

## 8 Prehistoric Extinctions and Ecological Changes on Oceanic Islands

H.F. JAMES

### 8.1 Introduction

*"In addition to the absence of native land birds over large areas in Hawaii, there is another interesting, as well as frustrating, feature about the distribution of the birds: some ecological niches are virtually devoid of native birds.*

*No native land bird inhabits the forest floor. The long-extinct rail on Hawaii did so, but almost nothing is known about either the habits or the ecological distribution of this small bird."*

A. Berger (1972: p. 24)

The body of ecological theory that relates specifically to islands was developed mainly through inference from modern patterns of diversity. Observations of process are limited, because they are usually restricted to the relatively short and recent periods of time covered by most field studies and experiments. Whether the processes that are important in these contexts can be extrapolated to explain biogeographic patterns that have been thousands to millions of years in genesis, is an essential question for which there are few relevant data. In this chapter, I argue that greater reliance on paleontological data would strengthen our understanding of island ecosystems, by linking modern patterns to processes that occur on evolutionary timescales.

The first step in this direction is to recognize the limitations to the information that can be obtained. Paleontological data have inherent biases, and are usually not directly comparable to ecological data. For example, fossil assemblages may be subject to time-averaging, or the mixing of diachronic populations in a single sample. Ecologists can pose research questions in terms that call for data collected with fine temporal resolution. To examine the same phenomena paleontologically, the questions have to be recast in terms that are tolerant of time-averaging. The discussion of turnover rates in this chapter is an example of such a problem.

The inability to observe organisms in life, interacting with their environment, is another obstacle to ecological interpretations of paleontological evidence. To an extent, this loss of autecological detail can be compensated for by reconstructing parameters of ecological importance, such as the weight, diet, and

---

Department of Vertebrate Zoology, National Museum of Natural History, Washington, DC 20560, USA

---

Ecological Studies, Vol. 115  
Vitousek et al. (eds) Islands  
© Springer-Verlag Berlin Heidelberg 1995

paleohabitat of extinct animals (e.g., Atkinson and Millener 1991). In this chapter, the absence of autecological detail makes it necessary to use a very coarse-grained approach when grouping extinct Hawaiian birds into feeding guilds.

Turning to the island fossil record itself, the salient observation that has emerged from many years of research is of an extinction event that significantly reduced vertebrate species richness during the postglacial period (the Holocene epoch, 10 000 years ago to the present). Within the island realm, these extinctions were global in scope. They can be traced through the Pacific, Atlantic, Arctic, and Indian Oceans, and the Mediterranean and Caribbean Seas. A recent review lists over 200 species of extinct island birds known from fossils (Milberg and Tyrberg 1993), a number that is steadily increasing with new discoveries. Many other endemic island vertebrates were lost, such as tortoises, lizards, bats, giant rodents, and dwarf ungulates.

Quaternary extinctions on continents are variously attributed to climatic reversals, geophysical activity, and to human impacts on the environment. During the same time frame (1.64 million years ago to the present), islands probably suffered extinctions from each of these causes as well. During the lowered sea levels of glacial maxima, the shallow marine shelves that surround some islands were exposed as emergent land, sometimes forming land bridges to continents or to other islands. Conversely, islands with low physical relief have been partly (sometimes entirely) inundated by the sea during marine transgressions. In theory, extinctions can result from competition after faunal exchange in the former case, or from reduced carrying capacity in the latter.

Knowledge of the historical geology of islands is receiving the benefit of renewed interest in catastrophism, leading to intriguing research, for example on the immense submarine (and partly subaerial) debris avalanches that affect Hawaiian shield volcanoes. Enormous avalanches can cause a sudden reduction in island area, and give rise to waves that have reached up to 365 m elevation on nearby islands, stripping away top soil below this elevation (Moore et al. 1989). Sudden devastation to islands can result from volcanic eruptions as well. Such catastrophic geophysical events have the potential to cause significant disturbance, and even to lead to extinctions on islands.

Delayed vegetation change following the Holocene climatic reversal may explain the extinction of dwarf mammoths 4000 years ago on Wrangel Island in the Arctic Ocean (Vartanyan et al. 1993). Change from drier Pleistocene to wetter Holocene climate has been advanced to explain extinctions in the West Indies (Pregill and Olson 1981), although chronological data are needed to support this. In Madagascar, paleoecological evidence of climatic desiccation during the late Holocene, coupled with evidence for several types of human impacts, has given rise to the hypothesis that synergistic interactions among climatic and anthropogenic factors contributed to the extinctions (e.g., MacPhee 1986; Burney 1993a). This explanation has been suggested for some late Quaternary extinctions outside Madagascar as well (Burney 1993b).

