

LIMITING FACTORS AFFECTING HAWAIIAN NATIVE BIRDS

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Abstract. Hawai'i has lost more than half of its endemic avifauna. Causes have varied, but habitat loss, hunting, predation by introduced predators, and disease are those for which we have the best evidence. With the exception of actions taken on behalf of birds in the Leeward Islands, the scale of management actions has not matched the scale of the threats. Species like the 'Akiapōlā'au (*Hemignathus munroi*), 'Ākepa (*Loxops coccyneus*), Palila (*Loxioides bailleui*), and Po'ouli (*Melamprosops phaeosoma*) are threatened over their entire range. Despite this, management actions are typically limited to areas less than 1% of species ranges. In the absence of any near future means to eliminate avian diseases, the survival of Hawai'i's endemic avifauna depends on elimination of habitat modifiers such as feral cattle (*Bos taurus*), pigs (*Sus scrofa*), goats (*Capra hircus*), feral sheep (*Ovis aries*), and mouflon (*Ovis musimon*). Introduced predators such as cats (*Felis catus*), rats (*Rattus* spp.), feral dogs (*Canis familiaris*), and small Indian mongoose (*Herpestes auropunctatus*) must be eliminated or significantly reduced in numbers over all, or a significant part of, the ranges of the threatened and endangered species of the islands. Failure to do so will result in all but two or three of the commonest species becoming extinct.

Key Words: disease; Hawai'i; honeycreeper; endangered species; management; predation.

Limiting factors responsible for the declines and extinctions of so many native Hawaiian birds have long interested biologists. Virtually every imaginable factor has been set forward at one time or another for the demise of this avifauna, but too often with little supporting evidence. Many have claimed one factor or another as "the" cause of extinction, but with endangered species, there is virtually never a single limiting factor. Instead, a spectrum of intertwining causes all contribute toward what exists today (Ehrlich et al. 1992).

We will critically examine six limiting factors that have been operative on the native Hawaiian avifauna: habitat changes, human predation, nonhuman predation, avian competition, avian parasites/diseases, and abiotic factors. Each factor will be discussed along a time line, starting with pre-human contact (prior to 500 BC), followed by post-Polynesian contact (400–1700 AD), and ending with post-European contact (1778–1998 AD). We will then try to understand the historical and current factors impacting native birds of the Hawaiian Islands. Hopefully, this will provide a foundation from which future research and management can be soundly based. Without some appreciation of these factors, we will have little hope of taking positive steps toward preventing further losses of this unique avifauna.

LIMITING FACTOR I: HABITAT CHANGES

PRE-HUMAN CONTACT

To properly examine anthropogenic habitat change in the Hawaiian Islands, it is necessary to recreate the condition of habitat and birds prior to arrival of the first humans. This is of course largely speculative, because the early humans in

Hawai'i kept no written accounts of the habitat conditions that they encountered. Therefore, we must use archaeological records, observations of the first European explorers, paleontological records, pollen profiles from bogs, and general knowledge of the reactions of biota to various types of impacts.

In pre-human Hawai'i, major habitat changes were restricted primarily to plant community succession and abiotic factors. However, arrival of new species and subsequent adaptive radiation resulted in a constantly changing composition, structure, and function of native ecosystems. One significant influence to vegetation communities was undoubtedly the frequent volcanic eruptions that occurred in the islands, both directly through the impact of lava and volcanic dust and indirectly through fire, as it still does today. The creation of kīpuka's (habitat islands) by lava served to isolate the less mobile species, especially the flightless ones, and must have greatly contributed to the high degree of insular avian adaptive radiation in Hawai'i. Vegetation changes were also wrought by climate shifts caused by El Niño and the ice ages (Allen 1997). Changes in sea level modified low-lying coastal habitats (Nunn 1990). Another factor influencing habitat, and thus the pre-Polynesian birds, would have been infrequent tropical hurricanes. These storms can have a devastating effect on forests and species inhabiting them (Pérez-Rivera 1991, Wauer and Wunderle 1992, Wunderle et al. 1992, Herbert et al. 1999), and any avian species restricted to small forest patches would be subject to local extinctions. Raffaele (1977) attributed the extinction of a Bullfinch (*Loxigilla portoricensis grandis*) from St. Kitts Island to two hurricanes.

Carlquist (1970:173) claimed that before human occupation, no significant herbivory occurred on the islands because there were no grazing land mammals. These ancient forests had, in fact, a considerable array of large herbivorous birds that were probably quite common. One such grazer, a goose, was described from fossil remains more than 50 years ago (Wetmore 1943). Since then, Olson and James (1982b:33–34) have found an array of geese and other potential grazing birds, up to 3 or 4 species from each island, including 10 extinct species, as well as the still extant Hawaiian Goose (*Bran-ta sandvicensis*), hereafter referred to as Nēnē. Some of these extinct birds were quite large, flightless, and even possessed toothlike projections on their beak, apparently an adaptation for grazing on plant parts. In addition, there was a plethora of finch-billed Hawaiian honeycreepers, some of which fed on leaves of plants, as a few still do today. This large grazing avian component undoubtedly influenced habitat changes in pre-human Hawai'i, as did plant feeding insects.

