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Extinction patterns in the avifauna of the Hawaiian islands

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ABSTRACT

Through the continuing accumulation of fossil evidence, it is clear that the avifauna of the Hawaiian Islands underwent a large-scale extinction event around the time of Polynesian arrival. A second wave of extinctions since European colonization has further altered this unique avifauna. Here I present the first systematic analysis of the factors characterizing the species that went extinct in each time period and those that survived in order to provide a clearer picture of the possible causal mechanisms. These analyses were based on mean body size, dietary and ecological information and phylogenetic lineage of all known indigenous, non-migratory land and freshwater bird species of the five largest Hawaiian Islands. Extinct species were divided into 'prehistoric' and 'historic' extinction categories based on the timing of their last occurrence. A model of fossil preservation bias was also incorporated. I used regression trees to predict probability of prehistoric and historic extinction based on ecological variables. Prehistoric extinctions showed a strong bias toward larger body sizes and flightless, ground-nesting species, even after accounting for preservation bias. Many small, specialized species, mostly granivores and frugivores, also disappeared, implicating a wide suite of human impacts including destruction of dry forest habitat. In contrast, the highest extinction rates in the historic period were in medium-sized nectarivorous and insectivorous species. These differences result from different causal mechanisms underlying the two waves of extinction.

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Keywords

Body size, extinction, Hawaii, island birds, overkill, palaeoecology, Polynesians.

INTRODUCTION

A catastrophic wave of extinction accompanied the arrival of humans in the Hawaiian archipelago (Olson & James, 1982a). These extinctions began when seafaring Polynesians sailed north from East Polynesia and arrived in the Hawaiian islands about 1600 years ago (Kirch, 1985). As on other Pacific Islands, Hawaiian land birds disappeared as colonists cleared forests, cultivated crops and raised domestic animals (Steadman, 1995). Since European contact in the 18th century, human impacts on the islands have intensified, leading to a second wave of extinctions of the native avifauna.

Over the past 25 years, knowledge of the native avifauna of the Hawaiian Islands has been enhanced by significant fossil discoveries on the five largest Hawaiian Islands (Kauai, Oahu, Molokai, Maui, and Hawaii). Approximately 56 species of land birds are now known only from pre-European fossil remains. These extinct taxa include birds of prey, crows, flightless and volant waterfowl, flightless rails, endemic genera of flightless ibises and of owls and Drepanidine finches, known as honeycreepers (James & Olson, 1991; Olson & James, 1991).

Numerous authors have found that prehistoric extinction of the avifauna of many Polynesian islands was a result of human activities (Milberg & Tyrberg, 1993; Steadman *et al.*, 1999; Duncan *et al.*, 2002; Roff & Roff, 2003; Duncan & Blackburn, 2004). The relative importance of direct and indirect human impacts in the prehistoric extinction remains controversial. Direct hunting of native birds was widespread prehistorically. Charred bones of extinct birds are often found in prehistoric human middens in the Hawaiian Islands and elsewhere providing plentiful evidence that the ancient Polynesians used birds for food (Olson & James, 1982b; Steadman *et al.*, 2002). Human foraging often targets larger prey, which can lead to a telltale size-bias in extinctions caused by human 'overkill' (Martin, 1984; Martin & Steadman, 1999). Additionally, in Polynesia humans placed unique hunting pressure on smaller birds, which were harvested for the manufacture of feather capes and other decorative items (Kirch, 1985). In Hawaii, these activities were limited to the most colourful species, including various species of *Drepanis*, *Moho* and

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Vestiaria, but their precise impacts on those populations are unknown (Sykes *et al.*, 2000).

Indirect human impacts, such as habitat destruction and the activities of introduced predators, also likely played a role in the extinction. Several novel predators including domestic pigs, dogs and the Pacific Rat, *Rattus exulans*, were introduced, either intentionally or inadvertently, by the first Hawaiians. Pigs and dogs may have been a threat to flightless and ground-nesting birds of various sizes. Potential prey of the Pacific Rat include ground-nesters with eggs less than 57 mm in length and adult birds of less than 100 g (Holdaway, 1999). These predators could introduce a bias in extinction probability towards small or medium-sized species. Clearing of lowland forest, primarily by fire, for agricultural purposes was widespread in Hawaii and eliminated vast areas of habitat (Olson & James, 1982a; Athens *et al.*, 2002). Modern habitat loss is thought to be neutral with respect to body size, affecting species of all sizes (Lyons *et al.*, 2004). However, evidence suggests that larger species may require larger geographical ranges to maintain viable populations (Brown, 1995; Diniz-Filho *et al.*, 2005). Thus, the effect of habitat loss on the relationship between body size and extinction probability is difficult to predict.

