CHAPTER 7

Physiology

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This chapter is about the physiological characteristics that allow birds to live in the places that they do and take advantage of the many resources that they use; it is about how birds work. Birds can be found from sea level to flying over the world's highest mountains, and they can feed on foods that range from nectar to toxic leaves. Natural selection has shaped all aspects of their physiology, from the pigments in their blood to the structure of their kidneys. However, rather than just describing the functions of the molecules and organs of birds, we focus on how these mechanisms can be used to explain the features of birds that allow them to live in different habitats (and sometimes prevent them from using others), perform amazing athletic feats, and feed on a wide variety of foods. We adopt both an ecological and a broadly comparative approach because it is only by placing the characteristics of birds in these contexts that one can fully appreciate their remarkable physiological diversity. We also take an integrative perspective. This means that we consider case studies of how birds work from the properties of the molecules within their cells and the genes that code for them, all the way up to how they function as fully integrated feathered organisms. Physiology has two major complementary branches. One branch deals with the structures and mechanisms that make up animals' bodies and their performances. The other branch of physiology is about how the nervous system, together with a system of hormone-producing glands, regulates the function of these structures and mechanisms (see chapter 8). This chapter emphasizes the former branch. It focuses on the design of structures and systems that allow birds to cope with environmental and ecological challenges.

WHY BODY SIZE MATTERS

George Bartholomew was one of the greatest comparative physiologists of the twentieth century. He stated that "the most important attribute of an animal, both physiologically and ecologically, is its size" (Bartholomew 1981). Body size is a major determinant of how an animal functions and of the role that it plays in ecological communities. In a subsequent section, we will argue that you can make coarse (but useful) predictions of many features in birds and other animals if you know how big they are. This is because many features of animals depend on body size in a predictable way. The metric that we use as an estimate of an animal's size is its body mass. Using very simple equations, we can estimate many of an animal's characteristics just by knowing the animal's body mass. The dependence of animal functions and traits on body mass requires that we take an animal's mass into account when we make comparisons. For example, we will see that hummingbirds tend to do things at a rapid pace. Hummingbirds have incredibly high heart and breathing rates. Per unit of body mass they use energy very rapidly, and they must feed frequently and abundantly. Is this because they feed on nectar, a high-octane food, and fly by hovering, which is a demanding way to move? Or is it because they are tiny?

Birds range in body mass from the diminutive Bee Hummingbird (*Mellisuga helenae*), which weighs slightly over two grams (less than one-tenth of an ounce), to the Ostrich (*Struthio camelus*), the largest living bird species, which can weigh over 100 kg (220.5 lb). If we consider extinct species, the range of avian body sizes gets even larger. The flightless Elephant Bird (*Aepyornis maximus*) from Madagascar and the gigantic carnivorous *Dromornis* from Australia could weigh half a ton (500 kg, or over 1,000 lb) and reach over three meters in height (9.8 ft; fig. 7.1). One of the largest flying birds to ever live, *Argentavis magnificens,* weighed around 80 kg (176.4 lbs). These vulture-like birds had wingspans of as much as seven meters (23 ft) (Palmqvist and Vizcaíno 2003). *Argentavis magnificens* was at least five times heavier than the California Condor (*Gymnogyps californianus*), which weighs up to 14 kg

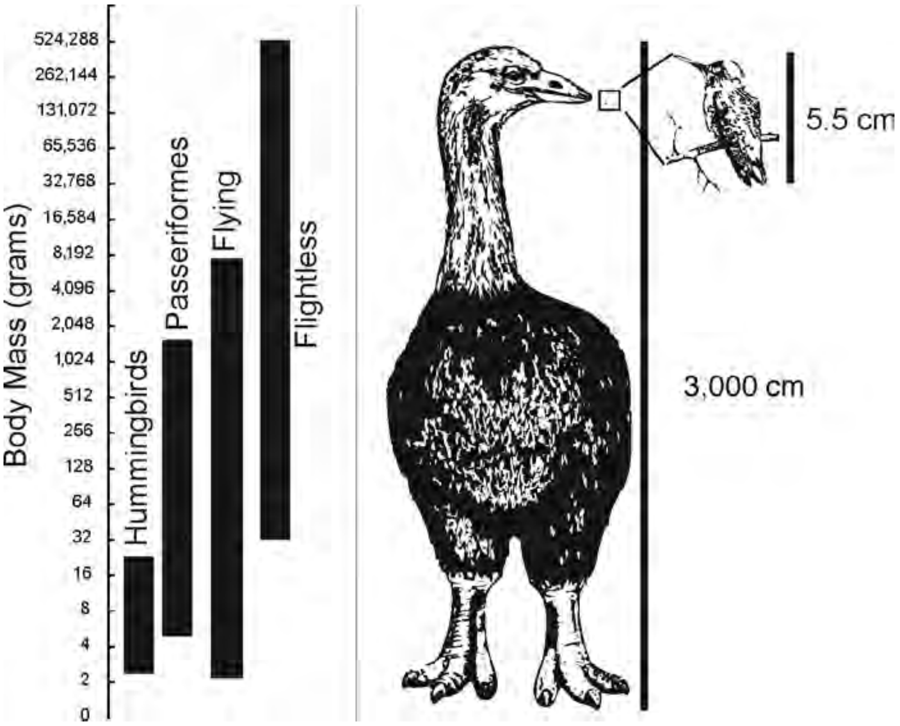


Figure 7.1. The body masses of birds span five orders of magnitude, from the tiny Bee Hummingbird (*Mellisuga helenae*) to the massive Elephant Bird (*Aepyornis maximus*). Using the same scale for both species turns the hummingbird into a tiny speck. Flightless birds tend to be bigger than those that fly. Hummingbirds are the smallest group of birds.

(31 lb) and can have a wingspan of up to three meters (10 ft). Kori Bustards (*Ardeotis kori*) can also be very large (up to 15 kg or 33 lb) and compete with California Condors as the largest extant flying birds. Thus, there is about a 250,000-fold difference in body mass between the Bee Hummingbird and the largest known birds; the masses of birds span five orders of magnitude (fig. 7.1). This large spread in body masses has profound physiological and ecological consequences. Table 7.1 shows a few of the physiological and ecological traits that are dependent on and can be predicted by body mass. The study of the relationship between body mass and biological function is called allometry, and the equations that relate body mass with form and function are called allometric equations.

BODY SIZE AND METABOLIC RATE

Knowing how much energy a bird spends per unit time is useful. We will call this rate of energy use **metabolic rate**. A bird's metabolic rate determines how much the bird should eat each day, and hence the size of the area that it must travel around to find food (the bird's home range), or the size of the area that it must defend (its territory). Consequently, if we know the abundance of resources, we might be able to predict, from an estimate of metabolic rates in individual birds, the number of birds that an area could support (Nee et al. 1991, table 7.1). Physiologically, we expect that the rate at which birds breathe air in and out of their lungs and transport blood to their tissues (and hence the rate at which their hearts pump blood) should be also dependent on metabolic rate. Many bird characteristics ranging from the physiological to the ecological depend on metabolic rate, and metabolic rate depends on body size (table 7.1).

The dependence of all these properties on body size is, not surprisingly, because larger birds use more energy than smaller ones. Field metabolic rate, basal metabolic rate, and summit cold-induced metabolism (these three measures are defined below) all increase with body mass. However, the relationship between the rate at which birds use energy and their size is not one of proportionality. You cannot just take the metabolic rate of a small bird and multiply it by a constant factor to get the metabolic rate of a larger bird. Elephant Birds did not have metabolic rates that were 250,000 times larger than that of Bee Hummingbirds; the rate was much lower. The relationship between metabolic rate and body mass is a power function of this form:

$$\text{Rate of energy use} = a * (\text{body mass})^{b}$$

where a is a constant and b is less than one (typically a value around 2/3 or 3/4; Hudson et al. 2013). Recall from your mathematics courses that if the value of b in a power function is less than 1 but larger than 0, then the relation between the dependent and the independent variable is an increasing, but decelerating, function. Therefore, standardizing metabolic rate by body mass (this is called mass-specific metabolic rate) produces a negative relationship between

Table 7.1. **Several Characteristics of Birds that Depend Predictably on Body Mass**

Type of trait	*Equation*	*Reference*
Morphological		
Skeletal mass (kg)	$Y = 0.06X^{1.1}$	Calder (1983)
Heart mass (kg)	$Y = 0.009X^{0.91}$	Calder (1983)
Kidney mass (kg)	$Y = 0.009X^{0.91}$	Calder (1983)
Physiological		
Respiratory rate (breaths/min)	$Y = 18.6^{-0.33}$	Calder (1968)
Heart hate (beats/min)	$Y = 155.8X^{-0.23}$	Calder (1968)
Glomerular filtration rate (ml/hour)	$Y = 141.1X^{0.73}$	Bakken et al. (2004)
Basal metabolic rate (J/second)	$Y = 3.5X^{0.67}$	McKechnie and Wolf (2004)
Maximum lifespan potential of flying birds (years)	$Y = 30.2X^{0.25}$	Healy et al. (2014)
Maximum lifespan potential of non-flying birds (years)	$Y = 41.6X^{0.13}$	Healy et al. (2014)
Ecological		
Population density (individuals/km^2)	$Y = 24.7X^{-0.604}$	Silva et al. (1997)
Raptor home range (ha)	$Y = 3664X^{1.34}$	Ottaviani et al. (2006)

Note: We emphasize that the predictions from these scaling equations are approximations that are often very inaccurate. The characteristic in question (Y) depends on body mass (X), but also on a variety of other factors. For example, population density depends not only on body mass but also on diet, the productivity of the habitat inhabited by the species in question, and the taxonomic affinities of a group.

mass-specific metabolic rate and body mass ($b-1 < 0$). Consequently, small birds have higher mass-specific metabolic rates than large birds. Hummingbirds have extraordinarily high mass-specific metabolic rates, but these are simply the result of their tiny size (fig. 7.2). Recall also that we can make power functions look linear if we plot them on log-log axes:

$$\text{Log(rate of energy use)} = \text{Log}(a) + b * \text{Log(body mass)}.$$

Figure 7.2 shows the relationship between the **field metabolic rate** of birds and their body mass in a log-log plot. Field metabolic rate is the rate at which birds use energy during the day and under natural conditions. The slope of this relationship (or the exponent *b*) is about 0.7 (Hudson et al. 2013). If this rate is standardized by 24 hours, this rate is called daily energy expenditure. The two primary methods for estimating field metabolic rate are described in some detail in box 7.1 on page 00.

Metabolic rate is measured in a variety of units and at a variety of time scales. You will find that metabolic rate is expressed in kilocalories per unit time, kilojoules per unit time, watts (joules/second), and as the rate of oxygen consumption or carbon dioxide production (in units of volume per unit time). Box 7.1 explains how to transform among different units of measurement. We often use the rate at which birds exchange respiratory gases with the atmosphere to estimate metabolic rate; this method is called **respirometry** (see box 7.1 on page 00). Our knowledge of the biochemical process of cellular respiration allows us to estimate metabolic rate because oxygen is consumed and carbon dioxide produced and exhaled in rather specific proportions during respiration.

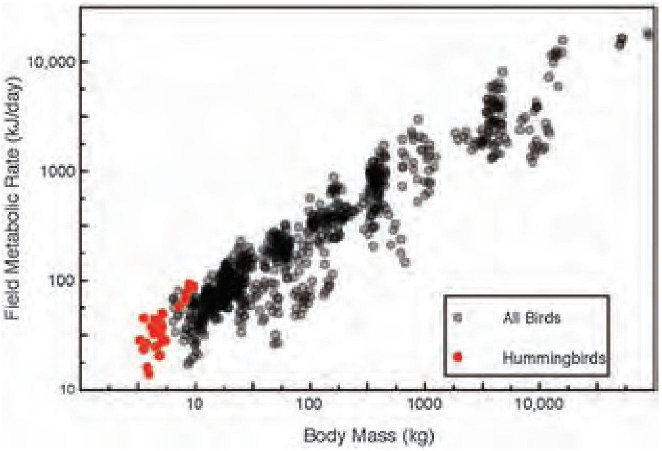


Figure 7.2. The relationship between field metabolic rate and body mass is roughly linear on a log-log scale. Each point is a measurement on an individual bird. The figure represents 895 individuals in 90 species and 15 orders. Note that measurements for hummingbirds fall roughly where they would be expected. Because the slope of the line is lower than 1 (it is about 2/3), the mass-specific field metabolic rate of small birds is higher than that of larger birds. *After Hudson et al. 2013.*

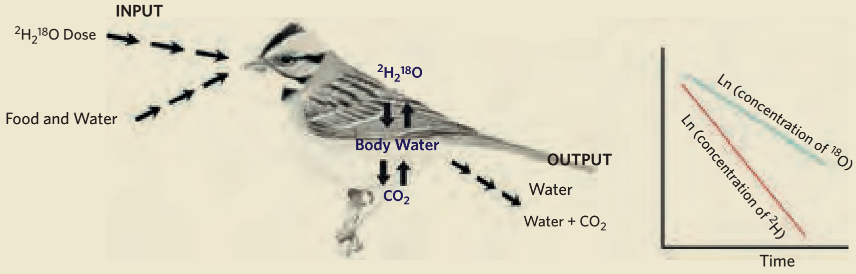
Birds spend energy to produce heat and maintain a relatively constant body temperature that is independent of that

METHODS OF MEASURING METABOLIC RATE

Metabolic rate is the rate at which chemical energy is converted to heat and external work. Energy is expressed in calories (cal) and joules (J; 1J = 4.184 cal), and metabolic rates are expressed as energy units per units of time, usually in cal/s or watts (W). When an animal oxidizes glucose or any other chemical foodstuff, a fixed proportional relation is obtained between the heat produced and the amount of O_2 used. The same is true for CO_2 production. Although the volumes of O_2 consumed per gram of each of the main foodstuff types that are oxidized (carbohydrates, lipids, and proteins) are very different, the amount of heat produced by a liter of oxygen consumed is quite similar (4.8 Kcal per liter O_2 in average). Thus an indirect measure of metabolic rate is the rate of O_2 consumption. The rate of heat produced per liter of CO_2 produced is very dependent on the type of food oxidized; therefore, researchers prefer to measure O_2 consumption as an indirect measure of metabolic rate.

Two methods are commonly used for estimating rates of O_2 consumption: open and closed system respirometry. In the open system, a continuous flow of air flows past the animal placed inside a chamber, and the difference in O_2 concentration between incurrent and excurrent air is measured. Knowing the airflow rate allows the rate of oxygen uptake by the animal to be calculated. In the closed system, the organism is placed in a sealed chamber, which leads to a decrease of O_2 concentration due to respiration. The average rate of oxygen consumption can be computed by using the difference in gas concentration at the start and end of a period of measurements, the chamber volume, and the time of measurement. The advantage of these methods lies in the fact that metabolic rates can be estimated in controlled conditions.

^{18}Oxygen and ^{2}Hydrogen are artificially enriched in the body water pool and their subsequent elimination is measured. This occurs at different rates for the two isotopes because hydrogen is primarily eliminated by the outflow of body water, while oxygen is eliminated both by water loss and from expiration of respiratory CO_2. The difference between the elimination rates of the two isotopes therefore provides an estimation of CO_2 production in an individual over a given time. The use of the doubly labeled water method is useful for estimating the average metabolic rate (field metabolic rate) in free-living birds. When animals spend energy in the body, carbon dioxide (CO_2) and water are produced; this technique measures the production of carbon dioxide over relatively long periods of time (days or weeks). The technique requires the administration (usually by injection) of water in which both the hydrogen and oxygen have been substituted partially or completely, for tracking purposes (i.e., labeled), with an uncommon stable isotope of these elements: deuterium (^{2}H) and oxygen (^{18}O). The method is based on the principle that, after a loading dose of $^{2}H_2{}^{18}O$, ^{18}O is eliminated as CO_2 and water, while deuterium is removed from the body as water. The rate of CO_2 production can be estimated from the difference between the two isotope elimination rates and the total amount of water in the bird's body (see figure). Knowing the production rate of CO_2, total oxygen consumption (metabolic rate) can be estimated from the respiratory quotient, defined by the ratio of CO_2 produced to O_2 consumed while food is being metabolized. This ratio can be measured by respirometry and usually exhibits values of from 0.7, when fat is being oxidized, to 1.0 when carbohydrates are being used; and in a mixed diet is usually about 0.8 (Frayn 1983). One can find out the "fuels" that birds use to power their metabolism by measuring the rate at which they consume oxygen and produce carbon dioxide. More recently, measurement of the heart rates of free-living birds have also been used to estimate field metabolic rate (Steiger et al. 2009). This approach is called heart rate telemetry, and it offers some key advantages over the doubly labeled water method. Most importantly, it allows for "real-time" measures of changes in heart rate (and thus metabolic rate) that are associated with specific activities or behaviors. To use heart rate telemetry to estimate field metabolic rate, however, changes in heart rate must be related to changes in O_2 consumption or CO_2 production. This is accomplished using respirometry on birds that are equipped with heart rate monitors, effectively calibrating the heart rate monitors so that they can be used as a proxy to measure respiratory gas exchange.