POST-POLYNESIAN CONTACT

The early Hawaiians kept no written records of what habitat changes they wrought to the islands (Kirch 1974). So again, we are forced to rely on inferential reasoning as to what occurred to Hawaiian habitats following Polynesian arrival. We argue that habitat, between the post-Polynesian period of 440 and 1700 AD, would have experienced dramatic changes. The lowlands up to about 1,500 m would have been burned and converted to agricultural lands, thus eliminating a large portion of the very distinct avifauna of these habitats (Cuddihy and Stone 1990). Many of the native plant species, found today only in remnant lowland patches, undoubtedly flourished (Rock 1913). Evidence from Kirch's (1982b) studies of land snails and Olson and James's (1982b) studies of pre-Polynesian fossil birds leaves little doubt that the diversity of the fauna and flora in the lowlands was astounding. Analysis of soil cores dating to 3660 BP in a limited number of sites found that *Pritchardia* palms and other tree species throughout the lowland forests on O'ahu steadily declined following arrival of Polynesians (Allen 1997, Athens 1997). Additionally, soon after the arrival of humans in the islands, signs of cultivation and erosion were evident. Cultivation of hillsides accelerated erosion, and sediment began to fill coastal lagoons inhabited by species such as the Common Moorhen (*Gallinula chloropus sandvicensis*) and Hawaiian Duck (*Anas wyvilliana*), hereafter referred to as Koloa.

The Polynesian pig's (*Sus scrofa*) impact on forested regions away from human habitation is

unknown. There is some evidence that it was not widespread in remote mountainous areas (reviewed by Cuddihy and Stone 1990), although the evidence varies (Ellis 1917, Tomich 1986). They almost certainly foraged widely in lowland areas where they would have significantly modified the vegetation in a manner similar to their activities today. The Polynesian rat (*Rattus exulans*) consumes many of the fruits, seeds, and drupes of native plants.

Much of the reasoning surrounding the thought that Polynesians greatly altered avian habitat in the islands comes from estimates of the human populations, which range from 200,000 to twice that many (Schmitt 1971). Whatever the true population, it was of a size that has not yet been reached even today on six of the eight main islands. This was a population largely dependent upon resources of the land. The warm and relatively deep waters surrounding Hawai'i are not the most productive for fish or invertebrates, although these resources were used extensively and supported large numbers of seabirds.

A massive agricultural system was necessary to support this human population. The excellent work of archaeologists in Hawai'i has provided extensive evidence of intense cultivation, pointing to widespread agriculture ranging from the coast up to 900 m and in some areas to 1,500 m elevation (Yen et al. 1972, Smith and Schilt 1973, Kirch and Kelly 1975; Kirch 1982a,b). The early Hawaiians diverted streams and had massive irrigation projects that enabled them to grow crops in many areas that did not have adequate rainfall and were thus marginal for agriculture.

Fire was used extensively by Polynesians to clear land for cultivation (Kirch 1982a,b; Cuddihy and Stone 1990), and the resultant loss of habitat was a major factor in the massive extinction of birds in the lowlands, and also an important factor in the upland areas. This use of fire in the clearing of large areas of native forest was a regular practice. As we can see today in other Pacific Islands, fire results in a steady encroachment of "cultivated" land, as each burn enters a bit farther into the normally wet, fire-resistant mesic forest (Allen 1997, Spriggs 1997).

The pervasiveness of this land clearing is apparent from pollen records that suggest a lowland vegetation much different from that experienced by early European explorers, who described lowlands on all islands as largely devoid of trees and shrubs and very similar among all the islands. For example, Cook (1785) and Vancouver (1798) describe a scene of dry lowlands devoid of trees and covered with grass on all the

main islands. Some of the smaller islands, such as Kaho'olawe, Lāna'i, and Ni'ihau, were also reported to be completely barren of trees by members of Cook's crew. All this argues that by the time Europeans arrived, much of the damage to lowland birds and their habitats had been done.

The extensive modifications of pre-Polynesian landscapes by the first human inhabitants of the islands is counter to the popular notion that the Polynesians were somehow special in the annals of humans, living harmoniously with their environment and taking only the surplus production of the land and the sea. The evidence that we have today suggests that what forests and avian habitat that were left at European contact remained only because the limited Polynesian technology prevented them from more fully exploiting their environment.

POST-EUROPEAN CONTACT

With the arrival of the Europeans, alteration of upland habitats, which in part had escaped the massive destruction by Polynesians, began in earnest. The first commercial use of Hawaiian forests was the harvesting of sandalwood (*Santalum* sp.), a tree prized for its fragrant wood, in the late 1700s and early 1800s and subsequent exportation to China (Rock 1974). This over-exploitation caused the demise of what once was a fairly common species whose flowers and fruits provided nectar and food for many native birds.