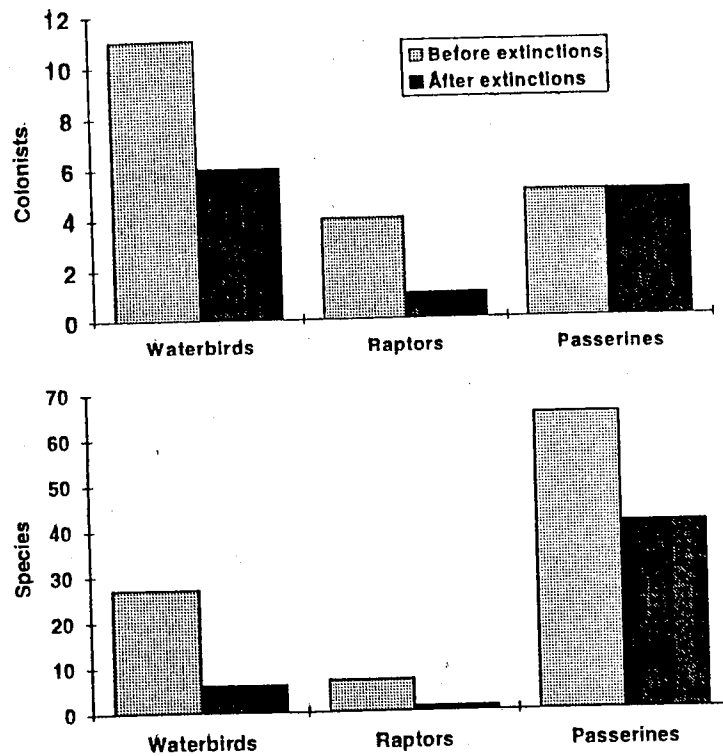
The most widely held hypotheses to explain Holocene island extinctions include a strong component of anthropogenic change. When the fossils have been radiometrically dated, it is usually apparent that most extinctions postdate the arrival of humans on the island (e.g., Steadman 1989; Steadman and Olson 1985; Steadman et al. 1984). Overharvesting and habitat destruction by humans, and collateral impacts resulting from their introduction of foreign competitors, predators, and even pathogens, are thought to have played a role. The human-caused extinction of island endemics is an ongoing phenomenon, and a matter of historical record in many instances (Greenway 1958). For prehistoric extinctions, the most thorough demonstrations of the human role have come from multidisciplinary studies that associate vertebrate fossils with evidence drawn from sedimentology, palynology, archeology and ethnography (e.g., Anderson 1989; Kirch et al. 1992).

For island ecosystem studies, it is important to understand that prehistoric anthropogenic change has intervened between modern patterns and the long-term processes that we infer from them. To what extent can modern patterns of diversity on islands be attributed to natural factors, to what extent to anthropogenic change? What exactly caused the extinctions, and how was ecosystem function affected? I review data relevant to some aspects of these questions, and where further research is needed, discuss the types of paleontological data that can be brought to bear.

## 8.2 Diversity

Holocene extinctions of vertebrates have been detected on most islands where fossil surveys were carried out. The proportion of native vertebrates lost from individual islands varies, but in the most extreme examples, some islands lost all resident, terrestrial species (e.g., Easter Island and Kahoolawe). New Zealand lost about 30 species of birds prehistorically (Millener 1991). The Hawaiian Islands lost 35 to perhaps 57 (James and Olson 1991; Olson and James 1991), an estimate that is continually being revised upward as more new species are discovered (e.g., Giffin 1993). Madagascar lost at least 30 species of mammals, birds, and tortoises (Dewar 1984; Godfrey et al. 1990; Goodman and Ravoavy 1993; and James pers. observe). In recent centuries, even the relatively pristine Galapagos Islands have lost at least 29 to 34 island populations of vertebrates (Steadman et al. 1991).

The Hawaiian Islands can serve to illustrate how prehistoric extinctions obscured our perception of natural faunal development on islands. When the extinct birds are added to the avifauna, it becomes apparent that many more avian species successfully colonized the archipelago and gave rise to endemic lineages than would be recognized without the fossil evidence (Fig. 8.1). The lineages that became extinct in prehistoric times fall into two distinct categories. They were either derived from waterbirds (ibises, rails, geese, ducks), most of which had shifted to terrestrial habitats after colonizing the islands, or they were



**Fig. 8.1.** The native avifauna of the main Hawaiian Islands, before and after prehistoric extinctions. *Above* The number of colonizing species necessary to account for the resident species of birds; *below* the number of resident species of birds. Data on the number of colonists are from James (1991). Note that all successful colonists were either waterbirds, raptors, or passerines. Many of the waterbirds shifted into terrestrial habitats after colonizing the islands

raptors (eagles, hawks, owls). No passerine lineages became entirely extinct, and passerines suffered proportionately less extinction at the species level as well (Fig. 8.1, below). In this way, extinction masked the success of waterbirds and raptors in colonizing the remote Hawaiian Islands and diversifying there, while it artificially exaggerated the importance of passerines in the fauna.

The impact that extinction may have had on individual island ecosystems is suggested by Figure 8.2, which contrasts the number of resident, native species recorded from specific Hawaiian islands, before and after prehistoric extinctions. Fossil collecting has been the most thorough on Maui and Oahu. On these islands, the high proportion of extinct species suggests that a prehistoric faunal collapse occurred, affecting not only the larger species that are conventionally thought to be vulnerable, but also many smaller species that presumably would have been relatively abundant and less extinction-prone.

