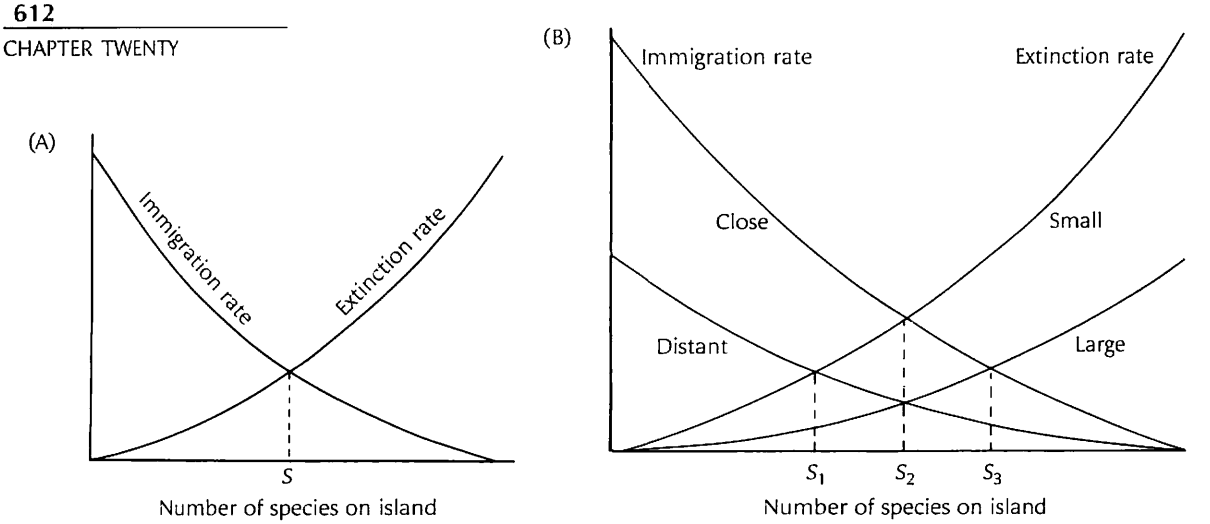


FIGURE 20–5 (A) The number of species found on an island reflects the balance between the rate of immigration (colonization) and the rate of extinction. (B) Immigration rates on islands that are distant from source areas are lower than rates on islands close to source areas. Extinction rates on large islands are lower than those on small islands. Extinction rates increase as the number of species present on an island increases. The point of intersection of the two curves for any particular island defines the expected equilibrium number of species, *S*. [*From Ricklefs 1976a*]

Conversely, the rate of immigration falls as the number of species increases. Fewer new species from source areas are possible, and the colonization of an island full of competitors is more difficult.

Rates of extinction and colonization vary among islands of different sizes and degrees of isolation. In general, the observed relations between the number of species and island size are in accord with the model (Figure 20–6). However, they do not take into account massive prehistoric extinctions caused by humans, such as the Polynesian colonists on the Hawaiian Islands and elsewhere in the South Pacific (Olson and James 1982).

The number of equilibrium species for large land-bridge islands, which were once part of a mainland with a full complement of species, is much greater (often three times) than that for large distant oceanic islands, which depend solely on colonists that cross the seas. Land-bridge islands have lost species steadily since they were isolated by rising sea levels at the end of the Pleistocene epoch (10,000 years ago). Small land-bridge islands have lost a greater proportion of their initial populations of birds than have large land-bridge islands of comparable age (Table 20–2).

Barro Colorado Island in Panama is a land-bridge island that was separated from the mainland in recent times by the opening and flooding of the Panama Canal in 1914. The island is home to the prestigious Smithsonian Tropical Research Institute. Its scientists thoroughly documented the species that were present and how they fared in 85 years of isolation (Robinson 1999). The result: 65 bird species have disappeared from the

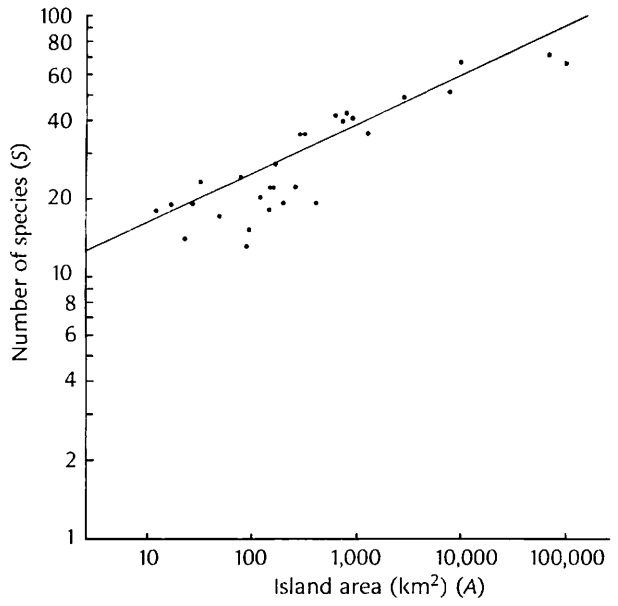


FIGURE 20–6 The number of species, *S*, found on islands increases in direct relation to island area, *A*. This graph is plotted for islands of the West Indies. [*From Ricklefs and Cox 1972*]

island. Once gone, sedentary forest-dwelling species in particular have not recolonized the island. Many of them were lost before 1970. At least 14 species disappeared after 1970, and three others (Slate-colored Grosbeak, Speckled Mourner, and Rufous Piha) that were abundant in 1970 now persist only in small numbers.

Extinction can result simply from the inevitable fluctuations in the size of small populations. The probability of extinction, therefore, depends on population size and on the area containing the population.

What has been causing this loss of bird species from Barro Colorado Island? Several changes contribute to the loss, but one of them highlights the importance of large predators, such as jungle cats and eagles. These

TABLE 20–2 Present and probable past land-bird faunas of five major land-bridge islands

Island	Area (km²)	Number of Species			Extinct Species (%)
		Original	Present	Extinct	
Fernando Po	2,036	360	128	232	84
Trinidad	4,834	350	220	130	37
Hainan	33,710	198	123	75	38
Ceylon	65,688	239	171	68	28
Tasmania	67,978	180	88	92	51

From Terborgh and Winter 1980.

predators disappeared soon after isolation, leading to increases in their prey—small forest mammals and other predators of ground-nest birds. Similarly, mainland forests are increasingly reduced to small island fragments that are subject to loss of species in what is sometimes called the small-island effect (see Chapter 21).

Open and Closed Communities Compared

Historical forces add and subtract species from local communities over long time periods. Evolutionary changes, on one hand, combined with seasonal changes and daily species interactions on the other hand, mold the actual compositions of local assemblages of species. Whether communities achieve stable equilibria through short-term or evolutionary adjustments remains uncertain.

Classical community ecology was largely an equilibrium science that assumed that both population and community processes tended strongly toward equilibrium states (Ricklefs 2005). Replacing that assumption now is a growing recognition that dynamic evolutionary and ecological adjustments may prevail. A continuum of possible community structures indicates the diversity of these processes in play.

Derived from early botanical thought are two polar views that embrace the continuum of community formation and dynamics (Figure 20–7). Open communities are fortuitous, dynamic assemblages of essentially noncompeting species. The species in these communities each align themselves independently along environmental gradients according to their own ecological requirements (Gleason 1926; Wiens 1990). Closed communities are stable combinations of species that separate themselves from a pool of possible colonists and competitors. Community efficiency, stability, and resistance to invasion by additional species increase with evolutionary adjustment among members of the community. In this view, competition for limited resources structures the local composition of species. The closed-community concept has been a dominant theme of modern studies of bird communities.

These views are extreme, but evidence exists for both. For example, the birds that breed in upland hardwood stands in southern Wisconsin form open-community assemblages of species (Bond 1957). Their habitats range from open, dry, deciduous forests dominated by black oak trees to denser, moist forests dominated by sugar maple trees. Certain bird species, such as the Red-eyed Vireo, are more common in wet-climate forests. Others, such as the Black-capped Chickadee, are more common in dry-climate forests. Some, such as the American Redstart, are most common in intermediate forest types. Each species has specific preferences or needs and chooses its habitat accordingly. These overlapping distributions suggest independent, ecologically related associations, not coincident relations of coadapted species.

Disturbance and unpredictable climate changes foster open-community assemblages. Series of unpredictable wet and dry years or of severe and benign winters are the norm worldwide. Pronounced year-to-year variations

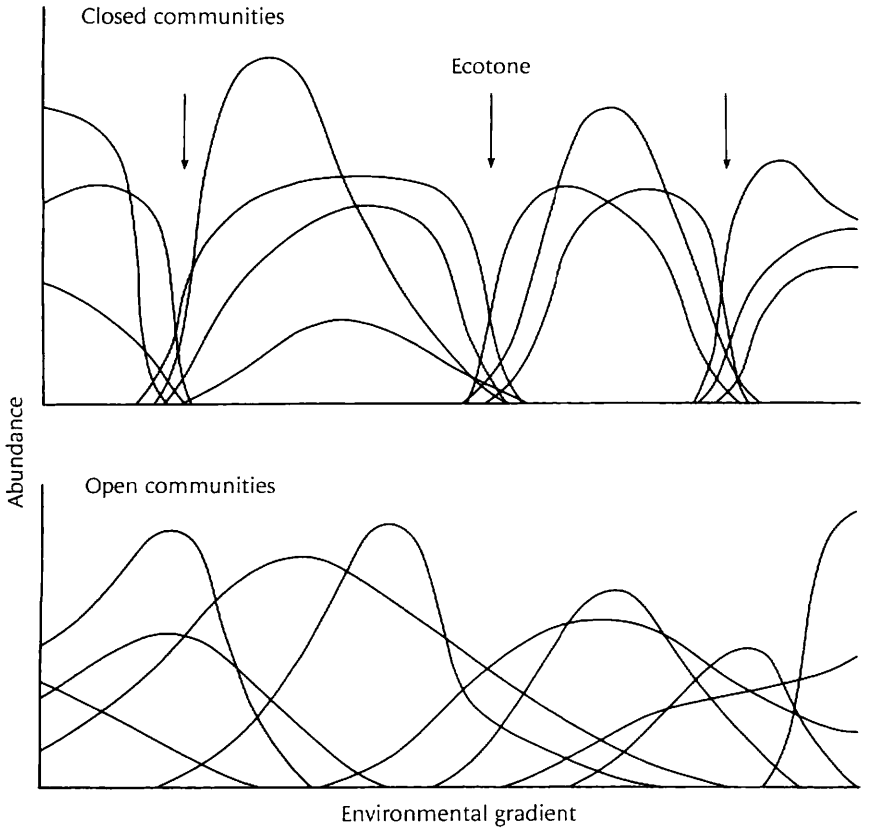


FIGURE 20–7 Open and closed communities are extremes on the continuum of possible community structures along environmental gradients, such as dry forest to wet forest. In open communities (*bottom*), species are arrayed independently according to their particular ecological needs. In closed communities (*top*), distinct sets of species occupy particular habitats with breaks at the interfaces between habitats, called ecotones (arrows). [*From Ricklefs 1979a*]

are typical even of tropical rain forests, once thought to be the most stable of ecosystems. Fire, an extreme form of disturbance, naturally and periodically devastates chaparral communities in California and the grasslands of both Africa and the western United States. Regrowth after a burn proceeds through regular patterns of plant succession and associated bird communities. Through the years, localized burns and recoveries create an ever-changing mosaic of unstable habitats. The local communities that occupy them are therefore dynamic ones rather than self-perpetuating systems at equilibrium.

Similarly, fire controls the shrub–steppe bird communities of the Great Basin of western North America. Interspecific competition does not seem to be an important force in such dynamic communities (Dunning 1986). Instead, these birds appear to be limited principally by winter food availability rather than by summer food availability. They respond opportunistically and without competition to locally abundant, nonlimiting resources on their breeding grounds.

Communities of hummingbirds also are dynamic ones centered on current blooms of favored flowers. The evolutionary history of hummingbirds features physiological adaptations to high altitudes, such as those of the Andes of South America, and specializations of bill structure for feeding and pollinating particular flowers (see Figure 1–9). It also features intense competition within and among species for nectar.

Hummingbirds, as well as other nectar-feeding birds, provide some of the best examples of closed assemblages of species that compete for food. Coexisting hummingbirds organize themselves in predictable, but often temporary, sets around one or two large, territorial species that control access to preferred flowers. In the highlands of Costa Rica, for example, the aggressive Fiery-throated Hummingbird and Green Violetear control the clusters of flowers that are rich in nectar (Wolf et al. 1976). Complementing such territorial species in each local set of species are (1) a large, nonterritorial, long-billed species, which visits scattered flowers containing large nectar volumes; (2) a small-sized, nonterritorial, short-billed species, which visits small flowers containing small amounts of nectar; and (3) a small-sized, sharp-billed filcher, such as the Tufted Coquette, which steals nectar from undefended big flowers by piercing the base of the corolla (Figure 20–8A).

Ornithologists frequently discover that the ranges of closely related species are mutually exclusive. Each island in the West Indies, for example, is inhabited by only 2 or 3 hummingbird species, although 15 hummingbird species inhabit the region (Figure 20–8B). Only two resident species, a small one and a large one, inhabit low-lying islands. Mountainous islands are populated by three types of hummingbirds: a small, widespread species and two large ones, one of them in the lowlands and the other in the highlands. Competition can be inferred to be the process historically responsible for such replacement patterns of ecologically similar species.

If communities were truly closed, they would be resistant to invasion by new, introduced species. But so-called invasive species occupy many bird communities worldwide. Think of Common Starlings and Common Pheasants in North America. The avifaunas of the West Indies now include 23 established exotic bird species. The Hawaiian Islands have more than 45, and Florida has 58 plus more than 100 additional species that escape or are deliberately released each year but don't yet breed.

What is the distinction, if there is one, between what we call "invasive," "alien," "exotic," or "nonnative" species and what we call "native" species that expand their range or invade a new island naturally? It rests on the role of human transport in their dispersal (Ricklefs 2005). Whether introduced species are poor dispersers that advance because they are superior competitors that can penetrate a closed community is unknown. The many exotic species introduced into the Hawaiian Islands have largely failed to invade the intact native forest there (Scott 1986). Instead, they thrive only in disturbed and human landscapes, much like those of their origins. As with natural range expansions, exotic species may thrive because they temporarily escape from the herbivores, predators, or pathogens that formerly limited their numbers.

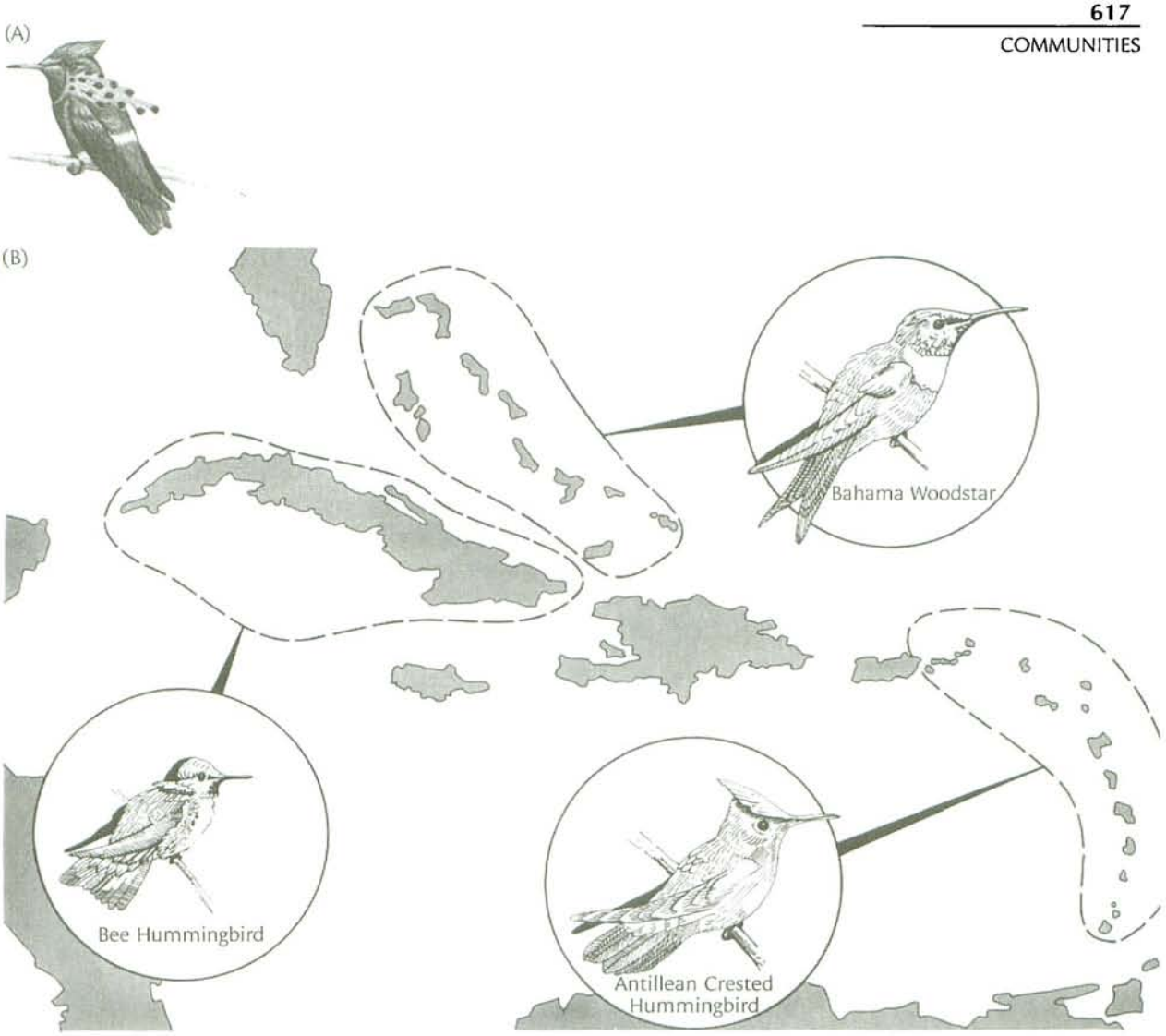


FIGURE 20–8 (A) The small Tufted Coquette uses its sharp bill to steal nectar from undefended big flowers by piercing the base of the corolla. (B) Geographical replacements of possible competitors. Different species of small hummingbirds do not coexist in the West Indies; instead, they have segregated distributions. [*After Lack 1971*]

What is known is that the success of an introduction corresponds primarily to the introduction effort itself—how many birds are released how many times. Many half-hearted introductions fail.

Species Diversity

The number and diversity of bird species in an area vary with habitat, among continents, and from one region of the planet to another. The major patterns of species richness—lowest in the Arctic, highest in the Tropics—have been known for years. The underlying causes of these

patterns, however, continue to challenge us. Understanding why there are so many more species in tropical communities than in temperate communities is especially challenging. The next sections review the patterns of species diversity in time and space, with special emphasis on tropical species diversity.

Differences among communities in numbers and relative abundances of their species relate to regional and historical processes as well as to local forces such as productivity and seasonal stability. Diversity in tropical communities, in particular, relates to their long, stable histories of accumulation of specialized species (Moreau 1966). Ancient communities may be the most species rich of all. For example, the forest faunas of Panama are richer than those of Africa, but the grasslands and savannas of Panama are relatively impoverished. The lowland forests in Africa were restricted in extent during the Pleistocene period, which prevented the development of rich forest avifaunas (Karr 1976). The man-made grasslands in Panama are quite young (15,000 years) relative to the ancient, natural grasslands and savannas of Africa. As a result, grassland communities in Africa are species rich, whereas those in Central America are species poor.

Spatial Components

The distributions of most bird species are restricted both globally and locally. Penguins are limited to the Southern Hemisphere, auks to the Northern Hemisphere, curassows (see Figure 3–14) to tropical South America, mousebirds and turacos to Africa (Figure 20–9), and the Dodo

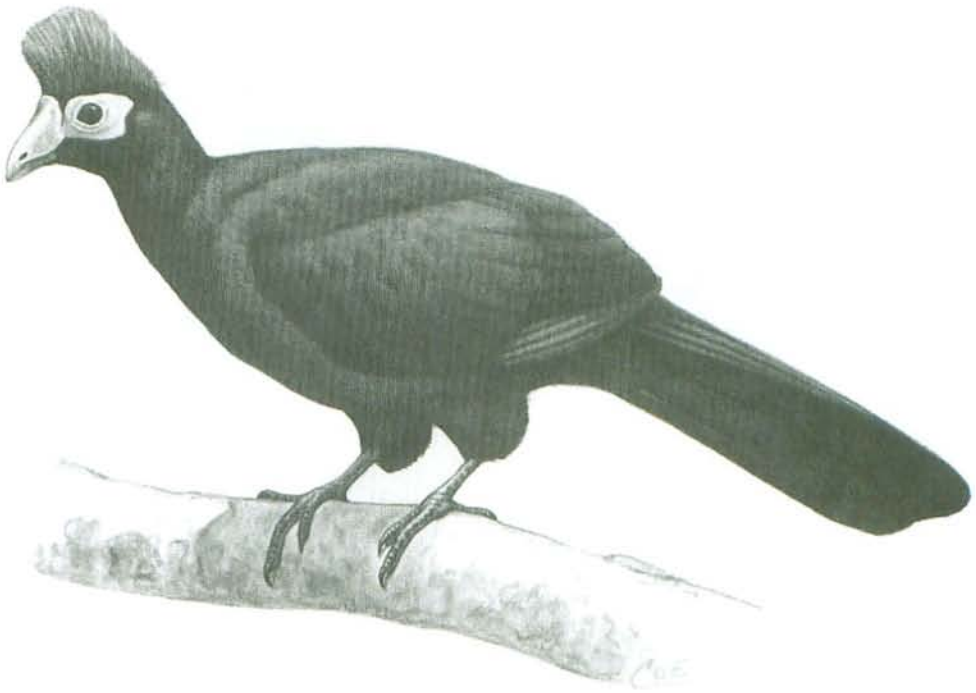


FIGURE 20–9 The turacos, such as this Ross's Turaco, are limited to Africa.

(once upon a time) to the island of Mauritius. Such boundaries may be due to physical restrictions. The flightless Dodo, for example, was limited to one oceanic island (see Box 21–1). More often, however, the limits of the distribution of a bird species, even on continents, are due to intrinsic limits of population growth, competitive replacement by another species, availability of resources, physiological tolerances, or some combination of these factors. Even at the local level of a county, parish, or shire perhaps, few birds use the full variety of habitats available to them.

Local diversity, or alpha diversity, corresponds to the structural complexity of the habitat. Plant species and physical form, amount of vegetative cover, and details of habitat structure all contribute to habitat complexity and to the local diversity of birds. The physical structure of habitats provides courtship and display stations, nest sites, protection from predators, shelter from climatic stress, and food.

The vertical distribution of vegetation roughly defines the variety of foraging opportunities and, hence, the variety of species that can occupy a habitat (Figure 20–10). The Hubbard Brook forests of New Hampshire, for example, contain ground feeders such as thrushes, Ovenbirds, and Dark-eyed Juncos; tree-trunk feeders such as woodpeckers and nuthatches; general canopy feeders such as Scarlet Tanagers, some vireos, and one species of flycatcher, which search widely in both deciduous and coniferous trees; and specialized canopy feeders such as Blackburnian Warblers and Black-capped Chickadees, which tend to restrict their searches for food to the outer twigs of conifers (Holmes et al. 1979). A closer look reveals that variations in foraging behavior among insectivorous birds are directly related to variations in foliage height.

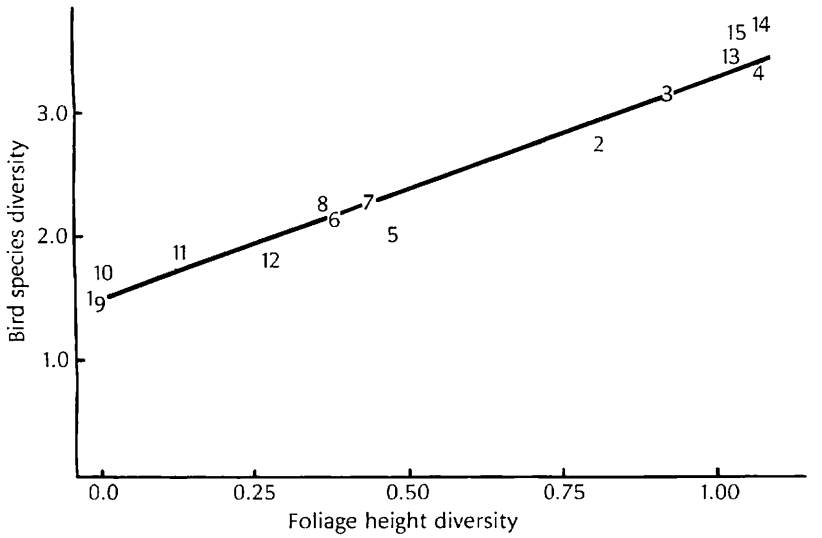


FIGURE 20–10 The local diversity and relative abundance of bird species are correlated with the relative height and diversity of the foliage, illustrated here for sites in Illinois (sites 1 through 4), Texas (sites 5 through 8), and Panama (sites 9 through 15). [*After Karr and Roth 1971*]

Nest predation can determine local species compositions by favoring bird species that nest at different heights and in different microhabitats. In a 20-year study of birds associated with the conversion of old, abandoned fields into shrublands and then into forest—called old-field ecological succession—on Long Island, New York, nine species of birds established nesting territories in a sequence that corresponded to the availability of nest cover (Lanyon 1981). Red-winged Blackbirds were the first to nest in a field, and Eastern Towhees were the last. As an open field converts into shrubland and then into forest, the availability of nest-supporting vegetation and the amount of shade for nests determine the suitability of the habitat for breeding. In this example, the procession of species of overlapping tenures caused the average number of territorial species present to peak 20 years after the field was last cultivated (Figure 20–11).