Under direct human hunting, we expect a strong bias in extinction risk towards larger birds, whereas indirect human impacts may lead to a variety of body size patterns. Additional ecological data, like diet and endemism, may help differentiate between these hypothesized mechanisms. Previously, this process has been hampered by a lack of quantitative data and by the tendency to examine individual or a few species in isolation. To date, body size estimates (e.g. Iwaniuk *et al.*, 2004) and ecological characterizations (e.g. James, 1995; James & Burney, 1997) of only a few extinct Hawaiian species have been published. Discussions of the extinction have not focused on the ecological characteristics associated with extinction risk, but on the individual circumstances of each species.

Here I take a macroecological view of the extinction by examining all known indigenous, resident land and freshwater bird species of the Hawaiian Islands. By characterizing each species in detail, I was able to make quantitative evaluations of the body sizes and ecological characteristics of the entire avifauna before and after initial human colonization. Because body size and ecological attributes could be the result of shared phylogenetic history, I also examined extinction patterns within phylogenetic lineages. A second wave of extinctions has occurred since European contact, thought to have been brought on by some combination of deforestation, urbanization, introduced predators and competitors and disease. Thus, I compared the ecological selectivity of the earlier extinction to these later ‘historical’ extinctions to compare and contrast the causal mechanisms.

Despite the considerable discussion and speculation, quantitative analyses of body size selectivity in Pacific island extinction events are largely based on data from New Zealand (Duncan *et al.*, 2002; Roff & Roff, 2003; Duncan & Blackburn, 2004), and none exist for the Hawaiian islands. Thus, these analyses represent the first quantitative ecological examination of extinction patterns in the pre-contact Hawaiian avifauna.

METHODS

Data

Relevant ecological data for all known indigenous, non-migratory land and freshwater bird species of the five best-studied Hawaiian islands were compiled into a data base. I obtained lists of extinct species from numerous sources (see Appendix S1 in Supplementary Material). These palaeontological data have inherent taphonomic (fossil preservation) biases and may not represent the entire prehistoric avifauna. However, these biases are minimized in limestone sinkholes that act as natural pitfall traps and provide excellent preservation of delicate passerine skeletons as well as bones of larger birds (Olson & James, 1982b). The data presented here are gathered from a combination of many types of palaeontological sites, including archaeological middens, lake bed and sand dune deposits, lava tubes and sinkholes (Olson & James, 1982b). All radiometrically dated fossil deposits are Holocene in age, except two sites, which dated to 120,000 and 25,000 yr BP (Olson & James, 1991). Using simple mark-recapture methods based on the presence of historically observed species in the fossil record (Pimm *et al.*, 1994), I estimated that approximately 30 prehistorically extinct species may remain undiscovered. I used a logistic regression approach to assign body sizes to these hypothetical species (see Appendix S3 in Supplementary Material) and used these data to check the robustness of any observed body size patterns in extinction probability.

Taxonomy of the Drepanidini followed James (2004). Species that are known only from pre-European fossil remains were classified as prehistoric extinctions, whereas species that were observed after European contact (1778 AD) but later went extinct were classified as historic extinctions. Lists of extant species were compiled from a variety of sources (see Appendix S1 in Supplementary Material). Underlying this analysis is the assumption that extant species were also present at initial human colonization. Archaeological evidence shows that most species predate the arrival of humans, but the Short-eared Owl, *Asio flammeus*, arrived later (Burney *et al.*, 2001), and hence was excluded from the prehistoric analysis. There is some speculation that certain freshwater birds (e.g. gallinules, coots, and the night heron) may not have established populations in the islands until suitable habitats were created by Polynesian aquaculture (Olson & James, 1982b). However, these species were included in the prehistoric analysis. Most Hawaiian bird species can be traced back phylogenetically to one of only a few archipelago colonization events (Slikas, 2003). I used published references (see Appendix S1 in Supplementary Material) to group species into monophyletic lineages for analysis.