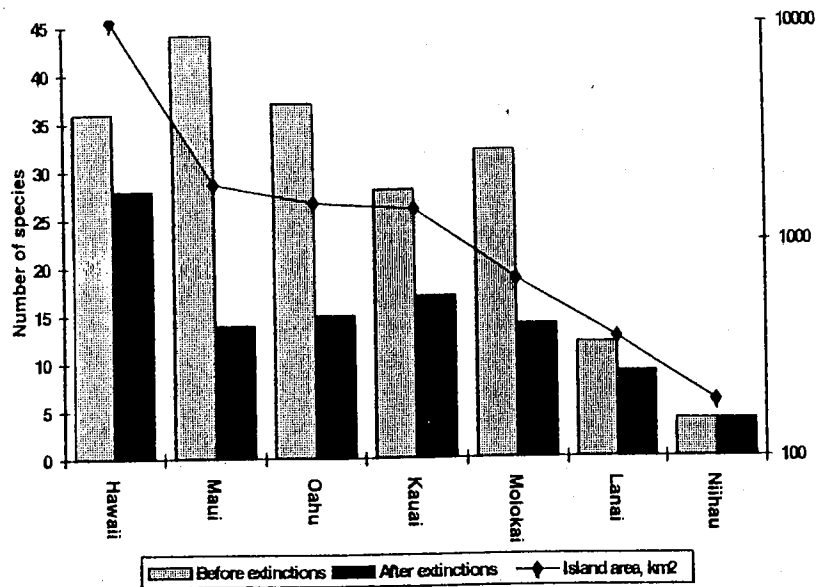


Fig. 8.2. The number of species in the resident avifauna of individual Hawaiian islands, before and after prehistoric extinctions. The scale on the *right* is for island area

Table 8.1. Comparison of cave faunas from Maui and northwest Madagascar

	Madagascar	Maui
Island area, km <sup>2</sup>	$5.87 \times 10^5$	$1.18 \times 10^3$
Human arrival, thousands of years before present	$\leq 2$	$\leq 2$
Local climate near caves	Tropical dry/mesic, seasonal rainfall	Tropical dry/mesic, seasonal rainfall
Cave system	Grottes d'Anjohibe and Anjohikely (S15° 33', E46° 53')	Puu Naio Cave (N20° 37', W156° 24')
Chronological range of fossil assemblage	7790 B.P. to modern	8820 B.P. to modern
Species of higher vertebrates		
<i>n</i> identified	$\pm 65$	35
<i>n</i> extinct	7–10	24–26
% extinct	11–15	69–74

In other island ecosystems the extinction event may have had a substantially different profile. A comparison of cave faunas from northwest Madagascar and Maui illustrates this point (Table 8.1). Radiocarbon chronologies establish that bones were accumulating in the two cave systems (Puu Naio on Maui, and Anjohibe and Anjohikely on Madagascar) during most of the Holocene. The

taphonomic origin of the collections is from natural traps and predator accumulations, supplemented with samples from bat roosts and archeological sites in the Madagascar caves. Thousands of bones were collected and identified from each cave system (James et al. 1987; James and Olson 1991; Burney et al. 1994). The revealing comparison is between the number and proportion of extinct species in the two localities. In northwest Madagascar, the evidence suggests that extinctions affected a much smaller proportion of the fauna and were more skewed toward larger species, compared to what occurred on Maui. If the model of faunal collapse with cascading extinctions is applicable to both extinction events, then the cascade appears to have proceeded much farther on Maui. Alternately, the difference may be explained to some extent by sampling error. Further field work may reveal a large number of undocumented extinctions of smaller animals on Madagascar.

Little is known about prehistoric extinctions of animals other than vertebrates. Insect extinctions probably occurred, but with few exceptions, there is no relevant record. Remains of extinct land crabs are frequently found in dunes and caves in the Hawaiian Islands. These may be the same species that was collected alive on Oahu in 1864 (Edmonson 1962), a record that has generally been overlooked because land crabs were never again taken alive in the islands. Land snails likewise suffered extinctions and local extirpations, and left behind an abundant record in caves and sediments, worthy of further study (e.g., Christensen and Kirch 1986).

The island record of fossil and subfossil plants generally has not produced evidence of anthropogenic extinction on the same scale as for vertebrates, but there are notable exceptions. For example, no native trees live on Easter Island, but lake cores contain pollen types representing about seven arborescent taxa (Flenley et al. 1991). Their extinction is attributed to complete deforestation of the island by humans. Ilha da Trindade in the South Atlantic is now virtually barren of trees, but dried stumps and branches found around the island vouchsafe the formerly wide distribution of a tree that was mentioned in early travel accounts (Eyde and Olson 1983). In the Hawaiian Islands, most of the Holocene plant microfossils identified by Selling (1946, 1947, 1948) in mid- to high-elevation bog cores belonged to extant taxa, although the spores of one fern were described as an extinct species (Selling 1946). The pollen types identified in late-Holocene sediment cores from the lowlands of Oahu were also attributed to extant taxa (Athens et al. 1992). However, the lowland cores provided evidence that there were major changes in plant communities during prehistoric times. These changes included the island-wide extinction of a leguminous shrub that had been fairly common on Oahu in the late Holocene. As one of the few nitrogen-fixing plants in the native Hawaiian flora, this legume may once have played an ecologically important role, but it is now too rare to do so. To summarize the botanical evidence, it is clear that prehistoric anthropogenic changes in island vegetation may have been extensive and have had important implications for ecosystem function. Yet current evidence suggests that plants were more resistant to extinction than animals (at least vertebrates) in the same ecosystems.

---

### 8.3 Prehuman Extinctions

In order to understand how island ecosystems respond to disturbance, be it natural or anthropogenic, we first need to know how these ecosystems behave in the absence of disturbance. When the evidence of disturbance is mainly a record of extinctions, we need to know the frequency of background extinction for comparison. In ecology, background extinctions are theoretically linked to species immigrations, which are often combined to calculate the overall rate of species turnover. Based on ecologists' estimates of species turnover in island avifaunas, summarized by Schoener (1983), we might expect 500 to 14 000 turnover events on a given island in the course of the Holocene.