Species that coexist in seemingly homogeneous habitats, such as grasslands or spruce forests, may segregate their niches more finely with respect to foraging station (Box 20–3). Consider the classic study of niche partitioning by warblers in northern spruce forests of Maine (MacArthur 1958). There, the Yellow-rumped Warbler feeds mostly in the understory below 3 meters, the Black-throated Green Warbler in the middle

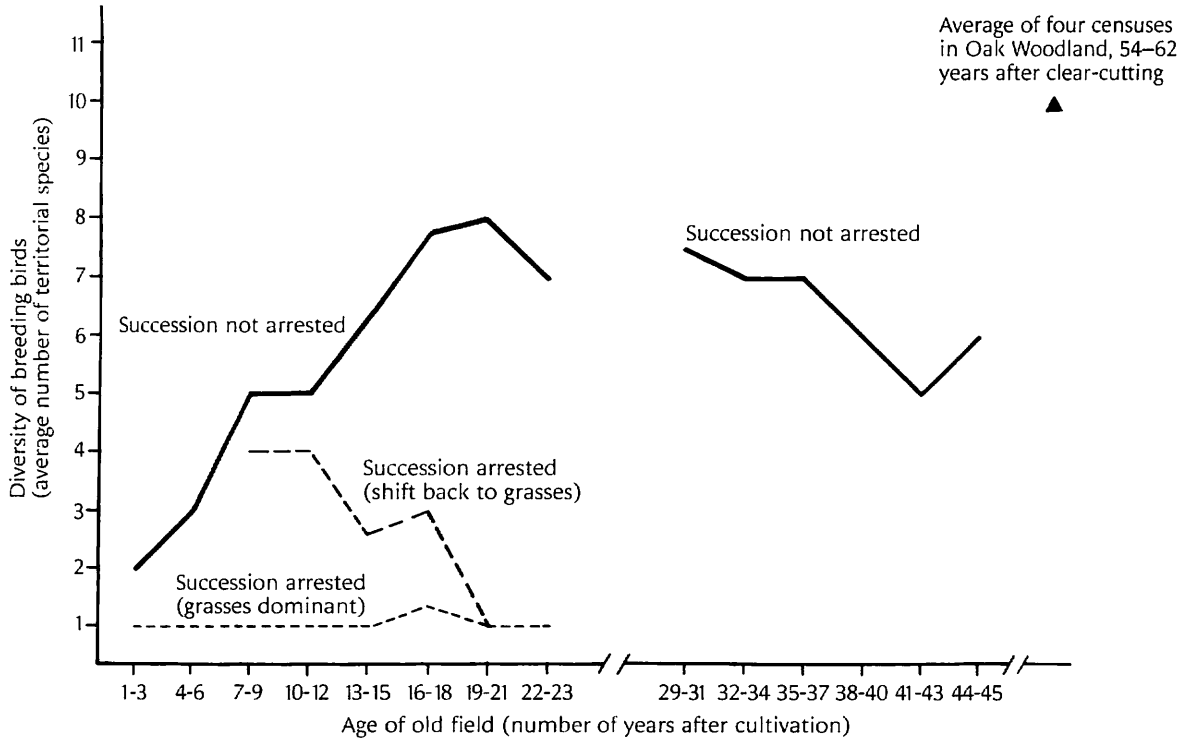
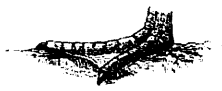


FIGURE 20–11 The diversity of species nesting in old fields changes with the age of the field and the successional change of the vegetation from grass, to bushes, and ultimately to trees. Successional change was arrested by cultivation. [*From Lanyon 1981*]

BOX 20–3

DISTANCE TO COVER DEFINES THE NICHES OF SPARROWS



Distance to protective cover affects the variety of sparrows that can coexist in open, simply structured grassland habitats (Pulliam and Mills 1977). In southeastern Arizona, four species of sparrows inhabit open grasslands that have scattered mesquite trees, which provide some protection from predators such as Prairie Falcons. From the sparrows' point of view, this habitat offers concentric rings of increasing distance from the nearest cover. The Vesper Sparrow stays closest to the mesquite trees (within 4 meters), the Savannah Sparrow feeds farther out (4–16 meters), the Grasshopper Sparrow still farther out (8–32 meters), and the Chestnut-collared Longspur feeds far from the trees in the most open grassland.

The behavior of these species when flushed corresponds to the risks of flying increasing distances to cover. Vesper Sparrows fly quickly to nearby cover. Savannah Sparrows fly to an exposed perch the first time they are flushed and then to full cover if flushed again. Rather than face the risks of a longer flight, Grasshopper Sparrows usually drop back into the grass when flushed, but they fly for cover if repeatedly flushed. Longspurs, however, either crouch to the ground to hide or fly off in tight flocks that help thwart predators.

story, and the Blackburnian Warbler at the tops of the same spruce trees. Sharing the midsection of the trees with the Black-throated Green Warbler, which searches the foliage for food, is the Cape May Warbler, which feeds on insects attracted to sap on the tree trunk. Sharing the tree tops with the Blackburnian Warbler, which feeds on the outer twigs and sallies out after aerial insects, is the Bay-breasted Warbler, which searches for insects close to the trunk. In Europe, different species of tits show parallel choices of their foraging stations (see page 629).

Bird species diversity increases from that in a single local habitat (alpha diversity), to that across multiple local habitats (beta diversity), to large-scale regional diversity (gamma diversity). Habitat preferences cause the variety of birds to increase as the number of distinct habitats increases. From the West Coast of the United States to the East Coast, the number of species peaks in the Sierra, Rocky, and Appalachian mountains, where markedly different habitats at various altitudes increase beta diversity. Some countries in South America—Colombia, Ecuador, and Peru—owe their extraordinary avifaunas in part to the topographical and ecological diversity of the Andes.

Tropical Diversity

The density of species in an area increases as in the procession southward from North America (Figure 20–12) and peaks in the tropical forests of western Amazonia. Tropical forests support more than 300 resident species in a 3-square-kilometer study plot, compared with only 30 to 50 species in temperate forests (Marra and Remsen 1997). A 400-square-mile section (160,000 square miles in area) of the United States contains from 120

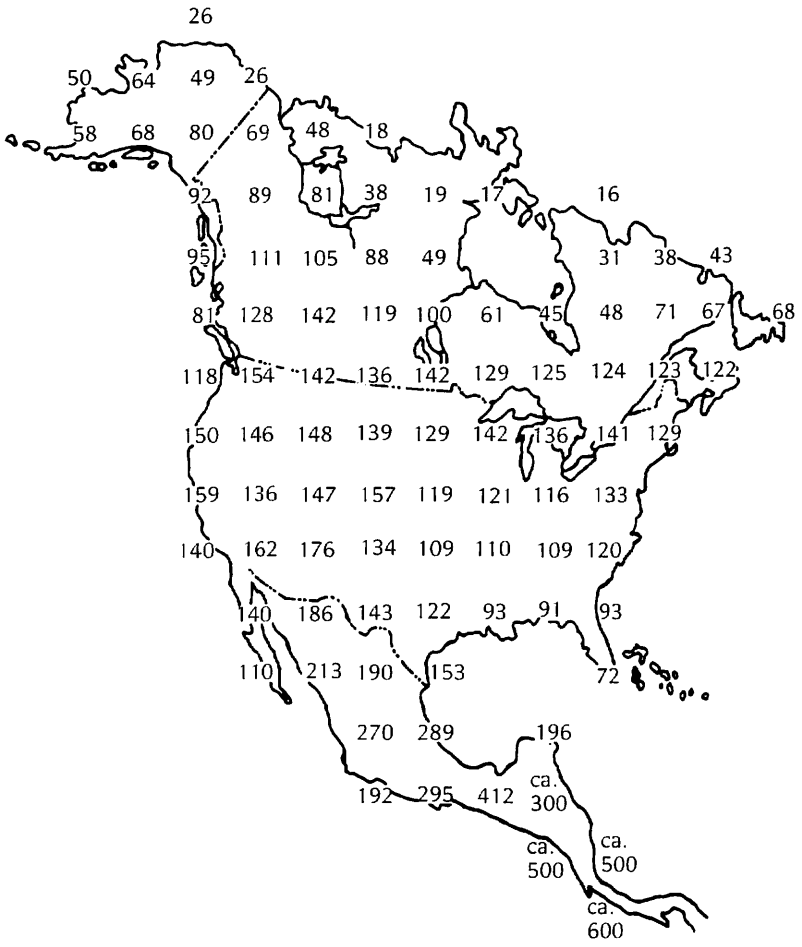


FIGURE 20–12 The number of land-bird species that breed in geographical areas of 400 square miles in North and Central America decreases with increasing latitude. [*From MacArthur 1969*]

to 150 species of breeding land birds, but the same area in Central America contains from 500 to 600. In western Amazonia, more than 1000 species can be found in such an area, and more than 535 species, including as many as 40 species of antbirds, can be found locally in a 100-hectare site (Terborgh et al. 1990).

The variety of species also increases downhill from high to low altitudes. In the Andean country of Colombia alone, 47 species reside above the timberline, 270 at lower temperate altitudes, more than 480 at even lower, subtropical altitudes, and more than 1000 in the tropical lowlands.

The greater diversity of species in the Tropics compared with diversity in the temperate zone is due in part to different and more varied food resources (Ricklefs and Travis 1980). For example, groups of fruiteaters—toucans, hornbills, barbets, trogons, cotingas, manakins, broadbills, and turacos—expand the dimensions of tropical bird communities. Parrots

large and small consume a wide variety of seeds, fruits, and nectars that are not available in northern forests. Hummingbirds and tanagers abound in New World tropical forests, but only a few species live in the north.

The diversity of insect sizes also is greater in the Tropics than in temperate-zone habitats, and the diversity of bill sizes of tropical birds increases accordingly (Figure 20–13). Some families of strictly tropical birds—puffbirds, motmots, antbirds, wood hoopoes, and jacamars—specialize in large insects and small reptiles that are not present in temperate ecosystems. Foraging specialists, such as ant followers and epiphyte probers, also add to the diversity of bird communities in tropical regions.

For decades, ornithologists thought that greater structural habitat complexity was responsible for the high diversity of species in tropical forests, but this conclusion may not be so (Marra and Remsen 1997). Despite their obvious differences, tropical and temperate forests do not differ in overall heterogeneity or complexity. Direct comparison of the use of the forest structure by foliage-gleaning insectivorous birds of the understory, however, exposes more specialized forest-floor foraging behaviors in the tropical species (Figure 20–14). Compared with temperate species, each tropical species is more selective of particular horizontal and vertical habitats and has narrower niche breadth in foraging substrates and foraging heights. In addition, the tropical species overlap less in foraging stations than do comparable temperate-zone species.

In general, tropical species tend to use a narrower range of habitats. They may be more specialized in their foraging behavior and less tolerant of climatic variation than their temperate counterparts. Greater ecological specialization leads to tighter packing of species in local communities, smaller geographical distributions, and greater species richness.

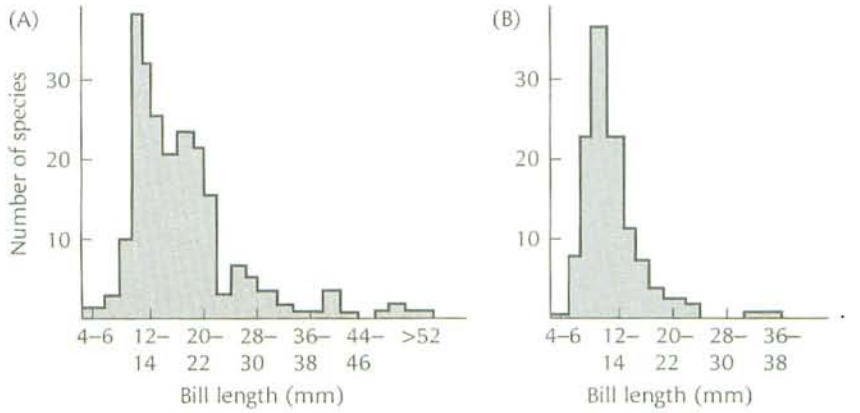


FIGURE 20–13 The existence of large-billed birds causes an increase in bird species diversity in the Tropics. Shown here are the bill lengths of insectivorous birds that breed in (A) tropical latitudes (8°–10° N) and (B) temperate latitudes (42°–44° N). [*From Schoener 1971*]

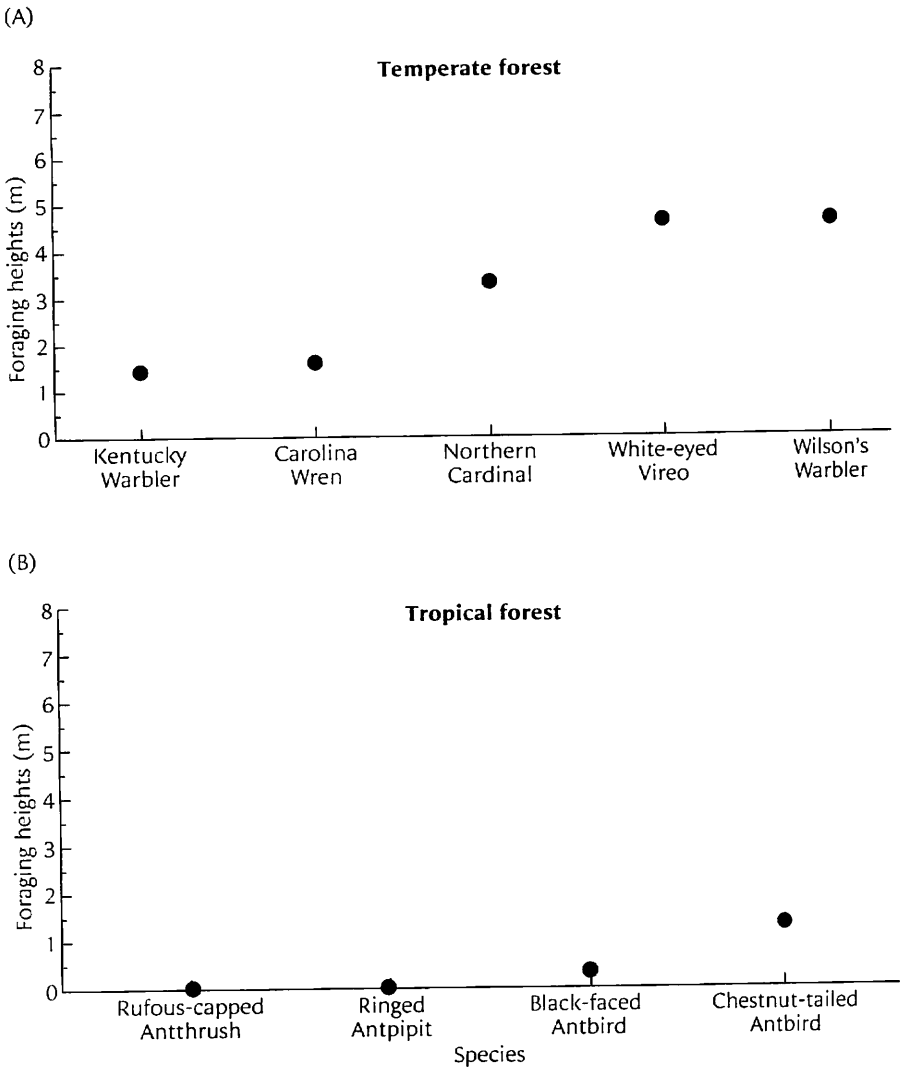


FIGURE 20–14 Mean foraging heights of (A) temperate and (B) tropical forest species. [*From Marra and Remsen 1997*]

Temporal Components

Local assemblages of species change with time as well as with space or geography. Their composition fluctuates regularly with the season and irregularly with climate and resource availability. Migrants coexist only temporarily with resident species and change their community membership with the seasons. Disturbances due to deforestation or fire or to colonization or extinction keep many habitats in flux.

Virtually all bird communities consist of both resident and nonresident species. Residents stay put and accommodate monthly changes in climate and food availability. Nonresidents are seasonal specialists that take advantage of predictable periods of local regional food abundance. The mobility of birds and the evolution of the migratory habit have made possible nonresidency and the opportunistic exploitation of variable environments (see Chapter 10).

Ephemeral resources attract opportunistic species. Temporary assemblages of highly mobile birds may last hours, weeks, or years. Flocks of seabirds over a shoal of fish, for example, are brief in duration (minutes or hours) and highly variable in species composition. Assemblages of hummingbirds and sunbirds at flowers feature high turnover of both individual birds and species during the brief blooming periods of days or weeks (Figure 20–15).

The regional diversity of small, short-billed hummingbirds depends on their ability to circulate seasonally among locally blooming flowers

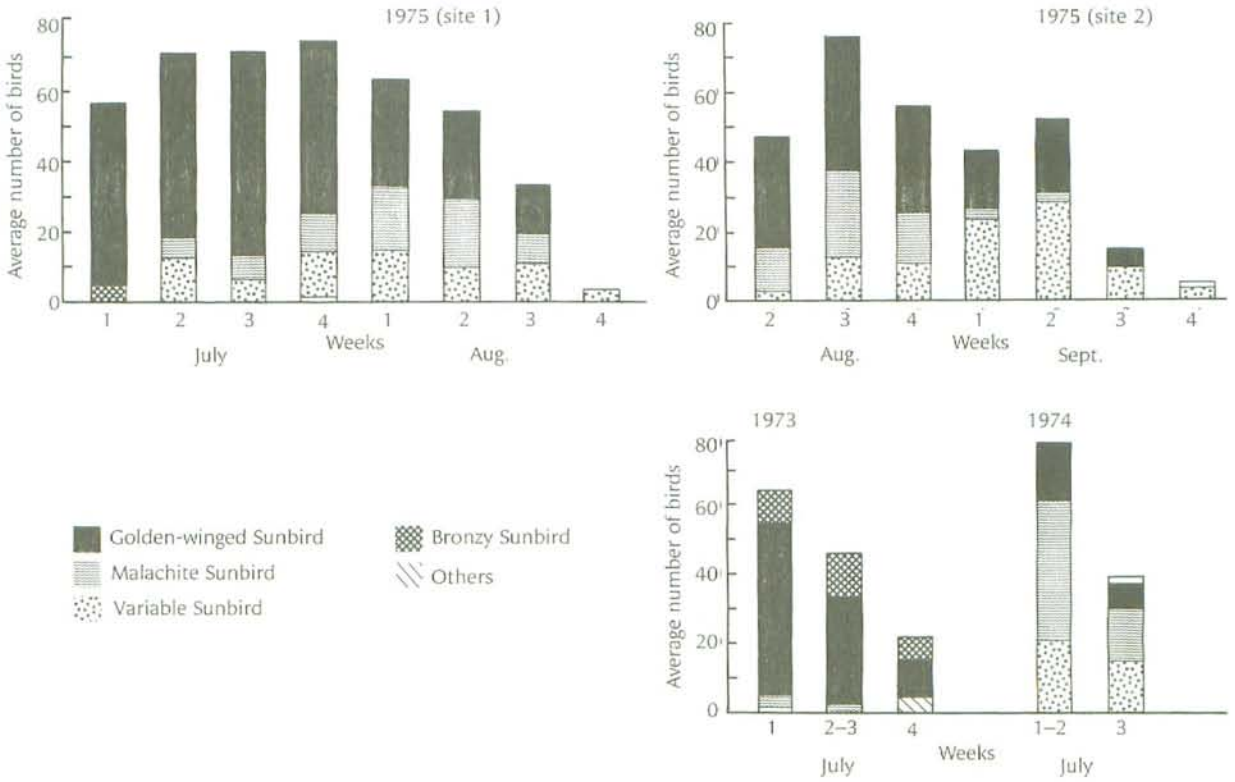


FIGURE 20–15 The composition of sunbird species feeding in fields of flowering mint in the Rift Valley of central Kenya changes weekly as a result of local competitive interactions, and varies through the years and over sites as a result of regional flower availability and colonization. [*After Wolf and Gill 1980*]

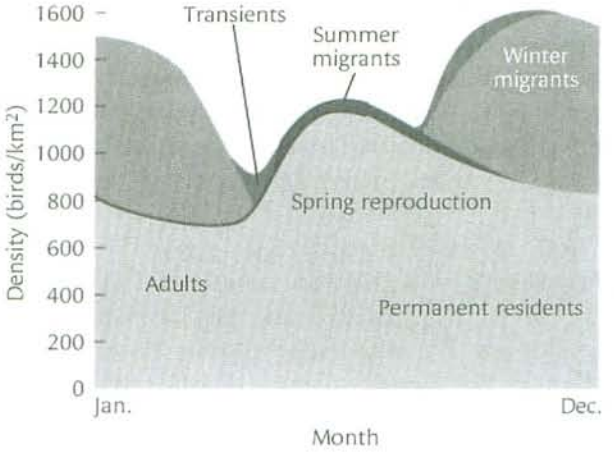


FIGURE 20–16 Model of seasonal composition of the pine-forest bird community of Grand Bahama Island. Local numbers increase with the addition of young birds in the summer and again with the arrival of wintering migrants, which leave in April. [*After Emlen 1980*]

(Feinsinger 1980). Only two short-billed species, the Copper-rumped Hummingbird and the Ruby Topaz, inhabit the small island of Tobago, where they must coexist year-round in the principal nonforested habitat. Seven similar species coexist on the larger island of Trinidad, where more diverse habitats enable segregations and seasonal patterns of local migration.

Seasonal residents form a major part of most bird communities. In season, migrant shorebirds can dominate the bird life of coastal wetlands. The influx of wintering migrants from the north triples the number of species found in the open pine forests of Grand Bahama Island and increases the density of birds from 900 to 1600 per square kilometer (Emlen 1980; Figure 20–16).

In the tropical evergreen forests of western Mexico, the density of small foliage gleaners increases from an average of 2 to 64 birds per hectare with the arrival of the migrants (Hutto 1980). These extraordinary densities of wintering birds result when large populations compress themselves into small areas. Migrant North American land birds from 16 million square kilometers of breeding range squeeze into 2 million square kilometers of winter range in northern Central America and the West Indies.

Competition

Competition arises when one bird's use or defense of a resource makes that resource less available to other birds. Interspecific competition arises when birds of coexisting species require some of the same limited resources. The use or defense of those resources by members of one species reduces the availability of resources to members of another species. Recall that competition among members of one species reduces the rate of

population growth in that species by limiting survival or reproduction. Competition among members of different species also can affect population growth.

The competitive exclusion principle—a fundamental concept of ecology also known as Gause's law after G. F. Gause, a pioneering Russian ecologist—states that two species with identical ecological niches cannot coexist in the same environment. Laboratory results support this concept. One species usually replaces another similar species when the two are forced to share the same environment in a laboratory.

Similarly, competitive interactions are expected to be most intense within sets of ecologically similar species, or guilds, that depend on the same set of resources (Root 1967).

Interference Competition

Competition can be expressed as the overt aggressive displacement of individual birds, called interference competition, or as the reduction of the fecundity and survival of one species by another, called exploitative competition. In an unambiguous example of interference competition, large, dominant species of hummingbirds aggressively exclude other species from the densest concentrations of flowers. Forced by dominant species to use other feeding grounds with fewer flowers, subordinate species quickly shift back to the best available feeding grounds whenever it is possible to do so. Coexisting antbirds that gather at swarms of army ants in tropical forests exhibit similar behavior (see Figure 11–8). So do Golden-crowned Sparrows wintering in California. They aggressively restrict the use by Dark-eyed Juncos of foraging space near shrubs (Davis 1973). The juncos increase their use of sites closer to protective cover when Golden-crowned Sparrows are removed experimentally but revert to infrequent use when the sparrows return.