Average body mass was estimated for each species in the combined data set (111 sp.). Masses for extant species came from a variety of books, field guides, web sources (see Appendix S2 in Supplementary Material), and generic averages in two cases (1.8% of species) where specific data were unavailable. Mass estimates of extinct birds (both prehistoric and historic) came from published estimates (see Appendix S2 in Supplementary

Table 1 Descriptions of body size distributions of the avifaunas analysed. Mean, median and range are given in units of ln mass (g).

	N	Mean	Median	Range	Skewness
Prehistoric avifauna and undiscovered species	139	4.05	3.50	6.50	1.44
Prehistoric avifauna	111	4.30	3.70	6.50	1.20
Historic avifauna	55	3.70	3.40	5.20	1.37
Extant avifauna	32	3.72	3.20	5.20	1.20

Material), or in the case of 68 species (61% of species), were based on linear regression of mass on skeletal measurements following the methods of Campbell & Marcus (1992). The majority of these regression equations were based on my own measurements of the hind limb bones of 442 specimens from groups with Pacific Island representatives. This method was very accurate in predicting mass ($r^2 = 0.946$) when tested on independent specimens of known body mass. Statistics describing the body size distributions of birds in each fauna are given in Table 1.

Species were also classified into broad dietary guilds and categories of endemism following published accounts (see Appendix S1 in Supplementary Material). Information on flight ability and nest type were also included based on osteological descriptions of fossil species and ecology of living relatives. The data base (see Appendix S2 in Supplementary Material) serves as a general reference for indigenous Hawaiian bird species and lineages.

Analysis

Extinction patterns were analysed first by comparing body mass distributions of prehistoric, historic, and extant species, foraging guilds and lineages using the Kolmogorov–Smirnov D-statistic. Body size bias was calculated, using logistic regression, for each time period and for each level of endemism. After inspection of the data, non-linear patterns in extinction probability appeared common. For example, predation and competition by the Pacific Rat and human hunting could combine to produce a pattern of high extinction in both large and small birds. To address the inherent non-linearities, regression trees were implemented in Matlab (The MathWorks, Inc.) using decision tree functions provided in Statistical Toolbox v5.0.

Regression trees are particularly well suited to this type of analysis because they partition the response data according to a suite of both categorical and continuous variables. Trees were fit to data through a recursive process of error minimization. A binary partitioning algorithm was applied at each node until either the node was homogeneous or the node contained a single observation. Partitioning was carried out on a one-step look ahead, which ensured an optimal split at each node but not necessarily the optimal performance over the whole tree. Once the nodes were determined, the tree was pruned to the smallest sub-tree that is within one standard error of the minimum-error sub-tree. Terminal nodes with only one observation remain in the tree if their inclusion adds substantial explanatory power. For more information on the use of regression trees to predict extinction see Roff & Roff (2003) and Sullivan *et al.* (2006).

In order to compare the factors leading to extinction in both the historic and prehistoric extinctions, I constructed two independent regression trees to predict probability of prehistoric and historic extinction based on five predictor variables. The prehuman fauna of 111 species was included in the prehistoric tree. Only the 55 survivors of the prehistoric extinction were included in the analysis of historic extinction. The following predictor variables were used:

- *Body size.* Estimated, natural log-transformed (ln) mass (g) of each avian species.
- *Dietary guild.* Species were divided into the following broad dietary categories: carnivore, insectivore, nectarivore, granivore, frugivore and herbivore.
- *Endemism.* Species were classified into three categories of endemism: 0- endemic at the subspecies level or not endemic to the Hawaiian Islands, 1- endemic at the species level, and 2- endemic at the genus level or higher.
- *Flightlessness.* Species were grouped into two flight categories: 0- volant and 1- flightless.
- *Nest type.* Ground-nesting species were coded as 1, whereas elevated nest types were coded as 0.

RESULTS

The body size data for the five best-studied islands revealed that, as in many continental bird and mammal faunas (Brown, 1995), the original Hawaiian avifauna showed a distinctive right-skewed distribution (Fig. 1, Table 1). Kolmogorov-Smirnov tests showed that extant land birds have a significantly different body size distribution than the victims of the prehistoric and historic extinctions (Table 2), meaning that the extinctions were not random with respect to body size. After accounting for undiscovered sub-fossils, differences remained significant.