For a number of reasons, it is likely that oceanic island communities are far more stable than these rates imply. Not all bird censuses yield similarly high estimates of turnover (Mayer and Chipley 1992). Arguing from modern patterns of diversity, we might predict low natural turnover rates on many oceanic islands. Turnover is inferred to be low when a high proportion of the species on an island are endemic, since endemism cannot develop or be sustained unless populations on the island are fairly long-lived (Diamond and Jones 1982). However, we have already discussed the prehistoric changes that make us suspicious of inference from modern patterns.

Estimating the turnover rate from ecological data has always been controversial. Early attempts were faulted because they relied on incomplete census data (Lynch and Johnson 1974), and attached undue importance to "ecologically trivial" events, such as the failure of small founder populations that had never played a significant role in ecosystem dynamics (Williamson 1989). In some studies of bird populations, most of the observed turnover was due to occasional breeders that were recorded in some years but not others (Diamond and Jones 1982). Considered over a longer stretch of time, these species are effectively part of the island's avian community. It may be inappropriate to equate their movements with turnover of long-established resident populations. In addition to these drawbacks, widespread anthropogenic disturbance makes it difficult to find island ecosystems where turnover can be studied under natural conditions. All of the above-mentioned factors will tend to inflate turnover rates estimated from ecological data, when compared with paleontological data.

Consider now the characteristics of paleontological data with respect to estimating turnover. In the light of time-averaging of fossil assemblages, census interval poses an even more serious problem than it does for ecological data (Diamond and May 1977). Time-averaging also means that paleontological records are unlikely to detect turnover due to occasional breeders. Small founder populations that fail to take hold are probably less likely to be observed by the paleontologist than by the field ecologist. Distinguishing breeding from non-breeding birds in fossil samples can be an additional problem. In these ways, paleontological and ecological estimates of turnover rate will not be directly comparable. However, if we wish to know to what extent extinctions and immigrations have shaped the modern ornithogeography of islands, then

paleontological data have some advantages. Only fossils offer the time-depth necessary to gauge the importance of turnover for long-established, resident populations. If such populations experience a constant rate of background extinction, this should be revealed by paleochronological data that record the distribution of extinctions through time.

Most available data show a cluster of extinctions in the human era, and very few before then. For example, in the Galápagos, of the 29 to 34 extinctions of vertebrate species or island populations that are on record for the Holocene, all but 3 are known to have occurred in the 5 centuries since humans began visiting the islands (Steadman et al. 1991).

Taking a step back in time, on the west coast of the South Island, New Zealand, avian species composition in cave faunas differs significantly between the last glacial maximum of the Pleistocene (25 000 to 10 000 years ago) and the Holocene (Worthy and Holdaway 1993). The authors interpret these differences in terms of the Pleistocene-Holocene climatic reversal. Evidently, climatic reversal caused major regional shifts in bird distributions within New Zealand, but as far as we know, no outright extinctions occurred. All of the late Pleistocene fossils of terrestrial birds known so far from New Zealand are attributed to species that survived until humans arrived, about 1000 years ago (Cooper and Millener 1993). The New Zealand avifauna suffered far greater stress during the human era, when half of the terrestrial species went extinct.

Taking another step back in time, on the island of 'Eua, Tonga, 21 species of birds were identified in a fossil collection dating to between 60 000 and 80 000 years ago (Steadman 1993). The fate of these species was traced by checking for their presence in archeological deposits on 'Eua, which date to < 3000 years ago. All but 5 of the 21 species were recorded in archeological contexts, indicating that at least three-fourths of the Pleistocene fauna survived until the human era. Eleven of these survivors (half of the Pleistocene fauna) disappeared from 'Eua during the human era. The Tongan data are consistent with the pattern of higher extinction rates in the human era, but they also suggest more prehuman faunal change than was observed in New Zealand. The author of the study notes that some of the apparent prehuman extinctions may be artifacts of sampling error.

A deeper Pleistocene record is available from the Hawaiian island of Oahu, where 17 species of land birds were recorded in a preliminary study of Pleistocene fossils from Ulupau Head, dating to > 120 000 years ago (James 1987). The fate of these species can be traced up through the Holocene to the present. Between > 120 000 years ago and the present, global climate passed through a complete cycle of glaciation and deglaciation, a potential cause of faunal change. However, in this case very little faunal change was observed in prehuman times. All but perhaps one or two (12% or fewer) of the species from Ulupau Head survived through the times of most pronounced climate change. These species were still extant in the mid- to late Holocene, when the Barber's Point fossil assemblage accumulated on Oahu. Tellingly, 13 (76%) of the Pleistocene survivors have met with extinction during the past few thousand years, when human impacts may have been important.



In summary, although we cannot hope to calculate annual turnover rates for comparison with ecological data, the paleontological evidence argues for long-term stability of vertebrate communities on oceanic islands. There is more evidence of prehuman faunal change in Tonga than in Hawaii or New Zealand. In New Zealand and Hawaii, the fossil evidence would not support species turnover as an important determinant of modern bird distributions, at least for native species. Perhaps more surprising is the paucity of evidence for climate-driven extinctions in the late Pleistocene, whether in tropical Hawaii or in temperate to subantarctic New Zealand. There are at least two possible explanations for this. One is simply that some island ecosystems resist climate-driven extinctions better than some continental ecosystems. Another is that late Pleistocene climate change actually caused relatively few extinctions, either on continents or on islands. It is still debated that late Pleistocene extinctions on continents were caused mainly by the spread of paleolithic peoples, rather than by climatic reversal (Martin 1984).