Today sandalwood is quite rare. Since the sandalwood trade died out, there has been relatively inconsistent use of the native forests. There have been numerous attempts at using extant forests for commercial ends, but almost all have been financially unsuccessful. Among these was the cutting of 'ōhi'a (*Metrosideros polymorpha*) trunks for a variety of products, including railroad ties in the western United States (Rock 1974:333). Koa (*Acacia koa*), the largest native tree, has had the longest history of commercial use in Hawai'i. Koa is highly prized among woodworkers because of its unique and interesting grain, being used today for specialty products, hardwood paneling, and flooring. The steady use of the larger trees has been a fairly continuous process, leaving now only remnant stands. Koa harvesting is usually coupled with the introduction of feral herbivores, especially cattle (*Bos taurus*). This tree, a legume, when young is exceedingly palatable to herbivores. Consequently, it is largely unable to regenerate under grazing pressure (Baldwin and Fagerlund 1943).

The conversion of native forests to pasture is probably the most comprehensive change to

have taken place in the post-European period in upland native bird habitat. The usual scenario is the initial felling of the forest, resulting in clearing and piling up windrows of logs. The cattle then have access to a variety of native plants, many of which are very palatable. The resulting grazing pressure of cattle prevents regeneration of any native plants except those that are growing on sides of steep gullies or as epiphytes (Cuddihy and Stone 1990).

The introduced animal that probably has had the greatest impact on altering native vegetation is the cow. Vancouver brought the first cattle to Hawai'i in 1793, placing seven ashore at two locations on Hawai'i Island. In the following year, he landed five more on that island (Vancouver 1798). Cattle were brought to Hawai'i in hopes of establishing a permanent food source for both the Polynesians and visiting ships' crews. To this end, Vancouver persuaded King Kamehameha I to place a kapu, or prohibition, for 10 years on the killing of any cattle.

The cattle soon multiplied and dispersed, and by 1801 were being used extensively for beef on Hawai'i (Tomich 1986). By 1813, 20 years after being introduced, cattle had so multiplied that they became a nuisance, and Brennan (1974) indicates that they were "devouring and trampling the natives' crops of potatoes, ravishing their taro patches, and, in short, raising havoc with whatever was planted." By 1846 there were an estimated 25,000 wild and 10,000 domestic cattle on the islands of Hawai'i. They not only ravished cultivated lands, but also devastated large tracts of native forest. There was little action taken to control them until the early 1900s. Judd (1936) presented a summary of actions taken, including fencing, shooting, trapping, and stock removal. Tomich (1986) credited cattle with totally denuding the Waimea Plain and much of the Hāmākua forests on Hawai'i. In fact, vegetation was damaged extensively on each of the islands that had cattle. Today, feral cattle exist in any numbers only on Hawai'i (van Riper and van Riper 1982).

Goat (*Capra hircus*) were first released in 1778 on Ni'ihau (Cook 1785), and Tomich (1986) felt that they were fairly well distributed throughout Hawai'i by 1793. Since the species originated in arid Mediterranean regions, it is well suited to the dry, rugged lava terrain in Hawai'i. The vegetation degradation that cattle started was compounded by the many feral goats that had proliferated in the late 1800s. Goats are much more agile than cattle, and they could, therefore, obtain forage in many areas where cattle had been excluded. Goats are prolific, and they move in small herds or family groups (van Riper and van Riper 1982). The product of this

was extensive browsing pressure in localized areas. Many of the fragile dry areas in Hawai'i were almost totally denuded of overstory vegetation because of high goat densities. Goats became a significant factor in forest and range deterioration and in the extinction of some specialized plant forms in the islands (Tomich 1986). At one time feral goats inhabited all the main islands, but today they are absent from Ni'ihau and Lāna'i. Indicative of the possibilities for eliminating goats from native ecosystems is the history of goat eradication in Hawai'i Volcanoes National Park. After years of mixed management, including sustained yield hunting, as late as 1970 park personnel fenced the park into quadrants from which goats could be removed using a variety of methods (Yocum 1964, 1967; Tomich 1986). Today the goat only occurs as an occasional straggler in the park. However, elsewhere in the islands it continues its negative impact on native ecosystems.

The effects of feral sheep (*Ovis aries*) on Hawaiian vegetation has been more localized than that of either cattle or goats, being restricted to the islands of Hawai'i and Kaho'olawe. Sheep were first introduced to Hawai'i by Captain James Colnett in 1791 (Wyllie 1850). Vancouver added more in 1793 and 1794. Like other introduced herbivores, feral sheep multiplied rapidly. By the mid-1800s, there were more than 3,000 on Hawai'i, and by the 1930s, there were over 40,000 just on Mauna Kea (van Riper and van Riper 1982). Domestic sheep were also raised on Ni'ihau and Lāna'i, and due to heavy overstocking, there was much damage to the vegetation (Tomich 1986). However, after the closing of the Humu'ula sheep ranch on Hawai'i Island in 1963 (Brennan 1974), the sheep industry all but disappeared in the islands.