^{18}O elimination rate (in water and CO_2) - ^{2}H elimination rate (in water) = CO_2 production

Field metabolic rate is commonly measured by injecting a bird with a dose of water labeled with Deuterium and 18O (the heavy stable isotopes of hydrogen and oxygen) and measuring the bird's water volume and the rate at which the concentration of the isotopes decreases with time.

of their environments. These features make them homeothermic endotherms. In birds, resting body temperature is lower in the larger Paleognathae (cassowaries and ostriches, mean body temperature about 38.5°C) than in other birds (average body temperature about 42°C; Clarke and Rothery 2008). In 1950, Per Scholander and Larry Irving, two adventurous, pioneering physiologists, proposed that we could study endotherms as if they were furnaces (Scholander et al. 1950). They suggested that in order to maintain a constant body temperature, an animal has to spend as much energy as it loses—much as the furnace that warms your house. The amount of energy lost to the environment, in turn, should be proportional to the difference in temperature between the animal's body and that of the environment. Thus, if you make a plot of an animal's metabolic rate against environmental temperature, you should get a straight line with a negative slope that projects into the x-axis at the value of the animal's body temperature (fig. 7.3). As temperature increases, rather than reaching a value of 0, metabolic rate becomes relatively stable. This minimal metabolic rate is called the **basal metabolic rate** if the animal is at rest and post-absorptive (meaning that it is not digesting a meal). The range of temperatures at which metabolic rate is constant is called the **thermoneutral zone**. The slope of the relationship between metabolic rate and ambient temperature is called **thermal conductance**. The slope is shallow if the bird is well insulated and steep if it is poorly insulated and loses a lot of heat (fig. 7.3).

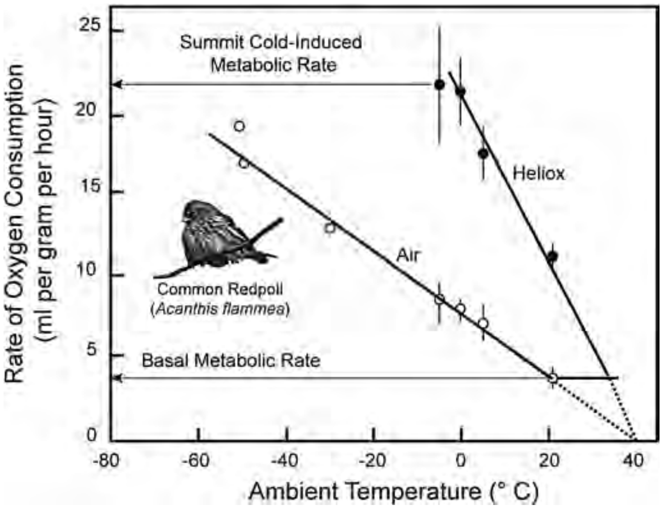


Figure 7.3. Scholander and Irving's model of thermoregulation in birds exposed to air and heliox. In order to maintain constant body temperature, heat output must match heat losses, which depend on the gradient between the bird's body temperature and air temperatures. Heat loss is steeper when insulation is low or when birds are exposed to a medium such as heliox that conducts heat efficiently. The relationship between energy used in thermoregulation and air temperature is flat for temperatures above a temperature called the **lower critical temperature**. *After Rosenmann and Morrison 1974.*

Basal metabolic rate estimates the minimal amount of energy that a bird needs to maintain its body temperature when it is resting and when ambient temperature is within the thermoneutral zone. How much can birds increase their metabolism in response to cold temperatures? Chilean physiologist Mario Rosenmann took advantage of the observation that a mixture of 80 percent helium and 20 percent oxygen (called heliox) conducts heat four times more rapidly than air (Rosenmann and Morrison 1974). If you place a bird in heliox, the gas increases heat loss. When they placed a Common Redpoll (*Acanthis flammea*) in heliox and measured its rate of oxygen consumption, they found that at 20°C it lost as much heat, and hence consumed as much oxygen per unit time, as if it was at −20°C. At only 0°C, the redpoll reached its maximal possible metabolic rate. This rate is called **summit** (or peak) **cold-induced metabolism**. To force the bird to reach this peak metabolic rate in air, Rosenmann would have had to lower ambient temperature to about −75°C. Many similar experiments have been conducted to find out the maximal rate at which birds can spend energy to keep body temperature in the cold.

Measurements of basal metabolic rate and summit metabolism are accomplished using respirometry to measure the rate at which an individual consumes oxygen or produces CO_2 at different environmental temperatures. This gives a standardized way to compare these values across species. Hundreds of measurements of the metabolic rates of birds have been made using respirometry, and we have learned a lot from them. But measuring the metabolic rate of a bird under these standardized conditions can be an oversimplification, because in nature there are lots of factors that influence the rate at which birds exchange heat with the environment (Wolf et al. 2000). Birds exchange heat with the sun and sky, with the ground, the air, and, in aquatic birds, with water. The rate at which these exchanges take place is affected by the speed of the wind or water. Figure 7.4 describes these mechanisms in detail. We have emphasized heat loss as a determinant of energy use. Other factors are also as important. All forms of locomotion are costly (see chapter 10); incubation, growth, and molt are also major determinants of how much energy is used by birds and are addressed in the corresponding chapters.

AVIAN ENERGETICS

How Do Birds Generate Heat?

The generation of heat is called thermogenesis. Because metabolic processes are inefficient, one of the end products of

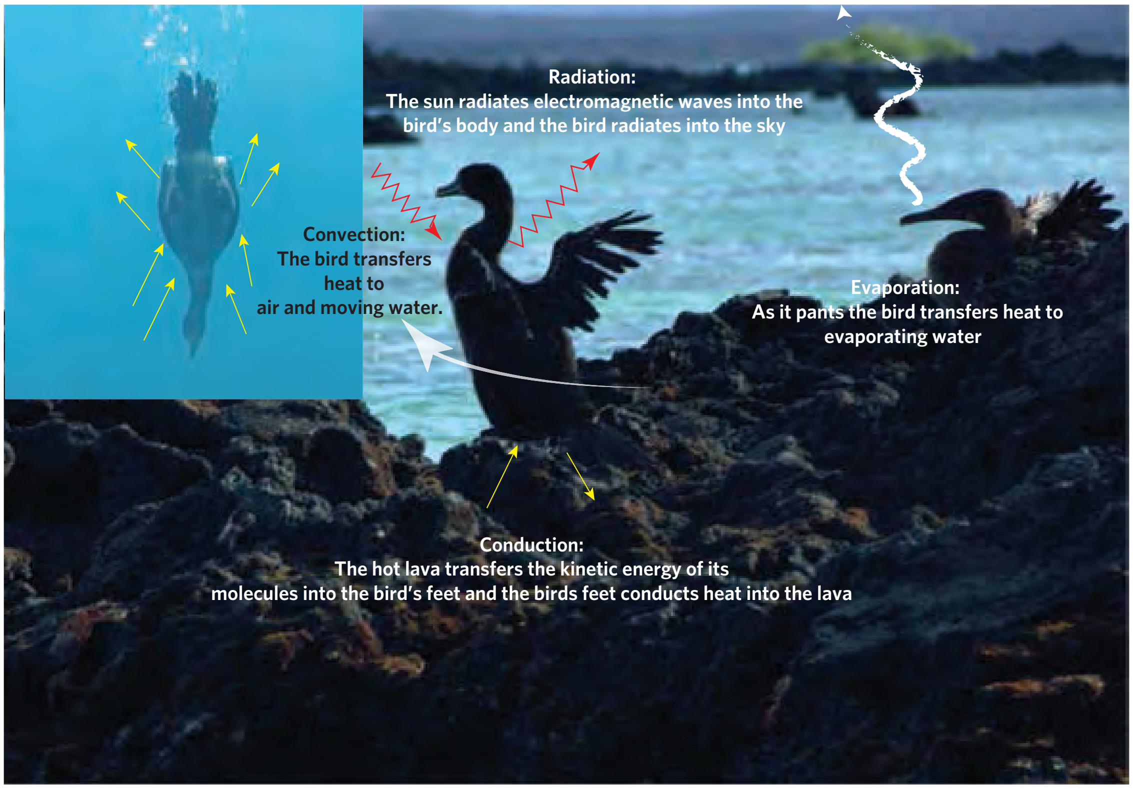


Figure 7.4. Birds exchange heat with the environment in many ways. When an object is in direct contact with another object, there is net transfer of the kinetic energy of the warmer object to the cooler one by conduction. The Flightless Cormorant (*Phalacrocorax harrisi*) is exchanging heat with the lava by conduction. Depending on the lava's temperature, net heat flow will flow into the bird's body or from the body into lava. Heat transfer is enhanced by a moving fluid, such as wind or water. This mode of heat transfer is called convection. Birds also emit and receive electromagnetic waves, with net movement of heat energy from high to low temperatures. The cormorant is emitting heat to the sky and receiving heat from the sun as it basks. Finally, because it takes energy to evaporate water, birds lose heat to the environment when they evaporate water. The cormorant evaporates water, and therefore cools down by panting. *Photo of birds on land by Nathan Bell; photo of diving bird by Greg Estes. With permission.*

their action is heat. Flight muscles (the *pectoralis* and *supracoracoideus*, chapter 6) represent a large fraction of a bird's body mass (from 15 to 25 percent) and are the most important heat generators (Swanson 2010). In some birds, leg muscles also contribute to thermogenesis. In mammals, non-shivering thermogenesis can be an important contributor to an individual's heat budget. In these animals, proteins found in mitochondria uncouple the electron gradient from the production of adenosine triphosphate (ATP) and therefore generate heat rather than store it in chemical bonds. These uncoupling proteins (or UCPs) are found in a type of fatty tissue called brown fat. The occurrence of non-shivering thermogenesis in birds is controversial, because birds do not have brown fat. However, several studies show that when Muscovy Ducks (*Cairina moschata*) and Chickens (*Gallus gallus*) are exposed to cold temperatures for several weeks, they express an uncoupling protein in their muscles and may experience non-shivering thermogenesis. Perplexingly, this protein does not seem to uncouple electron transport from ADP phosphorylation. No one knows exactly how (or if) this protein contributes to thermogenesis (Bicudo et al. 2001), making this an area of exciting new research.

Birds in the Cold

Tiny birds such as chickadees can survive the winter, even in places with very cold winters. Birds survive cold temperatures by increasing heat production to counteract heat loss and by conserving heat. David Swanson and Karen Olmstead (1999) captured Black-capped Chickadees (*Poecile atricapillus*), Dark-eyed Juncos (*Junco hyemalis*), and American Tree Sparrows (*Spizella arborea*) during several winters in South Dakota. They immediately brought them to the laboratory and measured their basal and summit metabolic rates. They found that basal and summit metabolic rates were higher in birds caught in colder than in warmer winters. They also found that a good predictor of how high these rates were was how cold it was the week before the birds were caught. Recent studies of juncos in the lab have revealed that cold exposure leads to dramatic increases in summit metabolic rate and the expression of genes that encode key metabolic enzymes (Stager et al. 2015a). These changes were more dramatic than those induced by changes in photoperiod, an environmental cue that signals the onset of winter. These results suggest that increases in the capacity to generate heat in juncos is a direct response to cold exposure, rather than an anticipatory response to winter onset. Chickadees also appear to use cold temperature as a cue to up-regulate their capacity to generate heat (Swanson and Olmstead 1999). Moreover, in comparisons among species that occur in a variety of environments, mean daily winter temperatures strongly predict mass-specific summit metabolic rates among species, and minimum winter temperature predicts variation in metabolic scope (the difference between mass-specific basal and summit metabolic rates) (Stager et al. 2015b). Taken together, these results demonstrate that the ability to up-regulate thermogenic capacity in response to cold temperatures strongly influences the geographic distributions of birds.

Small birds in winter not only increase their ability to generate heat, they also reduce heat losses. Agnes Lewden and her collaborators (2014) measured the body temperature of Black-capped Chickadees in the winter and found that on colder days chickadees become hypothermic. The normal temperature of chickadees is 41°C, whereas that of some individuals on really cold days (−15°C) was as low as 35.5°C. During the night, Black-capped Chickadees find an old nest or a hollow stump to roost and lower their body temperature even more than during the day, to about 30°C. By lowering their body temperature on cold days and nights, chickadees reduce the gradient with the environment and hence decrease the rate of heat loss. The increase in metabolic rate and body temperature that birds can undergo when exposed to natural cold temperatures is an example of both flexibility in physiological characteristics (what is called **phenotypic flexibility**; box 7.2 on page 00) and of **acclimatization**. The term acclimatization refers to changes in the expression of a characteristic that result from exposure to changes in environmental conditions in free-living birds. In contrast, the changes of bird characteristics due to changing conditions in the laboratory is called **acclimation**.

Emperor Penguins (*Aptenodytes forsteri*) are the only birds that breed in the Antarctic winter. Males and females court for about six weeks. Females then lay a single egg and pass it

PHENOTYPIC PLASTICITY IN BIRDS

The phenotype of an organism (i.e., the set of an individual's observable traits) is the result of the interaction between genes and the environment. The phenomenon of genotypes that lead to different phenotypes under different environmental conditions is called **phenotypic plasticity**. Phenotypic plasticity can take many forms: birds can differ in phenotype because they developed in different environments. This is called **developmental plasticity** and is typically irreversible. For example, when Peter Boag (1987) fed Zebra Finch (*Taeniopygia guttata*) nestlings on diets with high and low protein content, the chicks fed low-protein diets were smaller than those fed high-protein diets and remained small throughout their lives. Birds can also change their phenotypes reversibly and temporarily in response to changing environments or ecological demands such as migration and reproduction. This chapter has many examples of this type of **phenotypic flexibility**. The laboratory studies of physiological acclimation and the field studies of acclimatization that bird physiologists do all the time are examples of research into the phenotypic flexibility of birds. Finally, many bird species change their morphology and physiological characteristics seasonally. Rock Ptarmigan (*Lagopus muta*) are cryptic most of the year. In summer, their plumage is mottled dark brown, black, and grayish—a good camouflage for the tundra's summer vegetation. In winter, it is spotless white and matches the snow-covered ground. The ptarmigan's changing colors are an example of **life-cycle staging**, in which phenotype depends on season and/or the life stage of the individual. The following table, extracted from Piersma and Drent (2003), summarizes the three types of phenotypic plasticity that we often find in birds.

Plasticity Category	*Is phenotypic change reversible?*	*Does it occur within a single individual?*	*Is it seasonally cyclic?*
Developmental Plasticity	No	No	No
Phenotypic flexibility	Yes	Yes	No
Life-cycle staging	Yes	Yes	Yes

to a male who cradles it in a skinfold between his legs called a brood pouch. Then the female departs in a long march to the ocean to feed. Males incubate the eggs for over two months. Males fast from the beginning of courting to the time when females return to feed chicks after they have hatched. The success of males while courting and incubating the egg depends on how good they are at using their energy reserves efficiently. To save energy, Emperor Penguins aggregate in huge groups packed close together. Huddling in groups has two major advantages: (1) it reduces cold-exposed surface area and (2) it increases the temperature inside of the group. Huddling penguins have a metabolic rate that is about half of what they would have if they were alone (Gilbert et al. 2008), and they burn a lot less body reserves. Penguins constantly shuffle from the cold-exposed edge of the group to the inside, forming wavelike movements within the huddle (Gerum et al. 2013). The result is that all penguins in the group share energy savings fairly. Huddling has been studied in 25 bird species in nine families (Gilbert et al. 2010), but it is likely more widespread. Wojciechowski et al. (2011) found that migrating Blackcaps (*Sylvia atricapilla*) huddle when they stop to rest and feed at stopover sites. Huddling reduces metabolic rate and therefore facilitates the accumulation of fat reserves at stopover sites. Huddling is common in small birds that must cope with very cold winters, such as chickadees and Golden-crowned Kinglets (*Regulus satrapa*), and may be more common in small, migratory birds than previously thought.