Body size distributions of dietary guilds show that certain guilds dominated specific size classes (Fig. 2). Each dietary guild had a significantly different body size distribution, except that frugivores and insectivores were each statistically indistinguishable from nectarivores (K-*S*-test, $P = 0.15$ and $P = 0.77$). Foraging guilds were affected differently by the two extinction waves in

Table 2 Pairwise comparisons of body size distributions of Hawaiian avifauna. *P*-values for Kolmogorov-Smirnoff tests are shown. Values based on inclusion of hypothetical undiscovered species are given in parentheses.

	Extant species	Prehistoric victims
Prehistoric victims	0.0004 (0.02)	–
Historic victims	0.02	0.03 (0.33)
All extinct species	0.0004 (0.01)	–
Prehistoric survivors	–	0.01 (0.37)

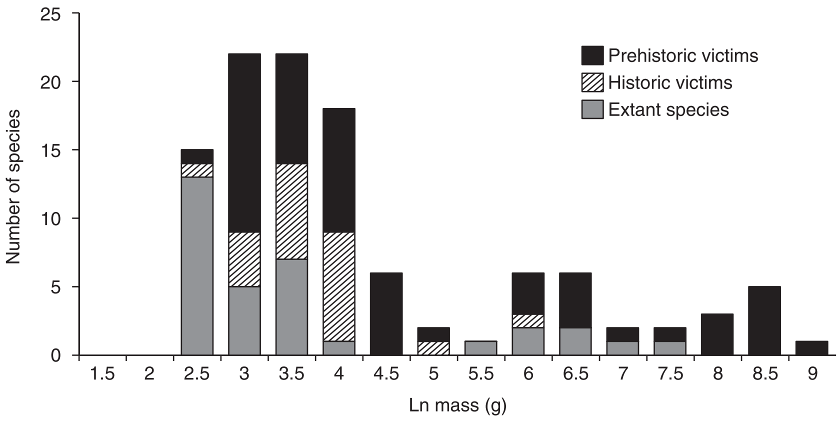

Figure 1 Body size frequency distributions of Hawaiian bird species. Extant species are shown in grey bars, prehistoric victims are shown in black bars, and historic victims are shown in hatched bars. Hypothetical undiscovered prehistoric victims add 11 species to size-class 2.5, 8 to class 3.0, 5 to class 3.5, 3 to class 4.0 and 1 to class 4.5.