#### 8.4 Prehuman Biological Invasions

Humans can cause disturbance on oceanic islands through their own activities, but they also frequently assist other alien species to invade, sometimes with very deleterious results. However, we know that island ecosystems have been invaded by alien species many times in the past, and presumably suffered adverse consequences even before the advent of humans. To put human-assisted invasions in perspective, it would be useful to know how island ecosystems have responded to invasions when humans were absent. This is another aspect of island ecosystem dynamics that paleontology may help to illuminate.

For example, several lines of evidence suggest that the subfossil sea eagle of the Hawaiian Islands is a relatively recent, but prehuman invader. First, the Hawaiian eagle does not show morphological adaptations to the island environment. Osteologically, it cannot be distinguished from either the palearctic White-Tailed Sea Eagle (*Haliaeetus albicilla*), or from the nearctic Bald Eagle (*Haliaeetus leucocephalus*; see Olson and James 1991). Second, chronological data are consistent with recent colonization. Collagen from eagle bones found in Puu Makua Cave on Maui was dated as being over 3000 years old ( $^{14}\text{C}$  sample 88NM-22,  $3000 \pm 60$  B. P.; 2 sigma calibrated range, 3389–3689 B. P.). This date establishes the presence of the eagle in the islands at least 1300 years before human arrival. More tentatively, the eagle may not have been present as long ago as  $> 120\,000$  years, as it has not been collected from the Pleistocene lake beds at Ulupau Head. We know that most of the elements of the Hawaiian vertebrate fauna (such as large flightless anseriforms, small ducks, coots, hawks, owls, crows, and flightless rails) were already present  $> 120\,000$  years ago (James 1987). The subsequent arrival of an eagle would have introduced a new trophic level to Hawaiian ecosystems, where flightless birds may have evolved in the absence of large predators. If adjustments occurred in response to predation by the eagle,

there is no evidence that they included rapid extinctions. Radiocarbon chronologies indicate that the extinctions of flightless birds took place centuries after humans arrived, and at least 2000 years after the arrival of the eagle (Stafford and James, unpubl.).

It is possible to cite contrary examples in which the human-assisted invasion of an island by a predator leads to rapid extinctions, as when the brown tree snake was transported to Guam (Savidge 1987). Further development of the fossil record associated with prehuman invasions of oceanic islands would lend historical perspective to the many studies of biological invasions that are underway at this time.

### 8.5 Anthropogenic Deletions

The ecological effects of biological invasions have received more research attention than the effects of deletions, perhaps not surprisingly in light of the difficulty of studying something that is no longer there. Nevertheless, deletions should not be ignored, since the fossil record repeatedly points to their importance in shaping modern communities. Consider the rainforest of the Kipahulu Valley on Maui, one of the few seemingly pristine forests remaining in the Hawaiian Islands. Seven species of birds that no longer occur in the valley constitute the faunal list of Holocene fossils from lava tube caves here (Medeiros et al. 1988; James, pers. observ). Only one of these species, the Hawaiian dark-numped petrel (*Pterodroma phaeopygia*), still survives anywhere on the island. The forest has also lost an herbivorous flightless anatid (*Ptaiochen pau*), a goose related to the Hawaiian Goose but with reduced flight capability (*Branta hylobadistes*), a flightless rail (*Porzana* sp.), a flightless ibis (*Apteribis* sp.), a thrush (*Myadestes* sp.), and a finch (*Orthospiza howarthi*). The fossil sample is small and the list is undoubtedly incomplete, yet even with this limited information, it is evident that the valley has undergone considerable Holocene change. Although the exact dietary habits of the missing species are unknown, we can surmise that the forest has been released from pressure from herbivores, frugivores, probably granivores, and from two species that were probably omnivorous feeders among forest floor detritus. What specifically caused these species' disappearance from the valley is not known, but human impacts of some sort are a strong possibility.

On many islands, prehistoric deletions may still be affecting forest ecosystems in unseen ways. Relevant observational data are hard to come by, leaving this a subject for current speculation and future research. Some possible effects of prehistoric deletions are the loss of certain ecological roles (e.g., with the extinction of land crabs), the breakdown of mutualisms (e.g., between rare plants and their extinct pollinators), habitat change due to loss of keystone species (e.g., the New Zealand moas, whose extinction may have inhibited the regeneration of native conifers; Cooper et al. 1993), and limitations to plant dispersal (e.g., due to the widespread extinction of avian frugivores in Polynesia; Steadman 1991). A factor worth investigating is the role that breeding seabirds may have played in

transferring marine nutrients to terrestrial ecosystems. Breeding seabirds were extirpated in some regions and greatly reduced in numbers in others by prehistoric overharvesting.

## 8.6 Vertebrate Feeding Guilds

Compared to the possible effects mentioned above, prehistoric changes to vertebrate feeding guilds are fairly amenable to analysis. Patterns can be discerned, for instance that extinctions left a false impression of relatively predator-free communities on many islands. From giant owls in Cuba, to giant eagles in Crete and New Zealand, to foxes in Sardinia and Corsica, predators at the highest trophic level seem to have been particularly vulnerable to prehistoric extinction. Large, endemic herbivores were vulnerable as well. Moas, swans, and geese are gone from New Zealand; elephant birds, giant tortoises, pygmy hippos, and giant lemurs from Madagascar; ground sloths and monkeys from the Greater Antilles. Many, but not all, of these extinctions have been shown to postdate human arrival.

The Hawaiian Islands can serve once again to illustrate how prehistoric extinctions altered the structure of vertebrate feeding guilds. Based on a very rough division of the resident avifauna into guilds, it is clear that extinction affected some groups more than others (Fig. 8.3). All but one species of native predator became extinct prehistorically. The one survivor (the Hawaiian Hawk, *Buteo solitarius*) became restricted in distribution to the largest island, so that most regions of the islands lost all native predators. To some extent, native raptors were replaced by owls that arrived after human settlement, but the new arrivals tend to feed on rodents, while their extinct counterparts specialized in eating the native birds.