Maintaining a high body temperature by the production of metabolic heat is very costly. As we have seen, birds reduce these costs by behavioral and physiological means: they choose microenvironments that reduce heat loss, they huddle, and they sometimes lower their body temperature. Birds can lower their body temperature to save energy in response to increased energy demands caused by cold temperatures or reduced availability of food, or to be able to gain more reserves from food even if it is abundant. This lowering of body temperature is not an uncontrolled process, which is why physiologists call the phenomenon **facultative hypothermia**. Facultative hypothermia has been observed in birds ranging in size from tiny hummingbirds (Booted Racket-tails, *Ocreatus underwoodii*, 2.7 g) to massive Eurasian Griffons (*Gyps fulvus*, 6,500 g). McKechnie and Lovegrove (2002) found reports of facultative hypothermia in 96 bird species in 29 families and 11 orders. The phenomenon is clearly widespread. Lowering of body temperature comes in two forms: rest-phase hypothermia and torpor. Birds in rest-phase hypothermia remain alert and are capable of flight. In contrast, birds in torpor are lethargic, often completely immobile, and unable to respond to external stimuli.

Facultative hypothermia appears to be very common in birds, and torpor has been reported in eight orders (Coraciiformes, Coliiformes, Apodiformes, Trochiliformes, Strigiformes, Caprimulgiformes, Columbiformes, and Passeriformes; Ruf and Geiser 2015). Because they are small, hummingbirds have very high mass-specific metabolic rates, and therefore they must feed on prodigious amounts of nectar. Because they find flowers by sight, they cannot feed at night. If hummingbirds maintain their high rates of metabolism throughout the night, they use their fat reserves very quickly. This is especially true if the night is cold. Furthermore, migrant hummingbirds can accumulate fat faster if they reduce the rate at which they use energy to thermoregulate at night. To save energy, hummingbirds often enter into torpor. When they enter into torpor, their body temperature drops precipitously, and with it their metabolic rate (Bicudo 1996). The metabolic rate of a torpid hummingbird can be 20 times lower than that of an active one (fig. 7.5). Hummingbirds can maintain a low metabolic rate for several hours. To arouse from torpor, hummingbirds increase their metabolic rate by shivering vigorously. Their body temperature increases by about 1°C per minute (Bicudo 1996). The rate at which temperature increases during arousal is faster in smaller than in larger birds (this is yet another example of a trait that depends predictably on body size). Hence, it is not very surprising that deep hypothermia and torpor are more common in small than in large birds (Ruf and Geiser 2015). The eight-gram Andean Hillstar (*Oreotrochilus estella*) can drop its body temperature to about 7°C (Carpenter 1974), whereas the Australian Tawny Frogmouth (*Podargus strigoides*, 500 g), one of the largest birds capable of entering torpor, drops it to slightly less than 30°C (Körtner

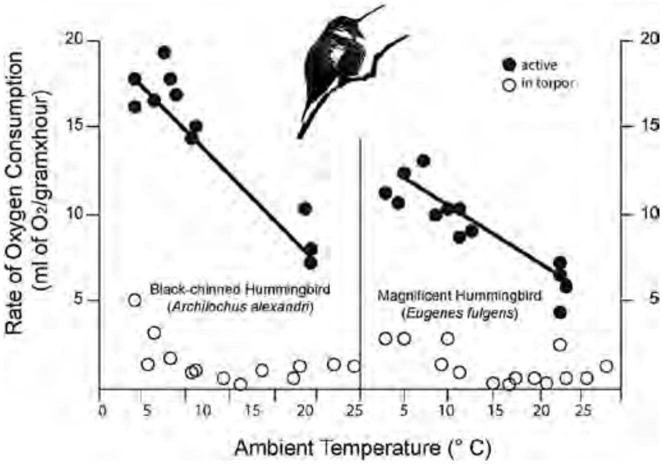


Figure 7.5. When in torpor, hummingbirds lower their body temperature and therefore the gradient between body and environmental temperature. Their metabolic rate drops and they save energy. *Redrawn from Hainsworth and Wolf 1978.*

et al. 2001). Hibernation is a form of torpor that lasts longer than 24 hours (Ruf and Geiser 2015). Many mammals hibernate, but as far as we know only one bird species, the Common Poorwill (*Phalaenoptilus nuttallii*), does. The Native America Hopi call Common Poorwills Hölchoco, "the sleeping ones." They likely knew that these birds were capable not only of entering torpor, but of staying inactive and seemingly torpid for over 10 days in the winter (Woods and Brigham 2004).

Birds in a Warming World

In 1932, a heat wave hit south central Australia. Temperatures reached over 49°C (over 120°F) and thousands of Budgerigars (*Melopsittacus undulatus*) and Zebra Finches (*Taeniopygia guttata*) died (McKechnie and Wolf 2010). The frequency of heat waves in the arid and semiarid areas of the world is increasing as the planet's atmosphere warms due to human emission of greenhouse gases. How will birds cope with these extreme events? Will we witness bird die-offs resulting from heat waves more frequently? Birds rely on both finding suitable cooler microclimates to avoid the hottest part of the day and on the evaporation of body water to cool themselves. Several species of storks and New World vultures excrete on their legs, and the evaporation of the liquid cools them down (Kahl 1963). When ambient temperature is higher than body temperature, birds lose water through their skin (**cutaneous evaporation**) and through the respiratory tract by panting. Some bird species supplement panting by vibrating the throat muscles in a behavior called gular fluttering. As ambient temperature increases above body temperature, the rate at which birds evaporate water (evaporative water loss) increases linearly (fig. 7.6). When temperatures become too high, though, birds lose the capacity to thermoregulate, become too hot (**hyperthermic**), and die. Andrew McKechnie and Blair Wolf (2010) combined data on body mass and evaporation rates and predicted ambient temperatures in two desert localities in Australia (Birdsville) and the United States (Yuma) to estimate bird survival during heat waves. Their results are sobering. They predicted reduced survival times and presumably increased frequency of bird die-offs caused by heat waves in the near future. Because the rate of evaporative water loss with temperature is steeper in smaller birds, they predicted stronger effects on smaller than on larger birds. Climate change, therefore, might have an impact on bird community composition in hot deserts (McKechnie and Wolf 2010).

Figure 7.6. If ambient temperature (Ta) becomes too hot, the rate at which birds lose water by evaporation to regulate their body temperature increases linearly. After Whitfield et al. 2015. The photographs depict a Sociable Weaver and the massive nests of this species. *Photo of Sociable Weaver by Johan Grobbelar. Photo of nest by Robert Thomson. With permission.*

RESPIRATION

Pathway of Oxygen

To maintain their active lifestyles and high body temperatures, birds need to transport oxygen efficiently from the atmosphere to respiring cells inside their bodies (fig. 7.7). The transport of oxygen from the lungs, through the blood, and on to working tissues is accomplished by the coordinated efforts of the respiratory and circulatory systems. Birds have evolved remarkably efficient lungs, powerful hearts, and extensive capillary networks to accomplish this vital, life-sustaining process. Perhaps the most distinctive feature of

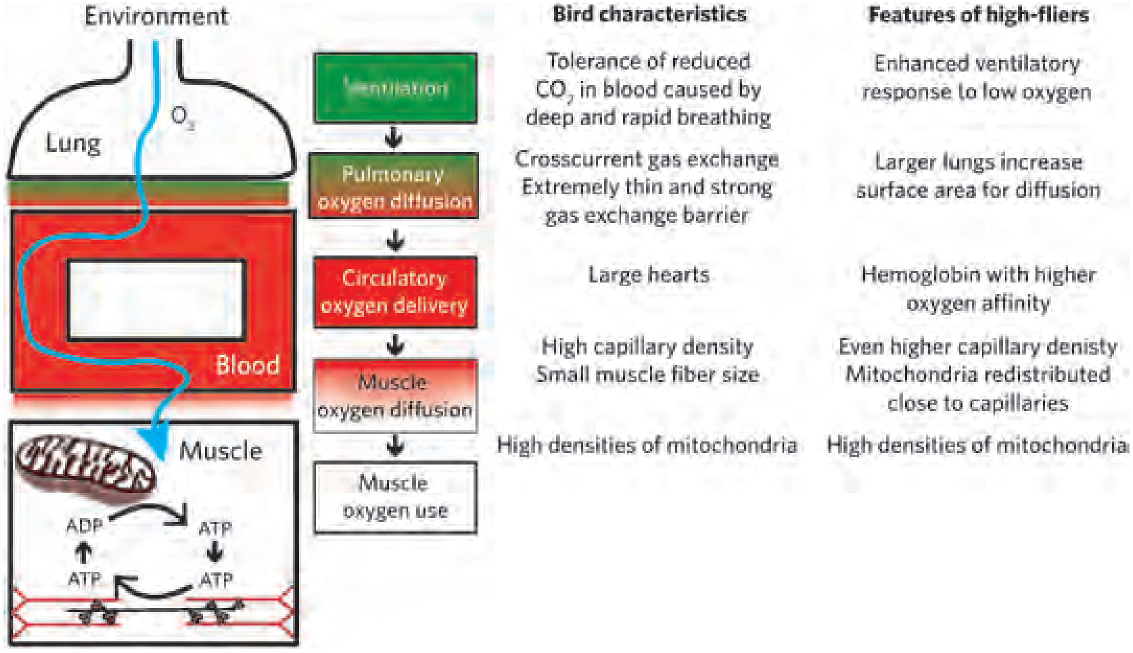


Figure 7.7. Increased aerobic performance under hypoxia requires modifications of several integrated steps in the oxygen transport cascade: these include breathing, diffusion of oxygen at the lung into the bloodstream, bloodstream circulation to transport oxygen throughout the body, diffusion of oxygen from the bloodstream into the cells of respiring tissues (e.g., muscle cells), and, finally, transport of oxygen to mitochondria to generate ATP via oxidative phosphorylation. All birds may be preadapted for increased aerobic performance under hypoxia due to modifications of each of the integrated steps in the oxygen cascade. The features that are common to all birds and enhance aerobic performance are accentuated in birds that fly at very high altitudes, such as Bar-headed Geese. *Modified from Scott 2011.*

the avian respiratory system is related to the structure and function of the lungs. In contrast to mammalian lungs, air flows in a single direction across the gas exchange surfaces of the avian lung. This unidirectional flow of air is accomplished by structural modifications of the lung itself, and by the presence of air sacs that act as baffles to store and move air through the respiratory system (fig. 7.8). A single breath of air moves through the respiratory system in a four-step process that includes two inhalation and exhalation cycles (fig. 7.8). Birds lack a diaphragm, the muscle that mammals use to create the changes in pressure within the thoracic cavity that inflate and deflate the lungs. Instead, birds breathe by muscular contractions that lower and raise the sternum and expand and contract the rib cage. The movement of the sternum and rib cage allows the air sacs to inflate (inhalation) and deflate (exhalation), forcing air to move through the intricate series of air sacs and across the parabronchioles within the lung.

With the first inhalation, the sternum lowers and the rib cage expands, allowing a breath of air to travel down the trachea and into the posterior air sacs. Upon the first exhalation, muscular contractions again raise the sternum and compress the posterior air sac, which forces the fresh, oxygen-rich air into the lungs through a series of finely subdivided parabronchioles. Radiating from the parabronchioles are air capillaries, the surfaces where gas exchange occurs. A dense network of capillaries within the lung crosses the parabronchioles perpendicularly, and this orientation has important consequences for the efficiency of oxygen and carbon dioxide exchange (see below). With the second inhalation, the oxygen depleted, carbon dioxide–rich air moves from the lungs into the anterior air sacs, where it is held until the second exhalation. During this final exhalation, the air leaves the anterior air sac, returns to the trachea, and is expelled. This four-step process ensures that nearly all of the air within the lung is turned over with each cycle—nearly all of the air within the lung is expelled, and it prevents mixing of fresh incoming air with expelled oxygen-depleted air. Birds avoid the problem that mammals have of having a dead space of stale air that stays in the lungs when breathing in and out. The bird's complex breathing pattern is enhanced during powered flight, which is an exceptionally aerobically demanding form of locomotion (chapter 10). During flight, contractions of the flight muscles enhance the movement of the sternum, rib cage, and furculum (or wishbone) to pump air more forcefully through the respiratory system (Jenkins

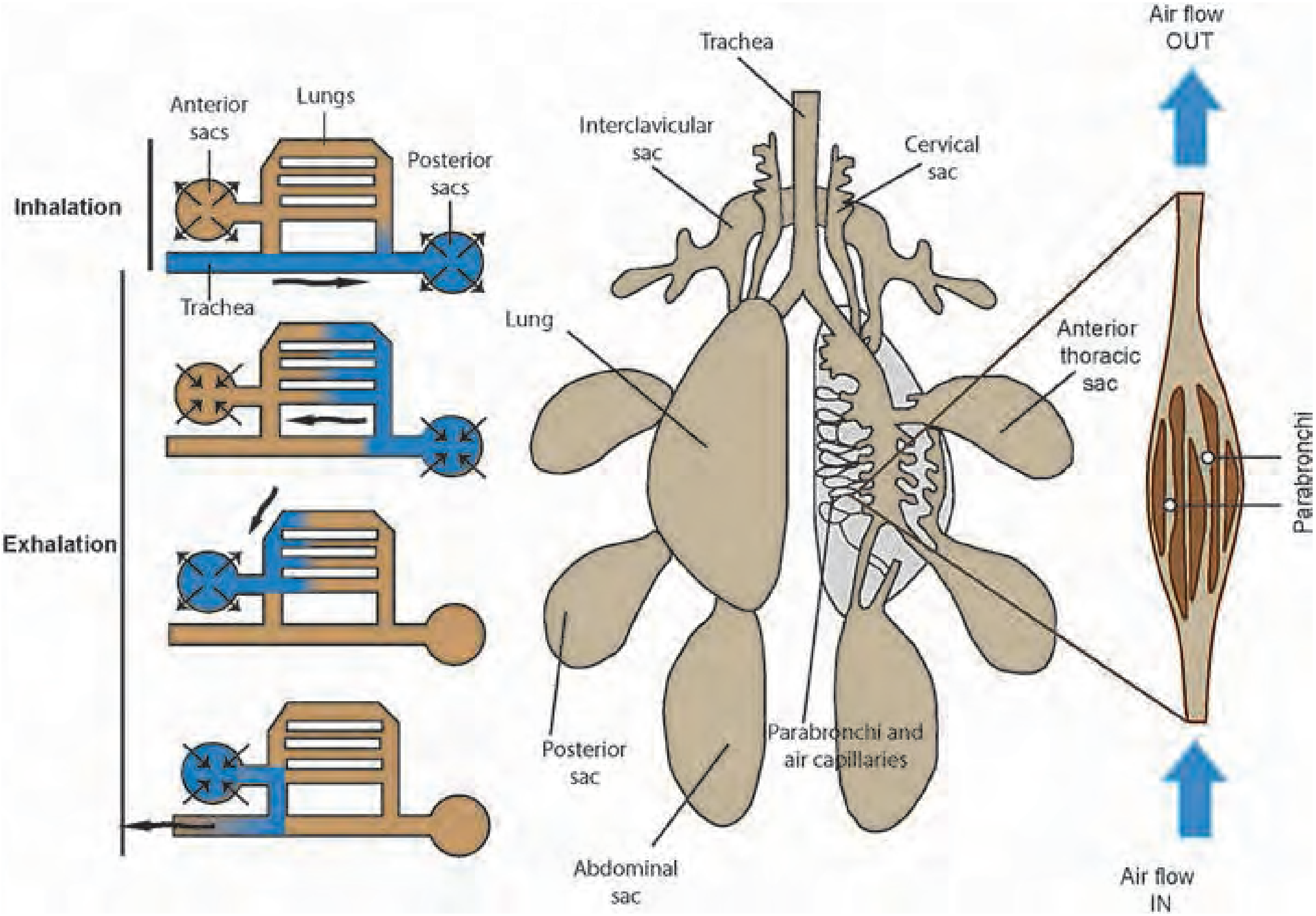


Figure 7.8. The avian respiratory system. *A*, Air movement is unidirectional through the avian respiratory system and a single breath of air requires two full respiratory cycles to move through the system. In the first inhalation, air moves into posterior air sacs through the trachea. Upon exhalation, air is forced from the posterior air sac across the lung, completing the first respiratory cycle. In the second inhalation, air move from the lungs into the anterior air sacs, and a new second breath enters the system. Upon the second exhalation, the first breath is forced out from the anterior air sacs and out the trachea, completing the second respiratory cycle, while the second breath is moved into the lungs. This cycle then repeats in a living, breathing bird. *B*, Major components of the avian respiratory system. *C*, Detailed view of air movement through primary and secondary bronchi within the lung, and the orientation of the parabronchi.

et al. 1988). Thus, the action of flying allows birds to breathe more deeply just when they need it the most.