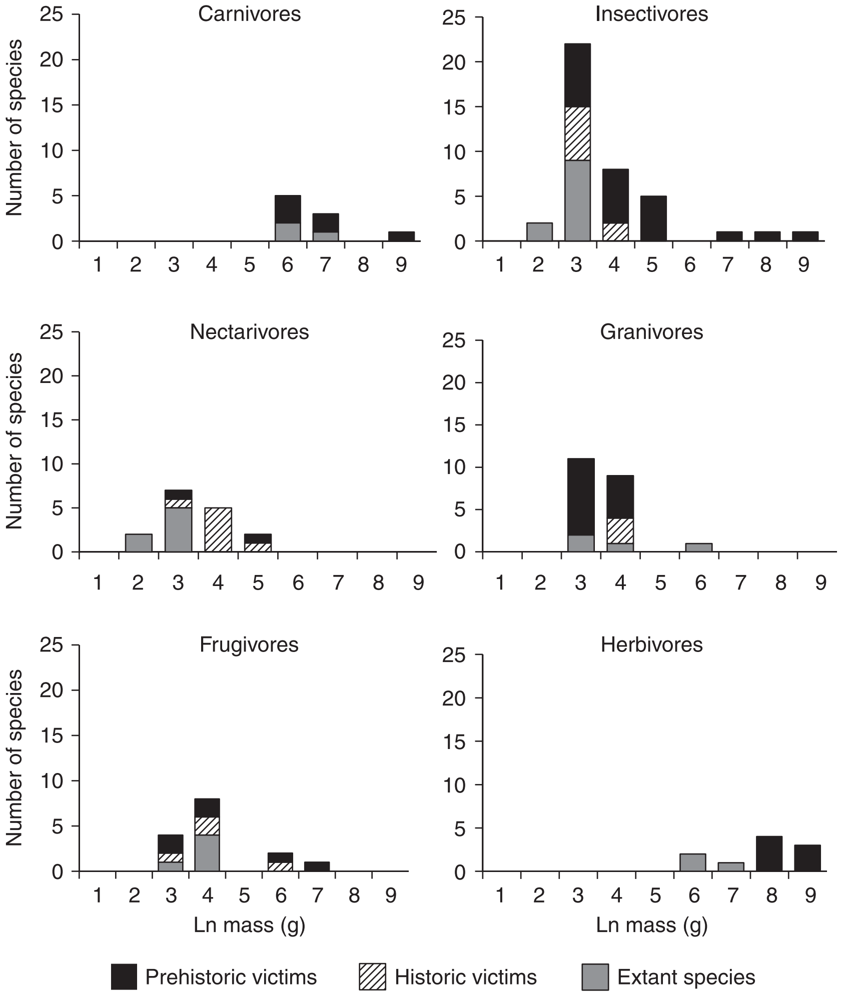

Figure 2 Body size frequency distributions of Hawaiian avifauna showing losses of each dietary guild. Extant species are shown in grey bars, prehistoric victims are shown in black bars, and historic victims are shown in hatched bars.

Hawaii. For example, nectarivores were only mildly affected by prehistoric extinction, but were dramatically reduced by extinctions in historic time (Fig. 2). The various avian lineages also suffered different extinction rates in the prehistoric extinction (ANOVA, $P = 0.002$, Table 3).

The prehistoric extinction showed significant size-bias wherein every ln unit increase in body size led to a 46% increase in the probability of extinction (Fig. 3a). After correcting for undiscovered species, size bias remained marginally significant. However, historical extinctions did not show a significant size-bias (Fig. 3a), but instead showed a non-linear, unimodal, relationship with body size. Endemic genera showed a significant bias in extinction probability toward larger body sizes in both time periods (Fig. 3b,c), whereas endemic species did not show a significant bias toward large size. Endemic species did show an interesting trend toward higher extinction rates in smaller

Table 3 Lineage-level analysis of extinction patterns. Proportions of original avifauna lost in each extinction are given, with significant differences between clades indicated by superscripts (Tukey HSD test). Results of logistic regression of ln body size against extinction probability are shown for lineages with more than four species in each time period. Significant size-bias is indicated in bold type.

Lineage	Number of species	Proportion extinct prehistorically	Proportion extinct historically	Proportion extant	Prehistoric size bias (*P*-value)	Historic size bias (*P*-value)
Anatidae: Anatinae	5	80%	0%	20%	0.99	–
Plataleidae: *Apteribis*	3	100%^{A}	–	–	–	–
Anatidae: *Branta*	4	75%	0%	25%	0.35	–
Corvidae: *Corvus*	3	66%	33%	0%	–	–
Fringillidae: Drepanidini	61	43%^{B}	21%	36%	**0.02**	**0.006**
Strigidae: *Grallistrix*	4	100%^{A}	–	–	–	–
Meliphagidae	6	17%^{B}	83%	0%	0.41	–
Turdidae: *Myadestes*	6	17%^{B}	33%	50%	0.91	**< 0.001**
Rallidae: *Porzana pusilla* clade	4	100%^{A}	–	–	–	–
Rallidae: *Porzana tabuensis* clade	7	86%	14%	0%	0.84	–
Individual colonists	8	25%^{B}	0%	75%	0.24	–
All species	111	51%	20%	29%	**< 0.001**	0.87

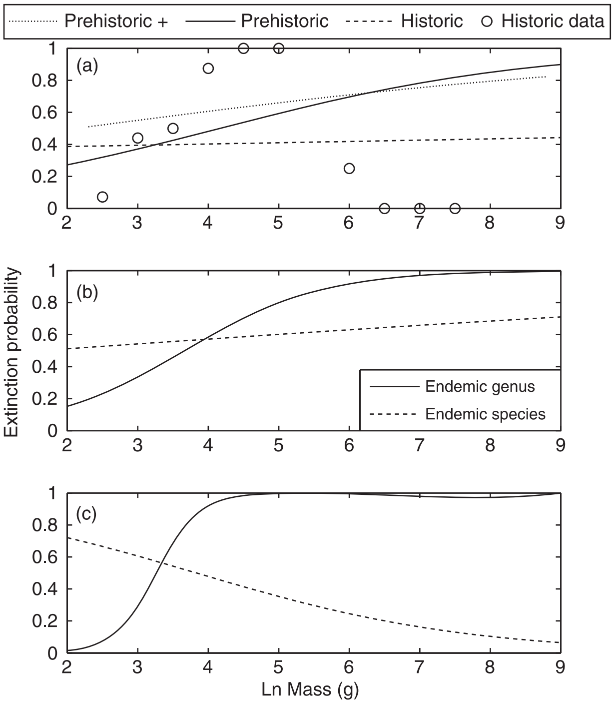

Figure 3 Results of logistic regression on body size and extinction probability. (a) Overall size-bias in prehistoric ($P = 0.0009$, solid line), after accounting for undiscovered species ($P = 0.05$, dotted line), and historic extinctions ($P = 0.87$, dashed line and circles). Endemism and size-bias in the (b) prehistoric and (c) historic periods. Endemic genera ($P = 0.005$ and 0.001) are shown with solid lines and endemic species ($P = 0.64$ and 0.31) in dashed lines.