Similarly, all terrestrial herbivores became extinct except the Hawaiian goose (*Branta sandvicensis*), which survived only on the largest island. The extinct herbivores include the large flightless anseriforms called moa-nalos, which are thought to have been browsers on understory foliage (Olson and James 1991). Their universal extinction may still be affecting understory vegetation in Hawaiian forests. Terrestrial omnivores (flightless rails and ibises) had been an important component of Hawaiian ecosystems, but they too all but disappeared prehistorically. The absence of avian terrestrial omnivores, coupled with the extinction of Hawaiian land crabs, may have continuing implications for nutrient cycling on the forest floor.

Most of the species of vertebrates that survived the Hawaiian extinction event are perching birds (order Passeriformes). Of 67 passerine species in the Holocene fauna of the main islands, 25 (37%) became extinct prehistorically, and another 15 (22%) have become extinct since European contact. These figures are approximate, because some postcontact extinctions probably went undetected, and undoubtedly some prehistoric extinctions have not yet been discovered.

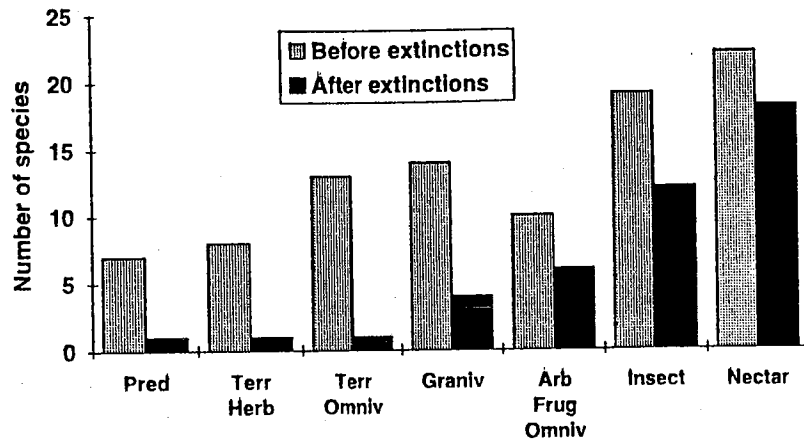


Fig. 8.3. The effect of extinction on avian feeding guilds in the Hawaiian Islands. Guilds are as follows: predators (*Haliaeetus*, *Buteo*, *Circus*, *Grallistrix*); terrestrial herbivores (*Chelychelynechen*, *Thambetochen*, *Ptaiochen*, *Branta*, *Geochen*, very large Hawaii goose); terrestrial omnivores (*Apteribis*, *Porzana*); granivores (*Telespiza*, *Loxioides*, *Chloridops*, *Rhodacanthis*, *Xestospiza*, and questionably *Orthospiza*); arboreal frugivores/omnivores (*Corvus*, *Myadestes*, *Psittirostra*); insectivores (*Chasiempis*, *Pseudonestor*, *Hemignathus*, *Oreomystis*, *Paroreomyza*, *Vangulifer*, *Aidemia*); and nectarivores (*Moho*, *Chaetoptila*, *Loxops*, *Vestiaria*, *Drepanis*, *Himatione*, *Palmeria*, *Ciridops*). Wetland species and non-native species are excluded from the analysis. Snail-eaters (*Melamprosops* and questionably *Dysmorodrepanis*) are excluded from the figure.

Not enough is known about the diets of the extinct species to permit a precise division of the passerines into feeding guilds at this time. Instead, I have divided them into four very general categories, an approach that will reveal only the broadest patterns (Fig. 8.3). Examined in this way, prehistoric extinctions among insectivores (37%) and arboreal frugivores/omnivores (40%) are proportional to extinctions among passerines generally.

The same is not true of granivores or nectarivores. Granivores have suffered grievously from extinction, beginning in the prehistoric phase of extinctions, and continuing historically until they were obliterated from all but one area of the main islands, high on the slopes of Mauna Kea. Meanwhile, nectarivores enjoyed an opposite fate. They began as the most speciose guild and remained so. Their extinctions were especially light during the prehistoric phase, when most of the granivores were disappearing. Indeed, the changes that Hawaiian forest communities have undergone seem to favor certain nectarivores (i.e., *Himatione sanguinea*, *Loxops virens*, *Vestiaria coccinea*), which at the present time are the most abundant native birds in the forests (Scott et al. 1986). With predators disappearing, habitats shifting, and species richness plummeting during the extinction event, it is plausible to suppose that some species, even some guilds, might gain an advantage, and perhaps end up being more widespread and abundant than they had been under prehuman conditions.

## 8.7 Future Directions

More than any other factor, the Holocene fossil record of islands reflects the repercussions of one significant addition to the fauna, that of *Homo sapiens*. As humans became established on island after island, an extinction event ensued. In effect, the experiment that can tell us how ecosystems respond to anthropogenic change, and particularly to reduced species richness, has already been set in motion. The experiment has been replicated numerous times on different islands, under varying conditions of climate, geography, ecosystem structure, human economy, and cultural evolution. The challenge is to exploit this source of information more effectively, to better understand what caused the extinctions, and how ecosystems were affected.