Feral sheep and goats were cited as major factors in the decline of the māmane (*Sophora chrysophylla*) forest on Mauna Kea (Warner 1960). In a precedent-breaking decision, the United States Ninth Circuit Court stated that the presence of sheep, goats, and mouflon (*Ovis musimon*) in the māmane forest inhabited by the endangered Palila (*Loxioides bailleui*) was a violation of Section 9 of the Endangered Species Act by causing "harm" to the Palila. In 1979 the state of Hawai'i was directed to remove the feral ungulates from Palila habitat (Bean and Rowland 1997). Twenty years later there are still hundreds of feral sheep, mouflon, and hybrids on the mountain. The example provided by the National Park Service in Hawai'i Volcanoes National Park indicated it is possible to remove ungulates from areas the size of Mauna Kea. Why this population has been allowed to persist is a mystery, as the damage caused to native plants

and the response when ungulates are removed is well documented (Scowcroft 1983, 1992; Scowcroft and Giffin 1983, Scowcroft and Sakai 1984, Scowcroft and Hobdy 1987).

Damage to the vegetation of Hawai'i by feral pigs has been extensive (Giffin 1978, Cooray and Mueller-Dombois 1981, Ralph and Maxwell 1984, Tomich 1986). Pigs of English stock were brought to Hawai'i by Cook (1785) on his first voyage, and a number of subsequent introductions have occurred (Tomich 1986). When new strains were introduced, the Polynesian pig interbred readily with the European varieties. Feral pigs are now distributed throughout the upland pastures and forests of the six largest islands that they inhabit (Tomich 1986). Hawai'i Island has the largest and densest pig population in the archipelago, and pig populations may reach densities of 0.4 animals per ha in pasture areas and 1.2 per ha in rain forest habitat (Giffin 1978). At these high densities, damage to the environment can be extensive. In some remote forested areas, such as Kohala Mountain, pigs have totally removed the understory vegetation, and all that remains are tree-fern skeletons and a quagmire of mud. This removal of understory vegetation and suppression of regeneration of canopy species has undoubtedly had a negative impact on native birds. For example, Rock (1974) noted that the Kohala Mountain area was one of the richest for lobelioids, a favorite nectar source of many native birds. Today, lobelioids are rare on Kohala Mountain and elsewhere as well, and the forest has also lost many of its native birds (van Riper 1982).

Recently introduced plants have resulted in marked vegetation changes in the islands (Cuddihy and Stone 1990). More than 1,000 species of nonnative plants were outplanted in forest reserves between 1910 and 1960 (Skolman 1979). This was in part the result of early statements that native plants were doomed (Lyon 1918). In the 1930s a number of the higher forests were cleared and replanted to eucalyptus (*Eucalyptus* sp.) plantations (Judd 1936). Other mid-to-upper native forests have been converted to nonnative conifers. However, the affected area has been relatively small as compared to conversion to pasture. Other species such as lantana (*Lantana camara*), firetree (*Myrica faya*), and banana poka (*Passiflora mollissima*), as they spread throughout the islands have had negative effects on the composition, structure, and function of native ecosystems. This is perhaps best documented in the national parks (Loope et al. 1992) where firetree has had a major impact (Vitousek 1992, Whiteaker and Gardner 1992). Recent studies have shown changes not only in the species composition of Hawaiian ecosystems but

also in their structure and ecological processes (Vitousek 1992). Those forests where nonnative species have become pervasive have usually been perturbed severely by other factors, apparently enabling the entry and spread of introduced species. Not all the impacts have been negative; in fact, the prolific flowers of the banana poka are a favored food source by some native birds (e.g., Berger 1981:155). The introduction of predaceous insects has resulted in the decline of many native insects, many of which serve as prey for native birds or as pollinators of flowering plants on which the nectivorous species feed (Banko and Banko 1976, Howarth and Mull 1992).

Post-European habitat changes were also greatly influenced by new types of agriculture. With the influx of Europeans in the early 1800s, the types of crops grown in the lowland areas changed (e.g., sugar cane and pineapple), and there was some increase in area farmed by the Polynesians, but this increase has not been well documented. Many areas, especially along streams, that were once used by the Polynesians for banana and wetland taro have now reverted back to second-growth habitat. However, they have not usually reverted to native forest but to introduced species of trees and shrubs. Many of the former lowland taro fields were converted to rice cultivation, and this shift probably had a temporary positive effect upon water birds. Early accounts describe the large numbers of ducks frequenting ponds (Berger 1981). Fossils of Laysan Ducks (*Anas laysanensis*) in lava taken on Pu'u Wa'awa'a and other upland locations suggests they may have been more wide-ranging than previously thought. However, more recently, drainage for housing developments and the decrease in farming has resulted in a reduction of wetland habitat. Thus, the advent of western farming continued to have a negative impact on native birds, albeit much reduced from that of the Polynesians.