Behavioral dominance forces sexes of the same species, as well as birds of different species, to use different habitats. Peter Marra (2000) tested the habitat preferences of American Redstarts wintering on Jamaica. There, adult male redstarts mostly occupy mangrove habitats, where they establish and defend winter territories. Female redstarts mostly occupy nearby low-quality secondary scrub habitats. The females that winter in scrub habitat suffer a measureable decline in body condition, which affects their migration back to breeding grounds in North America and, potentially, their future reproductive success (Marra and Holberton 1998).

Before a series of removal experiments, yearling male and female redstarts arrived first and settled in both habitats. Adult males arrived next and increased the competition for territories. They displaced subordinate redstarts, especially females, from the high-quality mangrove study areas to the low-quality scrub habitat. Marra then removed equal numbers of established redstarts from both habitats to test the response of the remaining redstarts to the experimental vacancies. No longer excluded from the best habitat by dominant males, subordinate redstarts, primarily females, quickly filled the vacancies in the mangroves first.

Exploitative Competition

Rather than overt aggression, most interspecific competition subtly depresses a species' survival or breeding success by reducing critical resources. Such competition is exploitative competition. Some of the best evidence of the effects of one species on the fecundity, survival, and population recruitment of another comes from research on Great Tits and Blue Tits. This research is an extension of the work on population regulation of the Great Tit (see Chapter 18).

The local assemblages, or guilds, of titmice have been the focus of intense research on the role of interspecific competition in bird communities. The reduction of the food supplies by tits can affect the reproductive success of species outside their guild, such as Collared Flycatchers in Sweden (Gustafsson 1987). However, the details of competitive interactions between Great Tits and Blue Tits are of particular interest. These two species negatively affect each other in a variety of ways, both trivial and consequential (Dhondt 1989). Whereas competition between them affects their annual population dynamics, the balance of their interactions leads to coexistence rather than the exclusion of one species by the other.

Recall that reproductive success, or fecundity, in Great Tits decreases as population density increases. In addition to being sensitive to the local densities of members of their own species, the fecundity of Great Tits is sensitive to the numbers of coexisting Blue Tits. Even though they tend to use different foraging stations, there is overlap. High densities of Blue Tits during the breeding season reduce food availability. Reduced food availability increases nestling mortality and causes fewer Great Tits to attempt second broods. In this way, high densities of Blue Tits reduce the reproductive output of Great Tits. The effects of Blue Tits on the reproductive output of Great Tits during the breeding season, however, are only temporary ones and have little final effect on the population density of Great Tits. Instead, their density is controlled primarily by winter survival and the recruitment of juveniles (see Chapter 18).

The reproduction of Blue Tits is neither density dependent nor greatly affected during the breeding season by the local numbers of Great Tits, with one caveat: Great Tits control nest boxes if they are in short supply. They may even kill Blue Tits in the process (Löhrl 1977). This form of interference competition is extreme.

Of greater consequence is the reversal of competition between these two species outside the breeding season. Then Great Tits truly limit the number of Blue Tits in a woodlot by controlling the availability of roost holes. When the number of Great Tits in a population that depended on man-made boxes for roosting (as well as for nesting) was halved (by narrowing the nest entrances from 32 to 26 mm and thereby excluding the larger Great Tits), many more male juvenile Blue Tits were recruited into the woodlot in the autumn and subsequently joined the breeding population in the following year (Figure 20–17).

The measurable competitive interactions between Great Tits and Blue Tits affect their annual successes. Although it does not result in the ex-

FIGURE 20–17 Experimental demonstration of interspecific competition. When Great Tits were excluded from nest boxes (from 1976 to 1978, screened area) in the experimental area at Gontrode, Belgium (white circles), more Blue Tits established themselves there than in a control area at Zevergem (black circles) that had the normal number of Great Tits. [*After Dhondt and Eyckerman 1980*]

clusion of one species from a woodlot by the other, competition favors different foraging behaviors, body sizes, and nest-site preferences. Segregation by habitat is another potential consequence in some species.

Ecological Segregation

A corollary of the competitive exclusion principle is that competition should increase directly with overlap in the use of limited resources. Detrimental ecological overlap may foster changes in behavior or morphology that reduce competition. Observed ecological differences between related species, therefore, may be the "ghosts of competition past" (Connell 1980).

Local separation by habitat and feeding stations is typical of titmice. In Europe, the Great Tit, Blue Tit, and Marsh Tit inhabit broadleaf forests. The Crested Tit and Coal Tit live primarily in coniferous forest used by the other three species only as a suboptimal habitat. The species that live together feed in different places: Great Tits on the ground, Marsh Tits on large branches, and Blue Tits on the smaller twigs. Differences among European titmice in their feeding locations are associated with differences in body mass and beak size. Larger species feed at a lower level and on larger insects and harder seeds than do smaller species. Species that live in coniferous forests have longer and narrower beaks than those that live in broadleaf woods.

Each species of European tit has a counterpart in North America (Figure 20–18). However, only two of the North American species usually live together in the same habitat. In many areas, a small chickadee coexists with a large titmouse, which has different requirements. Where two species of small chickadees coexist, they inhabit different habitats. In New England, the Boreal Chickadee inhabits dark conifer stands, whereas the

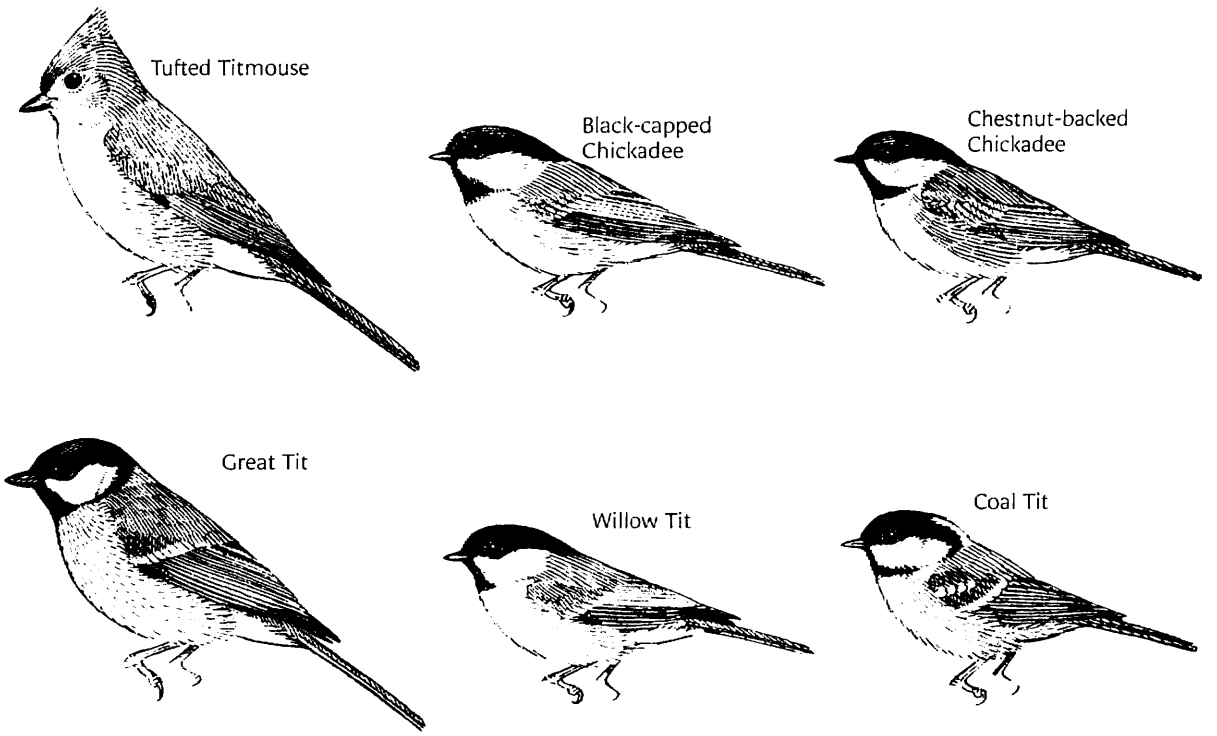


FIGURE 20–18 Certain species of North American (*top row*) and European (*bottom row*) chickadees and titmice act as ecological equivalents. [*From Lack 1971*]

Black-capped Chickadee inhabits more open, mixed deciduous and conifer forest. On the West Coast, Chestnut-backed Chickadees and Black-capped Chickadees similarly separate by habitat.

If competition actually restricts a species, one would expect shifts in the distribution, habitat use, or foraging behavior of a species when it is not limited by a competitor. The absence of a competitor allows ecological release. On the San Juan Islands of the Pacific Northwest, where there are no Black-capped Chickadees, the Chestnut-backed Chickadees inhabit broadleaf forests used elsewhere by the Black-capped Chickadees. Shifts in habitat use in the absence of other species are well documented among European tits. Marsh Tits, for example, inhabit pine plantations only in Denmark, where Willow Tits are absent from this habitat. In Ireland, Coal Tits feed regularly in the understory of evergreen forests in the absence of the Marsh Tits, Willow Tits, and Crested Tits that normally preempt this niche.

Ecological and Character Displacement

Darwin's finches of the Galápagos Islands provide a classic example of the apparent role of competitive exclusion and character displacement (Grant 1986). The adaptive radiation of these finches has propagated species with a variety of bill sizes that relate directly to seed sizes. Ground finches and

cactus finches with distinctly different bill sizes inhabit every island. The differences in the average bill size of coexisting species are consistent with the hypothesis of interspecific competition for food. Species with similar-sized bills replace one another on various islands, and the bills of various species are more alike when they do not live together (Figure 20–19).

Simple ecological displacements as a result of competition should lead to evolutionary reinforcement in the form of morphological character displacement, or enhanced differences (in size, for example) where two species coexist. On the Swedish island of Gotland, in the absence of larger competitors—specifically, Crested Tits and Willow Tits—Coal Tits are larger than on the mainland (Alatalo et al. 1986). Their larger size on

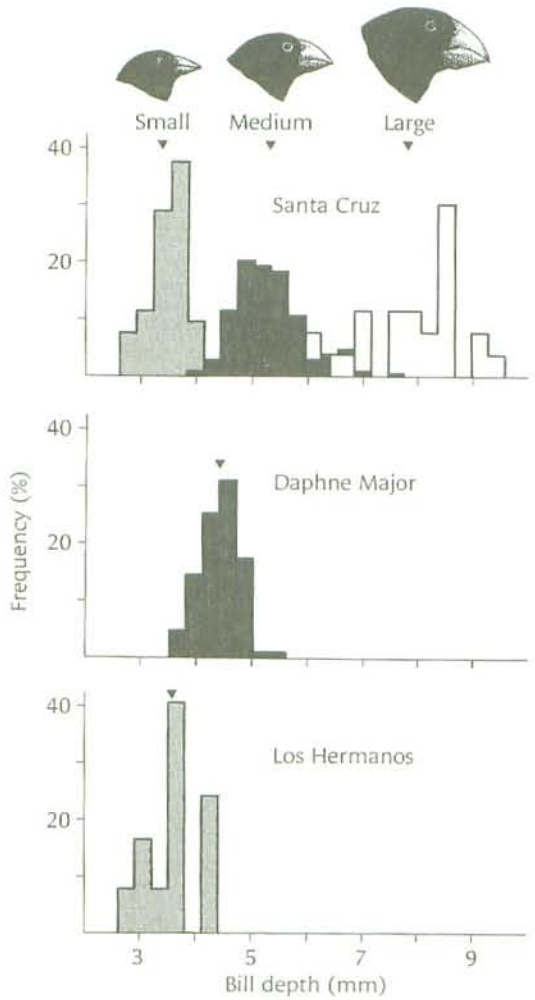


FIGURE 20–19 Three species of ground finches that coexist on the Galápagos island of Santa Cruz have bills of different depths (*top*), which enable them to feed on different seeds. Certain islands, such as Daphne Major and Los Hermanos, have only one species. In the absence of other species, the solo populations on these islands evolve intermediate-sized bills, as the lower two graphs show. [*After Grant 1986*]

BOX 20–4

COMPETITION AFFECTS THE USE OF FORAGING SITES BY TITS

The ornithological literature contains many, often anecdotal, observations of apparent niche shifts in the absence of a competitor. Controlled experimental demonstrations with the use of free-living birds in natural populations, however, are few. One exception is the study of foraging tits and Goldcrests in the coniferous forests of central Sweden (Alatalo et al. 1987). These small birds exploit nonrenewable insect and seed resources in their group territories during the long, cold winter. Two smaller and socially subordinate species, the Coal Tit and the Goldcrest, forage on the outermost branches and needles, whereas two larger and dominant species, the Willow Tit and the Crested Tit, forage inside the trees.

In this experiment, the ornithologists removed the Coal Tits and Goldcrests from three of six flocks to test whether Willow Tits and Crested Tits would change their foraging behavior. They did. In late winter, Crested Tits moved farther out on the spruce branches in experimental flocks than in control flocks. Willow Tits did so in pine trees but not in spruce trees.

The Swedish team concluded that exploitative competition directly based on food depletion, without any interference, influences the use of foraging sites by tits that coexist in coniferous forests.

Gotland coincides with a shift in foraging niche from the outside of the tree and on needles, where small size is advantageous, to the inner parts of the pine trees (Box 20–4).

The abrupt replacement of one species by another at various altitudes in the Andes and in New Guinea also suggests that competition from one species limits the distribution of another. New Guinea birds with well-defined altitudinal distributions replace one another abruptly at various elevations (Figure 20–20). The range of elevations occupied by a species seems to depend on the presence or absence of related species. For example, the Red-flanked Lorikeet is confined to low elevations in regions with one of the two highland species—either the Red-fronted Lorikeet or the Red-chinned Lorikeet. In regions in which the Red-flanked Lorikeet is alone, however, it ascends to high elevations. Conversely, in regions in which either the Red-fronted Lorikeet or the Red-chinned Lorikeet is alone, it descends to sea level.

Similar patterns of altitudinal replacement are found in the mountains of eastern North America, where as many as five species of thrushes nest in the high mountain forests of New England (Noon 1981). Veeries share low elevations with the Wood Thrush and are replaced at higher elevations by the Swainson's Thrush and the Bicknell's Thrush. In the Great Smoky mountains, where the Swainson's Thrush and the Bicknell's Thrush are absent, the Veery shifts to higher elevations and overlaps only slightly with the Wood Thrush at low elevations.

Such studies of ecological replacement assume weakly that the locations are identical except for the presence or absence of the purported competitors. At best, the process of competitive replacement must be inferred from an observed pattern. The role of interspecific competition is

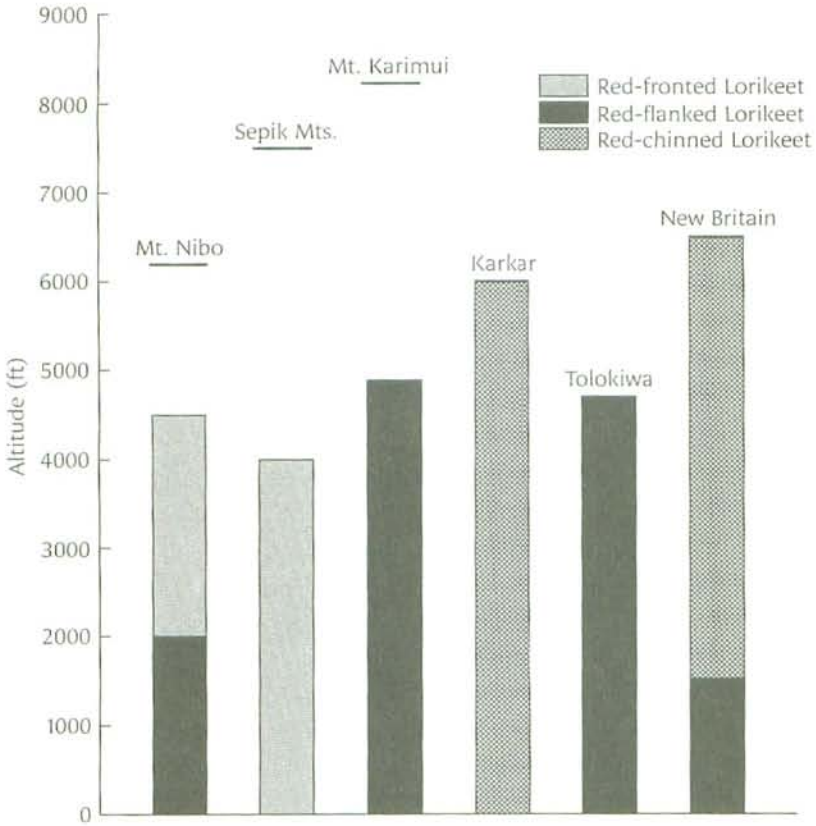


FIGURE 20–20 In regions inhabited by different species of lorikeets in New Guinea, they tend to occupy different elevations, but, in the absence of others, one species occupies a broader range of elevations (middle four bars). [*After Diamond 1975*]

still uncertain as a primary ecological force that defines the membership in bird communities and the geographical distributions of bird species. Few communities, if any, are truly "open" or "closed." Rather, assemblages openly compose and recompose on varied time scales with modest adjustments by local competitive interactions along the way.

Summary

The availability of resources, such as food and nest holes, determines not only the local population density of a given species but also the number and kinds of different species that can coexist in a given habitat. Two major theories attempt to explain the structures of avian communities. According to one theory, communities are open systems in which each species arrays itself independently along environmental gradients determined by its specific ecological requirements. According to the other theory, communities are closed, discrete, and integrated sets of mutually compatible species.

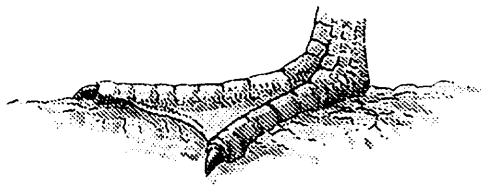
The number of species found locally increases from the Arctic to the Tropics. The local availability of key resources determines which species can live in a particular habitat. Habitat heterogeneity contributes to the species diversity of a region in mountainous regions. Interactions between residents and migrants in seasonally variable environments also affect species diversity.

Turnover—the addition and loss of species—drives the changing compositions of avifaunas. The composition of island avifaunas is due not only to ancient history but also to ongoing cycles of colonization and extinction, the frequency of which depends on the isolation and the size of the island. Small, isolated islands have the smallest equilibrium number of species, whereas large islands near continental source areas have the highest equilibrium number of species.

Competition is the key structuring force in the closed-community concept that dominates modern ornithology. Theoretically, the degree to which species compete should relate directly to overlapping use of shared resources. Competitive interactions between well-studied species of European tits illustrates this aspect of competition theory.

Another corollary of the competition theory is that ecological displacements should lead to evolutionary reinforcement in the form of morphological character displacements. The differing bill sizes of Darwin's finches on the Galápagos Islands are a classic example of character displacement. Patterns of geographical replacement in species too similar to coexist suggest but do not prove competitive exclusion. Replacement patterns are particularly well documented on the isolated islands of the West Indies and at different altitudes in the mountains of New Guinea and North America. Generally, however, competitive interactions simply adjust the habits of species that history assembles for limited periods of time.

CHAPTER 21



Conservation

Never have I seen such wonders, or met landlords so worthy of their land. They have had, and still have, the power to ravage it; and instead they have made it a garden.

[Fisher, page 418 in *Wild America* by R. T. Peterson and J. Fisher, 1955]

Birds have enormous conservation power, a power that can be harnessed for the conservation of all biodiversity. Their public appeal motivates millions of people to take time to observe them, to count them, to care about their well-being, and to act on their behalf. Their appeal adds economic value. Both public appeal and economic value translate into political power.

The single-minded goal of modern bird conservation initiatives is to stabilize bird populations worldwide and to prevent more extinctions. Fortunately, conservationists and governments increasingly recognize that the time to save species is while they are still common. Wise management of healthy bird populations can preempt future costly rescue efforts and protect the ecosystems on which our societies depend.

Preceding chapters highlighted many conservation implications of the biology of birds. This final chapter reviews specific bird conservation efforts—past, present, and future. The first two sections deal with the state of our birds, the threats that they face, and some historical perspective on the excessive exploitations that they suffered. Then follow successful initiatives that inspire hope, including those that catalyzed the modern conservation movement. Science-based stewardship of the intact ecosystems and habitats that remain is critical. Conservation by design includes not just the geometry of wildlife preserves but also how best to maximize the viability of populations on a fragmented landscape through sound restoration initiatives. In the end, public support and community participation will determine which initiatives are successful.

The State of Birds

The past plights of our most majestic bird species—Whooping Cranes, California Condors, Ivory-billed Woodpeckers in North America, to name a few—are renowned. Beyond them are substantial historical losses. At least 131 extinctions of birds diminished life on Earth from 1600 to the present time. The vast majority of these extinctions were island species exterminated by introduced species, habitat loss, and excessive human predation. Island species continue to be in trouble: many of the world's rarest birds persist only in small numbers on remote islands. More broadly, continental bird species are at equal or greater risk (Manne et al. 1999). On the larger landmasses, just 10 countries host more than 400 species of threatened birds with highly restricted geographical ranges (Figure 21–1A).

The authoritative Red List of the International Union for the Conservation of Nature (IUCN) classifies species in accord with their risk of extinction (http://www.iucnredlist.org/). The 2006 IUCN Red List classifies 532 bird species as globally endangered and an additional 674 species as vulnerable. A comparison of the threat statuses of all species on the list over five-year intervals produces the Red List Index for birds. This index documents coarsely, but quantitatively, a steady decline in worldwide bird species from 1988 to 2004 (Figure 21–1B).

History warns us not to take even common birds for granted. The once widespread Bewick's Wren, for example, disappeared from the eastern United States with little notice. Rusty Blackbirds and Eastern Meadowlarks are now in steep decline. Early danger signs prevail in Neotropical migrants and grassland species, migrant shorebirds, the seabirds of the Southern Hemisphere, and songbird species with restricted ranges.

Within the continent of North America, roughly half (208 of 414 species analyzed) of the bird species are declining. Some are declining at alarming annual rates of 10 to 15 percent (Butcher 2004). On the positive side, 118 species (28 percent) are increasing and 88 species (21 percent) are statistically stable. At the top of the list of species in serious decline are 19 of 27 North American grassland species. Eastern Meadowlarks, for example, have been declining throughout their range since 1966, especially in the developed northeastern states, where annual declines approach 10 percent (see Figure 18–21). Declining also are Loggerhead Shrikes, Greater Prairie Chickens, and five species of quail.

Embedded in the sprawling city and county of Boulder, Colorado, is one of the largest grassland open-space systems in North America (Jones and Bock 2002). Comparisons of bird-count data from the end of the twentieth century with data from 1900 and 1937 suggest that, if well managed, such municipal open spaces can support populations of many Great Plains grassland birds but not those associated with the shortgrass prairie. Species prominently associated with the shortgrass prairie, including the Burrowing Owl, Common Nighthawk, Loggerhead Shrike, and Lark Bunting, disappeared or declined. In contrast, species associated with mixed and tallgrass habitats increased or held steady. These species in-

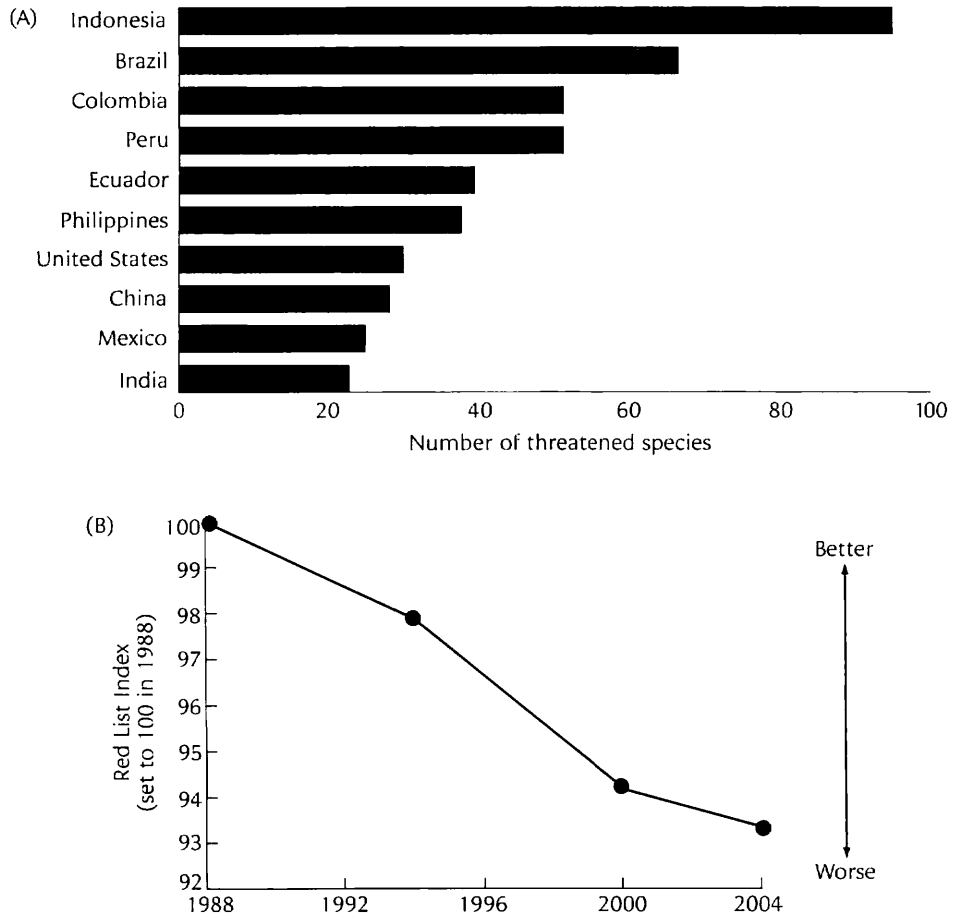


FIGURE 21–1 (A) Countries with the highest numbers of threatened bird species populating restricted geographical ranges. (B) The Red List Index (1988–2004) tracks the world's most threatened bird species, whose status as a group is worsening. The index describes the relative rate of change of species in a group. Change corresponds to overall threat status (relative extinction risk) as quantified by Red List categories (critically endangered, vulnerable, and so forth) over periods of about five years. [*(A) After Bibby et al. 1992. (B) From Butchart et al. 2005*]

cluded Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, Bobolink, and Western Meadowlark.