Reconstructing the complex history of prehistoric environmental degradation and identifying its precise causes is admittedly a difficult task. The use of comparative methods to search for common patterns in the extinction events that occurred on different islands is one promising approach to the problem. For this approach to be successful, we need to develop comparable data sets from various islands, dealing with such factors as vegetation change, human population and adaptation, and the ecological characteristics of extinct vs. surviving species. Excellent chronological data are needed, so that events that were separated in time will not be falsely correlated with each other. The comparative data on extinctions in northwest Madagascar and Maui, discussed in this chapter, is one small example of the types of comparisons that could prove to be informative.

The differential effects of extinction on vertebrate feeding guilds suggest that prehistoric changes may still be affecting island communities. When extinctions have occurred but the forest itself has endured, as is the case in the Kipahulu Valley on Maui, there may be continuing effects on ecosystem dynamics that are subtle and difficult to study. What happens to a forest when the native vertebrate predators, terrestrial herbivores and omnivores, and the granivores are removed from it? Increased collaboration between ecologists and paleontologists would promote a better understanding of natural ecosystem processes in the native habitats that still persist on islands.

A final point for emphasis is the potential of the fossil record to illuminate island ecosystem dynamics in prehuman times. Our perception of island ecosystems as fragile, and of island endemics as extinction-prone, is colored by the accelerated pace of change during the human era. In prehuman times, vertebrate communities on some islands underwent very little reorganization for tens of thousands of years, even through periods of pronounced global climate change. Stasis, however, is not the entire story. Before the advent of humans, island ecosystems were exposed to stress, for example from naturally occurring biological invasions, from reconfiguration of the landscape due to sea level change, from catastrophic geophysical events, and certainly from changes in climate. By developing the fossil record associated with such events, we could improve our understanding of the effects of natural vs. anthropogenic ecosystem disturbance.

*Acknowledgments.* I am grateful to Peter Vitousek and Hall Cushman of Stanford University and to Pericles Moillis of the Bahamas National Trust for organizing a very rewarding workshop. The field research that led to this summation was supported by the Wetmore Funds and the Scholarly Studies Program of the Smithsonian Institution, the Department of Defense Legacy Program, National Geographic Society grant 4493-91 to H. Wright and D. Burney, and NSF BSR-9025020 to D. Burney. David Burney, Lloyd Loope, Christopher Perrins, Storrs Olson, David Steadman, and Graham Wragg read a draft of the manuscript and made many useful suggestions.

## References

- Anderson A (1989) *Prodigious birds: moas and moa-hunting in prehistoric New Zealand*. Cambridge University Press, Cambridge
- Athens JS, Ward J, Wickler S (1992) Late Holocene lowland vegetation, O'ahu, Hawai'i NZJ Archaeol 14: 9-34
- Atkinson IAE, Millener PR (1991) An ornithological glimpse into New Zealand's pre-human past. Acta XX Congr Int Ornithol 1: 127-192
- Berger AJ (1972) *Hawaiian birdlife*. University of Hawaii Press, Honolulu, xii + 270 pp
- Burney DA (1993a) Late Holocene environmental changes in arid southwestern Madagascar. Quat Res 40: 98-106
- Burney DA (1993b) Recent animal extinctions: recipes for disaster. Am Sci 81: 530-541
- Burney DA, James HF, Grady FV, Rafamantanantsoa J-G, Ramilisonina, Wright HT, Cowart JB (1994) Environmental change, extinction, and human activity: evidence from caves in NW Madagascar. Natl Geogr Res Explor (in press)
- Christensen CC, Kirch PV (1986) Nonmarine mollusks and ecological change at Barbers Point, O'ahu, Hawai'i. Occas Pap Bernice P Bishop Mus 26: 52-80
- Cooper RA, Millener PR (1993) The New Zealand biota: historical background and new research. TREE 8(12): 429-433
- Cooper AJ, Atkinson IAE, Lee WG, Worthy TH (1993) Evolution of the Moa and their effect on the New Zealand flora. TREE 8(12): 433-437
- Dewar RE (1984) Extinctions in Madagascar: the loss of the subfossil fauna. In: Martin PS, Klein RG (eds) *Quaternary extinctions: a prehistoric revolution*. University of Arizona Press, Tucson, pp 574-593
- Diamond JM, Jones HL (1982) Species turnover in island bird communities. Acta XVII Congr Int Ornithol 2: 777-782
- Diamond JM, May RM (1977) Species turnover rates on islands: dependence on census interval. Science 197: 266-270
- Edmonson CH (1962) Hawaiian Crustacea: Goneplacidae, Pinnotheridae, Cymopoliidae, Ocypodidae, and Gacardinidae. Occas Pap Bernice P Bishop Mus 23(1): 1-27
- Eyde RH, Olson SL (1983) The dead trees of Ilha da Trindade. Bartonica 49: 32-51
- Flenley JR, King ASM, Jackson J, Chew C (1991) The Late Quaternary vegetational and climatic history of Easter Island. J Quat Sci 6(2): 85-115
- Giffin J (1993) New species of fossil birds found at Pu'u Wa'awa'a. 'Elepaio 53(1): 1-3
- Godfrey LR, Simons EL, Chatrath PJ, Rakotosamimanana B (1990) A new fossil lemur, *Babakotia* (Primates), from northern Madagascar. CR Acad Sci ser II Mec Phys Chim Sci, Univers Sci Tone 310(1): 81-88
- Goodman SM, Ravoavy F (1993) Identification of bird subfossils from cave surface deposits at Anjohibe, Madagascar, with a description of a new giant *Coua* (Cuculidae: Couinac). Proc Biol Soc Wash 106(1): 24-33
- Greenway JC (1958) *Extinct and vanishing birds of the world*. Spec Publ 13, Am Comm Int Wild Life Protect New York