In addition to the air sacs that allow for unidirectional air flow, another key innovation of the avian respiratory system lies in the structural properties of the parabronchioles and the orientation of the capillaries that service them. Air enters the lung from the posterior air sac through a pair of primary bronchi, which are further subdivided into parabronchioles, rigid air tubes that are intertwined with capillaries. Because the parabronchioles run perpendicular to the capillaries in the lung, they create a crosscurrent exchange system that is exceptionally efficient for oxygen and carbon dioxide exchange. As air flows through the parabronchioles, oxygen passively diffuses along its concentration gradient into the capillaries carrying the deoxygenated blood from the body. When blood flows through capillaries that are perpendicular to the flow of air through the parabronchioles, the orientation creates a crosscurrent exchange system that allows birds to obtain higher oxygen concentrations in their blood than that of the expired air. This mechanism is in stark contrast to that in mammalian lung, where air flows into tiny sacs inside of the lung (called alveoli) that are enmeshed in capillaries. Because the mammalian lung lacks the avian crosscurrent exchanger, the oxygen concentration in mammalian blood can be *at best* equal to that in the expired air. In addition, the gas exchange surfaces of birds are extremely thin, which reduces the distance over which oxygen must diffuse to enter the bloodstream. However, despite their thinness, the gas exchange surfaces of birds are mechanically stronger than those of mammals, which allows them to withstand greater increases in pulmonary pressure and blood flow (West 2009). Together these anatomical modifications allow birds to extract more oxygen from the air they breathe than do mammals.

Once oxygen enters the bloodstream, the vast majority is bound to hemoglobin within red blood cells, as it is in other vertebrates. Birds differ from other terrestrial vertebrates in their comparably large and powerful hearts, which pump this hemoglobin-bound oxygen throughout the body. Like mammals, birds have four-chambered hearts, but birds have larger hearts compared to similarly sized mammals. Birds also have slower resting heart rates than mammals (Grubb 1983). However, their increased size enables avian hearts to pump greater volumes of blood per stroke than those of a similarly sized mammal (Grubb 1983). These large heart masses and stroke volumes allow bird hearts to move more blood per unit time with fewer heart contractions than a mammal of similar size, suggesting that birds have a very high capacity for circulatory oxygen transport. Birds also have a very high capacity for oxygen diffusion from the blood into working tissues. Compared with the locomotory muscles of mammals, the flight muscles of birds have a much higher surface area of capillaries to muscle fiber ratio (Matheiu-Costello 1991). Bird brains and hearts also appear to have greater capillary densities than those of mammals (Faraci 1991). Because capillaries supply oxygen to muscles and other working tissues, these increases in capillary density should provide birds with a greater surface area for oxygen diffusion into metabolically active tissues.

In summary, modifications of nearly every step of the oxygen transport cascade allow birds to meet the demands of their active lifestyles and have transformed them into some of the most impressive aerobic athletes in the animal world. These modifications have also allowed them to exploit oxygen-poor environments during critical periods of their lives. During their annual migrations, some birds fly higher than any other terrestrial animal, and many species breed and forage at high-elevation habitats around the world. In the next section, we consider how the respiratory and circulatory systems of these amazing birds are modified to allow them to exploit these inhospitable environments.

Birds at High Altitude

Among the most remarkable aspects of avian physiological performance is that many birds utilize the most metabolically demanding form of animal locomotion—powered flight—under severely oxygen-poor high-altitude conditions. The partial pressure of oxygen drops rapidly with altitude. Although the percentage of oxygen in air is about the same at all elevations (21 percent in dry air), at high elevation there are fewer oxygen molecules than at sea level. For example, the partial pressure of oxygen in the air on the summit of Mount Everest is only 35 percent of that at sea level, which means that a single breath of air contains only about 35 percent of the oxygen that is available in a breath at sea level. Bar-headed Geese (*Anser indicus*) famously migrate over the highest peaks in the Himalayas while elite mountaineers struggle to climb the same peaks with the help of supplemental oxygen. Black-breasted Hillstar hummingbirds (*Oreotrochilus melanogaster*) hover in front of flowers on the Andean Altiplano at elevations above 4,000 m. In 1973, a soaring Ruppell's Griffon (*Gyps rueppellii*) collided with a commercial jetliner soaring at an altitude of 11,278 m (37,000 ft) (Laybourne 1974). Exposure to this altitude could induce unconsciousness and death within minutes of exposure in humans. The ability of these birds to perform such amazing physiological feats stems, in part, from the efficient cardiorespiratory systems that are common to all birds. Birds in general are preadapted for high performance in hypoxic environments, but extreme high flyers also exhibit a number of specific cardiorespiratory adaptations that underlie their remarkable abilities. High-altitude athletic performance has been best studied in Bar-headed Geese (Scott et al. 2015), so we use them as a case study in evolutionary adaptation for high-altitude performance.

In early reports, mountaineers described observing Bar-headed Geese flying over the highest peaks in the Himalayas during their spring migration to India (Swan 1970). Ever since these early reports, news of these remarkable flights have captivated avian physiologists, and several decades of research have documented the numerous physiological attributes that give Bar-headed Geese their abilities. First among these is an efficient breathing pattern: Bar-headed Geese take fewer but deeper breaths than lowland geese when exposed to low oxygen conditions, and this breathing pattern increases their total ventilation nearly twofold over their lowland counterparts (Scott 2011). These alterations of breathing pattern are enhanced by a dramatic increase in surface area of the lungs; the lungs of Bar-headed Geese are more than 25 percent larger than those of the lowland geese of similar body size (Scott 2011). In addition, Bar-headed Geese are also capable of greater circulatory oxygen delivery under hypoxia. This enhancement is driven in large part by changes in the functional properties of hemoglobin and physiological changes that enhance oxygen supply to the heart under hypoxia. The hemoglobin of adult Bar-headed Geese has much greater binding affinity for oxygen than that of lowland waterfowl, and this enhancement of binding affinity should help increase blood oxygen saturation under severe hypoxia. Changes in temperature also have profound effects on the ability of hemoglobin to bind oxygen. The hemoglobin of Bar-headed Geese is remarkably sensitive to changes in temperature. It has high affinity for oxygen in the lung's capillaries, where it takes up the scanty oxygen from the cold air, and low affinity when it delivers it to the hot flying muscles. These changes in hemoglobin function may allow Bar-headed Geese to extract more oxygen from the cold, hypoxic air at high altitude, while also allowing effective unloading of oxygen to warm muscles, to power their long-distance migratory flights.

Bar-headed Geese also possess cardiac adaptations to ensure that, once oxygen is bound to hemoglobin, it can be transported to the cells that need it. Their hearts have nearly 40 percent greater capillary density than those of geese that fly at lower altitudes, and this enhancement helps maintain adequate oxygen supplies to support high cardiac output during high-altitude flight (Scott 2011). Finally, Bar-headed Geese have also altered the structural properties and metabolic profiles of their flight muscles (Scott 2011). The flight muscles of Bar-headed Geese have greater capillary densities than lowland waterfowl, but the differences in muscle go even deeper. Within muscle fibers of the flight muscles, the mitochondria tend to be located closer to the cell membrane, which reduces the distance that oxygen must diffuse to reach these cellular power plants. Finally, the functional properties of a key metabolic enzyme that is expressed in the mitochondria of flight muscles, cytochrome c oxidase, are altered in Bar-headed Geese (Scott 2011). Although the physiological significance of this alteration is still being determined, it may play a role in reducing oxidative stress and cellular damage by reducing the production of damaging reactive oxygen species (ROS) during high-altitude flight (Scott 2011). In short, the amazing athletic performance of Bar-headed Geese is thanks to multiple complementary physiological traits that alter nearly every aspect of the oxygen-transport cascade (fig. 7.9). No other extreme high-altitude flyer has been as intensively studied as the Bar-headed Goose, but a number of these modifications have been documented in other high-altitude specialists. Modifications of hemoglobin function seem to be common among high-altitude bird species (see below), and Gray-crowned Rosy Finches (*Leucosticte tephrocotis*), which breed above the tree line in the mountain ranges of western North America, also have very high capillary densities in their leg and flight muscles compared with lowland finches (Mathieu-Costello 1998). Determining whether adaptation to life at high altitude generally involves the type of wholesale alteration of the oxygen transport cascade that is seen in Bar-headed Geese is an area of active research.

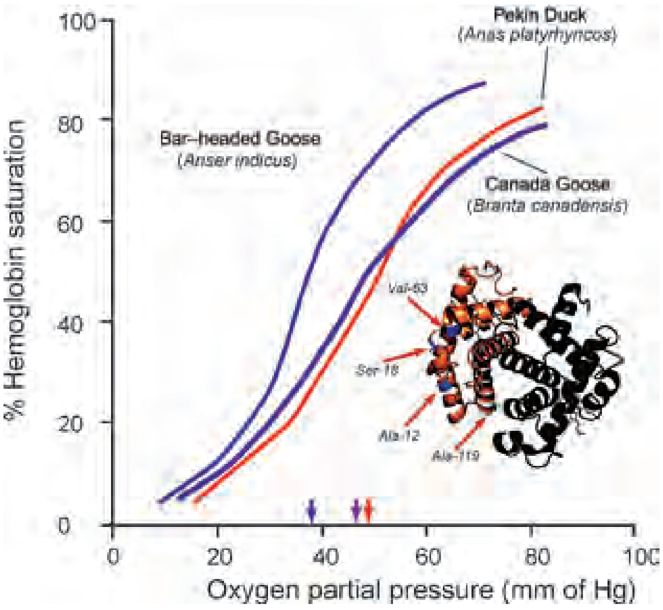


Figure 7.9. Hemoglobin oxygen dissociation curves for three species of waterfowl. The curve of the Bar-headed Goose is shifted to left, indicating that its hemoglobin has a higher affinity for oxygen than those of lowland species (Canada Goose and Pekin Duck). Hemoglobin oxygen affinity is often measured as a p50 value, the partial pressure of oxygen at which 50 percent of the hemoglobin in a sample is bound to oxygen. The p50 values for each species are shown as arrows in the x-axis and represent the partial pressures of oxygen at which 50 percent of the binding sites of hemoglobin are occupied by oxygen. The low p50 value and left-shifted curve for Bar-headed Goose indicates that its hemoglobin is better able to saturate at low partial pressures of oxygen, which is beneficial at high altitude where the partial pressure of oxygen is reduced. The inset depicts the four amino acid substitutions that distinguish the α- subunits of Bar-headed Goose hemoglobin from those of the lowland species (Natarajan et al. 2015). The increased hemoglobin affinity of Bar-headed Geese is due, at least in part, to the effects of these mutations. *Modified from Scott 2011.*

A recurring theme in avian adaptation to high-altitude flight and life in high-elevation habitats is the repeated adaptive modifications of hemoglobin function in high-altitude specialists. In addition to Bar-headed Geese, a number of other high-altitude species also possess hemoglobins with very high binding affinities for oxygen. An increase in hemoglobin oxygen affinity is beneficial at very high elevations because it helps ensure adequate oxygen loading at the lungs. To understand why this is the case, consider the relationship illustrated in figure 7.9, where it can easily be seen that at high oxygen partial pressures, the vast majority of hemoglobin is bound to oxygen, but the opposite is true at very low partial pressures of oxygen. The relationship between hemoglobin saturation and oxygen partial pressure is often referred to as the hemoglobin-oxygen dissociation curve, and this curve describes many of the functional properties of hemoglobin variants that are relevant for adapting to low-oxygen conditions. The oxygen affinity of a particular hemoglobin variant is often measured as a P_{50} value, which is simply the partial pressure of oxygen at which 50 percent of the hemoglobin in blood is bound to oxygen. Thus, when comparing two hemoglobin variants, the one with the lowest P_{50} value will have the highest oxygen affinity, because it is able to achieve 50 percent saturation at lower oxygen partial pressures. In fact, a variant with a low P_{50} values often has a higher percent saturation at most physiologically relevant oxygen partial pressures; its entire oxygen dissociation curve is shifted to the left. Because the primary challenge of high altitude is the reduced partial pressure of oxygen, a hemoglobin variant with a high oxygen affinity and a left-shifted oxygen dissociation curve would be beneficial to high-altitude specialists, because it would allow for greater hemoglobin oxygen saturation in face of the reduced oxygen partial pressure that occurs at high elevation. Consistent with this expectation, an increase in hemoglobin oxygen affinity is perhaps the most common evolutionary response to life at high altitude.

This pattern of repeated convergent evolution is perhaps best illustrated in Andean hummingbirds. Hummingbird diversity peaks in the Andes Mountains of South America, where several species occur at very high elevations, which is somewhat surprising, given that hummingbirds have exceedingly high oxygen demands. Upward of 150 species of hummingbirds are known to occur in the Andes. This impressive radiation is associated with several independent colonizations of elevations above 3,000 m, and subsequent recolonizations of lowland habitats by highland ancestors (McGuire et al. 2014, Projecto-Garcia et al. 2013). These elevational shifts are associated with repeated evolution of increased hemoglobin oxygen affinity in highland species. Remarkably, however, colonization of lowland habitats by highland ancestors is associated with evolved *reductions* in hemoglobin oxygen affinity (Projecto-Garcia et al. 2013). Why should reduced oxygen affinity evolve at low elevation? Again, examination of the oxygen dissociation curve in figure 7.9 holds the answer. Because a leftward shift in the oxygen dissociation curve means that oxygen will remain bound to hemoglobin at low partial pressures of oxygen, increasing hemoglobin's affinity for oxygen may reduce its ability to unload oxygen at the peripheral tissues. In working tissues, the partial pressure of oxygen is reduced through the consumption of oxygen in respiring cells. All else being equal, a hemoglobin variant with high oxygen affinity will necessarily unload less oxygen for a given reduction in the partial pressure of oxygen. Thus, at high elevations the challenge lies in simply ensuring that hemoglobin is able to saturate with oxygen at the lungs. Issues of oxygen delivery at the peripheral tissues are secondary if adequate arterial oxygen saturation cannot be maintained. Conversely, at low elevations, pulmonary oxygen loading is not a challenge, so the adaptive premium shifts toward enhancing hemoglobin's ability to unload oxygen at working tissues. Remarkably, these adaptive shifts in hemoglobin structure and function have been linked to repeated genetic changes at just two amino acid residues in the beta chains of adult hemoglobin (Projecto-Garcia et al. 2013). Whether this remarkable level of convergent evolution is common in other high-altitude birds remains to be seen. A similar study of Andean ducks has revealed similar patterns of convergent evolution in hemoglobin function at high altitude, but in these cases, the genetic basis for the convergent trait is not conserved. Different mutations tended to underlie the enhancement of hemoglobin oxygen affinity in independent highland lineages (Natarajan et al. 2015). In other cases, colonization of high elevations is not associated with modification of hemoglobin function at all (Cheviron et al. 2014), suggesting that modification of hemoglobin oxygen affinity is not necessarily a requirement for avian life at high elevation.

DIGESTION AND NUTRITION

The Gut and the Digestive Process

Birds feed on a wide variety of food types. These range from nectar and pollen to other animals. Chapter 15 illustrates the diversity of beak morphologies associated with these diets. Because different food types contain widely different compositions of macronutrients (lipids, proteins, and carbohydrates), and because each of these macronutrients must be assimilated by different processes, the digestive system of birds is also highly variable in morphology and physiological function. To appreciate the diversity in avian digestive systems (fig. 7.10), it is useful to review briefly how vertebrates assimilate different food types. We use the word **assimilation** to mean the chemical breakdown of complex molecules and the transport of the smaller molecules that result from these enzymatic processes across the walls of the gut. Box 7.3 on page 00 shows the mechanisms that birds use to assimilate macronutrients.