Throughout Europe, habitat generalists have remained stable from 1980 to the present and forest specialists declined slightly. Farmland specialists, however, declined sharply in the 1980s and more slowly in more recent years (Figure 21–2). Their declines correspond to the replacement of grasslands by modern agriculture. These declines also correspond to the spread of intensive herbicide- and pesticide-based monoculture farming practices that eliminate weeds and insects and leave no stubble or waste grain for the winter. In Britain, Corn Crakes, Corn Buntings, and Red-backed Shrikes stopped breeding and are endangered. The Gray Partridge

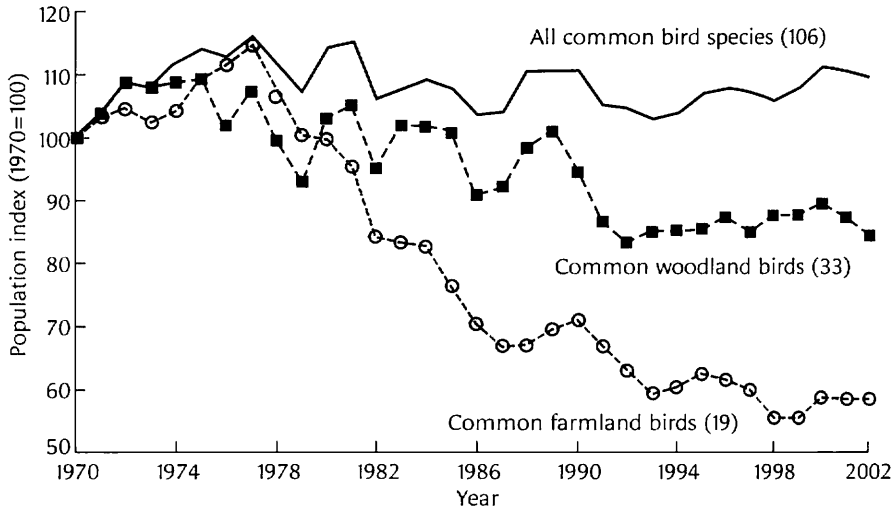


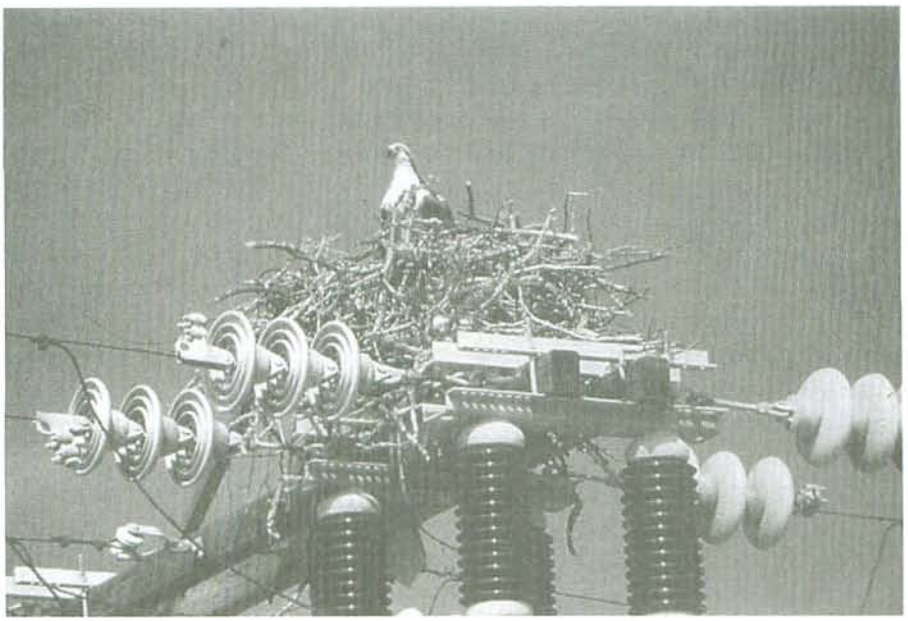
FIGURE 21–2 Common bird indicators in Europe, 1980–2002. The population index is based on national breeding-bird surveys from 18 European countries. Populations of farmland birds, particularly, exhibit the most severe declines due to the deterioration of farmland habitat quality, which affects both birds and other elements of biodiversity. [*From Gregory et al. 2005*]

declined by 43 percent from 1994 to 1999. The European Turtle Dove declined by 18 percent over the same period. In response to these warnings by farmland birds, the British government is investing billions of pounds sterling to encourage environmental farming such as mixed agriculture practices that separate fields with modest borders of habitat.

Birds of old fields, abandoned farmlands, shrub lands, and young or second-growth forests are declining, albeit at lower rates of 3 to 4 percent a year. In North America, they include the American Woodcock, Eastern Towhee, and Golden-winged Warbler. The conversion of these habitats into manicured yards of suburban sprawl and the maturation of young woods into mature forests are the main causes of the loss of this habitat.

Not surprisingly, species that adapt well to man-made environments are increasing. Introduced Common Pigeons, Common Starlings, and House Sparrows are now successful human associates. A redistribution of native species able to coexist with human societies also is under way. Canada Geese are thriving along urban streams and on golf courses. Ospreys nest on telephone poles, power lines, and channel buoys (Figure 21–3). Other raptors such as Red-tailed Hawks and Cooper's Hawks are colonizing our cities and suburbs. Turkey Vultures benefit from the increasing densities of road kills, especially car-struck deer. American Crows, known for 200 years as shy, rural birds in the United States, are invading suburban backyards and city parks, as House Crows and Common Mynas did in Asia centuries ago.

(A)



(B)

FIGURE 21–3 (A) The Osprey is a species benefiting from human structures that provide safe nest sites. (B) The Cooper's Hawk is one of the raptors that are now colonizing cities and suburbs. [*Photo courtesy of C. H. Greenewalt/VIREO*]

Threats

Despite a growing conservation ethic, expanding human populations continue to threaten native bird populations. Habitat loss is the primary threat. Other challenges to bird populations range from direct exploitation by hunting, overfishing, or commercial pet trading to the poisoning of food supplies with pesticides and other chemical contaminants. Added to these sources of mortality is the annual attrition due to predation by pets and collisions with cars, windows, and towers.

Domestic house cats in North America, for example, may kill hundreds of millions of songbirds each year. Farmland and barnyard cats kill roughly 39 million birds (and lots of mice, too) each year. Millions of hungrier, feral (wild) cats add to this toll. There is a common-sense solution. Letting cats roam outside the house shortens their expected life span from 12.5 years to 2.5 years and increases their risk of rabies, distemper, toxoplasmosis, and parasites. Evidence is mounting that cats help to spread diseases such as Asian bird flu. The message is clear: Keep pet cats inside for their own well being and for the future of backyard birds (http://www.abcbirds.org/cats/).

Collisions and Conservation

Collisions with man-made objects of all kinds in the aggregate are a significant source of bird mortality. Forty years ago, when cars were fewer,

vehicles killed a minimum of 57 million birds in the United States every year, assuming 15 bird deaths per road mile per year (Hodson and Snow 1965). There are no current estimates.

The U.S. Fish and Wildlife Service estimates that at least 4 million to 5 million birds fly fatally into communication towers each year. Collisions with plate-glass windows of homes and office buildings kill as many as 1 billion songbirds annually throughout the United States (Malakoff 2004). Systematic monitoring for one year registered 61 collisions at a house in Illinois and 47 collisions at a house in New York. Roughly half of the birds die of skull fractures and intracranial hemorrhaging. Collisions at single homes multiplied by the number of homes in suburban America projects to a truly huge annual loss of birds. We see only a fraction of these casualties because cats, raccoons, skunks, and opossums remove carcasses promptly.

Such sources of bird deaths are of great concern, but, with some notable exceptions, the essential challenges of bird conservation do not focus on them. Substantial annual mortality is a natural process, and populations compensate for losses of individual birds through increased (density-dependent) reproduction or survival (see Chapter 18). Among the worrisome exceptions are the accidental deaths of large, long-lived species, such as cranes, condors, and albatrosses, which can affect the future of their slow-reproducing populations. The losses of large numbers of albatrosses that drown after being hooked on the lines meant for fish, for example, are causing serious declines of these grand seabirds (see page 649).

More generally, healthy populations of birds typically produce surplus young. At least half of the total numbers of birds, swollen by the annual addition of young, die each year. That's half of the roughly 20 billion birds present at the end of the breeding season in North America alone. So each dead bird, although disturbing, is not a conservation problem.

Rather, population problems are conservation problems. Conservation problems arise when breeding productivity is reduced by the lack of food, loss of habitat, thinning of eggshells due to pesticides, or excessive mortality of adults, especially in long-lived species such as cranes and albatrosses. Of these effects on breeding productivity, habitat loss is by far the number one bird conservation challenge.

Habitat

Paramount among the threats that challenge wildlife everywhere is the rapid destruction of the natural habitats of the world. Examples include the replacement of virgin rain forest by pastures and coffee or banana plantations, the conversion of rich grasslands into agricultural monocultures or croplands, the draining of wetlands, and the consumption of diverse biological habitats by urban sprawl. Most birds require specialized habitats—old-growth forests, intact scrublands, and healthy wetlands (Figure 21–4). The complete loss and severe degradation of pristine habitats now affect the landscapes of all continents except Antarctica.

FIGURE 21–4 The Golden-cheeked Warbler nests only in the scrub oak–juniper forests of the Edwards Plateau of southern Oklahoma and central Texas. It is a strict habitat specialist that requires a particular mixture of junipers and oaks that is limited to only 10 percent of the vegetation in this area. One of its peculiarities is its dependence on mature, 50- to 80-year-old Ashe juniper trees, from which it peels the bark for its nests. Rapid suburban sprawl is replacing this essential habitat. [*Courtesy of H. Irby*]

The accelerating destruction of tropical rain forests has deservedly the highest profile as a global conservation problem because rain forests are the most diverse terrestrial ecosystems on the planet. They cover less than 7 percent of the Earth's landmass, but contain 66 percent of all species. Originally, rain forests covered about 12 percent of the Earth's landmass, but commercial logging, conversion into cattle pastures and into croplands for soy, banana, and coffee, and expanding civilizations reduced their extent by nearly half in recent decades (Figure 21–5). Half again of the remaining rain forests on Earth will be gone by the year 2022 if their destruction continues at the present rate (50 million acres annually). This loss extinguishes or dooms to extinction about 27,000 species each year, including many birds (Wilson 1992).

The challenges of habitat loss exist not only in distant tropical settings but throughout North America and Europe as well. Preceding the cutting of tropical rain forests by more than a century was our consumption of North American forests for fuel, lumber, and agriculture. The forests

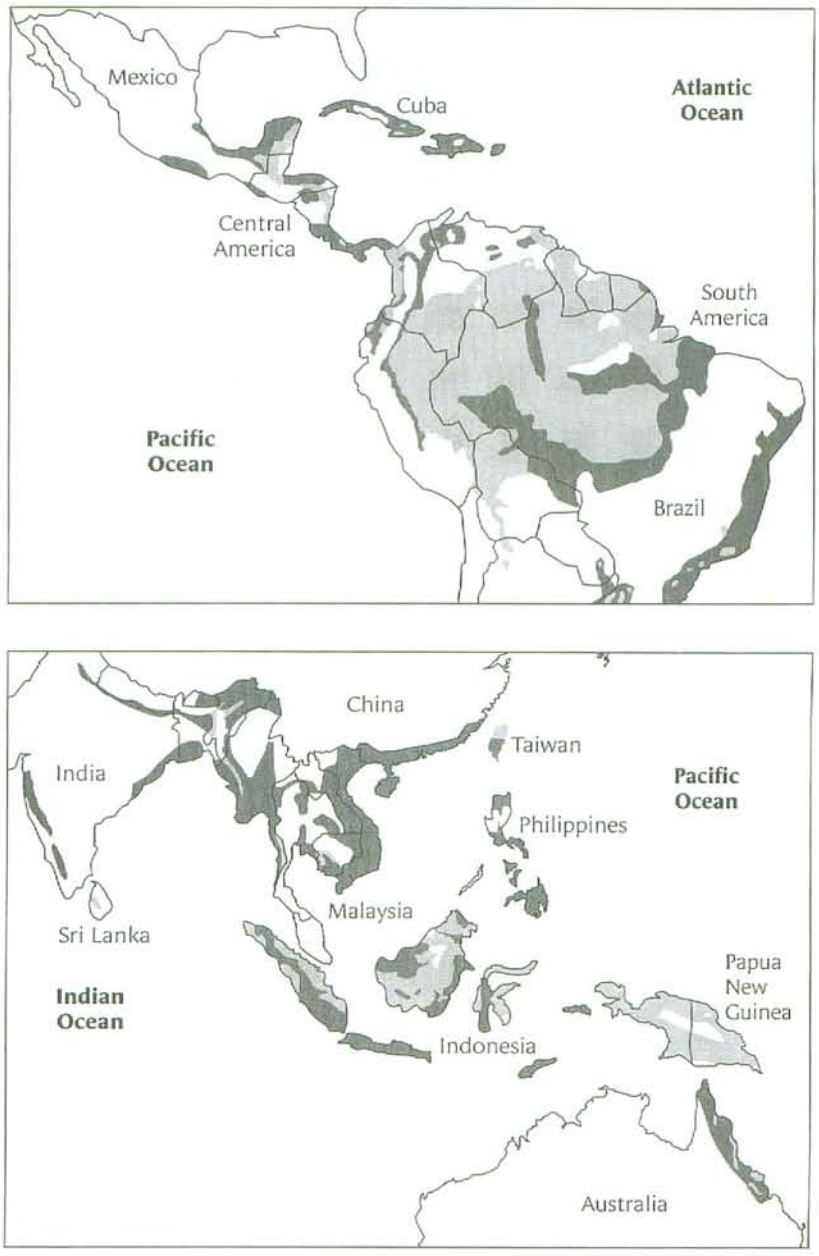


FIGURE 21–5 Tropical rain forest destruction in the New World Tropics and in Southeast Asia. Roughly half of the planet's rain forests have been destroyed *or* degraded in the past 50 years. Light gray areas identify the extent of tropical forests in the late 1980s. Dark gray areas identify forests destroyed or seriously degraded since 1940. [*After Philadelphia Inquirer/Kirk Montgomery, May 11, 1992*]

of the northeastern United States—east of the Finger Lakes in New York—were virtually cleared by 1800 (Foster and Aber 2004). The bottomland forests of the Southeast, home to the Ivory-billed Woodpecker, and the giant old-growth forests of the West Coast, home to the Spotted Owl, were next.

The good news is that birds, especially migratory species and dispersing young ones, quickly find and use newly restored habitat. The regrown forests of New England, for example, now support large populations of Broad-winged Hawks and Pileated Woodpeckers. Success stories of grass-

land restoration, beach protection, wetland management, and reforestation fuel the conviction that we can stabilize and rebuild many bird populations.

The Grasshopper Sparrow, for example, declined throughout the eastern United States. Yet fields on the eastern shore of Maryland converted from row crops into warm-season grasses attracted hundreds of them within two years (Figure 21–6), as well as Dickcissels and robust wild populations of Northern Bobwhites. More broadly, the Conservation Reserve Program (CRP) of the U.S. Department of Agriculture subsidized the switch from crops to native grasses on allowed acreages of farmlands

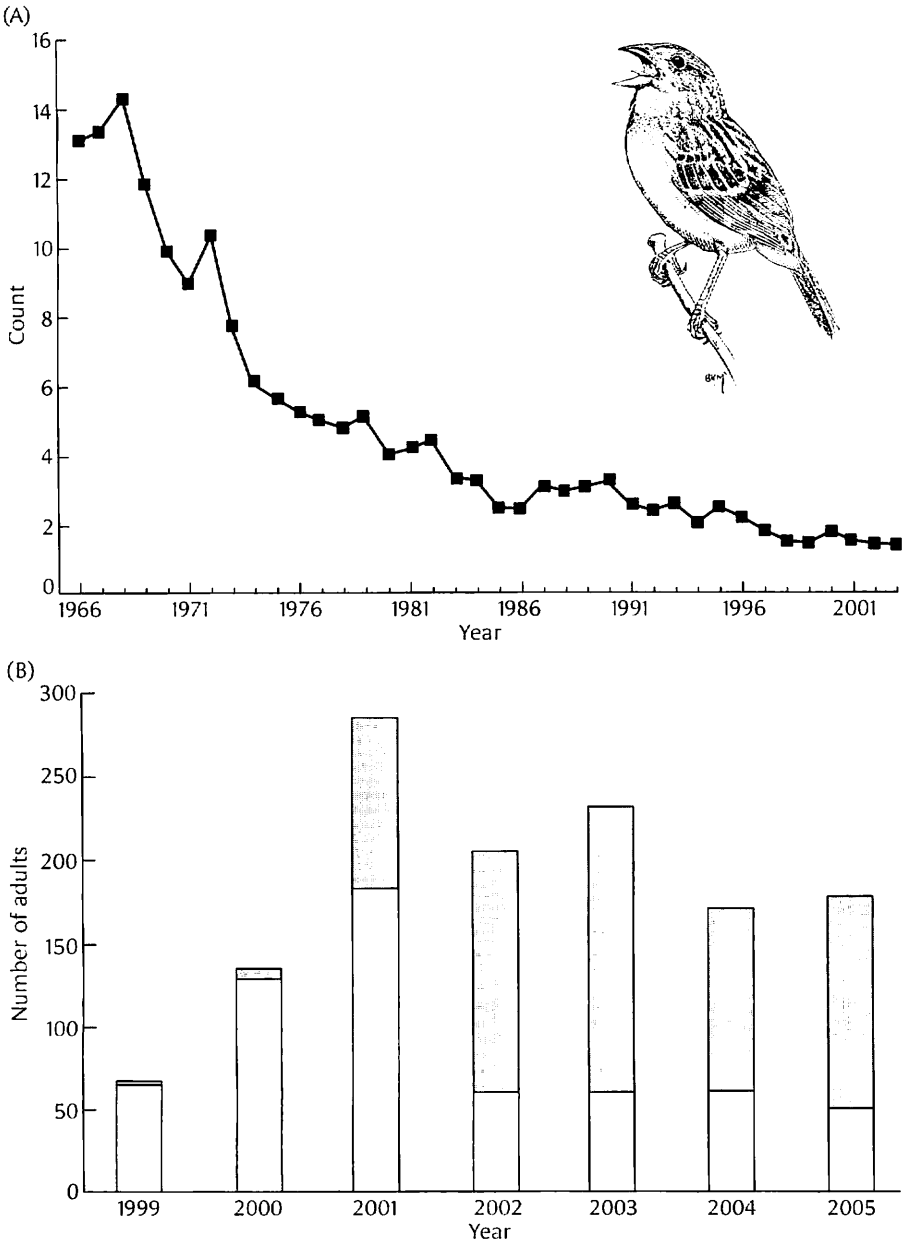


FIGURE 21–6 Grasshopper Sparrows find restored grasslands at Chino Farms in Maryland. (A) Breeding Bird Survey data document the decline of Grasshopper Sparrows in Maryland. (B) Numbers of adult Grasshopper Sparrows found breeding in a 250-acre restored grassland at Chino Farms near Chestertown, Maryland, starting two years after the conversion of row crops into grasslands. White parts of bars indicate new arrivals, and dark parts indicate banded birds returning from preceding year. [*(A) Sauer et al. 2005. (B) Courtesy of D. Gill*]

throughout the Midwest. Songbirds and game birds benefit together from the restoration or careful management of natural habitats. CRP grasslands foster robust populations of not only Common Pheasants and nesting ducks, but also grassland birds of many species: Eastern Meadowlarks and Western Meadowlarks, Bobolinks, and Vesper Sparrows. The management of eastern forests to provide areas of second growth and saplings favored by the Ruffed Grouse and American Woodcock also attract declining songbird species such as Golden-winged Warblers and Field Sparrows.

Emerging Challenges

Conservation threats will increase steadily in the years ahead with new and emerging challenges. Some challenges stem from the globalization of world health and economies. Others come from the growing perception of urban dwellers that the woods and fields are dangerous places to explore. Extreme climate events—heat waves, droughts, and extreme rainfall sessions—are increasing in frequency and intensity owing to global warming. These climate events foster local outbreaks of disease vectors such as mosquitoes and local amplifications of viruses, such as West Nile virus, which then spread rapidly throughout the world. Fast-spreading new diseases affect local populations of both common birds, such as American Crows and Great Horned Owls, and endangered birds, such as Sage Grouse and California Condors.

Wild birds tend to be victims rather than agents or primary vectors of disease. But there is historical precedence for new disease, as well as understandable public fear of it. The high-level concerns about Asian bird flu (H5N1), for example, include the role of migratory birds in its spread. Such concerns challenge the bird conservation community to be sensitive to the needs of both people and birds. In reality, high-density poultry farms and the globalization of human transportation systems are spreading the Asian bird flu, with migratory birds playing only a secondary, minor role (see Box 18–2, page 548).

Pollution comes in new and challenging forms. Certain chemicals disrupt the normal course of embryonic development, often without obvious manifestations until adulthood. This class of chemicals, called xenobiotics, includes fungicides, herbicides, and insecticides, plus assorted industrial chemicals, synthetic products including soy and pet-food products, and some metals including cadmium, lead, and mercury (Colborn and Clement 1992). The effects include, but are not limited to, thyroid dysfunction, compromised immune systems, decreased fertility, decreased hatching success, gross birth deformities, metabolic and behavioral abnormalities, and sex reversal.

Studies of Western Gulls breeding in California and Herring Gulls breeding on Lake Ontario and Lake Michigan showed some of the effects of these contaminants, including a high incidence of clutches with extra eggs, female–female pairings, and the feminization and high mortality of males (Gilbertson et al. 1991; Fox 1992). Gulls in these colonies also suffered from embryonic and chick mortality, edema, growth retardation and deformities, and altered nest-defense and incubation behavior.

All of these effects severely reduced reproductive success. Chemicals that impair birds in these ways can also affect human health.

World health officials have long worried about the possibility of new forms of drug pollution. A major episode surfaced on the Indian subcontinent, with birds—specifically, vultures—serving once again as leading indicators of environmental problems. Starting in 1997, three abundant species of vultures of the genus *Gyps* underwent severe, rapid, and widespread declines in India and neighboring Pakistan. Their populations crashed to just 3 to 5 percent of their starting numbers. The vultures were dying of renal failure and visceral gout, but thehe cause was mysterious. Disease was ruled out. Government concern escalated because the vultures were essential to public health. They reduced the risk of disease by cleaning up waste and carcasses on the landscape, aiding particular religious sects to whom cattle were sacred and could not be eaten or for whom cremation of their own dead was not allowed. Packs of wild dogs formed in the absence of vultures, adding new threats to local communities.

A veterinarian and his colleagues at the Peregrine Fund in Idaho and the Ornithological Society of Pakistan discovered the cause (Oaks et al. 2004). All three species of vultures were extremely sensitive to the anti-inflammatory drug diclofenac. Veterinarians in Pakistan and Indian used this drug with increasing frequency to relieve the suffering of dying sacred cattle. Diclofenac is a kind of ibuprofen (as in Advil) for pain relief. Vultures feeding on carcasses of recently treated cattle ingested the fatal drug as well. With little delay, an international team of scientists announced a solution on February 2, 2006, just two years after the diagnosis of diclofenac poisoning. An alternative drug named meloxicam that is safe for vultures can replace diplofenac. The transition to meloxicam as the veterinary choice of drugs for dying cattle is underway.