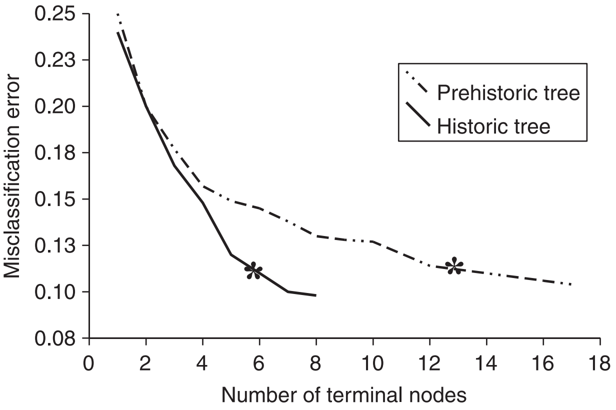

Figure 4 Error plots determined by resubstitution for fitted regression trees based on the number of terminal nodes in the tree. Asterisks indicate optimal pruning levels.

species during the historic extinction (Fig. 3c). These analyses suggest that the two extinction waves had different causal mechanisms.

The regression trees reflecting prehistoric and historic extinctions were pruned to 13 and 6 terminal nodes, respectively (Fig. 4). The primary risk factor for extinction in the prehistoric regression tree (Fig. 5a) was nest type. Within birds with elevated nests, larger species tended to have higher extinction rates. For species larger than 18.2 g (2.9 ln units), feeding guild was an important determinant of extinction (nodes 2–11). In the historic tree (Fig. 5b) extinction risk was a non-linear function of body size, with the highest extinction rates in medium-sized species. Feeding guild was also an important predictor of extinction in species between 22.2 g and 40.4 g (3.1–3.7 ln units; nodes 3–5).

DISCUSSION

The analyses presented here clearly identify two characteristics of species that are commonly associated with increased prehistoric extinction risk: ground-nesting and large body size. This vulnerability is apparent in the regression tree analysis (Fig. 5a)