The gut is a (relatively) simple organ in which each compartment is specialized to perform different functions (box 7.3 on page 00). The esophagus delivers food to the crop, an extensible sac where food can be stored temporarily and released into the stomach. Because birds do not have teeth, they swallow food mostly whole into the stomach. The bird's stomach has two parts. A glandular section called the proventriculus secretes hydrochloric acid and the enzyme pepsin. The function of this section is to initiate the digestion of protein. The proventriculus is followed by an organ called the gizzard. The gizzard is a muscular mill lined with

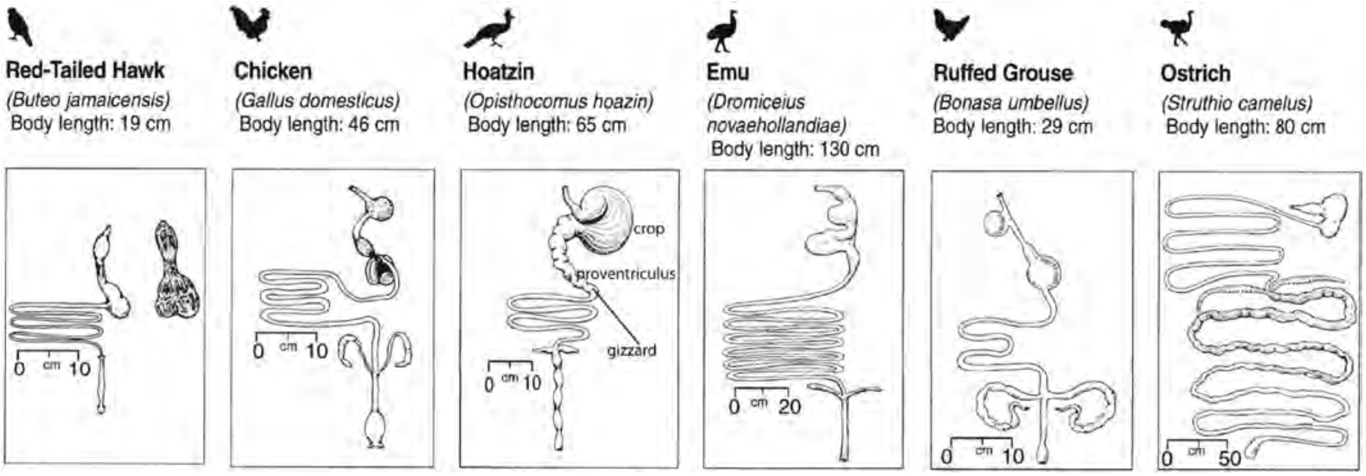


Figure 7.10. The morphology of the digestive system in birds varies among groups. For example, some bird groups lack cecae (hummingbirds and swifts, woodpeckers, and kingfishers). Others have very small ones (e.g. passerines, falcons, and storks). Some groups have large cecae (e.g., ostriches and tinamous, pheasants, quail, and grouse). The relative proportion of each segment of the gastrointestinal tract differs between species depending on diet. After Stevens and Hume 1998. *With permission from the American Physiological Society.*

a horny (keratinous) material (called koilin) that protects its inner walls and helps grind up food. The gizzard of birds appears to be as effective in reducing the size of food particles as the teeth of mammals (Fritz et al. 2011). The gizzard often contains small stones (called grit or gastroliths) that the birds ingest and that aid in the mechanical grinding of foods. Ducks and geese (Anseriformes), grain-eating birds such as quail (Galliformes), and many dove species (Columbidae) can confuse lead shotgun pellets and granular pesticides for grit and become poisoned (Gionfrido and Best 1996).

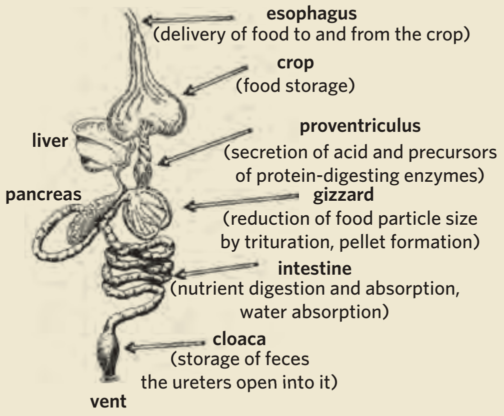
The gizzard varies in size and strength. It is large and very strong in granivores and herbivores and weaker in insectivores and carnivores (Piersma et al. 1993). Red Knots (*Calidris canutus*) feed on mollusks and use their muscular gizzards to crack the shell. When Theunis Piersma and his collaborators fed captive Red Knots on soft food pellets, their gizzards became smaller and they were reluctant to feed on hard-shelled molluscs (Piersma et al. 1993). Wild Red Knots have larger gizzards and feed on hard-shelled mollusks readily. This is an example of how a digestive feature of birds can shape feeding preferences. In another set of experiments, Matthias Starck (1999) fed Japanese Quail (*Coturnix japonica*) on diets with increased fiber content and measured the size of their gizzards using ultrasonography (much as physicians use ultrasound to evaluate a human fetus' growth). When they were fed on high-fiber diets, the birds ate more, and their gizzards became larger. When Starck shifted birds to low-fiber diets, their gizzards became smaller. The gizzard shows reversible changes in response to diet: it shows phenotypic flexibility (box 7.2 on page 00).

Many bird species use the gizzard as a filter that retains undigested parts of prey such as bones, feathers, and insect exoskeletons. The gizzard molds the indigestible materials in a pellet that the bird regurgitates. Owls (Strigidae), hawks (Accipitridae), falcons (Falconidae), and bee-eaters (Meropidae) regurgitate pellets daily. Terns (Sternidae), herons (Ardeidae), and gulls (Laridae) regurgitate them less regularly (Errington 1930). Another interesting use of the gizzard is found in Phainopeplas (*Phainopepla nitens*), which feed on the berries of mistletoes and use their reduced gizzard to separate the berries' exocarps (peels) from the seed and pulp. Unlike seed-eating birds that grind up and digest seeds, Phainopeplas defecate long strings of sticky intact seeds that alternate with neatly folded packets of peels (Walsberg 1975; fig. 7.11). The seeds attach to branches, germinate, and start a new mistletoe infection.

Food exits the gizzard by the pylorus (box 7.3 on page 00) and enters the small intestine. The small intestine is the site where most nutrients are digested and absorbed. The pancreas secretes its enzymes into the small intestine, and the cells that line the walls of the small intestine have digestive enzymes on their membranes. They also have transporters that carry small molecules from the lumen of the intestine into the bird's body. Enzymes secreted into the lumen of the intestine and those found at the surface of intestinal cells act in series. For example, if a bird eats a starchy seed, the enzyme amylase secreted by the pancreas breaks starch's long chain of glucose into molecules made of two or three glucoses. These smaller molecules are then broken down into glucose by enzymes bound to the membrane of intestinal

HOW BIRDS ASSIMILATE NUTRIENTS

The assimilation of nutrients in food can be divided into three steps: First, food must be processed mechanically to increase the surface area in relation to volume of particles. Second, large molecules must be broken down into smaller molecules by enzymes secreted into the lumen of the digestive tract by a variety of cells in the stomach and the pancreas. These smaller molecules must then be reduced in size further by enzymes bound to the membrane of intestinal cells. The third and last step is the absorption of these molecules across the wall of the gut. For example, if a bird eats an insect, it first grinds it in the gizzard. The pepsin secreted by the proventriculus begins breaking the insect's protein into smaller peptides. Digestion continues in the intestine as a result of protein-digesting enzymes secreted by the pancreas. The resulting smaller peptides are broken up further by enzymes bound to the membrane of intestinal cells. The resulting amino acids and very small peptides are then transported into these cells. The exception to this general description of assimilation as enzymatic digestion followed by nutrient absorption are lipids and complex carbohydrates such as cellulose. Lipids are emulsified in the small intestine by bile salts secreted by the liver, digested by pancreatic enzymes called lipases, and the resulting molecules (single fatty acids and monoacylglycerides) diffuse into the cells of the intestine. Complex carbohydrates can be difficult to assimilate and are sometimes assimilated with the aid of microorganisms, and we discuss them in a later section. Undigested materials end up in the cloaca, where they are mixed with excreta. The gastrointestinal tract illustrated here in the figure is a schematic representation of that of a woodpecker. Woodpeckers lack cecae.



Steps in Food Assimilation

mechanical particle reduction
(gizzard)
⬇
digestion by luminal enzymes
(proventriculus, gizzard, intestine)
⬇
digestion by membrane-bound enzymes
(intestine)
⬇
absorption/uptake
(intestine)

Birds assimilate the nutrients in food with a series of stepwise processes that take place in the gastrointestinal tract. First food must be physically processed to reduce the size of particles, then nutrients are broken by digestive anzymes, and finally, the smallest chemical components of nutrients are absorbed across the walls of the gut.

enzymes. Finally, intestinal cells transport glucose. As you would expect, birds that eat a lot of starchy seeds, such as House Finches (*Carpodacus mexicanus*) and House Sparrows (*Passer domesticus*) have higher levels of pancreatic and intestinal enzymes that break up starch than birds with low intakes of starchy foods, such as American Robins (*Turdus migratorius*) and Barn Swallows (*Hirundo rustica*; Kohl et al. 2011). Curiously, when Kevin Kohl and his collaborators (2011) measured pancreatic and intestinal enzymes that digest protein in these birds, they found no correlation with protein intake. They hypothesized that even animals with low protein intakes must maintain relatively high levels of protein-digesting enzymes to absorb adequate amounts.

Specialized nectar-feeding birds such as hummingbirds (Trochilidae) have very high levels of the intestinal and membrane-bound enzyme that breaks up sucrose in nectar into glucose and fructose (Schondube and Martinez del Rio 2004). These birds feed on nectar with very high sucrose content. Hummingbirds love to visit feeders that contain only a solution of table sugar (almost pure sucrose) and water. In contrast, starlings (Sturnidae), thrushes (Turdidae), and mockingbirds (Mimidae) seem to lack the ability to digest sucrose and get sick when they feed on sucrose-containing food (Martinez del Rio 1990). However, European Starlings (*Sturnus vulgaris*) and American Robins (*Turdus migratorius*) are notorious pests of plantations of blueberries and grapes. They can feed on these sweet fruits because their pulp contains glucose and fructose rather than sucrose.

Like the gizzard, the small intestine has remarkable phenotypic flexibility in both size and function. It grows and

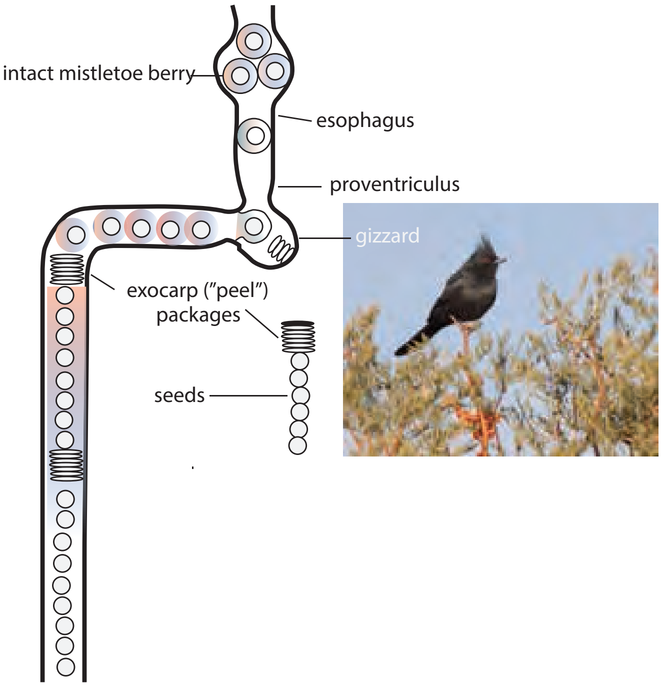


Figure 7.11. Phainopeplas (*Phainopepla nitens*) are fruit-eating birds that specialize in feeding on mistletoe berries. They use their gizzard to separate the seeds from the exocarps in order to assimilate the nutrients in the sticky pulp that surrounds the seeds. They defecate long strings of seeds that alternate with packages of peels/skins (technically called exocarps) neatly folded by the gizzard. You can sometimes find mounds of defecated mistletoe seeds under the perches favored by Phainopeplas. *After Walsberg 1975. Photo by Dave Kutilek used with permission.*

shrinks in response to environmental stimuli, and the enzymes in it change with diet (McWhorter et al. 2009). When birds are exposed to cold temperature, they must eat more to satisfy the increased energy costs of staying warm, and their gastrointestinal tracts grow. Scott McWilliams and his collaborators (1999) acclimated Cedar Waxwings (*Bombycilla cedrorum*) to either −21°C or 21°C. Cold-acclimated birds had to use more energy to thermoregulate and ate over 2.5 times more food. Their intestines were 22 percent heavier. Although the time that food stayed in the gut of cold-acclimated birds was shorter, the efficiency with which they extracted nutrients from it was only slightly (1.5 percent) lower than that of birds at 20°C (McWilliams et al. 1999). White-throated Sparrows acclimated to 21°C can increase their food intake by about 45 percent when temperature drops rapidly to −21°C. However this increase in intake in response to a quick change in energy demands is not sufficient to satisfy their energy costs, and they lose weight. If they are given enough time (50 days) to acclimate to −21°C, their guts increase in size, and they can then process enough food to maintain constant body weight (McWilliams and Karasov 2014). The bird gut has some spare capacity that can be harnessed immediately, but if energy demands increase too much, this spare capacity is not sufficient and the birds lose weight. Given time, birds can increase the gut's capacity and process more food, but clearly the gut can only increase in size up to a point (fig. 7.12). White-throated Sparrows increased their food intake by about 126 percent over their intake at 21°C when acclimated to really cold temperatures (−21°C), but could not increase it more.

Migratory birds also have phenotypically flexible guts. In preparation for migration, birds increase food intake (they become **hyperphagic**) so that they can store sufficient fuel reserves for the flight. The gut sometimes increases in size during these pre-migratory hyperphagic episodes (McWilliams and Karasov 2001). Migratory songbirds arrive to stopover sites to recover body condition and accumulate energy for the next leg of their journey. Often, these birds feed at low rates, and hence recover body mass slowly during the first days after arrival, and then much more rapidly. Birds in the laboratory also have this two-step recovery after they have been fasted and then fed as much as they want to eat. Why don't they eat as much immediately after they arrive to stopover sites? Most birds fast during migratory flights;

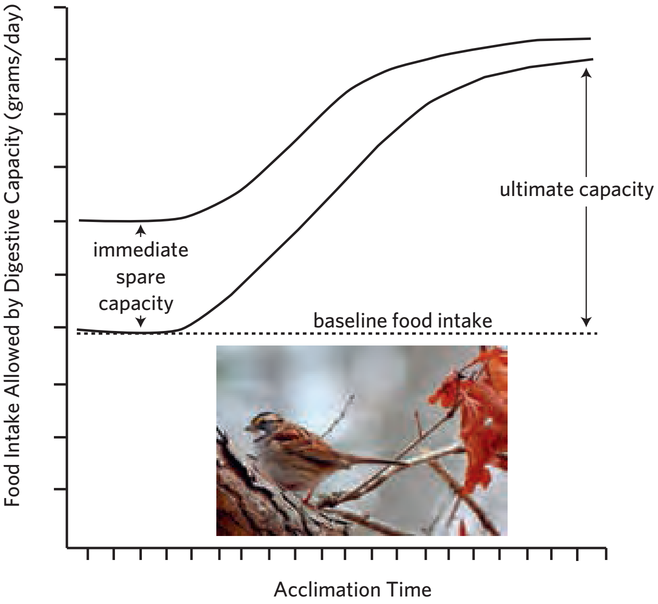


Figure 7.12. Schematic representation of the effect of the capacity to digest and absorb food (**digestive capacity**) and time of acclimation to conditions that demand higher intake such as increased energy losses in the cold. Birds appear to have modest instantaneous capacity to increase intake at first, but increase this capacity with exposure to the new conditions and to increased food intake. *After McWhorter et al. 2009. Photo by Shawn Billerman, used with permission.*

H. (BILL) KARASOV

Bill Karasov is a physiological ecologist that spends much of his time finding out how birds acquire resources such as food and water and how they cope with toxins and extreme environments.