Social challenges also loom large for the future of our environment and healthy bird populations. Urbanized societies are increasingly disconnected from the outdoors and, hence, tend not to value nature as much as earlier rural generations. That disconnection leads to fear of the woods and of nature generally, called ecophobia. It also leads to a spiritual or psychological handicap, recognized formally as "nature deficit disorder" (Louv 2005). The challenge, therefore, is to help young children of diverse ethnic and social backgrounds to discover birds, to value nature, and to take ownership of these resources for their own good health.

Before progressing to ongoing and increasingly successful conservation initiatives, let's first consider the early effects of human expansions on bird populations. These human excesses provide an essential historical perspective.

Past Excesses

The plight of birds and other wildlife worldwide due to human activities is not just a recent circumstance. Rather, global expansions of human civilizations started to transform landscapes and ecosystems more than 50,000 years ago (Fitzpatrick 2004). The effects of humans on natural landscapes intensified and then escalated greatly starting about 10,000 years ago.

BOX 21–1

SYMBOL OF EXTINCTION: THE DODO

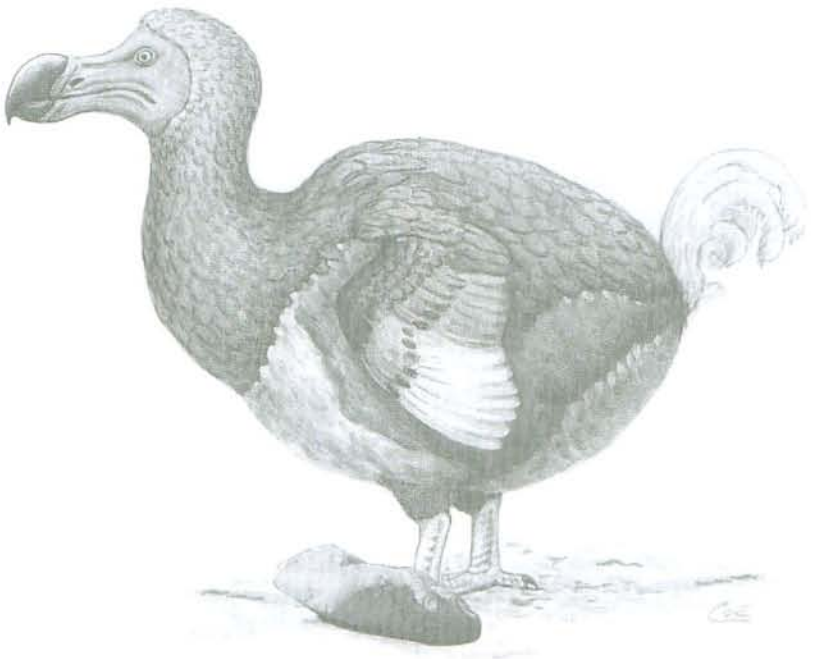
The legendary Dodo is a symbol for the process of extinction of vulnerable bird species by human beings. Not just a whimsical character in Lewis Carroll's *Alice in Wonderland*, the Dodo was a real bird that once lived on the remote tropical island of Mauritius, one of three Mascarene islands in the western Indian Ocean. The Dodo was a large, flightless, turkey-sized pigeon, assigned to the Family Raphidae. Cohabiting Mauritius with the Dodo was an amazing array of flightless pigeons, rails, parrots, waterfowl, and other birds. Almost all were exterminated in the seventeenth century (Hachisuka 1953).

The Dodo ate fruit, became extremely fat, and was easily captured (hence, the use of the name Dodo to indicate stupidity). It was prized as a readily available source of food. In the early 1600s, a few living Dodos were sent to Europe, where they captured public interest as a great curiosity. Few survived to the middle of the century, however.

The last eyewitness account of wild Dodos comes from the journal of Volquard Iversen, who was shipwrecked and stranded on Mauritius for 5 days in 1662 before being rescued (see Cheke 1987). He found no Dodos on the mainland but discovered some on a small islet accessible by foot at low tide, which he described:

> Amongst other birds were those which men in the Indies call doddaerssen; they were larger than geese but not able to fly. Instead of wings they had small flaps; but they could run very fast. [Cheke 1987, p. 38]

Perhaps the last Dodos learned to fear human hunters. But they did not run fast enough. Only fossils and a few preserved specimens remain as evidence of this odd species.



The Dodo.

Birds As Food

Bird flesh helped to fuel the global expansions of humans. Fossil records suggest that more than 9000 species of birds were lost to the first hungry waves of human civilization (Steadman 1995). That is roughly the same number of species as now prevail. By modern times, therefore, early human civilizations already had claimed half of the birds of the world that survived the last Ice Age.

Losses of island birds account for 90 percent of bird extinctions during historical times. Pioneering human colonists everywhere found abundant, tame, and edible birds, especially on oceanic islands. The extermination of the Dodo and other flightless birds on the Indian Ocean island of Mauritius in the late 1600s is a classic example of the loss of vulnerable island birds (Box 21–1). Dodos were slaughtered and salted to provision continued global exploration and colonization.

More recently, men had harvested the Great Auk of the North Atlantic to extinction by 1840. Valued as food to resupply ships that had crossed the Atlantic, these flightless birds were easy to catch and kill. One enterprising crew built a bridge of sail canvas from shore to ship and herded the helpless auks directly into the ship's cargo hold (Matthiessen 1959).

Dodos and Great Auks are the most famous birds lost to extinction in human history but not the only ones. The Maori peoples who colonized New Zealand consumed giant, flightless moas. Similarly, Indonesian peoples who colonized Madagascar 14,000 years ago downed the amazing elephant birds—3 meters tall with 9-liter eggs—plus a host of other species found only there.

These examples are only a few from the broad pattern of destruction of island avifaunas by early human colonists. Similar waves of extinctions of birds of all kinds followed the settlement of the Caribbean islands 3000 to 4500 years ago (Pregill and Olson 1981). Early camp garbage pits on islands throughout the South Pacific also contain the bones of species no longer there. The original civilization on Easter Island depended on the abundant birds, especially seabirds, as a primary source of food and on the forests for fuel. Their civilization collapsed when they exhausted the supplies of seabirds and wood (Diamond 2005).

In one way or another, humans destroyed most of the unique original avifaunas of the Hawaiian Islands. The early Polynesians leveled the lowland forests after landing there roughly 1500 years ago. Eliminated were at least 39 species of land birds, including 7 geese, 2 flightless ibises, 3 owls, 7 flightless rails, and 15 species of honeycreepers (James 1995). Captain James Cook then brought European civilization, mosquitoes, and diseases to the islands in the eighteenth century. Island birds lose resistance to mainland diseases, in addition to losing their fear of predators and their ability to fly. Consequently, bird pox and malaria destroyed the remaining lowland populations of the Hawaiian honeycreepers when mosquitoes that carried these diseases were accidentally introduced.

Species still extant in the South Pacific face new challenges. One dramatic and current challenge is the brown tree snake, an arboreal, prolific bird-eating snake that grows to as much as 8 feet in length. Native to the Solomon Islands, New Guinea, northern and eastern Australia, and eastern Indonesia, it was accidentally introduced on the island of Guam between 1947 and 1952. Native bird species became easy prey. The brown tree snake swiftly extirpated 9 of the 11 species of native forest-dwelling birds. Five of them were endemic species or subspecies. Two of these species, the Guam Rail and the Micronesian Kingfisher, are being bred in zoos in the hope that they can eventually be released back into the wild. Several other native species persist in precariously small numbers. Aggressive control efforts that employ specialized snake viruses are under way. For more information, see the Web site at http://nationalzoo.si.edu/Publications/ZooGoer/2000/1/curingguamsnake.cfm.

Returning to the main theme and closer to home, the wholesale consumption of wildlife was a national pastime in the new nation of the United States in the eighteenth century and, especially, in the nineteenth century (Matthiessen 1959). The earliest settlers of the United States lived off the abundant game, severely depleting local stocks of turkey and deer. Larks, bobolinks, robins, and many other songbirds also were fair game. Full-scale market gunning took its toll later in the mid-1800s. First, the great bison herds and other large mammals of the Great Plains were exterminated. Then, cannonlike punt guns mounted on low close-approaching "sinkboats" dropped flocks of waterfowl. Many of the market gunners in later years on the Texas Gulf Coast averaged taking 200 ducks each daily (Nighthawk Publications 2006). One man figured to have killed about 360,000 ducks in his 16 years of market gunning. By 1900, only 150 million ducks and geese survived in the United States, down from 500 million in 1700.

Populations of the most common birds number in the hundreds of millions or more, but such abundance did not prevent extinction. Legendary are the estimated 1 billion Passenger Pigeons that flew over colonial America. Advancing European colonists cut down the beech forests that provided abundant food for the pigeons. Aided in the late nineteenth century by telegraph communications about the locations of the flocks and by new railroads that enabled transport to major city markets, market hunters harvested and sold vast numbers of the pigeons for food. The seemingly unlimited flocks of Passenger Pigeons disappeared. The last wild Passenger Pigeon was killed in Ohio in 1900. The last captive birds died soon after.

Shorebirds fell, too, particularly the vast flocks of American Golden Plovers and Eskimo Curlews that migrated north in the spring through the Great Plains and then south in the fall from maritime Canada to South America. John James Audubon reported millions of American Golden Plovers near New Orleans in the early nineteenth century and compared curlew flights with those of the Passenger Pigeon. Occasionally, southbound plover and curlew flocks appeared on the New England coast.

> On August 29, 1863, both curlew and plover appeared on Nantucket in such numbers as to "almost darken the sun"; seven or eight thousand were destroyed before the island's supply of powder and shot gave out. [Matthiessen 1959, p. 162]

Excessive exploitation continues in modern times. The commercial fishing industry, for example, challenges not just fish populations but also the future of many seabirds, both indirectly and directly. The depletion of fish stocks—anchovy off the coasts of Peru and South Africa and in the North Sea—has caused major seabird colonies to decline. More directly, gill nets catch large numbers of diving seabirds as well as fish. In the North Pacific, an estimated 750,000 seabirds, including the threatened Marbled Murrelet, drown in gill nets each year.

The long-lived, slow-reproducing albatrosses of the world's oceans are particularly vulnerable to accidental mortality when they are caught on the hooks meant for large pelagic fish such as tuna. Albatrosses traditionally follow fishing ships for food and can't resist the baited hooks tossed out on miles of longlines. Mortality due to drowning when hooked on longlines is estimated to be roughly 100,000 albatrosses each year. Nineteen of the 21 species of albatross in the world are threatened with extinction largely because of longline fishing. Fortunately, there are practical solutions for the fishing industry to implement. Adding weights to the baited hooks to sink them before the surface feeding albatross can get them significantly reduces fatal bycatch rates.

Commercial harvesting of horseshoe crabs on the mid-Atlantic coast is another high-profile modern conservation problem. Red Knots and other shorebirds are the victims in this case. Thousands of horseshoe crabs emerge each spring from the depths of the inshore bay waters to lay their nutritious eggs in the beach sand. Those eggs are a primary fuel for shorebirds on the last stages of their northbound migration (see Chapter 10). Coasts of the Delaware Bay of New Jersey, Delaware, Maryland, and Virginia provide traditional stopover sites, where horseshoe crabs and shorebirds have converged each spring for thousands of years. Horseshoe crabs are also harvested locally for fertilizer and for bait. Intensive harvesting has caused the numbers of crabs emerging to decline each year. In parallel, the Atlantic population of the Red Knot has declined 80 percent in the past 10 years. Regulations that start to control the harvest rates are now in effect in most states.

Birds As Decorations

As the flocks of shorebirds and pigeons fell as sources of food in the late nineteenth century, another threat materialized—plume hunting for the millinery trade. The mounting of bird feathers, as well as whole birds, on ladies' hats became the height of fashion in the 1870s and 1880s. Entrepreneurs killed an estimated 5 million birds for this purpose alone.

At first, the breeding plumes of large wading birds—egrets, herons, and spoonbills—were prized, with devastating effect on their nesting

colonies. The millinery trade next turned to gulls and terns and then to a full array of species from brightly colored songbirds to crows. Drawing rave reviews was an entire crow—beak, feet, and all—seen on a hat in New York City in 1886. Frank M. Chapman, distinguished ornithologist at the American Museum of Natural History and an early officer of the budding Audubon Society, amused himself by identifying the species on hats as he strolled through New York City. In one census, 542 of 700 hats sported mounted birds of at least 20 species, including a Ruffed Grouse and a Green Heron (Matthiessen 1959, p. 168).

Few people are aware of the dimensions of the modern caged-bird industry and its effect on the populations of certain wild birds. Millions of birds are harvested from the wild as decorative pets. The exotic pet-bird trade is a multi-million-dollar industry, much of it illegal. From 2 million to 5 million birds move annually from tropical habitats to the living rooms of developed countries. The United States, currently the largest importer of exotic birds, legally imported nearly 1 million birds annually throughout the 1980s. Forty-three percent were parrots, and the remainder represented various other birds of the world—no fewer than 77 different taxonomic families. Parrots command especially high prices. At the top of the price list are rare macaws, such as the Hyacinth Macaws. A pair sells for $5,000 to $30,000.

Millions of other cage birds are harvested from wild populations. Because the exotic cage-bird trade is growing rapidly, it increasingly threatens some wild bird populations and even some species. Controlling the international pet trade is the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In response to a list compiled by this organization, Congress passed the Wild Bird Conservation Act of 1992 in an effort to eliminate the importation of endangered wild bird species. By 1994, imports of cage birds dropped to 80,000 birds annually. Also on the positive side of the issue, captive breeding stocks increasingly satisfy the appetites of the pet market.

Hope

There is hope, despite the catastrophic losses of species, the ongoing declines, and the continuing excesses. We have the knowledge and ability to stabilize threatened bird populations and even to reverse their declines. The legacy of recent and past successes testifies to our ability to succeed, if we have the will. Birds are amazingly resilient and will rebound if given just half a chance. Vigilance and regular monitoring of bird populations are among the keys to their future health.

Major conservation initiatives responded to the harvesting of birds for food and decoration. Formal protections were instituted. Federal and state governments now place populations of birds and other wildlife on lists for special protection when they decline to small and vulnerable sizes. Conservation biologists assign bird species in trouble to one of two official categories—Endangered or Threatened—as defined in the United

BOX 21–2

SAVING THE WHOOPING CRANE

Cooperation between the governments of the United States and Canada has restored hope for the future of the stately black-and-white Whooping Crane, an endangered species that inspired international concern and constructive action. The population of Whooping Cranes, which once nested widely in the upper midwestern states and prairie provinces during the nineteenth century, declined to a low of only 18 birds (in 1939) that wintered at Aransas National Wildlife Refuge on the Texas coast (U.S. Fish and Wildlife Service 1986; McMillen 1988). In addition, three nonmigratory cranes lived year-round in southwestern Louisiana, but they had not bred since 1939, when the conservation efforts began.

International concern about this endangered species impelled the governments of the United States and Canada to work together to prevent the extinction of the Whooping Crane. This accomplishment overcame many setbacks—accidental deaths, fatal diseases in captive flocks, the consequences of imprinting on foster-parent Sandhill Cranes, and the need to teach young birds how to migrate to Florida (see Chapter 10).

As of May 2006, the main Wood Buffalo–Aransas (Texas) flock was up to 189 adults and 25 young. At least 72 pairs are expected to breed. The total population of Whooping Cranes increased slowly at first but dramatically to roughly 336 birds in four free-living populations, plus an additional 134 in captivity (Whooping Crane Eastern Partnership, http://www.bringbackthecranes.org/).

States by the Endangered Species Act of 1973, as amended in 1978 and 1982.

An endangered species is one that is in danger of extinction throughout all or a significant portion of its range. A threatened species is one that is likely to become an endangered species in the foreseeable future throughout all or a significant portion of its range. A third category—Species of Special Concern—carries lower legal protection, but accords proactive management status to species that are in local or regional decline.

Being classified as endangered invokes broad new powers and resources for the care of threatened birds such as the Whooping Crane. Its rescue required the protection of threatened habitats and well-coordinated rescue efforts (Box 21–2).

Rediscovery

Even more encouraging are the rediscoveries of species thought to be extinct (Table 21–1). Among them, the Ivory-billed Woodpecker has by far the highest profile. Last seen for sure in 1944 in the Singer tract of Louisiana, the majestic Ivory-billed Woodpecker, or Lord God Bird, is the signature species of the old-growth bottomland forests of the southeastern United States (Figure 21–7). One of the largest woodpeckers in the world, the Ivory-bill first was hunted by Native Americans and then was collected as a desirable rarity by early ornithologists. Critical

TABLE 21–1 Some rediscovered bird species thought to be extinct for at least 50 years

Species	Location	Year Rediscovered
White-winged Guan	Peru	1977
Gurney's Pitta	Thailand	1986
Jerdon's Courser	India	1986
Madagascar Serpent Eagle	Madagascar	1988
Night Parrot	Australia	1990
Sao Tome Grosbeak	Gulf of Guinea	1991
Cebu Flowerpecker	Philippines	1992
Edwards's Pheasant	Vietnam	1996
Congo Bay Owl	DR Congo	1996
Kinglet Calyptera	Brazil	1996
Forest Owlet	India	1997
Cherry-throated Tanager	Brazil	1998
Chinese Crested Tern	China Sea	2000
Kalinowski's Tinamou	Peru	2000
White-masked Antbird	Peru	2001
Long-legged Thicketbird	Fiji	2003
Ivory-billed Woodpecker	United States	2004?

bottomland forests were cut. Despite regular reports of sightings of Ivory-billed Woodpeckers, in the absence of any confirming photograph, Ivory-bills became as legendary and as elusive as Elvis himself.

Then, a report by a kayaker in southeastern Arkansas on February 11, 2004, followed by 4 seconds of video, sparked fevered excitement, renewed hope, and led to a public media blitz in April 2005 (Fitzpatrick et al. 2005). Field teams searched the bottomlands. Additional land was secured to protect the ecosystem. Local entrepreneurs and townships profited from the rush of ecotourism. But the woodpecker disappeared, prompting professional debates and doubts (Sibley et al. 2006; Fitzpatrick et al. 2006; Jackson 2006).This spike of rediscovery, however, revitalized the hopes of conservationists everywhere. Other lost species also might survive if such a large and dramatic species as this one could persist undetected for 60 years.

Restoration

Viable bird populations can be restored from remnant individual birds on the brink of extinction. Among the modern highlights are the remarkable comebacks of some signature species: Bald Eagles, Brown Pelicans, Sandhill Cranes, and colony-nesting herons, egrets, and ibises decimated 100 years ago by the plume hunters. Some, such as the Whooping Crane, are large, long-lived species that multiply slowly. Protection combined with deliberate restoration programs rebuilt their populations.

FIGURE 21–7 Ivory-billed Woodpecker, the signature species of the bottomland forests of the southeastern United States. Apparently extinct and not seen for more than 60 years, it was sighted in Arkansas in 2004, raising hopes for the survival of this species and for other endangered species. [*Courtesy of National Audubon Society*]

Most small populations have an intrinsic potential to rebound from severe reductions. One legendary case is that of the Short-tailed Albatross (see Box 18–1. page 534).

The return of the Wood Duck was one of the early conservation triumphs in North America (Figure 21–8). Uncontrolled hunting and the destruction of the bottomland forests that also supported the Ivory-billed Woodpecker had almost eliminated this abundant species by 1900. In 1918, the U.S. government closed the hunting season. The Wood Duck population rebounded vigorously by the 1930s. Nest boxes supplemented natural production in tree holes and allowed the reopening in 1941 of carefully controlled hunting with limited daily bag limits in 14 states. Wood Ducks are now common throughout their original range with a

FIGURE 21–8 Male Wood Duck in breeding plumage. Wood Ducks made a comeback in the twentieth century after overhunting and habitat destruction led to their decline. [*Courtesy of Garry Kessler*]

total population size of more than 2 million. In addition, Wood Ducks are expanding widely into new parts of the continent. Annual harvests of Wood Ducks are now second only to those of Mallards.

The DDT story offers further testimony to our ability to remove threats and rescue declining bird populations. Human poisoning of the environment has had a devastating effect on the fecundity of some birds, directly endangering them (see Chapters 14 and 18). DDT affects all animals, including human children, with symptoms ranging from growth deformities to neurological damage. After the effects of DDT were recognized, its use was widely banned, with dramatic positive results.

Given a chance by the banning of DDT and related pesticides, supplemented by captive breeding and reintroduction programs, Bald Eagles and Ospreys recovered strongly. Bald Eagle populations now nest in growing numbers throughout most of the continent (except Arizona). Also a signature of success, Peregrine Falcons now nest on almost every traditional cliff in the northeastern United States as well as on every suitable bridge that crosses major rivers such as the Hudson, the St. Lawrence, and the Mississippi. Less well known is the return of the Aplomado Falcons, among the fanciest of all falcons. Extirpated from southern Texas, New Mexico, and Arizona, Aplomado Falcons are back nesting on the South Texas Coast and in southwestern New Mexico, thanks to a major reintroduction program.

Rescue of the Peregrine Falcon

Restoration programs have the goal of reestablishing self-sustaining natural populations of a species. The successful effort to restore the Peregrine Falcon to eastern North America engaged the public as well as the professionals (Figure 21–9).

Peregrine populations in North America, particularly in the eastern United States and Canada, virtually disappeared in the 1950s and 1960s,

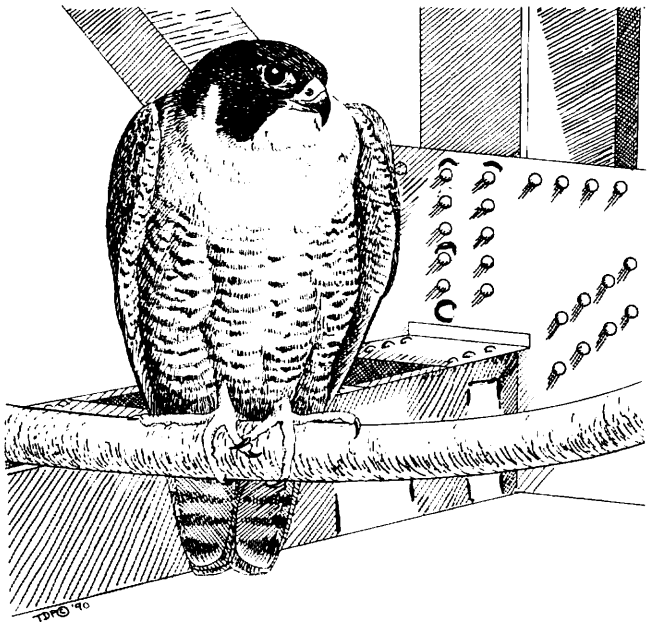


FIGURE 21–9 Peregrine Falcon, a raptor whose extinct populations have been replaced by local restoration programs releasing captive-raised young birds. [*Courtesy of T. Pedersen*]

primarily as a result of reproductive failure due to DDT pesticide poisoning. The ban on DDT for most uses in the United States removed the immediate problem and set the stage for a bold conservation initiative. The goal was to rebuild a free-living population of eastern Peregrines by raising young falcons in captivity and then releasing them into the wild in a procedure called hacking. Private falconers joined the program led by Thomas Cade, then at the Cornell Laboratory of Ornithology, to help breed the large numbers of young birds necessary for the success of the hacking effort.

To reestablish a self-sustaining breeding population in midwestern North America, one group of volunteer conservationists led by Bud Tordoff and Pat Redig of the University of Minnesota worked with local business communities of the major cities. Peregrines were hacked from boxes on the window ledges of the cities' finest office buildings and then returned to nest themselves on these ledges. In all, the communities hacked 1249 young falcons and fledged 3178 wild young from 1140 successful pairs between 1982 and 2005. This effort produced 169 territorial pairs that fledged 421 young themselves in 2005. Fecundity of the new midwestern Peregrines now averages the same as in healthy, wild Peregrine populations: 1.5 fledged young per pair annually. From a genetic standpoint, the rebuilt population also is healthy. Minnesota Peregrines are mixing with populations to the west, north, and east, fostering increased genetic variability.