Even the leeward island habitats were greatly altered, illustrated by the destruction of native vegetation by the European rabbit (*Oryctolagus cuniculus*) introduced to Laysan Island by guano miners in 1903. By the time of the Tanager Expedition in 1923, four of the five endemic landbirds were heading to extinction (Wetmore 1925). The last Laysan Honeyeater (*Himatione sanguinea freethii*) was observed just prior to a three-day windstorm on Laysan Island in 1923 (Wetmore 1925, Bailey 1956).

We are thus left today, on all the Hawaiian Islands, with only remnants of habitat suitable for native bird occupancy and a fraction of the original avifauna.

LIMITING FACTOR II: HUMAN PREDATION

PRE-HUMAN CONTACT

What would have impressed people the most, if they could have viewed pre-human Hawai'i, would have been the spectacular assemblage of seabirds. The large land area and relative absence of predators probably made the Hawaiian Islands home to many millions of terns, shearwaters, petrels, boobies, albatrosses, and other seabirds, the remnants of which today throng only on the leeward and some offshore islands. Due to the remoteness of the islands, insular adaptive radiation flourished and there was a suite of flightless birds, including geese, moa nolas ibises, and rails on each island (James and Olson 1991, Olson and James 1991, Curnutt and Pimm *this volume*). Thus the stage was set for human exploitation of the native avifauna through indiscriminate hunting, as has been demonstrated on other isolated oceanic islands (Steadman 1997a,b).

POST-POLYNESIAN CONTACT

The large number of flightless Hawaiian birds must have been a welcome sight to the early Polynesians. Such a food source, probably fairly abundant, soon succumbed to human predation. Flightless Hawaiian birds followed the same path to extinction as the moas (e.g. *Dinornis torosus*, *Eurapteryx gravis*) in New Zealand (Anderson 1984, 1989) and other oceanic island birds (e.g., Anderson 1984, Diamond and Veitch 1981; Steadman 1997a,b). Another group that was particularly hard hit by Polynesian hunting was seabirds. Especially vulnerable were the burrow nesting species, such as the Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*), whose young were collected by skewering them with a barbed stick just prior to fledging (Munro 1944). Adult petrels and other nocturnal seabirds were also netted as they flew into their nesting grounds after dark (Simons 1985). By 1778, nesting seabirds were all but gone except for the most isolated or inaccessible areas. Their absence was a direct result of continued egg, chick, and adult predation by humans. For example, after protection, Sooty Terns (*Sterna fuscata oahuensis*) increased from few or no birds on Mānana Island off O'ahu to about 100,000 breeding pairs in 1972 (Brown 1976). The large numbers of seabirds transported large masses of nutrients from the sea to the land. This has been demonstrated to be a major factor in the growth of plants and other species elsewhere (Ryan and Watkins 1989, Polis and Hurd 1996, Polis et al. 1997; Anderson and Polis 1998, 1999; Stapp et al. 1999).

After the flightless and unwary birds had been disposed of, the Polynesians resorted to a great variety of bird-catching techniques including birdlime and nooses for the other species (Perkins 1903). Most of these methods were indiscriminate. Polynesians hunted a number of native Hawaiian birds for their feathers, but the prized species included the 'Ō'ō (*Moho* spp.), Hawai'i Mamo (*Drepanis pacifica*), 'Ō'ū (*Psittirostra psittacea*), 'Apapane (*Himatione sanguinea*), and 'I'iwi (*Vestaria coccinea*; Brigham 1899). Not only were feathers collected, but also, in all likelihood, the birds were themselves eaten (Wilson and Evans 1890–1899, Berger 1981), especially considering the relative scarcity of protein in this agricultural society. Although it took an estimated 80,000 birds to construct a small feather cape (Rose et al. 1983), harvesting by prehistoric Hawaiians probably did not have a major detrimental effect on native birds that could fly.

POST-EUROPEAN CONTACT

With the introduction of firearms to the islands, coupled with an active trade of feathered artifacts, hunting probably contributed significantly to the final demise of several highly prized species, particularly the Hawai'i Mamo and 'Ō'ō. Perkins (1903) reports on over 1,000 'Ō'ō (*Moho nobilis*) shot over several weeks above Hilo, Hawai'i. The mid-elevation species were probably hardest hit by hunting for the feather trade, as were the leeward island birds (Berger 1981).

Historic hunting for food and sport during the post-European period had its greatest impact on the extant larger native birds. Swedberg (1967) was convinced that the demise of the Koloa could be attributed directly to hunting pressure. The Nēnē was also subjected to intensive hunting, and there is little doubt that its precipitous decline was directly related to this factor (Baldwin 1945, Kear and Berger 1980). The goose was hunted during its breeding season (September through February) in the early 1900s, thus magnifying the impact.