As a junior at the University of Minnesota, Bill Karasov took a semester off to work at a kibbutz in Israel. Ironically, he was assigned to work at the chicken house. Little did he know that observing and doing research on birds would occupy a lot of his time during his future as a researcher. In the free time left from tending the chicken flock, he read Michael Evenari and colleague's (1982) book on the ecology of the Negev desert, and he became fascinated by the questions that physiological ecologists ask: How is it that birds can survive the scorching temperatures of tropical deserts or the frigid ones of the tundra? How is it that they can meet their nutritional requirements on diets as different as grass and nectar? Although his doctoral research at the University of California Los Angeles (UCLA) was on the adaptations of desert ground squirrels and lizards, he had been a bird-watcher since college and was soon hooked on birds as research organisms while working as a postdoctoral researcher in Jared Diamond's lab at UCLA. In his stint as a postdoc, Bill studied the digestive system of birds as well as that of members of all vertebrate classes. His work illustrates the great benefits of a broad comparative perspective, and of an integrative approach to research. Bill's work runs the gamut from working with molecules and cells in the laboratory to capturing and studying animals in the field. Because Bill's work is comparative and integrative, it is of interest to a broad swath of biologists. He has published over 200 papers, and a book, and has made remarkable discoveries (some of which are described in this chapter). As important as his scientific contributions are his efforts to train and mentor future generations of comparative biologists. Bill has trained many comparative physiologists over his career, both formally, as trainees in his laboratory (24 doctoral students, 16 masters students, 17 postdocs, and myriad undergraduates), and informally as one of the wise gurus of ecological physiology. When he was a graduate student, one of us (CMR) received a life-changing phone call from Bill. Bill invited Carlos to spend time in his laboratory in Madison, Wisconsin, to pursue common interests. He invited him and funded his research, although they had never met. Scientists can be competitive; we care about priority in discovery and of receiving credit for our findings. Bill Karasov's generosity as a mentor and adviser is unusual and, therefore, legendary.

exceptions are some swifts and swallows that feed on the wing. The guts of birds often decrease in size during long fasts and long migratory flights (see box 7.4 on page 00). Scott McWilliams and Bill Karasov (2001) suggest that, because birds lose gut tissue and therefore digestive function during migratory flights, they must rebuild the gut before they can take advantage of the food at stopover sites.

Herbivory in Birds

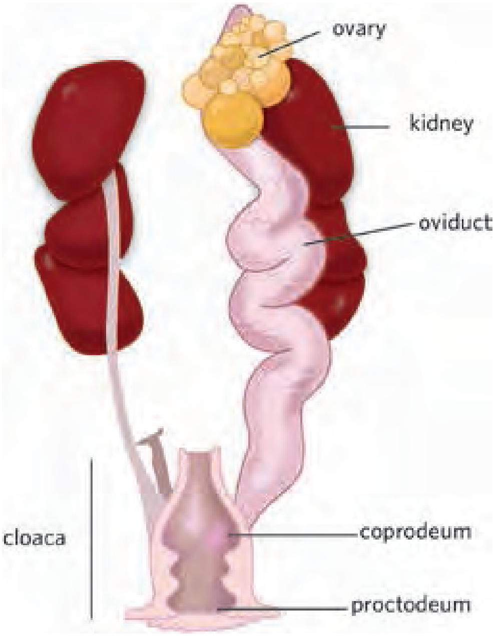
Herbivory is rare among birds, even though it is very common in mammals. We use the word herbivory to refer to the eating of plant parts (leaves, buds, and twigs). We exclude nectar, fruit, and seeds from this definition. Plant parts are difficult to process because cell walls contain materials such as cellulose and lignin that are difficult to digest (nutritionists call these substances **refractory**). Although cellulose is one of the most abundant substances in terrestrial ecosystems, no vertebrate is able to produce the enzymes necessary to digest it. Herbivores, including birds, follow two strategies: they either eat and process large amounts of plant materials and assimilate only the cell contents (they skim the digestible "cream"), or they enlist the help of microbes capable of breaking up and fermenting cell wall materials. Small herbivorous birds such as the South American plantcutters (genus *Phytotoma*, Cotingidae), follow the former strategy. They use their sturdy serrated bills to "masticate" young leaves and buds. Plantcutters have short robust intestines with very high digestive enzyme levels (Meynard et al. 1999), but they have to be very selective and eat primarily nutrient-rich young plant parts. Another example of a bird that relies on cell contents of plant parts is the Kakapo (*Strigops habroptilus*). The Kakapo is found in New Zealand and is the largest parrot. Although they were once widespread and common, they are now endangered. Kakapos are nocturnal, flightless, and herbivorous. They pull foliage through their beaks with their feet while squeezing the nutritive juices out with their tongues. They leave small crescent-shaped fibrous bundles attached to the plant. The underside of the Kakapo's thick tongue has a hard and keratinized band that facilitates mashing foliage (Kirk et al. 1993).

Relying on microbes to assimilate the refractory materials in plant cell walls requires that the gut has a compartment that houses large microbial populations. The Hoatzin (*Opisthocomus hoazin*) is the only example of a bird species with a crop that has evolved into a fermentation vat (Grajal 1995; see the Hoatzin's enlarged crop in fig. 7.10). Hoatzins are the only known **foregut fermenters** among birds. Like cows, their fermentation vat is anterior to the stomach. Filipa Godoy-Vitorino and her collaborators (2012) characterized the microbial communities of Hoatzin crops (called **microbiomes**) and found a very diverse community of bacteria (many of which were completely new to science) with similarities between them and those of cows. Having the fermentation chamber before the stomach allows Hoatzins to digest the bacteria that they are associated with and benefit from bacterial protein. Many other herbivorous species house fermenting bacteria in paired structures called cecae. Cecae are sacs that open at the junction between the small and the large intestine. Herbivorous birds that use the cecae to house microbes are **hindgut fermenters**. Hummingbirds and swifts (Apodiformes) and parrots (Psittaciformes) lack cecae; passerines (Passeriformes) have tiny ones with unknown function; grouse (Tetraonidae), waterfowl (Anatidae), and ostriches (Struthionidae) have large ones. Herbivorous ducks and geese have larger gizzards and cecae than omnivorous and carnivorous species (Barnes and Thomas 1987). A. Starker Leopold (1953) measured the cecae of herbivorous and granivorous Galliformes and found that herbivorous grouse (Tetraonidae) had much larger cecae than seed-eating quail (Odontophoridae), pheasants (Phasianidae), and turkeys (*Meleagris gallopavo*). Avian cecae have diverse microbiomes that seem to help birds assimilate materials in cell walls (Waite and Taylor 2014), but birds in general appear not to be as good as mammals at digesting this abundant but hard-to-digest material (McWhorter et al. 2009). The explanation for the paucity of herbivorous birds with the capacity to assimilate refractory plant materials is likely that birds fly and cannot afford to carry a large chamber to house a big microbiome. The cecae of herbivorous birds might play a role in their nitrogen economy. The ureters are the conduits that deliver urine to the rectum. The uric acid in urine can then be refluxed up to the cecae and used by bacteria to synthesize protein that can then potentially be used by birds. The problem with this scenario is that bacterial protein must be digested. You might recall that protein digestion takes place first in the stomach and then in the small intestine. Many mammals solve this problem by eating their own feces. Although there are anecdotal observations of birds eating their own feces, the significance of these sparse observations is very unclear. The function of the cecae and of avian microbiomes remains an area where we still have much to learn.

OSMOREGULATION: COPING WITH SALT AND WATER

Bird Kidneys

Birds must maintain water balance. If they live in hot and dry environments, they must reduce losses. If they inhabit oceanic environments without freshwater, they must get rid of the salt in seawater and their food. In addition birds can lose astounding amounts of water through their respiratory system when they are engaged in active flight. The converse challenge is that birds that feed on nectar can sometimes ingest prodigious amounts of water and then must eliminate it. Birds meet these challenges with kidneys and other organs such as salt glands, and with the help of the lower end of the digestive system. This section is about how birds in different environments cope with water and salts. It begins with kidneys. The two bird kidneys are embedded in recesses on each side of the ventral side of the synsacrum. The ureters carry urine to the urodeum of the cloaca—there is no urinary bladder as in mammals (fig. 7.13). Unlike mammals, which void feces and urine through different orifices, birds void it into the cloaca, where it mixes with undigested material from the gastrointestinal tract. Therefore birds do not defecate, they excrete, and the appropriate way to refer to bird poop is excreta. Bird kidneys filter and reabsorb water and substances such as electrolytes and small molecules. They also secrete toxins. Kidney size depends on need and therefore on the habitats occupied by birds. Birds that live in marine environments must cope with salt and drink large amounts of water; so, their kidneys are larger (over 1 percent of body mass) than those of birds that live on land (under 1 percent of body mass; Hughes 1970). In contrast, birds that live in the desert have very small kidneys. The functional units of kidneys are called nephrons. These tiny structures filter, reabsorb, and secrete substances. Some birds have nephrons that lack a loop of Henle, located in the external layer of the kidney (the renal cortex). Because these nephrons resemble those of reptiles, they are called reptilian. Birds also have nephrons with a loop



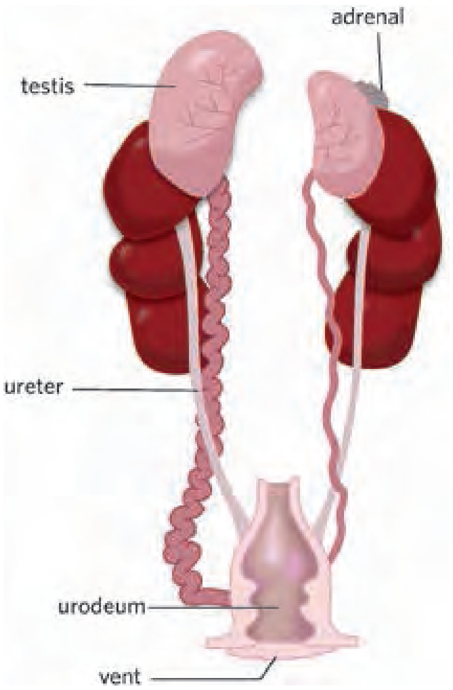


Figure 7.13. A schematic of the urogenital organs of birds. The kidneys are lodged within the synsacrum. The urine that they produce joins the rectum by the ureters at the urodeum. Note that the digestive, urinary, and reproductive systems converge in the cloaca.

of Henle, located in the kidney's interior. Because, in addition to birds, mammals are the only vertebrates with nephrons with loops of Henle, these nephrons are called mammalian. In addition to these two extreme nephron types, birds have an intermediate type, in which nephrons empty their filtered (and modified by reabsorption and secretion) contents into collecting ducts. Bird kidneys are composed of a multitude of lobules, each of which has a bundle of medulla surrounded by connective tissue called the renal cone and associated cortical tissue (fig. 7.14).

Ecological Correlates of Kidney Structure and Function

Only two groups of vertebrates are capable of making urine that is more concentrated than blood plasma: mammals and birds. We recommend Poulson's (1965) and Goldstein and Skadhauge's (2000) descriptions of the mechanisms that birds use to concentrate urine. It is sufficient to say that mammalian nephrons are responsible for the concentration of urine and that having more of them is associated with the production of more concentrated urine. Although birds can produce urine that is up to two to three times more concentrated than plasma, birds are not nearly as good urine concentrators as many mammals. Desert Hopping Mice (*Leggadina hermanburgensis*), for example, are champion urine concentrators and can produce urine that is 27 times more concentrated than plasma. There are no birds that can even come close. The

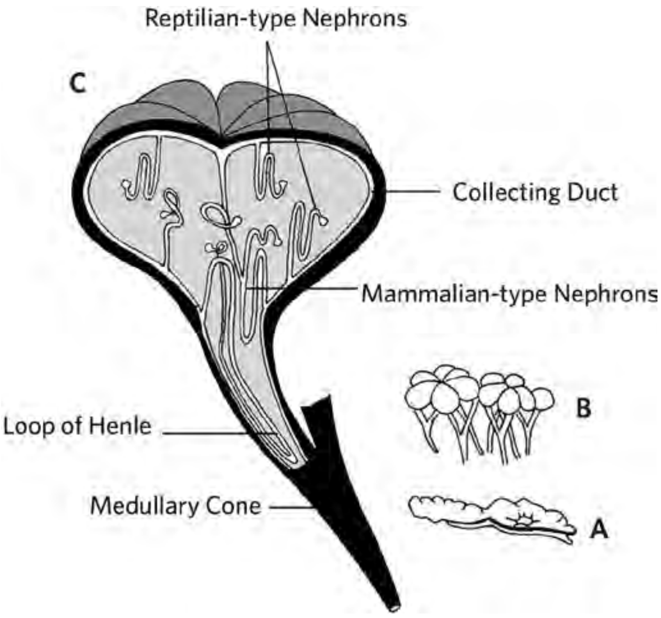


Figure 7.14. Renal structure in bird kidneys. Avian kidneys have two types of nephrons, mammalian-type and reptilian-type (this is a slight simplification, as these nephron types are extremes in a continuum). Only mammalian-type nephrons have the ability to generate a significant osmotic gradient to produce a urine more concentrated than other body fluids, but the functional link between both nephron types through the collecting duct inside of the medullary cone determines that the ability to concentrate the urine is less efficient than in mammals. The whole kidney is shown in *A*, and two successive enlargements (*B* and *C*) are shown, each showing greater detail than the previous one. *Modified from Braun 1982*.

presence of longer cones (i.e., cones with nephrons with longer loops of Henle) in some birds enables them to retain more water and produce more concentrated urine. Therefore, the ability to produce concentrated urine (maximum urine concentrating ability), and cope with aridity and diets with high salt loads, is correlated with the relative size of the kidney, with the fraction of the kidney that is made of medullary tissue, and with the number of medullary cones (Goldstein and Braun 1989).

Giovanni Casotti and Eldon Braun (2000) compared the kidney morphology of Savannah Sparrows (*Passerculus sandwichensis*) that live in dry salt marshes without freshwater with those of House Sparrows (*Passer domesticus*, Passeridae) and Song Sparrows (*Melospiza melodia*, Emberizidae) that live in semiarid and mesic environments, respectively. They found that Savannah Sparrows were capable of producing more concentrated urine than the other two species and had kidneys with more mammalian-type nephrons and larger medullas than the other two species. This pattern seems to be repeated in other bird groups: Casotti and Richardson (1992) found that honeyeaters (Meliphagidae) from arid areas have kidneys with a higher percentage of tissue made of renal medulla than those from humid environments. McNabb (1969) found that desert Gambel's Quail (*Callipepla gambelii*) have kidneys with a larger proportion of renal medulla than Northern Bobwhite (*Colinus virginianus*) and California Quail (*Callipepla californica*), which occupy humid and mesic areas. Birds, such as hummingbirds, that must process large volumes of nectar and hence produce copious dilute urine, have kidneys in which 99 percent of nephrons are of the reptilian kind with almost no medullary tissue (Casotti et al. 1998). These birds are unable to produce concentrated urine and may face a difficult challenge. Like other birds, they absorb almost all the water they ingest, and the renal system has to eliminate it. When they are feeding, hummingbirds are diuretic. However, when they are not feeding, their high metabolic rates (and hence high rates of respiration) cause them to lose a lot of water by evaporation. Hummingbirds must get rid of a lot of water when they are feeding but conserve it when they are not. Unlike other birds, they cannot save water by making concentrated urine. Bradley Bakken and his collaborators (2004) found that Broad-tailed Hummingbirds (*Selasphorus platycercus*) solve this quandary by decreasing how much water gets reabsorbed by the kidney when they are feeding and by ceasing to filter water in the kidneys when they are not. Ceasing filtration in the kidneys in humans is called acute renal failure, which is a serious medical condition. Hummingbirds cope with it just fine.

Unlike seabirds (see following section), songbirds (Passeriformes) lack functional salt glands. Because birds are not very good at concentrating urine, the renal traits of this very large group of birds might limit their ability to use marine environments that impose a heavy salt load. Pablo Sabat and his collaborators (2006) studied the renal structure and the ability to concentrate urine in five species of ovenbirds (Furnariidae) in the genus *Cinclodes*. Because carbon molecules in food from marine sources have a higher content of ^{13}C, the heavy isotope of carbon, they used the content of this isotope to estimate how much individuals of each species fed on marine invertebrates relative to terrestrial ones (Sabat and Martinez del Rio 2002). They assumed that birds feeding on marine sources, with more ^{13}C in their tissues, would face higher loads of salt in their food. They found that birds with more ^{13}C in their tissues, and thus more marine invertebrates in their diets, had larger kidneys with a higher fraction of the kidney made of medulla and with a higher number of medullary cones per unit of kidney mass than closely related birds that fed on terrestrial invertebrates (fig. 7.15). One of the species, the Chilean Seaside Cinclodes (*Cinclodes nigrofumosus*), fed almost exclusively on seafood plucked from intertidal pools. Chilean Seaside Cinclodes are the most marine of all passerines. They have huge kidneys and are unusual among passerines in their capacity to deal with salt by producing concentrated urine. This ability allows them to live by the ocean in the Atacama Desert, one of the world's driest deserts, while feeding on marine invertebrates.