The cost of such restoration programs is significant, but it stays modest because of the volunteer contributions. In the entire Midwest, hacking

1265 young falcons at $2500 each cost $3,162,500. In the whole of North America, about 7000 peregrines were produced and hacked, for a total cost of $17,500,000. By comparison, one F-16, the least expensive of modern U.S. fighter planes, cost $28,000,000 in 2001. A spectacular bird that had been extirpated in much of its range was restored for less than the cost of a single fighter plane. For the full details of this success story and access to the database, visit the following Web site: http://www.midwestperegrine.umn.edu

Rescue of the California Condor

The California Condor, North America's largest vulture, is a relict of the past. Other condor species, many of them much larger, once prospered along with the continent's prehistoric large mammals. Today, only two species remain: the Andean Condor of South America and the California Condor of North America. The California Condor once roamed widely across the United States as far east as New York in search of carrion. Through the millennia, the large populations shrank to a single remnant population in southern California. Illegal shooting and lead poisoning from bullet fragments in deer carcasses were the main terminal causes.

The rescue of the California Condor illustrates some of the conflicts between using a species as a symbol for habitat preservation and saving a species for its own sake (Kiff 2000; Snyder and Schmitt 2002). The initial efforts to save the California Condor polarized two political factions. In one camp were those who considered the condors an untouchable symbol of the remaining wilderness expanses of southern California threatened by expanding populations of people. Protecting it would also protect the wilderness reserves. No protection in captivity should take place. At worst, they reasoned, the condor should be allowed a noble death that would conclude an era of Earth's history. In the other camp were those who believed that intervention was both warranted and essential to save the species, even if only as captives in zoos, because we ourselves brought the condors to their sorry state.

With the wrenching decision to capture the last free-living condor in 1987, the prospects for their return to the skies of southern California shifted to the release and successful rehabilitation of condors hatched and raised in captivity (see Box 16–4, page 495; Figure 21–10). The first six young condors were released back into the wild in January 1992. One of the first ones released died after drinking water contaminated with antifreeze, an unfortunate accident. Despite the setbacks, increasing numbers of condors now fly over the Grand Canyon from the nearby Vermillion Cliffs release site in Arizona and over Big Sur of central California.

The success of this high-profile initiative will depend not only on teaching naive young condors to forage and survive on their own but also on a new political challenge—the ability of conservation groups and government agencies to reduce the use of lead bullets in release areas. Soon after their release, young condors die of poisoning by lead fragments that they ingest from carcasses of deer and wild pigs shot by hunters. Lead is a poison that has been banned from our homes and office build-

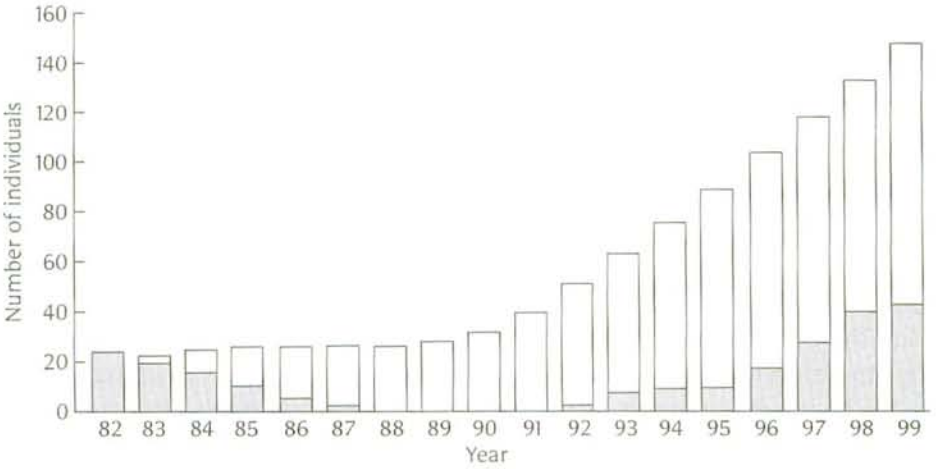


FIGURE 21–10 California Condor numbers in the wild (gray part of bar) and in captivity (white part of bar) from 1982 to 1999. [*After Kiff 2000*]

ings and from waterfowl marshes. It should also be banned from terrestrial landscapes.

Special Facilities

Other success stories correlate with the provision of special nesting facilities. Eastern Bluebirds responded to the network of well-designed nest boxes on the bluebird trails pioneered by Thomas Musselman of Quincy, Illinois, in 1926, now a nationwide network of trails maintained by members of the North American Bluebird Society (see the Web site http://www.nabluebirdsociety.org). Aided by regular cleaning and maintenance of the nest boxes in backyards, on farmlands, and in parks and refuges, Eastern Bluebirds are now widespread and common to the delight of all. Mountain Bluebirds and Western Bluebirds also respond to bluebird boxes erected in the western states.

Special nest platforms also aid water birds, such as the Great Northern Loon (Sutcliffe 1979; Piper et al. 2002), by reducing nest predation by raccoons and nest flooding due to rising lake levels. This initiative started on Squam Lake, New Hampshire, as a local conservation initiative of volunteer "Loon Rangers." It caught on. Summer-camp owners now proudly protect their loons as a feature of the vacation experience on northern lakes. Like the California Condor, however, loons now also must contend with lead poisoning (Box 21–3).

Island Conservation

Island-bound birds and nesting seabirds are particularly vulnerable to hogs and goats, cats and rats, and other such exotic mammals brought to once-safe islands by ships and sailors. Hogs and goats eat everything down to bare rock. Introduced predators, such as rats and cats, are directly responsible for the extirpation of many island populations of birds, land birds and seabirds alike. Rats, which infest most (80 percent) of the islands of

BOX 21–3

LOONS AND LEAD

Lead poisoning is a significant source of mortality of Great Northern Loons on the lakes where they nest in the northern United States and Canada. Lead poisoning causes from 25 to 50 percent of documented cases of death on some lakes. Lost lead fishing tackle—jigs and sinkers—is responsible for this mortality.

How does fishing tackle poison birds? Loons ingest small pebbles as "grit" to help digest fish bones in their gizzards. They pick up lead fishing tackle by mistake, sometimes large sinkers and jigs. More than 20 other species of water birds accidentally ingest lead fishing tackle while feeding.

Under way are many educational and political campaigns to reduce the use of lead fishing tackle. New York State passed legislation banning the sale of small lead sinkers weighing less than 0.5 ounce, starting on May 8, 2004. Some New England states (New Hampshire, Maine, and Vermont) also have legislation regulating the use or sale of lead fishing tackle. They also promote educational programs for anglers about nontoxic alternatives. More broadly, the use of lead sinkers has been banned in national parks and wildlife refuges across the United States.

For more information, visit the Web site http://www.adkscience.org/loons/lead.htm.

the world, participated in roughly half of the historical extinctions of island birds (and reptiles). One pregnant cat imported in the 1950s onto Kerguelen Island in the southern Indian Ocean multiplied into 3500 cats in 30 years. They killed 1.2 million seabirds each year (Krajick 2005).

Professional staff of New Zealand's Department of Conservation are the world leaders in the conservation of endangered island bird species, especially their own shattered avifauna. Aggressive eradication through hunting, trapping, and poisoning exotic species that ruin New Zealand's fragile ecosystems is one of their trademarks. Other organizations, government and private, are following suit and adopting similar techniques to remove, for example, every one of the thousands of goats that are destroying the natural vegetation on the Galápagos island of Isabela. In another effort, the U.S. Fish and Wildlife Service eradicated Arctic foxes introduced onto the Aleutian Islands for their fur industry. The results of these efforts have been spectacular. Fork-tailed Storm Petrels, eiders, and native geese increase as much as fivefold within 10 years after the foxes are gone.

A similarly aggressive and model program is under way to eradicate invasive mammals from the hundreds of islands in the Sea of Cortez and off the coast of Baja California in northwest Mexico (Tershy et al. 2002; and Figure 21–11). The array of more than 250 islands supports diverse plants and animals, including 180 endemic terrestrial vertebrates and 50 kinds of seabirds. Invasive alien mammals—rats, cats, goats, rabbits, and so on—are present on at least 44 islands. They are responsible for the disappearance of 22 endemic vertebrate taxa (species and subspecies) and the local extinction of seabirds from 10 islands.

A consortium of organizations supported by Island Conservation, a small nonprofit organization in California, developed a master collaborative plan that ranked islands by their level of threat and prospects of recovery. They then deployed teams of hunters, trappers, and Jack Russell

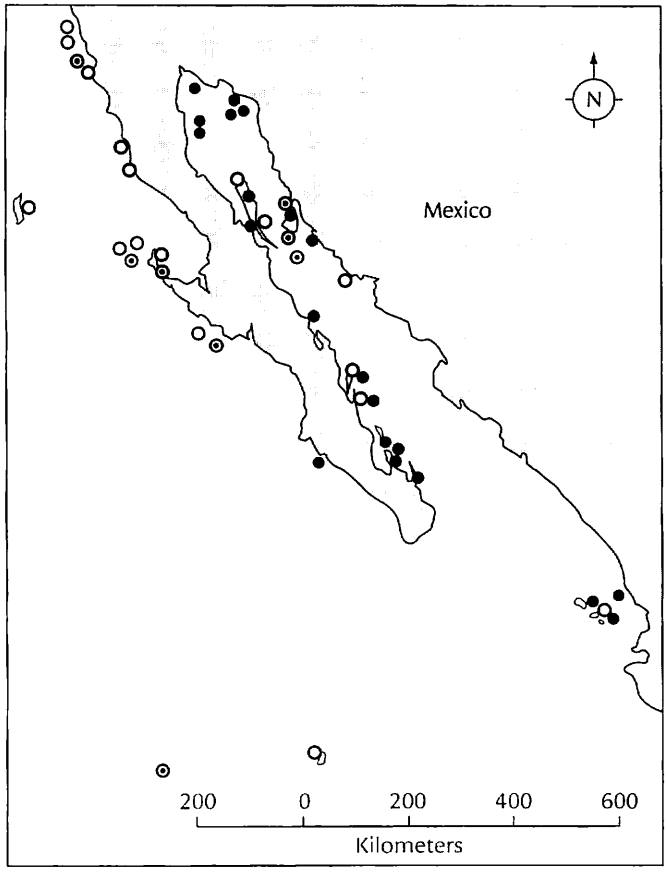


FIGURE 21–11 Islands off northwest Mexico with invasive mammals in 1994. White circles indicate islands that suffered local extinctions of seabird species. White circles with a black dot indicate islands that lost endemic vertebrates. Black circles indicate islands that have not lost species. [*From Tershy et al. 2002*]

terriers to systematically eradicate one or more invasive mammals from 23 small islands. As a result, 27 seabird taxa, such as the Black-vented Shearwaters on Natividad Island, and 38 endemic terrestrial vertebrates are protected and on the rebound. Lessons learned from these initial experiments enable even more ambitious eradication efforts on large islands.

Many colonial seabirds that nest on islands require social stimulation to breed. They respond well to decoys and vocal broadcasts of their own species' calls (Jeffries and Brunton 2001; Ward and Schlossberg 2004). Audubon's Steve Kress (1997) pioneered the use of social attraction to bring Atlantic Puffins back to the coast of Maine. Harvesting of their eggs and young had extirpated these colonies by the 1880s. Now, Atlantic Puffins are back as nesting species on the islands in the Gulf of Maine (http://www.audubon.org/bird/puffin/what.html).

How were they brought back? Steve Kress lured them back. It took decades of dedicated effort. The formula required transplanting nestlings from Great Island, Newfoundland, and hand rearing them in specially constructed burrows. Between 1973 and 1986, they successfully fledged

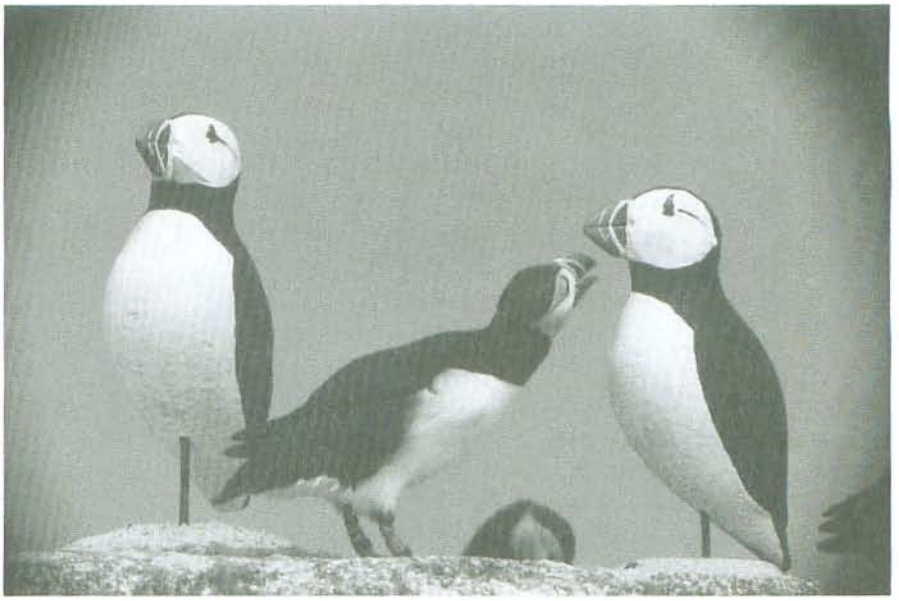


FIGURE 21–12 Decoys (*at left and right*) were the key to attracting sociable Atlantic Puffins back to deserted islands in the Gulf of Maine. [*Courtesy of Stephen W. Kress*]

914 of 954 puffin chicks transplanted to Eastern Egg Rock. Fledged young puffins then wait from two to three years to return to their home island to nest. But they prefer not to be the first of their kin to settle down on an empty island. Prospecting young puffins flew by but did not stop and stay.

Success followed the discovery that social cues were essential. Placing decoy puffins on prominent rocks on the island and playing back recorded puffin calls made the difference (Figure 21–12). Young puffins stopped to consort with and sometimes court the decoys, building up to a critical mass of real puffins that now thrive in robust colonies on many of the islands. Summer communities on the shores of the Gulf of Maine are proud to have their puffins back, and they cater to growing numbers of tourists eager to see them.

Conservation by Design

Conservation biology is a burgeoning scientific discipline that sets priorities and then integrates specific objectives into large-scale plans of ecosystem management. These plans address both the integrity of healthy ecosystems and the broad spectrum of plants and animals that will benefit from scientifically smart management. Birds are often the signature species of projects that foster biodiversity as a whole.

With commitments for the protection and restoration of habitat come the significant challenges of designing effective networks of conservation reserves. The basic guidelines for reserve networks in fragmented landscapes are now well established (Figure 21–13). For purposes of bird

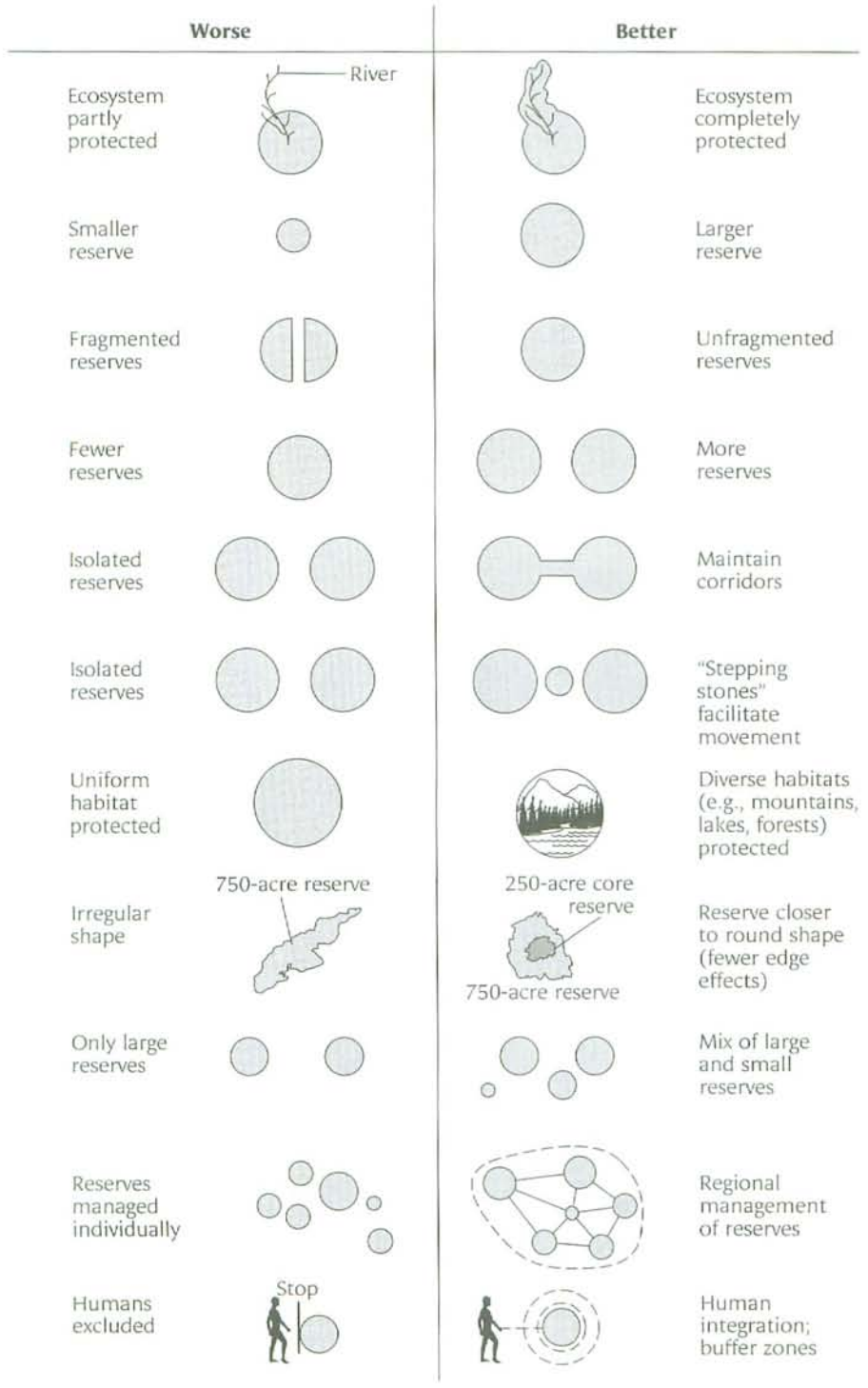


FIGURE 21–13 Guidelines for designing networks of nature reserves. Attention to their size, shape, and arrangement on the landscape increases their conservation effectiveness. [*After Fitzpatrick 2004; Shafer 1997*]

conservation, the geometry and scale of the design must take into consideration the substantial movements of birds and meet their seasonal requirements. Corridors are an essential part of that geometry to facilitate dispersal among reserves so as to maintain genetic variability and to reduce the probability of extinction due to the small-island effect.

Looking ahead, we see that global warming challenges the past designs and locations of reserves. Coastal reserves on the Norfolk coasts of Britain, for example, will be under the North Sea in this century owing to rising sea levels and the continued downward tilting of the land itself, causing a net loss of freshwater and brackish habitat of about 4000 hectares (Lee 2001). In response, the Royal Society of Bird Preservation is building new marshland preserves inland to restore declining populations of threatened marsh species such as the Eurasian Bittern. The projected costs of freshwater and brackish habitat replacement will be roughly £50 million to £60 million.

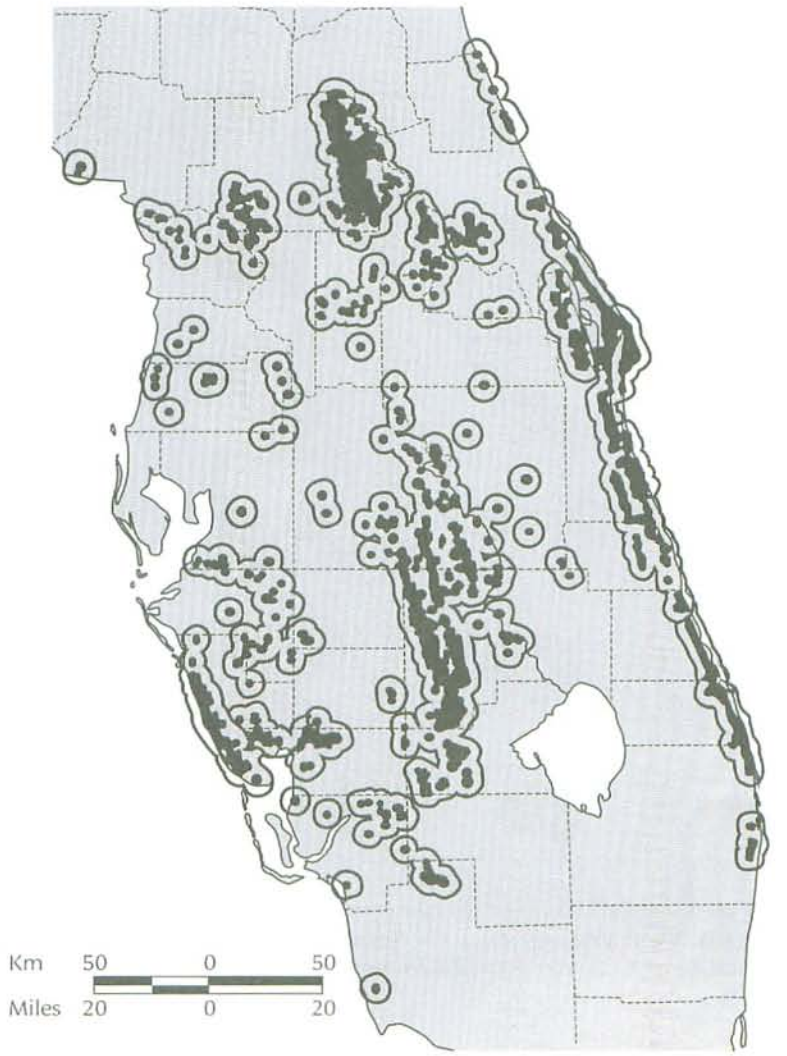


FIGURE 21–14
Metapopulation map of Florida Scrub Jays. Each black dot indicates one or more family groups of this cooperatively breeding species. Solid outlines group sets of territories into 42 separate metapopulations within which dispersal offsets local extinctions. [*After Fitzpatrick 2004, Courtesy of Island Press/Metapopulations and Wildlife Conservation (1996), D. R. McCullough, Ed.*]

Population Viability

Populations of plants and animals typically comprise numerous local populations distributed across the landscape in patches, or fragments, of preferred habitat. Dispersal and gene flow between the local populations unites them into so-called metapopulations (Figure 21–14). Small, local "sink" populations prone to extinction disappear temporarily and then reappear when new colonists arrive from nearby or larger source populations.

Metapopulation structures are an intrinsic property of the Biological Species Concept (see Chapter 19). Understanding them is central also to conservation plans that ensure the viability of populations that occupy fragmented habitats. Two elements are most important: (1) the probability of the extinction of populations of different sizes and (2) maintaining adequate genetic diversity.

Population viability analysis (PVA) is now a standard tool of conservation planning. PVA computer models incorporate life-table statistics (age-specific birth rates and death rates; see page 506) of the species under study to simulate rates of growth or decline of populations of different sizes through time. The simulated population trend leads to extinction in some runs but not others. These results define their probability of extinction. For the well-studied, cooperatively breeding Florida Scrub Jay, only populations with 40 to 100 territories are likely to persist as long as 400 years (Figure 21–15). These analyses can be executed for single

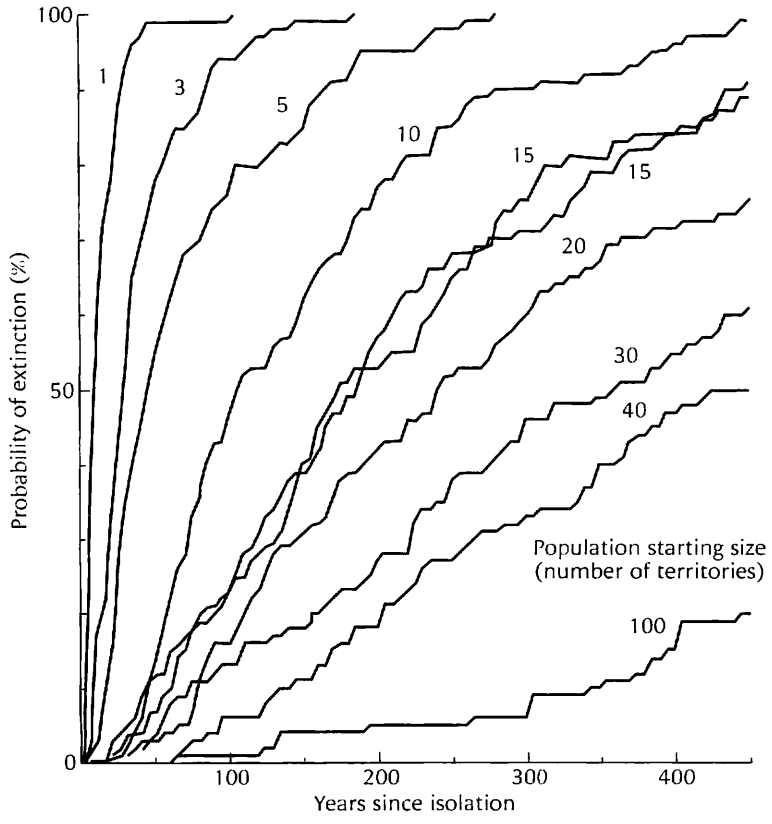


FIGURE 21–15 Population viability model for the Florida Scrub Jay. Computer simulations, based on the analysis of life-table parameters, show that the probability of short-term extinction of an isolated set of territories decreases with the size of the starting population (see numbers). Populations with only a single family group territory are likely to disappear within 50 years, but populations with 100 territories will last for hundreds of years. [*From Fitzpatrick et al. 1991*]

populations or, with more assumptions about dispersal, for multiple local populations that represent a metapopulation.