Today, hunting seasons are closed for all native birds in Hawai'i. However, occasional shooting still occurs. In 1970 we found the plucked remains of two Nēnē on the summit of Hualālai. During the private release of introduced birds in the early 1970s at Pu'u Wa'awa'a, the Hawaiian Hawk (*Buteo solitarius*) was eliminated from this area (pers. obs.). Through the 1980s, the Hawaiian Crow (*Corvus hawaiiensis*), hereafter referred to as 'Alalā, was shot for sport (J. Giffin, pers. comm.). Munro (1944) believed that shooting was one of the

chief reasons for the 'Alalā's decline at the turn of the century.

LIMITING FACTOR III: NON-HUMAN PREDATION

PRE-HUMAN CONTACT

Undoubtedly, many of the seabirds that nested on cliffs along the coasts of the main Hawaiian Islands lost young to predatory fish, who would concentrate off shore to prey on young that had just fledged into the ocean. The majority of terrestrial predation on the native avifauna, prior to the arrival of humans, was limited primarily to other avian species. Many of the Hawaiian paleontological specimens have been retrieved from fossilized owl pellets of extinct bird-eating owls in sinkholes (Olson and James 1982b, Olson and James 1991, Giffin 1993). Researchers have also found a number of extinct predatory birds such as Long-legged Owls (*Grallistrix* spp.), an eagle (*Haliaeetus* sp.) and a harrier (*Circus dossenus*) (Olson and James 1991). We know that the Hawaiian Hawk, although a buteo, takes a number of avian prey species (Griffin et al. 1998), as does the Hawaiian subspecies of the Short-eared Owl (*Asio flammeus sandwichensis*) or Pueo. The 'Alalā diet includes a large number of other passerine species (Sakai et al. 1986, Sakai and Carpenter 1990).

POST-POLYNESIAN CONTACT

The Polynesians brought the pig (Kirch 1985, Tomich 1986), Polynesian rat, and dog (*Canis familiaris*), and these early introductions must have greatly affected birds that had never encountered mammalian predators. Native Hawaiian birds evolved in the absence of mammalian predators and were thus extremely vulnerable to these introduced mammals. What portion of the prehistoric avian extinctions can be attributed directly to mammalian predation cannot be determined. However, the view that these introductions by the Polynesians were essentially without impact seems to us without merit. The Polynesian rat, widespread and abundant, is a known predator on 15 species of seabirds (Atkinson 1985) and consumes many of the fruits, seeds, and drupes of native plants. The Polynesian rat is carnivorous and will readily take birds and their eggs (e.g., Kepler 1967, Woodward 1972). Introduced rats have been implicated in the complete breeding failure of several seabird species on Kure Atoll (Moors and Atkinson 1984). Feral pigs are well-known predators of ground-nesting seabirds (Challies 1975). The feral dog is a known predator on seabirds and their eggs (Moors and Atkinson 1984, Atkinson 1985, Johnstone 1985) and has been implicated in the extinction or extirpation of a number of seabird

species and populations. Feral dogs almost certainly preyed on eggs and young of both ground-nesting and burrowing colonial nesting seabirds in the lowlands (Johnstone 1985). They are known predators on Nēnē (reviewed in Tomich 1986) and colonial nesting seabirds such as the Wedge-tailed Shearwater (*Puffinus pacificus chlororhynchus*; Byrd and Boynton 1979, Stone et al. 1983).

The Polynesian pig and rat most likely confined initially to the areas around settlements, but within a very few years undoubtedly experienced explosive population increases and dispersed into the forests. (See previous discussion on this topic.) An introduction of an animal into a novel environment often results in such a population explosion, overrunning an area, and only in later years drops to a more restrained population level. Ground-nesting and -feeding birds were probably most affected, and many did not survive long after these mammalian predators were introduced (Olson and James 1982a, 1991; James and Olson 1991). The declines and extinctions caused by these introduced predators is a pattern that was repeated throughout the world (King 1985, Steadman 1995, 1997a,b).

POST-EUROPEAN CONTACT

A number of additional potential predators of birds were introduced into Hawai'i following European discovery, including the cat (*Felis catus*), small Indian mongoose (*Herpestes auro-punctatus*), two species of rat (roof rat, *R. rattus*, and Norway rat, *R. norvegicus*), and the Barn-Owl (*Tyto alba*). Of these, the one with probably the most impact on birds was the roof rat. Atkinson (1977) provides convincing evidence implicating this rat as one of the major causes of the declines of native birds in the early 1900s. He observed that the chief effect of the roof rat on passerine birds was through predation on eggs, nestlings, and sometimes adults. It is fairly certain that this rat caused the extinction of the Laysan Finch (*Telespiza cantans*) and Laysan Rail (*Porzana palmeri*) from Midway Island (Munro 1944; Baldwin 1945, 1947b). More recently, Seto and Conant (1996) showed that 46 of 58 known nest failures of Bonin Petrels (*Pterodroma hypoleuca*) on Midway Island were due to loss of eggs thorough rat predation. Eddinger (1970) found that roof rats destroyed a number of 'Anianiau (*H. parvus*) and 'I'iwi nests that he had studied on Kaua'i. On Hawai'i, van Riper (1978) reported predation of roof rats at two Hawai'i 'Amakihi (*H. virens*) nests found on Mauna Kea. Roof rats have been implicated in the loss of five species of birds from South Cape Island in New Zealand (Bell 1978). The Norway rat is a known predator on more than 100 bird

species (Atkinson 1985), has caused significant declines in many, and has been implicated in the extinction of the Lord Howe Island Starling (*Aplonis fuscus carunculatus*) and South Island Saddleback (*A. f. hullionus*; Hindwood 1940, Atkinson and Bell 1973). King (1985) stated that rats have been implicated in the greatest number of extinctions due to any predator (54%).