- James HF (1987) A late Pleistocene avifauna from the island of Oahu, Hawaiian Islands. *Doc Lab Geol Fac Sci Lyon* 99: 221–230
- James HF (1991) The contribution of fossils to knowledge of Hawaiian birds. *Acta XX Congr Int Ornithol* 1: 420–424
- James HF, Olson SL (1991) Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part II. Passeriformes. *Ornithol Monogr* 46: 1–88
- James HF, Stafford TW Jr, Steadman DW, Olson SL, Martin PS, McCoy P (1987) Radiocarbon dates on bones of extinct birds from Hawaii. *Proc Natl Acad Sci USA* 4: 2350–2354
- Kirch PV, Flenley JR, Steadman DW, Lamont F, Dawson S (1992) Ancient environmental degradation: prehistoric human impacts on an island ecosystem: Mangaia, Central Polynesia. *Natl Geogr Res Expl* 8(2): 166–179
- Lynch JF, Johnson NK (1974) Turnover and equilibria in insular avifaunas, with special reference to the California Channel Islands. *Condor* 76(4): 370–384
- MacPhee RDE (1986) Environment, extinction, and holocene vertebrate localities in southern Madagascar. *Natl Geogr Res Expl* 2(4): 441–455
- Martin PS (1984) Prehistoric overkill: the global model. In: Martin PS, Klein RG (eds) *Quaternary extinctions: a prehistoric revolution*. University of Arizona Press, Tucson, pp 354–403
- Mayer GC, Chipley RM (1992) Turnover in the avifauna of Guana Island, British Virgin Islands. *J Anim Ecol* 61: 561–566
- Medeiros AC, Loope LL, James HF (1989) Caves, bird bones and beetles: new discoveries in rain forests of Haleakala. *Park Sci* 9(2): 20–21
- Milberg P, Tyrberg T (1993) Naive birds and noble savages – a review of man-caused prehistoric extinctions of island birds. *Ecography* 16: 229–250
- Millener PR (1991) The Quaternary avifauna of New Zealand. In: Vickers-Rich PV, Monaghan JM, Baird RF, Rich TH (eds) *Vertebrate paleontology of Australasia*. Monash Univ Publ Comm, Melbourne, pp 1317–1344
- Moore JG, Clague DA, Holcomb RT, Lipman PW, Normark WR, and Torresan ME (1989) Prodigious submarine landslides on the Hawaiian Ridge. *J Geophys Res* 94 (B12): 17465–17484
- Olson SL, James HF (1991) Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part I. Non-Passeriformes. *Ornithol Monogr* 45: 1–88
- Pregill GK, Olson SL (1981) Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. *Annu Rev Ecol Syst* 12: 75–98
- Savidge JA (1987) Extinction of an island forest avifauna by an introduced snake. *Ecology* 68: 660–668
- Schoener TW (1983) Rate of species turnover declines from lower to higher organisms: a review of data. *Oikos* 41: 372–377
- Scott JM, Mountainspring S, Ramsey FL, Kepler CB (1986) Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. *Stud Avian Biol* 9: 1–431
- Selling OH (1946) Studies in Hawaiian pollen statistics, Part I: the spores of Hawaiian Pteridophytes. *Spec Publ Bishop Mus* 37: 1–87
- Selling OH (1947) Studies in Hawaiian pollen statistics, part II: the pollens of the Hawaiian phanerogams. *Spec Publ Bishop Mus* 38: 1–430
- Selling OH (1948) Studies in Hawaiian pollen statistics, part III: on the late Quaternary history of the Hawaiian vegetation. *Spec Publ Bishop Mus* 39: 1–154
- Steadman DW (1989) Extinction of birds in eastern Polynesia: a review of the record, and comparisons with other Pacific island groups. *J Arch Sci* 16: 177–205
- Steadman DW (1991) Ecological impact of the human depletion of frugivorous birds in Polynesia. *Acta XX Congr Int Ornithol* 1: 424 (Abs)
- Steadman DW (1993) Biogeography of Tongan birds before and after human impact. *Proc Natl Acad Sci USA* 90: 818–822
- Steadman DW, Olson SL (1985) Bird remains from an archaeological site on Henderson Island, South Pacific: man-caused extinctions on an “uninhabited” island. *Proc Natl Acad Sci USA* 82: 6191–6195

- Steadman DW, Pregill GK, Olson SL (1984) Fossil vertebrates from Antigua, Lesser Antilles: evidence for late Holocene human-caused extinctions in the West Indies. *Proc Natl Acad Sci USA* 81: 4448-4451
- Steadman DW, Stafford TW Jr, Donahue DJ, Jull AJT (1991) Chronology of Holocene vertebrate extinction in the Galapagos Islands. *Quat Res* 36: 126-133
- Vartanyan SL, Garutt VE, Sher AV (1993) Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. *Nature* 362: 337-340
- Williamson M (1989) The MacArthur and Wilson theory today: true but trivial. *J Biogeogr* 16: 3-4
- Worthy TH, Holdaway RN (1993) Quaternary fossil faunas from caves in the Punakaiki area, West Coast, South Island, New Zealand. *J R Soc NZ* 23(3): 147-254

*Note added in proof.* The manuscript cited above as Burney et al. 1994 (in press) was accepted for publication, but the journal in question recently ceased publication and all manuscripts were returned to the authors. Another publication outlet is being sought.