Recovery plans for endangered species incorporate estimates of population size that ensure their long-term viability. The recovery plan for the Black-capped Vireo, which lives in the troubled oak–juniper habitats of Texas, Oklahoma, and Mexico, has the goal of downlisting this species from Endangered to Threatened status by the year 2020 (U.S. Fish and Wildlife Service 1991). Four criteria must be fulfilled before downlisting it from Endangered to Threatened status: (1) all existing populations must be protected and maintained; (2) a minimum of six viable breeding populations of 500 to 1000 pairs must exist in Texas, Oklahoma, and Mexico; (3) sufficient winter habitat must exist to support the priority breeding populations; and (4) the designated breeding populations must be maintained for at least five consecutive years with evidence of continued viability.

Small fragmented, or remnant, populations lose genetic diversity owing to chance and to increased inbreeding. The loss of genetic diversity affects survival and fertility and, hence, the ability of a population in trouble to recover. If natural dispersal does not offset local losses of genetic diversity, conservation biologists can offset these losses themselves by adding birds imported from other populations.

The conservation of the Greater Prairie Chicken in the midwestern United States provides an example of this process. The current distribution of the Greater Prairie Chicken is only a small fraction of its original range throughout the central and much of the eastern United States. In the early nineteenth century, native prairie covered most of Illinois. By

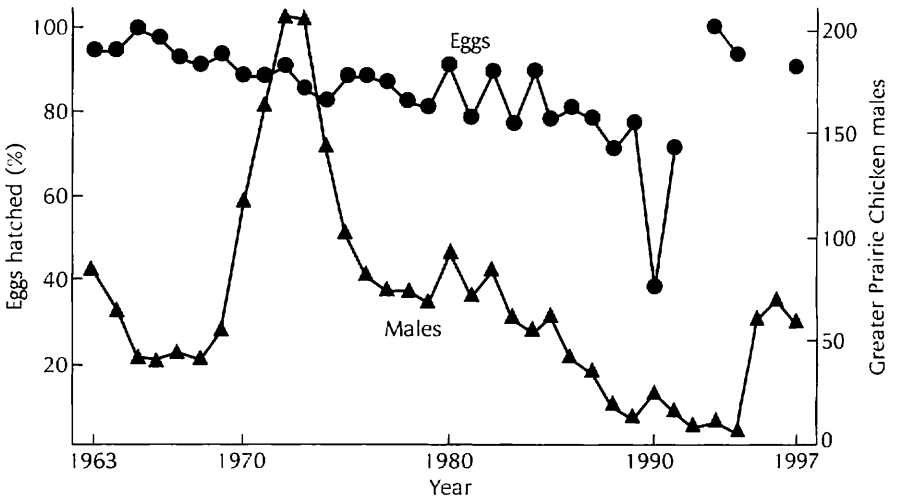


FIGURE 21–16 Population trends and fertility in a remnant population of Greater Prairie Chickens in southeastern Illinois. Counts of males on the lek (*bottom line*) declined steadily after a short-lived peak in 1972, until extra males were introduced from other larger populations. Genetic diversity and egg-hatching rates (*top line*) declined in this small shrinking population but then rebounded after birds from other populations were introduced in 1990. [*After Westemeier et al. 1998*]

1994, only a few small patches remained in the state. The same was true in Wisconsin. Greater Prairie Chickens and other grassland birds declined along with these prairies. The remnant population of prairie chickens in southeastern Illinois dropped from 2000 birds in 1962 to fewer than 50 by 1994 (Westemeier et al. 1998). Genetic diversity dropped significantly in both states.

Projections of continued loss of genetic variation suggest that, in 40 years, these prairie chicken populations would reach the reduced genetic diversity of the related Heath Hen 30 years before its extinction on Martha's Vineyard in 1932 (Johnson and Dunn 2006). In Illinois, egg fertility and hatchability declined significantly along with genetic diversity, a prelude to extinction (Figure 21–16). The good news is that conservation biologists were able to offset these handicaps and to increase egg viability in Illinois by importing prairie chickens from large and genetically diverse populations in other states.

Fragmentation and Corridors

Many human activities—cutting forests for timber, converting grasslands into croplands, and dividing shorelines for buildings—divide major blocks of quality habitat into remnant islands of habitat, or fragments (Figure 21–17). The small sizes and extensive edges of habitat fragments lead to increased predation, limited space, and invasion by exotic species. Reduced nest success and adult survival in fragments, compared with large intact blocks of habitats, are predictable results. Small fragments become unsustainable population sinks, with poor reproductive success and high mortality.

Unfragmented core areas of habitat, therefore, are an essential element of conservation planning. Forest fragmentation in North America, for example, promotes local reproductive failure due to increased nest predation

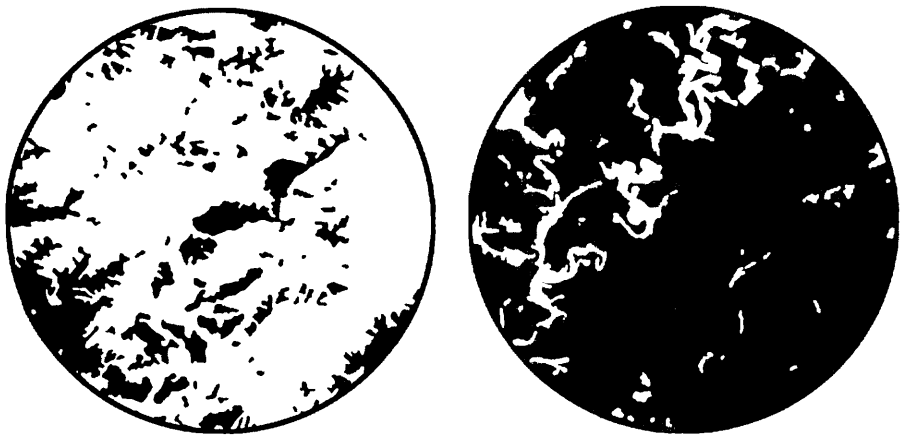


FIGURE 21–17 Forest fragmentation in Missouri. Computer maps of a nonforested landscape (*left*) and a forested landscape (*right*). Dark areas are forested. [*From Askins 1995*]

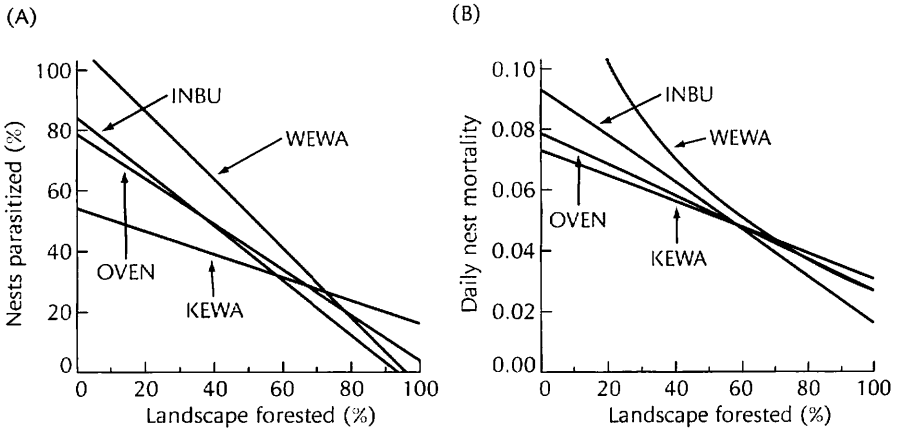


FIGURE 21–18 Forest cover improves nest success in the midwestern United States, but such cover is diminished in landscapes where forests are fragmented. (A) Correlations of the proportion of nests parasitized by Brown-headed Cowbirds and the percentage of forest cover. (B) Correlations of daily nest mortality and the percentage of forest cover. Abbreviations for species: INBU, Indigo Bunting; WEWA, Worm-eating Warbler; OVEN, Ovenbird; KEWA, Kentucky Warbler. [*After Robinson et al. 1995*]

and brood parasitism by Brown-headed Cowbirds. Scott Robinson and his colleagues (1995) documented the effects of fragmentation on the local rates of cowbird nest parasitism and daily nest mortality in the forested landscapes in the midwestern states of the United States (Figure 21–18). Migratory songbirds such as Ovenbirds, Kentucky Warblers, Worm-eating Warblers, Indigo Bunting, Scarlet Tanagers and Acadian Flycatchers were the focus of this study.

The highly fragmented landscapes of northern Missouri, southern Wisconsin, and Illinois are population sinks. Those populations cannot sustain themselves without the immigration of young birds from the extensive source forests of the Missouri Ozarks, northern Wisconsin, and south central Indiana, respectively. These costs are most severe within 100 to 200 meters of the forest edge (Figure 21–19). Most birds breeding in small fragments of habitat are affected. The interiors of large blocks, on the other hand, are relatively safe.

Scarlet Tanagers and the closely related Western Tanagers and Summer Tanagers are among the most attractive of North American bird species. All are sensitive to forest fragmentation (Rosenberg et al. 1999a). The Cornell Laboratory's continent-wide, citizen science initiative, Project Tanager, surveyed woodlots of different sizes for tanagers. The probability of finding a tanager dropped below 50 percent in highly fragmented landscapes. The sensitivity of Scarlet Tanagers to fragmentation, calculated in terms of the minimum area required to support them, was greatest in the highly fragmented forests of the Midwest. These studies enabled regionally specific recommendations for the management and restoration of forests that would attract tanagers, as well as other affiliated species of conservation concern, such as the Eastern Wood Pewee (Rosenberg et al. 1999b).

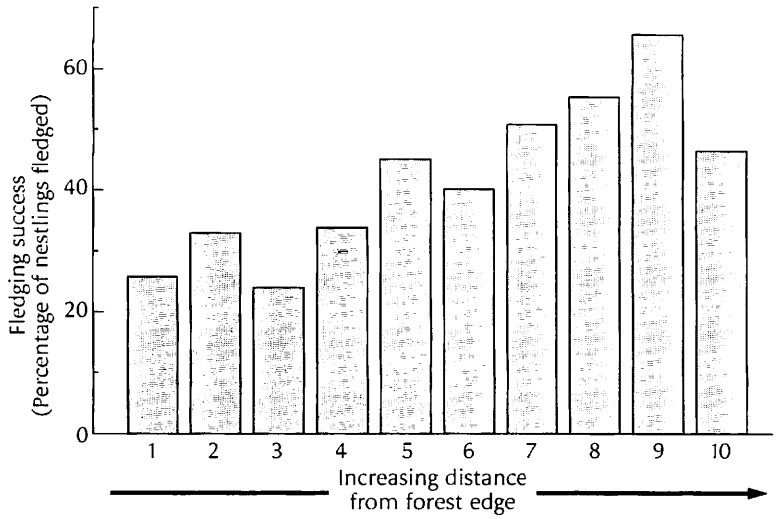


FIGURE 21–19 Songbird nesting success increases with distance (10 categories from 0 to 123 meters) from the forest edge, where nest predation and parasitism (by Brown-headed Cowbirds) is greatest. [*After Wilcove et al. 1986*]

Like islands in the ocean, islandlike fragments of habitat lose species at predictable rates owing to fluctuations in population size and the costs of edge effects. Small fragments lose species faster than large fragments. Several studies in Brazil illustrate this effect. In southern Brazil, for example, intact subtropical woodlands supported about 220 bird species (Willis 1980). Fragmentation of the woodlands for coffee plantations in the past century caused reductions of species. Now a large, isolated woodlot (1400 hectares) supports 202 species, a medium-sized woodlot (250 hectares) supports 146 species, and a small woodlot (21 hectares) supports only 93 species. The birds lost from the largest plots were mostly large species found in low densities, such as eagles, macaws, parrots, toucans, and tinamous. The birds most likely to disappear from the small woodlots were primarily large, canopy, fruit-eating birds and large, ground, insect-eating birds.

Thomas Lovejoy and his colleagues launched an ambitious landmark project in the Amazon rain forests near Manaus, Brazil. They started this long-term project in 1979 to document the specific effects of forest fragmentation on tropical biodiversity (Bierregaard et al. 1992). In an alliance with the government, farmers left blocks of forest of different sizes and configurations as they cleared the land. Teams of experts then monitored the changes that followed. The long-term minimum-critical-size (MCS) project demonstrated dramatic losses of species from tropical forest islands less than 10 hectares in size.

Especially vulnerable were specialized birds that follow army ants to catch flushed prey, because the ants themselves disappeared. Three species of obligate army ant followers disappeared immediately upon the isolation of small fragments. Also vulnerable were birds that participated

FIGURE 21–20 Resplendent Quetzal. Conservation reserves for the quetzal and other mobile species of the cloud forests of Central America must include different sites for different seasons and corridors that connect them.

regularly in mixed-species foraging flocks. Most of these species disappeared from all small rain-forest fragments in one to two years.

Local landscapes, the teams concluded, should include one or more forest tracts larger than 1000 hectares. Large source tracts would produce surplus birds to help populate smaller fragments. Corridors between isolated fragments of original habitat, however, are needed as an essential element of conservation planning. Corridors just 100 to 300 meters wide between blocks of forest helped to maintain species diversity in forest fragments as large as 100 hectares in area. Small forest fragments also require connections by corridors of rain forest to facilitate the dispersal of young birds among them.

Species of tropical mountain forests require corridors for seasonal altitudinal migration between separated living areas. One of the most dramatic of all tropical birds, the Resplendent Quetzal, a trogon of the cloud forests of Central America, is iridescent green and scarlet in color with lacy, 2-foot-long upper tail coverts (Figure 21–20). It feeds and breeds in mountain preserves, such as the popular 28,000-hectare Monteverde Cloud Forest Preserve in Costa Rica. But the quetzals also migrate downslope to find food during the nonbreeding seasons. By tracking the seasonal movements of quetzals wearing radio transmitters, George Powell and his colleagues (1995) discovered that the mountain slopes between 615 and 1540 meters altitude were critical corridors and nonbreeding residences for the quetzal. The preserve now provides a network of habitats required by the quetzal throughout the year.

Disturbance

Many habitats and their birds require regular ecological disturbances, especially by fires or floods, to maintain their vitality (Askins 2000; Brawn et al. 2001). Both the intensity and the frequency of local disturbance govern the character of habitats (Figure 21–21). In particular, the suppression of fires and floods is responsible for losses or declines of bird species, in addition to those lost on a broad scale to outright loss of habitat. On a landscape level, healthy ecosystems are those that include a mixture or mosaic of habitats in various stages of recovery from disturbance. Good stewardship of ecosystems, therefore, requires deliberate programs of burning and the flooding of floodplains.

Fire

Fire is an essential element in the ecological health of almost all habitats. It naturally affects the plant structure and species compositions of forests, grasslands, and scrublands and thereby what bird species will also be present. California's coastal chaparral, Yellowstone's scenic ponderosa pine forests, and Illinois's remnant prairies all require regular fires to sustain their special suites of species. Before the colonization of the United States by Europeans, regular fires started accidentally by lightning and deliberately by Native Americans swept unchecked across the landscape. One-half of the continental United States burned every 1 to 12 years (Brawn et al. 2001).

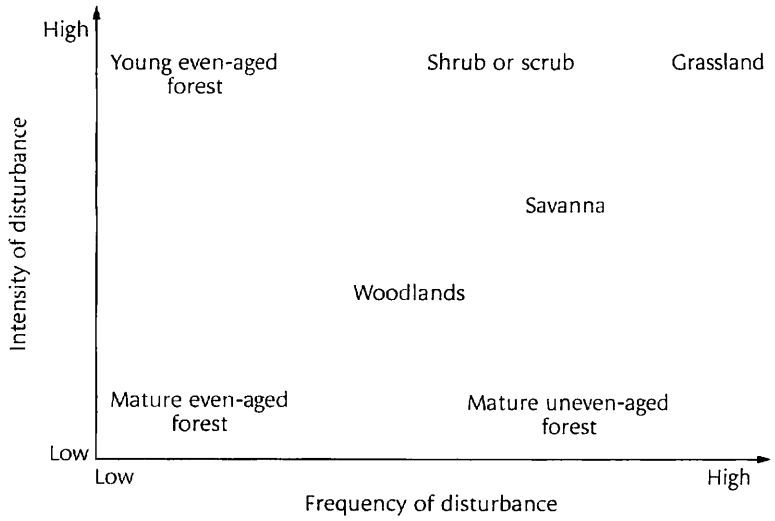


FIGURE 21–21 Intensity versus frequency of disturbance on selected terrestrial habitats. Fire, floods, severe winds, and forestry practices create even-aged forests by promoting growth of replacement saplings over large areas. Frequent fires of light to moderate intensity structure woodlands and savannas. Grazing and frequent, intense fires control the structure and species compositions of grasslands. [*From Brawn et al. 2001*]

Many bird species also are fire-dependent specialists. Among them, Black-backed Woodpeckers target the wood-boring beetles that flourish in scorched conifer trees from two to three years after fires in the boreal forests of Canada and Alaska. The endangered Kirtland's Warbler specializes in young jack pines that grow after fire releases seeds from mature pines in Michigan. Fire also controls critical long-leaf pine habitat for Red-cockaded Woodpeckers and Bachman's Sparrows of the southeastern United States.

Fire is an essential ingredient for the management of the birds in scrub and pine forests of the southeastern United States. Florida Scrub Jays, for example, are a fire-dependent species. They survive only in the remnant scrub habitats of the sandy ridges of central Florida, along with other endangered species. They depend on regular fires at 8- to 15-year intervals to refresh territories with optimal habitat.

Long-term studies at the Archbold Biological Station documented the effects of fire and fire suppression on the jay's use of habitat (Woolfenden and Fitzpatrick 1996; and Figure 21–22). Specifically, active fire suppression from 1980 to 1990 caused the number of territories on a 55-hectare (136-acre) study plot (18E) to decline from more than five to just one. Competition from Blue Jays and predation by hawks and snakes increase in the absence of fire. To improve the quality of the habitat, the station's staff burned the study plot in a carefully controlled "prescribed burn" in 1991. Scrub jays returned to the plot, reestablishing more than six territories by 1997. Repeating the cycle, they then started to decline, awaiting the next burn.

Grassland birds most of all respond to different regimes of prescribed burns to replace the lightning-sparked natural fires that once governed

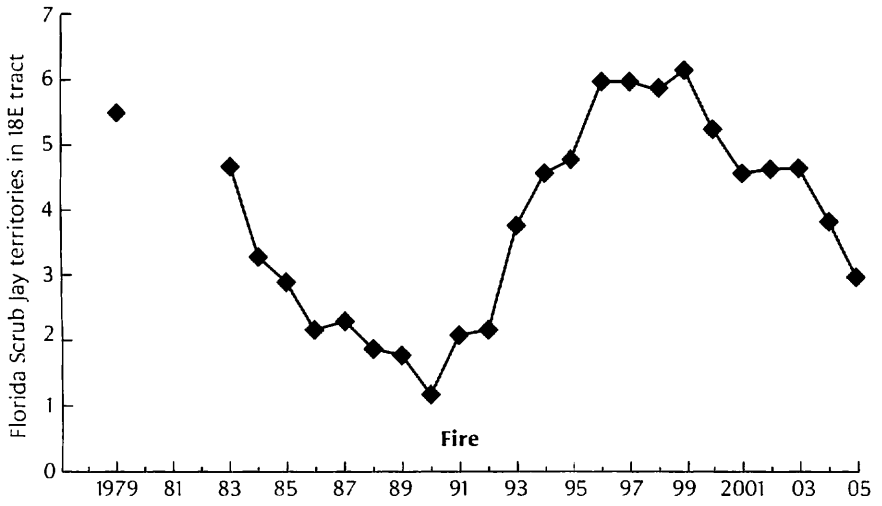


FIGURE 21–22 Beneficial effects of fire on habitat use by Florida Scrub Jays. The quality of the habitat and the number of territories that it supported declined from 1980 to 1991 as the scrub habitat grew in the absence of fire. A prescribed burn in 1991 promoted increased occupancy through 1997. Reversal of this occupancy trend points to the need for another fire. [*Courtesy of J. W. Fitzpatrick and G. E. Woolfenden*]

grassland ecology. Local populations of Henslow's Sparrows in the midwestern states, for example, prefer postburn grasslands two to four years of age (Herkert and Glass 1999). Such burns allow the development of thick protective ground cover for the nests as well as the growth of small flowering plants (forbes) that enhance the diversity of insect prey. More generally, regular burns of grasslands favor a variety of native grass species and thwart the growth of woody plant species that start to prevail through natural succession if left unchecked.

In addition to disturbance by fire, grasslands are subject to disturbance by grazing—originally, by great herds of buffalo, antelope, or elk and, now, mostly by domestic livestock. Overgrazing, especially on leased government lands, converts rich grasslands into deserts. Savvy ranchers, however, guard the health of grasslands and the sustainability of their ranges by rotating their livestock. A variety of widespread birds, including Horned Larks and Lark Buntings, as well as specialized local birds such as Montezuma Quail in Arizona, benefit from moderate grazing regimes.

Floods

The flooding of bottomlands along rivers is an essential source of disturbance. So-called floodplains depend on regular disturbance (Brawn et al. 2001). Historically, seasonal flooding, sometimes severe and sometimes not, created backwater lakes and habitats, replenished vital nutrients, and reset the initial stages of plant succession on new soils. Now, however, floodplain habitats are under severe threat due to the "protection" from normal flood regimes by dams, channels, and levees and other changes such as excessive siltation.

Changes in flooding disturbance affects the riparian forests of southwestern North America and the large river systems of central North America. The floodplain forests of the southeast once supported species such Carolina Parakeets (extinct), Bachman's Warblers (extinct?), Swainson's Warblers (declining) and, the Ivory-billed Woodpecker. The Amazon and Orinocan river systems of South America still undergo major cycles of disturbance by flooding. Many little-known bird species, such as the Black-and-white Antbird and the White-bellied Spinetail, benefit from these cycles. They inhabit only the early-succession-stage vegetation on ever changing sandbars and river islands (Ridgely and Tudor 1994).

Forestry

In developed countries such as the United States, commercial forest management practices cause more disturbance than do natural processes such as fire, wind blowdowns, floods, and pests. For example, silviculture disturbed 24 percent of the timberland in Michigan, Wisconsin, and Minnesota in the 1980s compared with 13 percent by natural events (Schmidt et al. 1999).

Timber harvests vary from clear-cuttings to highly selective logging and from uneven-aged to even-aged methods of tree removal. The

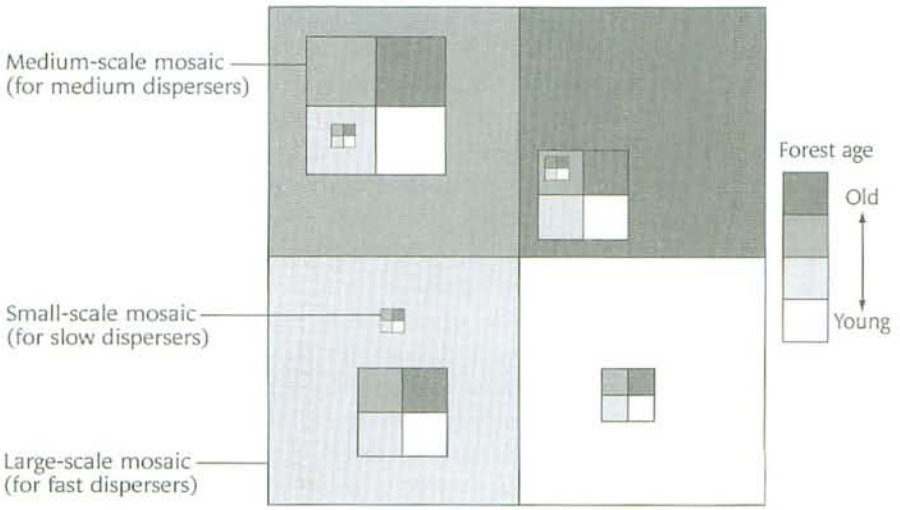


FIGURE 21–23 The shifting forest mosaic model. Forestry cutting of trees creates a variety of successional stages in the landscape. Different shades denote four stages of forest age from young to old. The stages "move around" over time as the forest grows and is cut in different years. Ideally, a full complement of plant and animal species adapted to a particular stage will colonize each stage. Different dispersal and colonization abilities enable some species to keep up and leave others behind. The inclusion of different-sized shifting mosaics in the landscape ensures the continued presence of fast dispersers such as birds and slow dispersers such as some plants. Small-scale mosaics should be embedded within large-scale mosaics to accommodate different kinds of dispersers and to maintain large blocks of adequate habitat. [*Courtesy of J. Hagan; after Harris 1984*]

sizes, distributions, and characters of the resulting timber harvests lead to landscape-scale mosaics of disturbed and successional habitats. These mosaics can be managed to ensure the sustained presence of disturbed forests of different ages, albeit at different locations in the mosaic. Shifting forest mosaic designs accommodate the needs of species with different habitat preferences and different dispersal tendencies (Figure 21–23).