At this point you might wonder if kidneys are as phenotypically flexible and plastic as guts are. Several studies have shown that the composition of diet can affect kidney structure and function in birds (Ward et al. 1975a, 1975b, Singer 2003). This is because kidneys are not only used to deal with water and salt, but also to get rid of the end products of the breakdown of protein. Unlike mammals, which excrete primarily urea, birds excrete primarily uric acid. They also secrete urea and ammonia (Tsahar et al. 2005), but in most species uric acid is the primary form of nitrogenated excretion product in urine. Unlike urea and ammonia, which are soluble, uric acid is very water insoluble. It is secreted by nephrons in the cortex of the kidney. The urine of birds has uric acid both in solution and as precipitate (the precipitated uric acid is the white material that you find in the bird excreta splattered in the windshield of cars). The uric acid that precipitates in the cloaca of birds is in the form of tiny spheres (Braun 1982). These microspheres form a stable colloidal suspension in the liquid phase of urine. Thus, birds can conserve water by excreting a semisolid paste that has little water (Braun 1982). The microspheres are not only osmotically inactive, they also contain ions (such as Na^+) within them. Birds, as we have seen, have limited ability to produce concentrated urine. They can use these spheres to dispose

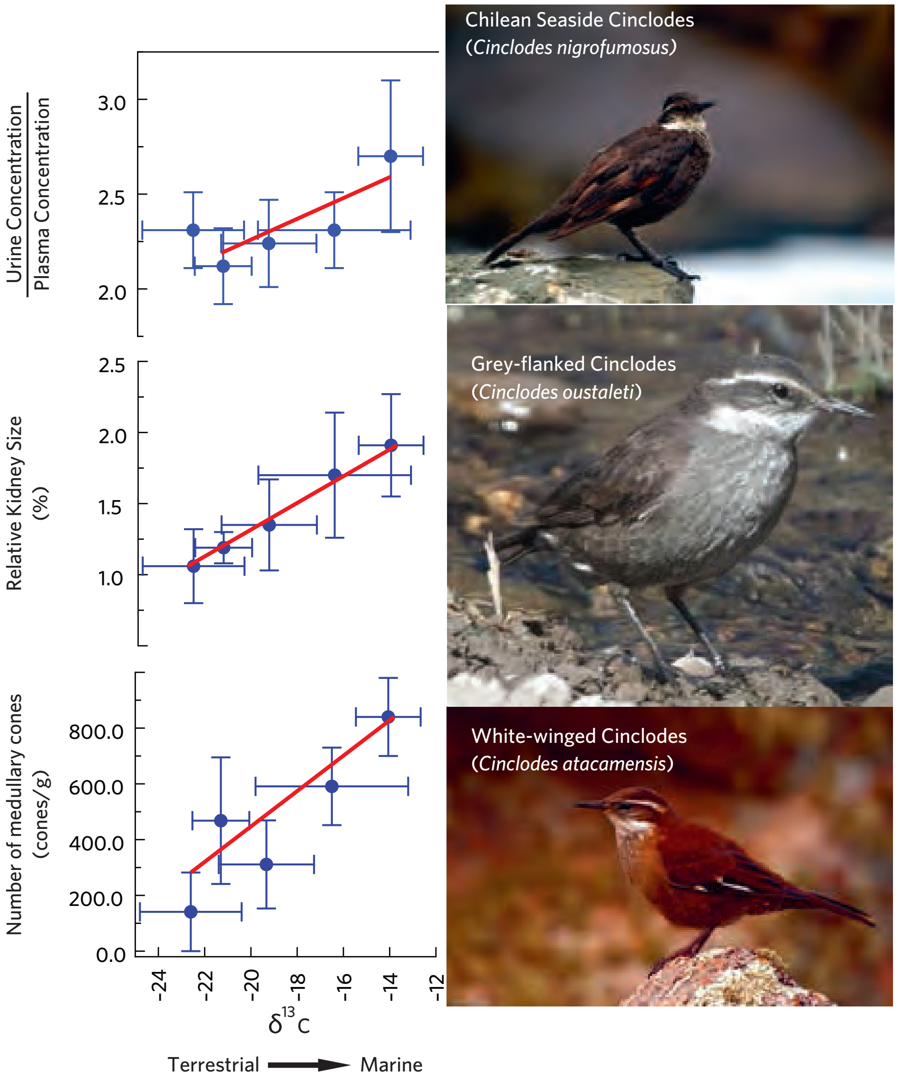


Figure 7.15. In the genus *Cinclodes* (Furnariidae), the relative size of the kidney, the number of medullary cones, and the ability to produce concentrated urine increases with the use of marine habitats as measured by the abundance of ^{13}C in tissues. The Chilean Seaside Cinclodes inhabits the intertidal areas on Central and Northern Chile, feeds on marine invertebrates primarily, and has the kidneys to cope with this very salty diet and a very dry environment. Like all passerines, this species lacks functional salt glands. *Photos (from top) by Pablo Sabat Kirkwood, Bob Lewis (https://www.flickr.com/photos/boblewis/), and Raúl Demoli. With permission.*

of ions. About 50 percent of the sodium excreted by European Starlings (*Sturnus vulgaris*) can be excreted associated with uric acid (Braun 1982). Birds that eat more protein must excrete more uric acid. Consequently, when birds are acclimated to diets with high protein content, the size of their kidneys increases, and the morphology of nephrons changes so that birds on high protein diets have kidneys with higher fractions of medullary tissue (Goldstein et al. 2001, Sabat et al. 2004). To evaluate whether the changes in kidney form and function observed in short-term experiments were also found in the renal characteristics of birds across species, Gonzalo Barceló and his collaborators (2012) measured the kidneys of 16 passerine species. They found the opposite of what they expected. The mass of the medullary portion of the kidney and the length of medullary cones were negatively correlated (rather than positively correlated, as expected) with the percentage of invertebrates in the birds' diet. They hypothesized that the renal medulla of grain-eating birds is large because there is very little water in seeds. They argued that although getting rid of nitrogenated waste products is important for the design of the kidney, across species this need might be overridden by the need to conserve water.

Salt Glands

Shearwaters (Procellariidae), albatrosses (Diomedeidae), and petrels (Procellariidae and Hydrobatidae) spend most of their lives at sea. They feed offshore on marine organisms and drink seawater. They come to land only to breed. Their kidneys, like those of most birds, are not very good at making concentrated urine and getting rid of salt. They can drink seawater and eat marine salty prey because they have salt glands. Salt glands are located in depressions in or above the eye orbits and empty their briny secretion into the nasal cavity (fig. 7.16) where it drips out or birds shake it off. The fossil skulls of two birds from the Cretaceous, *Ichthyornis* (Ichtyor-

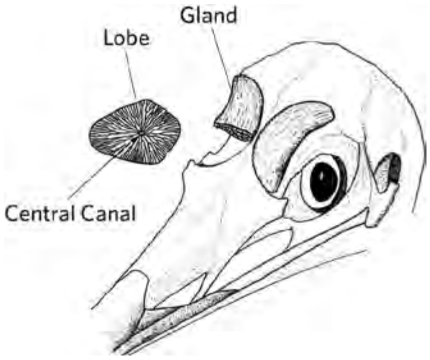


Figure 7.16. Many birds have salt glands, also called supraorbital glands, that can produce a concentrated salt solution. These glands are an extrarenal mechanism that allows many species to inhabit marine environments. *After Schmidt-Nielsen et al. 1958.*

niothidae) and *Hesperornis* (Hesperornithidae), show clear impressions of similarly positioned salt glands. These birds were most likely marine. Although the existence of salt glands in birds has been known for a very long time, their role in salt-riddance was discovered by Knuth Schmidt-Nielsen and his collaborators (1958) after they gave seawater to a Double-crested Cormorant (*Phalacrocorax auritus*) and, after a very short time, found drops of salty brine in the bird's nares.

Seabirds can drink seawater and eat seafood because the secretions of the salt gland can be more concentrated than seawater. Nevertheless, to get rid of salt, birds must drink a lot of water. Birds with salt glands have water fluxes (i.e., rates of water intake and loss) that are about twice as high as those of birds of the same size that lack them. The kidneys of birds that experience large salt loads must be able to get rid of absorbed water. Maryanne Hughes (1970) has shown that, for birds of similar sizes, birds with large salt glands have large kidneys as well. She found that marine birds that have larger kidneys and salt glands are capable of filtering more water. Jorge Gutierrez and his collaborators (2012) measured the size of salt glands in 29 species of shorebirds in the order Charadriiformes. They found that, for a given body mass, marine-dwelling species had larger salt glands than birds that live in terrestrial wetlands. They also found that Dunlins (*Calidris alpina*) living in marine environments had larger salt glands than those living inland in freshwater habitats. The salt gland is phenotypically flexible. Franklin Gulls (*Larus pipixcan*) breed in freshwater marshes in North America but spend the winter in the west coast of South America. They have larger salt glands in the winter than in the summer. When Mallards (*Anas platyrhynchos*) are acclimated to salty water, their salt glands quadruple in mass due to an increase in cell numbers and size. The cells in the glands increase the number of mitochondria and proteins that transport sodium in them (Hildebrandt 2001).

The Digestive System Aids in Osmoregulation

The last segment of the avian digestive system is the cloaca. The cloaca has three compartments. The first one, closest to the colon, is called the coprodeum; the second one is the urodeum; and the third one is the proctodeum, which ends in an opening called the vent (fig. 7.13). The ureters deliver urine into the urodeum. Before voiding urine, some birds can modify its composition and volume by refluxing it into the hindgut (the coprodeum, colon, and cecae). The hindgut of birds reabsorbs both salts and water and relies on bacteria to use uric acid. The Emu (*Dromaius novaehollandiae*), for example, produces dilute urine but has a big rectum with large folds capable of reabsorbing both salt and water. The capacity of the lower gut to save water allows Emus to live in semidesert areas in spite of having kidneys with relatively poor concentrating capacity. The salt that flows into the gut is reabsorbed, and Emus get rid of it using salt glands. The ability to recover salt depends on intake. When domestic chickens are fed on low-salt (NaCl) diets, their coprodeum and colon absorb sodium at a very high rate, presumably by increasing both the number of cells in the tissue and the number of sodium transporters in the membranes of the epithelia of these cells (Goldstein and Skadhauge 2000). When birds are fed on high salt diets, the recovery of salt is reduced. The hindgut differs in physiology and morphology among species. These differences are sometimes accompanied by differences in osmoregulation. For example, subspecies of Savannah Sparrows (*Passerculus sandwichensis*) inhabit salt marshes or upland environments. The most distal section of the large intestine (the rectum) of the salt-marsh subspecies (*P. s. beldingi*) has smoother apical surfaces and shorter microvilli than subspecies inhabiting upland areas with available freshwater (*P. s. anthinus*, *P. s. nevadensis*, and *P. s. brooksi*; Goldstein et al. 1990). These structural differences of the large intestine match the differences between chickens acclimated to either high or low intake of salts (Clauss et al. 1988).

The retrograde flow of urine into the large intestine represents a potential physiological complication for birds without salt glands. If urine is very concentrated, water may be drained from the plasma to the urine in the cloaca, counteracting the work of the kidney. Birds such as the House Sparrow (*Passer domesticus*) are capable of regulating the flow from the cloaca to the ileum when hydrated, but the flow is inhibited when birds are dehydrated and produce concentrated (hypertonic) urine (Goldstein and Braun 1988). The complementarity of the digestive and urinary systems in birds poses many interesting questions: Are many birds without salt glands capable of regulating the flow from the cloaca to the intestine? How many species can regulate the water permeability of the walls of the cloaca? These questions remain unanswered. They are some of the many questions that await answers by the bird physiologists of the future.

KEY POINTS

- Body size is a determinant of a bird's characteristics. It can be used to predict many traits, ranging from how much energy a bird uses to how dense the populations of a species are.
- Birds cope with cold temperatures by increasing heat production and by minimizing heat loss. They cope with hot temperatures by choosing cool microenvironments and by losing heat by evaporation of water.
- Many bird species are able to reduce their body temperatures to reduce the rate of heat loss in the cold, and many species are even capable of entering torpor. Only a single species, as far as we know, is capable of hibernation.
- Birds are very good at delivering oxygen to their tissues and thereby fueling their expensive mode of locomotion. Birds that live at the highest places on earth have very efficient lungs, hemoglobin with high affinity for oxygen, and extraordinary circulatory systems that include large hearts and dense capillary beds.
- The anatomy and physiology of bird digestive systems varies with diet. The characteristics of the gastrointestinal tract of birds are often phenotypically plastic and vary with energetic demands and diet.
- Bird kidneys have limited capacity to concentrate urine, at least compared with those of mammals. Marine bird species rely on supraorbital salt glands to get rid of the salt that they ingest with seawater and prey. The lower gastrointestinal tract of birds complements the function of the kidneys in the regulation of water and salt balance.

KEY MANAGEMENT AND CONSERVATION IMPLICATIONS

- Managers can use simple allometric equations to make predictions about avian traits of management and conservation interest.
- Habitat characteristics determine rates of heat gain and loss in birds. Thus, changes in bird habitat can have profound consequences for the rates at which animals spend energy.
- A warming earth can lead to changes in the composition of bird communities, especially in hot tropical and subtropical deserts.
- Although birds have remarkable phenotypic plasticity, this plasticity has limits, and thus rapid environmental changes can have deleterious effects on the performance of individual birds and, through these, on their populations.

DISCUSSION QUESTIONS

1. How is it that body size can be used to predict things as disparate as the rate at which kidneys filter urine and how long birds live?
2. Birds are much better at coping with high elevations than mammals. Why?
3. Can physiological traits (i.e., the capacity to cope with high and low temperatures, to get rid of salt in food and water, and to feed on certain types of food) shape the broad ecological characteristics of bird species, including their use of certain habitats and their geographical distribution?
4. How is it that gut microbiomes shape and are shaped by the ecological characteristics of a bird species?
5. Individuals of a species can differ from each other in physiological characteristics. Also, species can differ from each other. Discuss the factors that influence the "expression" of a physiological characteristic in an individual and in a species.

References

Bakken, B. H, T. J. McWhorter, E. Tsahar, and C. Martínez del Rio (2004). Hummingbirds arrest their kidneys at night: Diel variation in glomerular filtration rate in *Selasphorus platycercus*. Journal of Experimental Biology 207:4383–4391.

Barceló, G., J. Salinas, and P. Sabat (2012). Body mass, phylogeny and diet composition affects kidney morphology in passerine birds. Journal of Morphology 273:842–849.

Barnes, G. G., and V. G. Thomas (1987). Digestive organ morphology, diet, and guild structure of North American Anatidae. Canadian Journal of Zoology 65:1812–1817.

Bartholomew, G. (1981). A matter of size: An examination of endothermy in insects and terrestrial vertebrates. *In* Insect thermoregulation, B. Heinrich, Editor. Wiley, New York, pp. 45–78.

Bicudo, J. E. P. W. (1996). Physiological correlates of daily torpor in hummingbirds. *In* Animals and temperature: Phenotypic and evolutionary adaptation I, A. Johnston and A. F. Bennett, Editors. Cambridge University Press, Cambridge, UK, pp. 293–311.

Bicudo, J. E. P. W., C. R. Vianna, and J. G. Chaui-Berlinck (2001). Thermogenesis in birds. Bioscience Reports 21:181–188.

Boag, P. T. (1987). Effects of nestlings' diet on growth and adult size of Zebra Finches (*Poephila guttata*). The Auk 104:155–166.

Braun, E. J. (1982). Renal function. Comparative Biochemistry and Physiology 71A:511–517.

Calder, W. A. (1968). Respiratory and heart rates of birds at rest. The Condor 70:358–365.

Calder, W. A. (1983). Size, function, and life history. Harvard University Press, Cambridge, MA.

Carpenter, F. L. (1974). Torpor in an Andean hummingbird: Its ecological significance. Science 183:545–547.

Casotti, G., and K. Richardson (1992). A stereological analysis of kidney structure of honeyeater birds (Meliphagidae) inhabiting either arid or wet environments. Journal of Anatomy 180:281–288.

Casotti, G., C. A. Beuchat, and E. J. Braun (1998). Morphology of the kidney in a nectarivorous bird, the Anna's hummingbirds *Calypte anna*. Journal of Zoology 244:175–184.

Casotti, G., and E. J. Braun (2000). Renal anatomy in sparrows from different environments. Journal of Morphology 243:283–291.