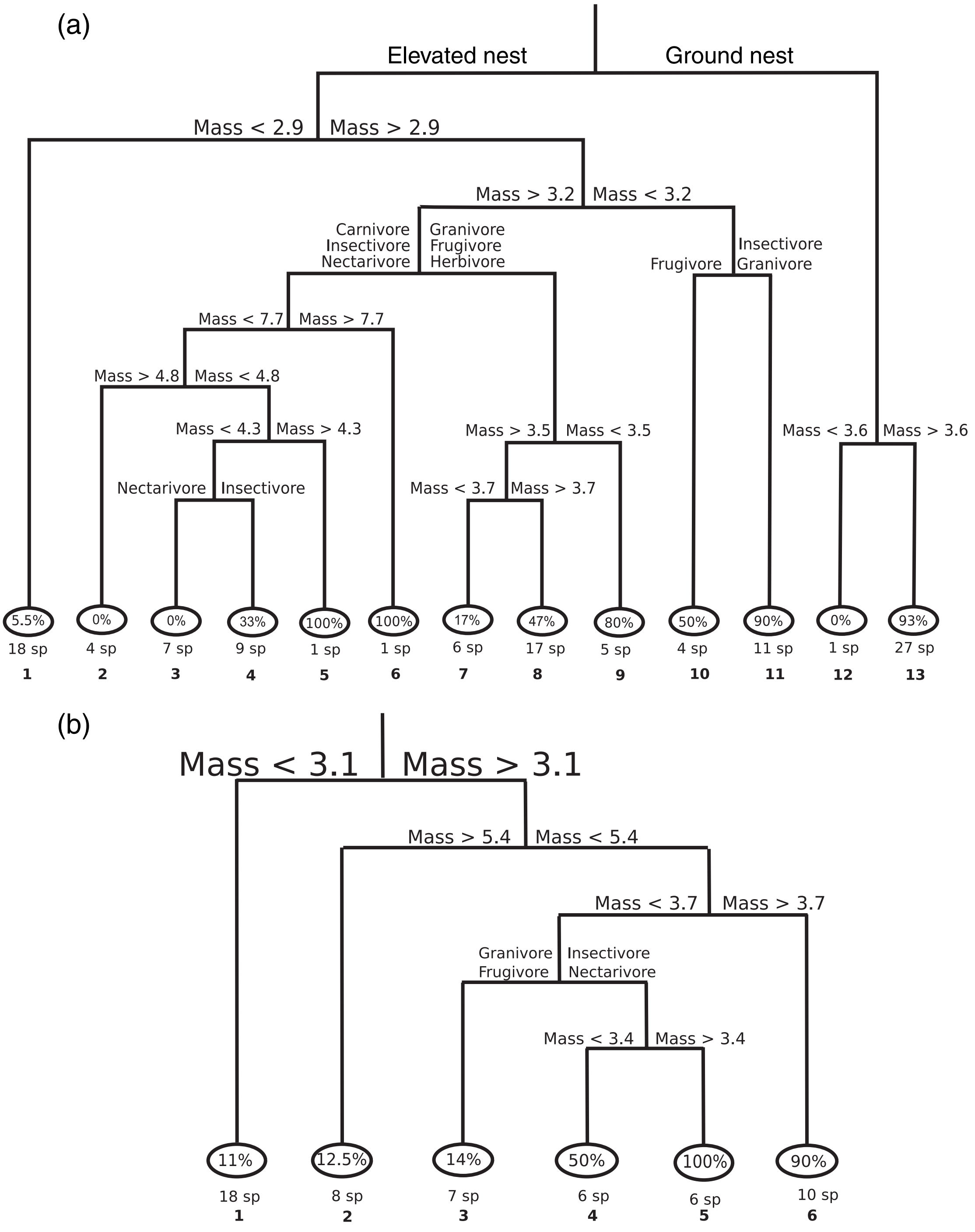

Figure 5 Regression trees predicting extinction probability based on flight ability, nest type, ln body size, dietary guild, and endemism for (a) prehistoric extinctions and (b) historic extinctions. Extinction probability increases to the right of each branch point. Terminal nodes show probability of extinction, number of species, and are numbered for reference.

where ground-nesting species (89.2% extinction) were immediately separated from those with elevated nests (37.3% extinction). Lineage-level differences in extinction risk (Table 3) also reflect the importance of shared phylogenetic history on body size and flightlessness. The largest birds of the prehistoric avifauna, the moa-nalos, ibises and *Branta* geese, are certainly within the range where human hunting would have been profitable and bones of these species have been found in association with human hearths and in middens (Olson & James, 1982b). Flightlessness, encapsulated entirely within the ground-nesting category, was also an immense disadvantage to birds faced with novel predators. Only the smallest flightless bird in the islands, *Porzana sandwichensis*, survived into the historic period (Fig. 5a, node 12). In 1892, collectors hunted intensively for the rail, but were unsuccessful and found its former habitat overrun with mongooses (Olson, 1999b).

Large body size may increase extinction susceptibility for at least two reasons (Brown, 1995; Gaston & Blackburn, 1995). Large size constrains population density and hence total population size on an island. Any environmental change that reduces population sizes could differentially affect larger species. This is especially true for those large species at higher trophic levels, such as birds of prey. Large organisms also have life history characteristics that make them slower to rebound from population declines, such as small clutch size and long intervals between clutches. This situation is exacerbated in insular species that tend towards even smaller clutch sizes (Cody, 1966).

Although nest type and large body size can explain some extinctions, not all the victims of the prehistoric extinction showed these characteristics. The relationship between feeding guild and extinction risk leads to interesting new hypotheses of extinction as a result of differential human activities in habitats utilized by birds. Recently, studies of the Hawaiian ecosystem have uncovered evidence of extensive habitat modification by humans and Pacific Rats. Much of the lowland forest of the ‘Eua Plain region of Oahu appears to have been destroyed by rats even before human settlement in the area (Athens *et al.*, 2002). Populations of early Hawaiians and Pacific Rats were concentrated in lowland areas where extensive areas in the windward valleys were cleared for irrigated taro fields and fish ponds, whereas large portions of the leeward slopes were divided into intensive dry land field systems (Kirch, 1995). Granivorous birds that relied on lowland dry forest resources, such as *Ciridops* (Fig. 5a, node 9), may have faced severe food competition from rats, as well as habitat loss from land clearing, whereas montane, wet forest species survived (Fig. 5a, nodes 2 and 3). The same is true for insectivores, which showed higher extinction rates than similarly sized frugivores and nectarivores in two nodes (Fig. 5a, nodes 4 and 11). This pattern could reflect severe disruptions in the food web of lowland forests caused by rats, which frugivores and nectarivores were able to avoid by ranging widely in search of their patchy food. An apparent interaction between feeding guild and body size led to an almost universal extinction of the largest birds in each feeding guild (Figs 2 and 5a).