Shifting forest mosaic designs support diverse bird communities that use them dynamically (Brawn et al. 2001). Some species, such as Winter Wrens, Eastern Bluebirds, and Northern Flickers, quickly colonize cutover regeneration stands. They use open slashpiles, herbaceous undergrowth, or residual snags. Within two to three years, additional species such as Mourning Warblers, Common Yellowthroats, and Swainson's Thrushes start using the regrowth saplings. About half of the Neotropical migratory bird species that breed in the hardwood forests of the central United States prefer early-succession stands of harvest regrowth. Well-designed forest regeneration mosaics can thus support high diversities of bird species that include clear-cut colonists and mature forest residents.

Forest management plans that protect old-growth forests are extremely important and controversial. Intense logging in the twentieth century reduced the old-growth forests in the Pacific Northwest to about 10 percent of their original extent. The environmentalists were eager to protect the remnant of what remained, and the loggers were eager to continue harvesting timber as the main source of their livelihoods. One species in particular—the Spotted Owl (Figure 21–24)—was at the center of the controversy.

FIGURE 21–24 The Spotted Owl, a threatened species that came to symbolize old-growth forests of the Pacific Northwest, which are now reduced to only 10 percent of their original extent. [*Victor Bakhtin*]

The Spotted Owl seemed destined to repeat the fates of the Passenger Pigeon and the Ivory-billed Woodpecker. Its typical habitat in the Pacific Northwest consists of low- to middle-elevation old-growth forests dominated by Douglas fir trees. These forests have mixed age classes of trees, including some large ones that are more than 200 years old, plus an abundance of dead trees and branches. The owls' preference for old-growth forests relates to the availability of large, old dead trees for nesting, the availability of small mammalian prey, especially flying squirrels, and protection from predators. Each pair requires from 500 to 2000 hectares of mature forest, depending on location. The owl symbolized the old-growth forest ecosystem and its biodiversity, including an endangered seabird—the Marbled Murrelet (Box 21–4).

Conservation research on the biology of Spotted Owls greatly affected land-use policy generally in the United States (Noon and Franklin 2002). It also spearheaded an understanding of many of the fundamentals of conservation biology. The research revealed the metapopulation structure of populations of three genetically distinct subspecies (Northern, California, and Mexican).

In addition to the raw loss of habitat due to logging, the fragmentation of the old-growth forests into isolated patches separated by second growth affects Spotted Owls. The fragmentation of continuous stretches of old-growth forest increases competition from larger and more aggressive Barred Owls that thrive in adjacent regrowth areas. Fragmentation also increases predation by Great Horned Owls, which frequent the forest edges and openings created by logging. Demographic data and life-table analyses project declines in the populations of the Spotted Owl, which delays breeding until it is three years old, later than most medium-sized owls. Breeding success is good in some years but bad in others, depending on the availability of prey. Poor breeding success stems in part from the high mortality of as many as 82 percent of dispersing juveniles.

Required by law to ensure viable populations of all native vertebrate species in the national forests, the U.S. Forest Service developed guide-

BOX 21–4

A SEABIRD OF THE OLD-GROWTH FOREST

Few birds have been as mysterious and have eluded study for as long as the quail-sized Marbled Murrelet, a declining and threatened species. The murrelet was the last North American species to have its nest discovered. By accident, a tree surgeon named Hoyt Foster discovered a moss nest containing one downy young murrelet 45 meters off the ground in a tall Douglas fir 16 kilometers from the ocean in California's Santa Cruz Mountains. These small seabirds, it turns out, fly inland to nest in tall, old-growth forest. Like the Spotted Owl, they depend on the disappearing old-growth forests of the Pacific Northwest (Nelson 1997).

The dependence of Marbled Murrelets on the old-growth forests from northern California to Alaska adds an extra threat to their future, because they are also highly vulnerable to coastal oil spills and to drowning in underwater fishing nets.

lines for the management of the Spotted Owl. Its plan in July 1986 was to set aside 500 Spotted Owl habitat areas in Washington and Oregon. The protected areas would vary in size—the average area containing 1000 hectares of old-growth forest—and would form a well-distributed network that allowed the dispersal of young owls. A review of the minimum population requirements by a blue-ribbon advisory panel of ornithologists convened by the National Audubon Society raised the stakes. They recommended protection of a minimum of 1500 breeding pairs by setting aside habitat areas with 2100 hectares each in Washington, 1100 hectares in Oregon and northern California, and 650 hectares in the Sierra Nevada (Dawson et al. 1986).

The Spotted Owl was listed as threatened in 1990, and a draft recovery plan was published in 1992. The Northwest Forest Plan of 1994 became the cornerstone for conserving and recovering the Spotted Owl on 24.4 million acres of federal land in Oregon, Washington, and California. A decade of research will be used to guide the completion of the recovery plan and final designation of critical habitat for the Spotted Owl by December 2007. Ongoing analyses of the viability of the scattered populations of the Spotted Owl confirm the original projections of their declines and sensitivity to habitat quality. These analyses also suggest that the declines of some populations are accelerating owing to decreased adult survival. Larger blocks of forest than originally projected may be needed to stop the declines.

Site-Based Conservation

Setting priorities is an essential first step in the process of conservation by design. Limited resources must be directed wisely to conservation programs at the highest-priority places among the many places that are under threat and for the many species that are declining. Public and community support of conservation programs is essential for their success.

Hot Spots and Important Bird Areas

To focus conservation resources on places of greatest need, conservation biologists led by Conservation International identified "hot spots" of biodiversity. Hot spots are those places under threat in the world that have the greatest concentrations of biodiversity, defined by the largest total number of species, the most threatened and endangered species, and the most endemic species. The initial selection of hot spots was based on measures of the richness of plant species.

Birds also stand out as one of the best indicators of biodiversity and ecosystem health. Birds are pivotal players in ecosystems. In the broad spectrum of biodiversity, birds are the most visible and accessible indicators of the interconnectedness of life on Earth.

By using computerized maps of the geographical distributions of all extant bird species, David Orme and his colleagues (2005) identified the places that host the greatest bird diversity, on the basis of the same three

principal criteria. The tropical Andes of South America topped the list of avian hot spot regions by all three criteria. Important in regard to species richness were other parts of South America (Amazon Basin, Atlantic Coastal Forest, Guyana highlands), the Himalayas, and the Rift Valley of Africa. Regions with high numbers of threatened species also included the Philippines, New Zealand, and Madagascar. New Guinea ranked high among the regions with lots of endemic species. Many, but not all, of these avian hot spots were also on Conservation International's list.

Responding to the challenge of protecting global diversity, the partnership alliance of Birdlife International created the Important Bird Areas (IBA) program. The IBA program is now the global paradigm for site-based conservation using the power of birds. It sets conservation priorities and provides a unified framework for national bird conservation initiatives. The goal is to protect a vast, well-designed, worldwide network of sites that stabilize bird populations and their essential ecosystems. Realizing their full potential, IBAs will keep common birds common, stop and reverse current declines, and prevent the extinction of our most imperiled bird species.

The IBA network includes protected public lands such as federal wildlife refuges as well as private and local community lands important for birds. The network features sites in the tropical Andes that harbor the most endangered forest species, wetland sites that are critical to stopover during seasonal migrations of shorebirds, including Western Hemisphere Shorebird Reserve Network sites (see Chapter 10) and the major wintering grounds of Arctic waterfowl. IBA initiatives in the Western Hemisphere have identified about 3000 sites of global significance, including 130 in the United States, 597 in Canada, and 230 in Mexico. More of them are identified each year. With the addition of sites of regional and continental significance, the network of IBAs in the Western Hemisphere will grow to include about 8000 sites under the supervision and conservation stewardship of nearby local communities (Figure 21–25).

The future quality of IBAs as primary conservation sites depends partly on the local management and restoration of quality habitat and on the abatement of major threats to those habitats. The future wildlife value of IBAs also depends on the care of the larger landscape of which they are a part. Most IBAs are surrounded by working lands of agriculture, high-impact human activities, or urban development. What homeowners do in their own backyards affects the quality of watersheds, flooding regimes, pollution, and frequency of predation by pets. The entire matrix of human activities thus governs the future value of sites in the network and of the network as a whole. Conversely, IBAs add value to the communities as recreational spaces for families and as magnets for ecotourism that brings revenue to the community.

Communities

Public and community support of conservation programs is an essential ingredient for their success. Public opinion matters. Therefore, conservation

FIGURE 21–25 Important Bird Areas in the Western Hemisphere. [*Courtesy of J. Cecil, National Audubon Society*]

initiatives must incorporate economic and social variables as well as tenets of landscape ecology. People are comfortable with birds and other wildlife and enjoy them as long as they do not become too common. Although rare species will delight the finder, the same species potentially become pests if they prosper to excess.

Conservation efforts can be too successful. For example, locally encouraged populations of resident Canada Geese now plague golf courses and city parks. Snow Geese in North America responded so well to management encouragement that they exceeded their resources on the Canadian Arctic breeding grounds, where they destroyed large expanses of sensitive tundra (see page 538).

Local pride is key to getting public support. Local pride can convert a community into an effective conservation force in just one year. The nonprofit conservation organization RARE uses the power of local pride to integrate conservation into the cultural, economic, and political aspects of community life (http://rareconservation.org). One of its initial programs in the Caribbean demonstrated the power of fully engaging public participation (Butler 1992). The revolution started on the island of St. Lucia, where Paul Butler, a British naturalist, transformed local indifference about wildlife into a passionate embrace of an endangered parrot, the St. Lucia Amazon, known locally as the Jacquot. The conservation blitz heightened awareness everywhere, with special attention given to schoolchildren, who educate their parents.

The Jacquot population had declined to a precariously small size as a result of being hunted for food and captured for the pet trade. The mountain forests where it lived had been cut for firewood and for farming. Now the island's national bird and center of pride, the Jacquot is increasing in numbers. As the island's conservation spokesman, the Jacquot exhorts fellow St. Lucians to save the island's forests, keep the water clean, protect their island's coral reefs, and engage in other environmental efforts.

> The parrot's colorful image now appears on billboards, bumper stickers, T-shirts, and St. Lucia passports. A lively combination of classroom visits [featuring a person dressed up like a parrot], reggae songs, music videos, church sermons, and puppet shows made saving the Jacquot a cause célèbre with all age groups on the island. As a result, the parrot not only stopped its slide toward extinction, but nearly doubled its population to about 350 birds. [Nielsen 1993, p. 48]

The Conservation Movement

Responding to the public concern about the welfare of birds in the late nineteenth century, states passed laws limiting the hunting season or protecting particular species. The work of the conservation committee of the American Ornithologists' Union, founded in 1883, led to the formation of state Audubon societies and soon thereafter to federal agencies such as the U.S. Bureau of Biological Survey charged with bird protection. In 1886, the American Ornithologists' Union proposed a model law that was adopted immediately by New York State and the Commonwealth of Pennsylvania. It eventually became the prototype for bird-protection legislation throughout the country.

Origins

The roots of such successful conservation initiatives in North America, as well as in other parts of the world, go deep into past practices of uncontrolled exploitation of the eighteenth and nineteenth centuries, outlined

earlier in this chapter. Public opposition to the killing and exploitation of native birds in the nineteenth century was inevitable and then prevailed. Famous conservation writers—Ralph Waldo Emerson, Walt Whitman, John Burroughs, and John Muir—stirred the public conscience with their writings.

Leading the initial battles for bird conservation were several amazing women in Massachusetts. Fannie Hardy and Florence Merriam founded the first Audubon society in 1887 at Smith College to rid the campus of feathered finery. A few years later, in 1896, Harriet Hemenway founded the Massachusetts Audubon Society with the mission of discouraging ornamental uses of wild bird feathers and protecting birds. From their first acts, the bird conservation movement grew steadily, led by women. The founding of Hawk Mountain Sanctuary Association is just one fine example.

Hawk Mountain

Sixty years ago, in 1934, a dedicated New York conservationist named Rosalie Edge challenged local traditions of shooting migrating hawks for fun. She put an end to it on a mountaintop in southeastern Pennsylvania. Rosalie Edge believed that the time to save a species is while it is still common. Her private initiative—now a classic conservation story—started the sport of hawk watching as an alternative to hawk shooting and created a model for the monitoring and conservation of migratory hawks and eagles worldwide (Bildstein et al. 1993).

On their way south in the fall, migrating hawks hug the tops of mountain ridges, riding favorable, rising air currents. They pass key sites in great numbers on days of favorable winds, providing living targets to those who wished to eliminate predators. The annual toll of tens of thousands of Sharp-shinned Hawks and other species was staggering. Determined to stop the shooting, Rosalie Edge raised the money to buy 567 hectares (1400 acres) on Hawk Mountain (Figure 21–26). She installed a brave young naturalist warden, Maurice Broun, to protect the hawks and to share his recognition of raptors as beneficial rather than harmful members of natural ecosystems. Since its founding, the Hawk Mountain Sanctuary Association has played a key role in protecting North America's raptors and their essential habitats by developing grass-roots support for state and national legislation. Each year, 70,000 visitors come to view the inspiring passage of hawks and eagles and leave Hawk Mountain with a greater commitment to conservation.

Relating to its long, pioneering history, Hawk Mountain also maintains the world's longest and most detailed record of raptor migration. The millionth raptor—an immature female Sharp-shinned Hawk—was officially logged at 12:41 p.m. on Thursday, October 8, 1992. This total increased to 1.4 million at the end of 2005. The annual counts of hawks and eagles that migrate past Hawk Mountain have proved to be effective tools in assessing long-term trends in raptor populations throughout eastern North America. This database played a key role in exposing first-generation organochlorine pesticides, such as DDT, as causative agents for the decline of several species of birds of prey, as well as measuring their

FIGURE 21–26 The lookout at Hawk Mountain near Reading, Pennsylvania. [*Courtesy of Hawk Mountain Sanctuary Association*]

population recoveries following a decreased use of environmental pesticides. Now, there is a continent-wide network of hawk watching and monitoring sites: Cape May, New Jersey, Duluth, Minnesota, and Vera Cruz, Mexico, complemented by others in Spain, Taiwan, and many more.

Momentum

A series of environmental crises—fatal air-pollution events, rivers afire with debris and chemicals, birds dying of pesticides on lawns—and a powerful book—*Silent Spring* by Rachel Carson (1962) —awoke the country and launched the modern environmental movement. Starting in the 1950s and continuing through the 1970s, the U.S. Congress enacted landmark legislation, including the Wilderness Act (1964), National Environmental Policy Act and the Environmental Protection Agency (1969), Clean Air Act (1970), Clean Water Act (1972), Endangered Species Act (1973), and the Safe Drinking Water Act (1974). President Nixon's administration (1969–1974) accomplished more significant environmental legislation than any before or since, with the possible exception of Theodore Roosevelt (1901–1909).

Bird conservation grew to be a local, national, and international priority as a variety of nonprofit organizations, national and local, formed to coordinate and focus public concern about their birds. In North America,

more than 1000 independent bird clubs, bird observatories, professional coalitions, and Audubon chapters look out for the welfare of birds. They maintain sanctuaries, restore habitat, and advocate on behalf of birds. Each organization has its own proud stories of accomplishment.

Worldwide, hundreds of national bird conservation organizations address priority matters locally. In Britain, the venerable Royal Society for Protection of Birds founded in 1889 now hosts more than 2 million members. Uniting national bird conservation organizations worldwide in the common cause, the BirdLife International coalition of country partners spearheads the conservation of globally endangered and threatened bird species.

Government agencies, both state and federal, pay increasing attention to the management of non–game bird populations. The restoration of the declining waterfowl populations led modern government bird conservation initiatives. Faced with continuing wetland destruction and accompanying declines in waterfowl populations, the governments of the United States, Canada, and Mexico initiated a new, intense effort to protect wetlands and associated wildlife in 1986. Participants in the North American Waterfowl Management Plan (NAWMP) vowed to protect millions of acres of important wetlands. With the participation of nearly 200 public and private organizations, the NAWMP strives to meet specific population goals for each of 32 species of ducks, geese, and swans.

The conceptual foundations of the NAWMP gave rise to two new remarkable initiatives in the 1990s: Partners in Flight, or PIF, followed by the North American Bird Conservation Initiative, or NABCI (Fitzpatrick 2002). The PIF initiative, a coalition of government agencies enhanced by the participation of nongovernment agencies, corporate leaders, and academic professionals, focused first on the growing plight of Neotropical migrant bird species, with the rallying cries "Keep common birds common" and "Birds are just like ducks." It set priorities on action plans through consensus and mobilized new resources—federal, state, and private dollars—to protect bird populations. Those plans are being implemented throughout the United States and Canada.

NABCI sprouted from these same roots, expanding the movement from Neotropical migrants to "All birds, all habitats." Upland game birds, shorebirds, colonial nesting birds, and resident songbirds all gained collective conservation attention. Building on the waterfowl plan that set regional population goals for duck species, the participants in NABCI are doing the same for all birds and then forging the local partnerships and funding to achieve those goals.

Birding and Citizen Science

Effective conservation requires countable units, usually acres or species. The average citizen also tends to take ownership of what he or she counts and then to act on their behalf (Flicker 2002). Ever increasing numbers of people participate in the local conservation of the birds that they count.

The importance of conservation-oriented birding is due to the efforts of pioneering ornithologists such as Frank Chapman. When he was not

censusing birds on women's hats in New York City, Chapman promoted winter bird watching in the form of bird counts during the Christmas holidays to replace the traditional end-of-the-year bird-shooting parties. The Christmas Bird Count of the National Audubon Society is now the largest and oldest citizen science project in the world. It fostered the founding and growth of more than a thousand bird clubs and Audubon chapters throughout the United States and Canada. It continues to expand throughout Central and South America.

With the Christmas Bird Count, Frank Chapman founded what we now call "citizen science," which harnesses an army of volunteers to monitor our bird populations as indicators of environmental health through a growing array of substantial projects, including the Breeding Bird Survey (see page 562).

In its broadest definition, citizen science is research done by people from every level of society in collaboration with scientists. By empowering voters and decision makers with science-based information, citizen science is central to the maintenance of a sustainable society and a healthy environment (Irwin 1995).

Citizen science has been a primary force for the growth of the modern conservation movements in North America and Europe. The citizen science and conservation movements in North America expanded together and diversified in participation and accomplishments. A similar grass-roots industry grew in parallel in Britain and the rest of Europe. Looking ahead, we can use the sheer volume of observations contributed daily combined with the power of modern databases to track bird populations in real time as a conservation radar with unprecedented power of timely public participation.

The growth of public interest in birds has been extraordinary. It powers the modern conservation movement in many respects. Birding now engages tens of millions of citizens (La Rouche 2001). The average birder is well educated, earns an income above the national average, and belongs to at least three conservation or birding organizations. On the basis of 15,300 interviews, the national survey estimates that 46 million U.S. citizens, 16 years of age or older, are birders. This projection defines birders as people who "closely observed or tried to identify birds around the home and/or took a trip a mile or more from home for the primary purpose of observing birds." So defined, most birders (88 percent, or 40 million) were backyard birders. Forty percent, or 18 million, including some of the former group, took trips to look at birds. Most (74 percent) were beginners who said they could identify from only 1 to 20 species, and 5 percent (2.3 million) kept a life list of species that they saw.

Birding is an economic force for local communities and governments as well as for conservation. In Britain, the presence of a nearby bird reserve maintained by the Royal Society for the Protection of Birds substantially improves the economies of small rural towns by increasing sales of petrol, beer, and pub lunches. The 2001 U.S. Fish and Wildlife Service survey estimates that, in that year, U.S. birders (84 percent) and other wildlife watchers (16 percent) spent an estimated $24 billion on binoculars, bird food, camping equipment, and related items and more than

BOX 21–5

BIRDING ETHICS: AMERICAN BIRDING ASSOCIATION

Everyone who enjoys birds and birding must always respect wildlife, its environment, and the rights of others. In any conflict of interest between birds and birders, the welfare of the birds and their environment comes first.

1. Promote the welfare of birds and their environment.

To avoid stressing birds or exposing them to danger, exercise restraint and caution during observation, photography, sound recording, or filming.

Limit the use of recordings and other methods of attracting birds, and never use such methods in heavily birded areas or for attracting any species that is Threatened, Endangered, of Special Concern, or is rare in your local area.

Keep well back from nests and nesting colonies, roosts, display areas, and important feeding sites.

Stay on roads, trails, and paths where they exist; otherwise keep habitat disturbance to a minimum.

2. Respect the law and the rights of others.

Do not enter private property without the owner's explicit permission.

Follow all laws, rules, and regulations governing use of roads and public areas, both at home and abroad.

3. Ensure that feeders, nest structures, and other artificial bird environments are safe.

Keep dispensers, water, and *food* clean and free of decay or disease. It is important to feed birds continually during harsh weather.

Maintain and clean nest boxes regularly.

If you are attracting birds to an area, ensure that the birds are not exposed to predation from cats and other domestic animals or to dangers posed by artificial hazards.

4. Group birding, whether organized or impromptu, requires special care.

Respect the interests, rights, and skills of fellow birders, as well as those of people participating in other legitimate outdoor activities.

Freely share your knowledge and experiences. Be especially helpful to beginning birders.

If you witness unethical birding behavior, assess the situation and intervene if you think it prudent.

Please follow this code—distribute it and teach it to others.

$7 billion on travel. These expenses leveraged $85 billion in overall economic output and $13 billion in state and federal income taxes.

To ensure their continued welcome as guests of local communities and wildlife refuges, responsible birders observe a code of ethics for behavior that is good for both the birds that they watch and the places that host them. Box 21–5 lists selections of this code endorsed by the American Birding Association.

Wild America

American icon Roger Tory Peterson and British ornithologist James Fisher took an epic journey and survey of the birds across North America in 1953. James Fisher saw North America for the first time and concluded their story of this journey in their book *Wild America* (1955) with the

quote posted at the beginning of this chapter. Fifty years later, Scott Weidensaul took a second look and observed

> I found the continent changed—for the better in some places, for the worse in others. Yet the land, the rugged heart of natural America, retains an essential timelessness. . . . Ours is still, at its core, a wild country. [Weidensaul 2005, p. xx]

Our knowledge of birds and our appreciation of them can assure their future and "the rugged heart of the planet." That has been the theme of this book. Each of us can make a difference. Please start now.

Summary

More than 10 percent of the world's bird species are either endangered or vulnerable. In the United States alone, about half of bird species are declining, some steeply. Paramount among the negative forces of humankind on bird populations is the rapid destruction of the natural habitats of the world, ranging from the tropical rain forests to grasslands worldwide. Excessive exploitation and nesting failures caused by pesticides or introduced predators were the primary causes of historical extinctions. Continuing and emerging threats include the commercial pet-bird trade, new diseases, and new forms of chemical pollution of the environment.

The goal of bird conservation is to stop declines and to prevent further extinctions. Attention to the habitat needs of birds also benefits a wide range of other species, as well as the health of ecosystems on which modern societies depend. Conservation successes inspire hope and confidence that we can reverse negative trends. Rediscoveries of lost species and determined restoration of populations on the brink demonstrate our ability to prevent extinctions. Bird populations respond spectacularly to the eradication of introduced mammals from islands and to the restoration of new grassland habitats.

With the commitment to set aside critical habitat for endangered species comes the challenge of designing these reserves. Conservation design includes the geometry of reserve shapes and sizes and their arrangement on the landscape, including connections by corridors. Population viability analyses include attention to the dynamics of local populations within larger metapopulations. Conservation plans must incorporate or replace natural forms of disturbance, including fires, flood, and blocks of successional-stage forest that suit the dispersal behavior of both plants and animals.

The economic value of bird watchers as ecotourists and the cultivation of local pride are powerful forces behind successful conservation projects. In addition to public concern, the key ingredients for the success of bird conservation programs worldwide are sound ornithological knowledge of a species' biology and the political will to help species prosper.

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