Cheviron, Z. A., C. Natarajan, J. Projecto-Garcia, D. K. Eddy, J. Jones, M. D. Carling, C. C. Witt, et al. (2014). Integrating evolutionary and functional tests of adaptive hypotheses: A case study of altitudinal differentiation in hemoglobin function in an Andean sparrow, *Zonotrichia capensis*. Molecular Biology and Evolution 31:2948–2962.

Clarke, A., and P. Rothery (2008). Scaling of body temperature in mammals and birds. Functional Ecology 22:58–67.

Clauss, W., V. Dantzler, and E. Skadhauge (1988). A low-salt diet facilitates Cl secretions in hen lower intestine. Journal of Membrane Biology 102:83–96.

Errington, P. L. (1930). The pellet analysis method of raptor food study habits. The Condor 32:292–296.

Evenari, M., L. Shanan, and N. Tadmor (1982). The challenge of a desert. Harvard University Press, Cambridge, MA.

Faraci, F. M. (1991). Adaptations to hypoxia in birds: How to fly high. Annual Review of Physiology 53:59–70.

Frayn, K. N. (1983). Calculation of substrate oxidation rates in vivo from gaseous exchange. Journal of Applied Physiology 55:628–634.

Fritz, J., E. Kienzle, J. Hummel, O. Wings, W. J. Streich, and M. Clauss (2011). Gizzards vs. teeth: It's a tie: Food processing efficiency in herbivorous birds and mammals and implications for dinosaur feeding strategies. Paleobiology 37:577–586.

Gerum, R. C., B. Fabry, C. Metzner, M. Baulieu, A. Ancel, and D. P. Zitterbart (2013). The origin of traveling waves in an emperor penguin huddle. New Journal of Physics 15. doi:10.108 8/1367 2630/15/12/125022

Gilbert, C., S. Blanc, Y. Le Maho, and A. Ancel (2008). Energy saving processes in huddling emperor penguins: From experiments to theory. Journal of Experimental Biology 211:1–8.

Gilbert, C., D. McCafferty, Y. Le Maho, J. Martrette, S. Giroud, S. Blanc, and A. Ancel (2010). One for all and all for one: The energetic benefits of huddling in endotherms. Biological Reviews 85:545–569.

Gionfrido, J. P., and L. B. Best (1996). Grit-use in North American birds: The influence of diet, body size, and gender. Wilson Bulletin 108:685–696.

Godoy-Vitorino, F., K. C. Goldfarb, U. Karaoz, S. Leal, M. A. Garcia-Amado, P. Hugenholtz, S. G. Tringe, E. L. Brodie, and M. G. Dominguez-Bello (2012). Comparative analyses of foregut and hindgut bacterial communities in Hoatzins and cows. ISME Journal 6:531–541.

Goldstein, D. L, and E. J. Braun (1988). Contributions of the kidney sand intestines to water conservation, and plasma levels of antidiuretic hormone, during dehydration in House Sparrows (*Passer domesticus*). Journal of Comparative Physiology B 158:353–361.

Goldstein, D. L., and E. J. Braun (1989). Structure and concentrating ability in the avian kidney. American Journal of Physiology 256:R501–R509.

Goldstein, D. L., J. B. Williams, and E. J. Braun (1990). Osmoregulation in the field by saltmarsh Savannah sparrows *Passerculus sandwichensis beldingi*. Physiological Zoology 63:669–682.

Goldstein, D. L., and E. Skadhauge (2000). Renal and extrarenal regulation of body fluid composition. *In* Sturkie's avian physiology, G. C. Whittow, Editor. Academic Press, San Diego, pp. 265–297.

Goldstein, D. L., L. Guntle, and C. Flaugher (2001). Renal response to dietary protein in the house sparrow *Passer domesticus*. Physiological and Biochemical Zoology 74:461–467.

Grajal, A. (1995). Structure and function of the digestive tract of the hoatzin (*Opisthocomus hoazin*): A folivorous bird with foregut fermentation. The Auk 112:20–28.

Grubb, B. R. (1983). Allometric relations of cardiovascular function in birds. American Journal of Physiology 245:H567–H572.

Gutiérrez, J. S., M. W. Dietz, J. A. Masero, R. E Gill Jr., A. Dekinga, P. F. Battley, J. M. Sánchez-Guzmán, and T. Piersma (2012). Functional ecology of salt glands in shorebirds: Flexible responses to variable environmental conditions. Functional Ecology 26:236–244.

Hainsworth, F. R., and L. L. Wolf (1978). Regulation of metabolism during torpor in "temperate" zone hummingbirds. The Auk 95:197–199.

Healy, K., T. Guillerme, S. Finlay, A. Kane, S. B. A. Kelly, D. McLean, D. Kelly, I. Donohue, A. L. Jackson, and N. Cooper (2014). Ecology and mode-of-life explain lifespan variation in birds and mammals. Proceedings of the Royal Society of London B 281. doi: 10.1098/rspb.2014.0298

Hildebrandt, J. P. (2001). Coping with excess salt: Adaptive functions of extrarenal osmoregulatory organs in vertebrates. Zoology 104:209–220.

Hudson, L. N., N. J. B. Isaac, and D. C. Reuman (2013). The relationship between body mass and field metabolic rate among individual birds and mammals. Journal of Animal Ecology 82:1009–1020.

Hughes, M. R. (1970). Relative kidney size in nonpasserine birds with functional salt glands. The Condor 72:164–168.

Jenkins, F. A., K. P. Dial, and G. E. Goslow (1988). A cineradiographic analysis of bird flight: The wishbone in starlings is a spring. Science 241:1495–1498.

Kahl, M. P. (1963). Thermoregulation in the Wood Stork, with special reference to the role of the legs. Physiological Zoology 36:141–151.

Kirk, E. J., R. G. Powlesland, and S. G. Cork (1993). Anatomy of the mandibles, tongue, and alimentary tract of Kakapo with some comparative information from Kea and Kaka. Notornis 40:55–63.

Kohl, K. D., P. Brzek, E. Caviedes-Vidal, and W. H. Karasov (2011). Pancreatic and intestinal carbohydrases are matched to dietary starch level in wild passerine birds. Physiological and Biochemical Zoology 84:195–203.

Körtner, G., R. M. Brigham, and F. Geiser (2001). Torpor in free-ranging tawny frogmouths (*Podargus strigoides*). Physiological and Biochemical Zoology 74:789–797.

Laybourne, R. (1974). Collision between a vulture and an aircraft at an altitude of 37000 feet. Wilson Bulletin 86:461–462.

Leopold, A. S. (1953). Intestinal morphology of gallinaceous birds in relation to food habits. Journal of Wildlife Management 17:197–203.

Lewden, A., M. Petit, M. Malbergue, S. Orio, and F. Vezina (2014). Evidence of facultative daytime hypothermia in a small passerine wintering at northern latitudes. Ibis 156:321–329.

Martinez del Rio, C. (1990). Dietary, phylogenetic, and ecological correlate of intestinal sucrase and maltase activity in birds. Physiological Zoology 63:987–1011.

Mathieu-Costello, O. (1991). Morphometric analysis of capillary geometry in pigeon pectoralis muscle. American Journal of Anatomy 191:74–84.

McGuire, J. A., C. C. Witt, J. V. Remsen Jr., A. Corl, D. L. Rabosky, D. L. Altshuler, and R. Dudley (2014). Molecular phylogenetics and the diversification of hummingbirds (Apodiformes: Trochilidae). Current Biology 24:910–916.

McKechnie, A. E., and B. G. Lovegrove (2002). Avian facultative hypothermic responses: A review. The Condor 104:705–724.

McKechnie, A. E., and B. O. Wolf (2004). The allometry of metabolic rate: Good predictions need good data. Physiological and Biochemical Zoology 77:502–521.

McKechnie, A. E., and B. O. Wolf (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biology Letters 6:253–256.

McNabb, F. M. A. (1969). A comparative study of water balance in three species of quail II: Utilization of saline drinking solutions. Comparative Biochemistry and Physiology 28:1059–1074.

McWhorter, T. J., E. Caviedes-Vidal, and W. H. Karasov (2009). The integration of digestion and osmoregulation in the avian gut. Biological Reviews 84:533–565.

McWilliams, S., E. Caviedes-Vidal, and W. H. Karasov (1999). Digestive adjustments in Cedar Waxwings to high feeding rate. Journal of Experimental Biology 283:394–407.

McWilliams, S. R., and W. H. Karasov (2001). Phenotypic flexibility in digestive systems structure and function in migratory birds and its ecological significance. Comparative Biochemistry and Physiology A 128:577–591.

McWilliams, S. E., and W. H. Karasov (2014). Spare capacity and phenotypic flexibility of a migratory bird: Defining the limits of animal design. Proceedings of the Royal Society of London B 281:20140308.

Meynard, C., M. V. Lopez-Calleja, F. Bozinoic, and P. Sabat (1999). Digestive enzymes of a small avian gerbivore, the rufous-tailed plantcutter. The Condor 101:904–907.

Natarajan, C., J. Projecto-Garcia, H. Moriyama, R. E. Weber, V. Munoz-Fuentes, A. J. Green, C. Kopuchian, et al. (2015). Convergent evolution of hemoglobin function in high-altitude Andean waterfowl involves limited parallelism at the molecular sequence level. PLoS Genetics 11:e1005681.

Nee, S., A. F. Read, J. J. D. Greenwood, and P. H. Harvey (1991). The relationship between abundance and body size in British birds. Nature 351:312–313.

Ottaviani, D., S. C. Cairns, M. Oliverio, and L. Boitani (2006). Body mass as a predictive variable of home-range size among Italian mammals and birds. Journal of Zoology 269:317–330.

Palmqvist, P., and S. F. Vizcaíno (2003). Ecological and reproductive constraints of body size in the gigantic *Argentavis magnificens* (Aves: Teratornithidae) from the Miocene of Argentina. Ameghiniana 40:379–385.

Piersma, T., A. Koolhas, and A. Dekinga (1993). Interaction between stomach structure and diet choice in shorebirds. The Auk 110:552–564.

Piersma, T., and J. Drent (2003). Phenotypic flexibility and the evolution of organismal design. Trends in Ecology and Evolution 18:228–233.

Poulson, T. L. (1965). Countercurrent multipliers in avian kidneys. Science 148:389–391.

Projecto-Garcia, J., C. Natarajan, H. Moriyama, R. E. Weber, A. Fago, Z. A. Cheviron, R. Dudley, J. A. McGuire, C. C. Witt, and J. F. Storz (2013). Repeated elevational transitions in hemoglobin function during the evolution of Andean hummingbirds. Proceedings of the National Academy of Sciences USA 110:20669–20674.

Rosenmann, M., and P. Morrison (1974). Maximum oxygen consumption and heat loss facilitation in small homeotherms by He-O2. American Journal of Physiology 226:490–495.

Ruf, T., and F. Geiser (2015). Daily torpor and hibernation in birds and mammals. Biological Reviews 90:891–926.

Sabat, P., and C. Martínez del Rio (2002). Inter- and intraspecific variation in the use of marine food resources by three *Cinclodes* (Furnariidae, Aves) species: Carbon isotopes and osmoregulatory physiology. Zoology 105:247–256.

Sabat, P., E. Sepúlveda-Kattan, and K. Maldonado (2004). Physiological and biochemical responses to dietary protein in the omnivore passerine *Zonotrichia capensis* (Emberizidae). Comparative Biochemistry and Physiology A 137:391–396.

Sabat P., K. Maldonado, M. Canals, and C. Martínez Del Río (2006). Osmoregulation and adaptive radiation in the ovenbird genus *Cinclodes* (Passeriformes: Furnariidae). Functional Ecology 20:799–805.

Schmidt-Nielsen, K., C. B. Jörgensen, and H. Osaki (1958). Extrarenal salt excretion in birds. American Journal of Physiology 193:101–107.

Scholander, P. F., R. Hock, V. Walters, F. Johnson, and L. Irving (1950). Heat regulation in some arctic and tropical mammals and birds. Biological Bulletin 99:237–258.

Schondube, J. E., and C. Martinez del Rio (2004). Sugar and protein digestion in flowerpiercers and hummingbirds: A comparative test of adaptive convergence. Journal of Comparative Physiology B 174:263–273.

Scott, G. R. (2011). Elevated performance: The unique physiology of birds that fly at high altitudes. Journal of Experimental Biology 214:2455–2462.

Scott, G. R., L. A. Hawkes, P. B. Frappell, P. J. Butler, C. M. Bishop, and W. K. Milsom (2015). How Bar-headed Geese fly over the Himalayas. Physiology 30:107–115.

Silva, M., J. H. Brown, and J. H. Downing (1997). Differences in population density and energy use between birds and mammals: A macroecological approach. Journal of Animal Ecology 66:327–340.

Singer, M. A. (2003). Do mammals, birds, reptiles and fish have similar nitrogen conserving systems? Comparative Biochemistry and Physiology B 134:543–558.

Stager, M., D. L. Swanson, and Z. A. Cheviron (2015a). Regulatory mechanisms of seasonal metabolic flexibility in the Dark-eyed Junco (*Junco hyemalis*). Journal of Experimental Biology 218:767–777.

Stager, M., H. P. Pollock, P. M. Benham, N. D. Sly, J. D. Brawn, and Z. A. Cheviron (2015b). Disentangling environmental drivers of metabolic flexibility in birds: The importance of temperature extremes vs. temperature variability. Ecography 39:787–795.

Starck, J. M. (1999). Phenotypic flexibility of the avian gizzard: Rapid, reversible, and repeated changes of organ size in response to changes in dietary fiber content. Journal of Experimental Biology 202:3171–3179.

Steiger, S. S., J. P. Kelly, W. W. Cochran, and M. Wikelski (2009). Low metabolism and inactive lifestyle of a tropical rain forest bird investigated via heart-rate telemetry. Physiological and Biochemical Zoology 82:580–589.

Stevens, C. E., and I. D. Hume (1998). Contribution of microbes in vertebrate gastrointestinal tract to production and conservation of nutrients. Physiological Reviews 78:393–427.

Swan, L. W. (1970). Goose of the Himalayas. Natural History 79:68–75.

Swanson, D. L. (2010). Seasonal metabolic variation in birds: Functional and mechanistic correlates. Current Ornithology 17:75–129.

Swanson, D. L., and K. L. Olmstead (1999). Evidence for a proximate influence of winter temperature on metabolism in passerine birds. Physiological and Biochemical Zoology 72:566–575.

Tsahar, E., C. Martínez Del Río, and A. Zeev (2005). Can birds be ammoniotelic? Nitrogen balance and excretion in two frugivores. Journal of Experimental Biology 208:1025–1034.

Waite, D. W., and M. W. Taylor (2014). Characterizing the avian gut microbiota: Membership, driving influences, and potential function. Frontiers in Microbiology 5. doi: 10.3389/fmicb.2014.00223

Walsberg, G. E. (1975). Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. The Condor 77:169–174.

Ward, J. M., R. A. McNabb, and F. M. A. McNabb (1975a). Effects of changes in dietary protein and water availability on urinary nitrogen compounds in rooster, *Gallus domesticus* I: Urine flow and excretion of uric-acid and ammonia. Comparative Biochemistry and Physiology A 51:165–169.

Ward, J. M., R. A. McNabb, and F. M. A. McNabb (1975b). The effects of changes in dietary protein and water availability on urinary nitrogen compounds in the rooster, *Gallus domesticus* II: Diurnal patterns in urine flowrates, and urinary uric acid and ammonia concentrations. Comparative Biochemistry and Physiology A 51:171–174.

West, J. B. (2009). Comparative physiology of the pulmonary blood-gas barrier: The unique avian solution. American Journal of Physiology: Regulatory, Integrative and Comparative Physiology 297:R1625–R1634.

Whitfield, M. C., B. Smit, A. E. McKechnie, and B. O. Wolf (2015). Avian thermoregulation in the heat: Scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. Journal of Experimental Biology 218:1705–1714.

Wojciechowski, M. S., M. Jefimow, and B. Pinshow (2011). Heterothermy, and the energetic consequences of huddling in small migrating passerine birds. Integrative and Comparative Biology. doi:10.1093/icb/icr055

Wolf, B. O., K. M. Wooden, and G. E. Walsberg (2000). Effects of complex radiative and convective environments on the thermal biology of the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). Journal of Experimental Biology 203:803–811.

Woods, C. P., and R. M. Brigham (2004). The avian enigma: "Hibernation" by Common Poorwills (*Phalaenoptilus nuttallii*). *In* Life in the cold: Evolution, mechanisms, and Applications, B. M. Barnes and H. V. Carey, Editors. Biological Papers of the University of Alaska 27:231–240.