The cat was introduced to Hawai'i with the first Europeans, quickly became feral, and is now established in the wild on all eight main islands (Tomich 1986). It lives in all habitats throughout Hawai'i, but is more abundant in drier areas. Cats worldwide are known to prey on birds (e.g., Johnstone 1985, Veitch 1985), and Hawai'i is no exception. Twenty-six percent of bird extinctions on islands by nonnative predators are attributed to cats (King 1985). Perkins (1903) reported that he found the bodies of no less than 22 native birds that were eaten by cats on a single trail over a two-day period on Lāna'i. Richardson and Woodside (1954) reported that cats preyed on the endangered Dark-rumped Petrel on both Hawai'i and Maui. Tomich (1969) found feral cats on Mauna Kea with remains of the introduced Skylark (*Alauda arvensis*) in their stomachs. On this same mountain, van Riper (1978) reported that 55% of trapped cats had bird remains in their stomachs. Native birds were the Hawai'i 'Amakihi and 'Elepaio (*Chasiempis sandwichensis*). He also found one nest of the endangered Palila from which the female had been taken by a cat. In the Kīlauea forest on Mauna Loa, Hawai'i, Tomich (1981b) found 'Oma'o (*Myadestes obscurus*) in a cat stomach. There is no doubt that the cat has had and continues to have a negative effect on the native birds of Hawai'i.

The small Indian mongoose was released in Hawai'i in 1883 along the Hāmākua coast of Hawai'i (Bryan 1938). Subsequent releases were made on all of the main islands except Lāna'i and Kaua'i (Baldwin et al. 1952). Mongooses are principally predators on ground-nesting birds (King 1985). They have been identified as a primary factor in the extinction of the ground-nesting Jamaican Least Pauraque (*Siphonorhis americanus americanus*) and at least one other Jamaican species also known as predators on seabirds (King 1985). Their impact would, therefore, be felt more heavily on native seabirds, ducks, geese, and those passerines that frequent the ground.

La Rivers (1948), Baldwin et al. (1952), Kami (1964), and Tomich (1986) have treated at length the question of whether the mongoose is a negative factor in relation to landbirds. They reported that the small Indian mongoose now preys principally on game birds, and occasion-

ally some of the introduced passerine species. King and Gould (1967) felt that this predator was responsible for the disappearance of the endemic subspecies of Townsend's Shearwater (*Puffinus auricularis newelli*), hereafter referred to as Newell's Shearwater, from most of the main Hawaiian Islands. The mongoose is probably now having the greatest impact on the Nēnē (Baldwin 1945, Elder 1958, Walker 1966, Baker and Russell 1979). Banko (1992, Banko et al. 1999) believes that the poor reproductive success of the goose in recent years is a direct result, in part, of mongoose predation on eggs, goslings, and adults. Without proper control of this predator, it is doubtful if the Nēnē will ever be able to maintain its numbers in the wild. However, inadequate food resources appear to be a significant factor in failure to restore the Nēnē to nonendangered status citation.

In studies conducted on the feeding habits of the Barn Owl (*Tyto alba*), native landbirds constituted only a small portion of their diet (Tomich 1971, 1981b, Byrd and Telfer 1980, Snetsinger et al. 1994; C. van Riper, pers. comm.). However, owls near seabird colonies have some effect (Byrd and Telfer 1980), and feral dogs and pigs have been known to prey on the Nēnē and Koloa (Swedberg 1967, Tomich 1969, Giffin 1982).

Perkins (1903:394) felt that the Common Myna (*Acridotheres tristis*) was a major predator on eggs and young of other avian species. He said that it "probably exceeds in numbers the whole of the native land-birds put together," and felt it had "greatly extended its range through the forest." In the 1890s the species was in an expansion phase of a population increase, and may well have had marked negative effects on native birds. Today, it is much rarer in native forests, and its impact on other birds probably not nearly so severe.

LIMITING FACTOR IV: AVIAN COMPETITION

PRE-HUMAN CONTACT

Interspecific avian competition was undoubtedly a significant force driving evolution of the pre-human avifauna on the Hawaiian Islands. The disharmonic fauna and equitable environment rapidly selected for different forms, each sped along their evolutionary pathways through avoidance of competition from their avian counterparts.

POST-POLYNESIAN CONTACT

The only additional component of potential interspecific competition added to the Hawaiian avifauna during the Polynesian era was the Red Junglefowl (domestic chicken—*Gallus gallus*).