The data also suggest that granivores were more susceptible to prehistoric extinction regardless of habitat, as granivory is associated with higher extinction risk in two nodes in the regression tree (Fig. 5a). This pattern may reflect the coevolution of birds and plants and the resulting specialization of many native birds on particular plant species, consistent with a taxon-cycle (Ricklefs & Bermingham, 2002; Duncan & Blackburn, 2004). These specialized species may have had limited geographical ranges, and may have been unable to shift into new habitats where their principal food plants were absent, whereas surviving endemics generally were more nomadic and generalist feeders. For example, the extinct koa-finches (*Rhodacanthis*), as their name implies, were adapted for harvesting the green pods of the leguminous koa tree, *Acacia koa* (Olson, 1999a), whereas the surviving ‘Apapane (*Himatione sanguinea*) and ‘O’u (*Psittirostra psittacea*) are nomadic foragers on native and introduced fruits and nectar (Snetsinger *et al.*, 1998).

In the historic period, body size effects were mixed. It seems that the most vulnerable large-bodied species had already disappeared, leading to a non-linear effect of body size. Large size was associated with decreased extinction probability in endemic species (Fig. 3c) because only one large (> 221 g or 5.4 ln units, Fig. 5b, node 2) endemic species went extinct historically. The remaining large species had traits that helped them survive both extinction waves. However, three of these species are now listed as endangered or vulnerable by the IUCN (2007). In the historic period, habitat destruction, introduced predators and mosquito-borne disease struck lowland forest species, leading to the disproportionate loss of insectivores and nectarivores (Fig. 5b, nodes 4 and 5). This trophic effect could be a result of the loss of so many granivores and frugivores in the prehistoric period, so that the surviving granivores and frugivores were more likely to survive the historic period. Because the introduced mosquito, *Culex quinquefasciatus*, is limited by temperature to areas below approximately 600 m in elevation (Atkinson *et al.*, 2000), disease also acted to eliminate much of the remaining lowland forest habitat for birds.

Several lines of evidence support the conclusion that the two waves of extinction resulted from different causal mechanisms. In the prehistoric period, the degree of size-bias observed clearly implicates human hunting, whereas the non-linear size-extinction pattern in the historic period points to the complex interactions of endemism with disease and exotic predators. However, the body size distributions of prehistoric and historic victims are indistinguishable below 244 g (5.5 ln units; KS test: $P = 0.83$). Because habitat destruction was a major factor in both extinctions, the similarity of these distributions may reflect the consistent loss of vital habitat over time. Knowledge of the effects of prehistoric habitat loss may thus help to predict the impacts of modern habitat destruction.

This paper presents the most complete ecological picture of the extinctions of Hawaiian birds currently available. More detailed and perhaps slightly different conclusions will likely emerge with accumulation of additional fossil evidence and information on the extinct and extant avifauna. Nevertheless, human colonization of the Hawaiian Islands initiated sweeping changes in the island environment including the extinction of more than 50% of native bird species. On every other island and continent examined so far, similar size-selective extinctions have followed human colonization (Alcover *et al.*, 1999; Burney, 1999; Roberts *et al.*, 2001; Roff & Roff, 2003; Duncan & Blackburn, 2004; Lyons *et al.*, 2004). One clear message from previous studies and the results presented here is that human-mediated extinction often follows predictable patterns. We must use this knowledge to help prevent further extinctions today.

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SUPPLEMENTARY MATERIAL

The following supplementary materials are available for this article:

Appendix S1 List of data sources.

Appendix S2 Data spreadsheet (.csv).

Appendix S3 Description of methods for estimating taphonomic bias.

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http://www.blackwell-synergy.com/doi/abs/10.1111/
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