It is not clearly understood how this species interacted with the terrestrial native birds, how it competed for resources, and what diseases might have been introduced with it, but the introduction of this bird by the Polynesians as a domestic animal probably had some impact. At present the Red Junglefowl is found in numbers only on Kaua'i, which lacks the mongoose, but it was formerly established in the wild on all the main islands. Its reproductive potential is high, and it is omnivorous. It seems very likely to us that this species in large numbers could have been a potent competitor to some species of ground-foraging native birds, such as the smaller rails, only one of which survived into historical times.

POST-EUROPEAN CONTACT

Competition with native birds by introduced avian species is one of the favorite themes of biologists who have compiled armchair lists of potential causes of the demise of the Hawaiian avifauna. In addition, much of yesterday's ecological literature emphasizes the role of competition in shaping communities (e.g., MacArthur 1972). There have been, however, no unequivocal studies establishing competition as a cause of extinctions in Hawai'i, and none is likely to be soon forthcoming. The study of competition in birds is one of correlation and comparison because of the difficulty in designing a crucial experiment with field populations. The Japanese White-eye (*Zosterops japonicus*) is considered a prime candidate as a harmful competitor. Although introduced about 1929, after most native bird extinctions had already occurred, it is widely known as an abundant generalist, spending a good deal of time gleaning for insects but also venturing with facility into frugivory and nectarivory (van Riper 2000).

There have been few published studies that actually examined data that may have some relevance to introduced versus native bird competition in Hawai'i (Moulton and Pimm 1983, 1986a; Mountainspring and Scott 1985). Mountainspring and Scott (1985) examined the correlations between densities of different birds in different areas to determine if any negative relationships emerged. That is, if one bird became less common while another became more common, it could indicate a competitive interaction. Of 170 partial correlations, just 6% were significantly negative, only slightly more than the 5% expected by chance alone. However, the authors felt that two relationships were especially important: (1) the Japanese White-eye and the 'Elepaio, and (2) the Japanese White-eye and 'I'iwi. Even if competition is involved in these two cases, clearly by this measure at least, it is not a pervasive and continuous force. However,

when they examined the entire set of set of correlations, Mountainspring and Scott (1985) found that there was a more pervasive pattern. The native/introduced species pairs had a significantly greater proportion of negative partial correlations (37%) than either native/native (8%) pairs, or introduced/introduced (0%) pairs. The authors suggest that many of the native/introduced species pairs experience at least small population depressions due to competition.

It seems unlikely to us that introduced granivores and frugivores could be competitors with native birds, since critical seed and fruit resources are used by relatively few historic native birds and because they are superabundant (Wagner et al. 1990a,b). Some native birds that use fruit resources (largely the thrushes) are themselves still generally common (van Riper and Scott 1979, Wakelee 1996). Similarly, the presumed granivores that became extinct, such as the large-billed finches, used food resources that are still common, and there were essentially no introduced species that could have competed with them for this food resource (however, see Moulton et al. *this volume*).

LIMITING FACTOR V: AVIAN PARASITES/DISEASES

PRE-HUMAN CONTACT

Because of Hawai'i's isolation, many avian diseases and their vectors were not able to reach the islands prior to the arrival of humans. The first avian parasites to reach the islands undoubtedly arrived with early immigrating birds, and they subsequently evolved with their avian hosts. Endemic coccidia and nematodes have been reported from Hawai'i (Levine 1980, Cid del Prado Vera et al. 1985) and many ectoparasites also appear endemic (Garrett and Haramoto 1967, Goff 1980). It is unknown what impact these diseases had on prehistoric bird populations.

POST-POLYNESIAN CONTACT

It is not known what avian parasites/diseases arrived in Hawai'i from 400 to 1700 AD. Alicata (1947) lists a number of diseases in gallinaceous birds, and it is possible that some of these were introduced to Hawai'i with the Polynesian chicken. Additional avian parasites could have been introduced to the islands during this period by migrating birds, but because of distances to mainland source areas (e.g., 5,000 km to North America), certainly birds with heavy parasite levels would have been less likely to survive the long flight. The impact of infectious diseases introduced by Polynesians and their commensals is unknown but may have been significant (Daszak et al. 2000).

POST-EUROPEAN CONTACT

The parasites and diseases that have accumulated in Hawaiian birds subsequent to European contact are varied. Protozoa, various helminths, ectoparasites, viruses, bacteria, and fungi are all represented (van Riper and van Riper 1985). Although most diseases appear to be of little importance in regulating avian populations in Hawai'i, avian poxvirus and malaria have had an important influence. These two diseases have such an influence on the native birds that of all the limiting factors presently operative in Hawai'i, disease is now recognized as the single factor having the greatest impact on the continued survival and potential recovery of native birds.

The negative impact of diseases on native Hawaiian birds was probably felt most strongly when avian poxvirus, one of the first new diseases, was introduced to the islands following colonization by Europeans. Perkins (1893) recorded a number of native species from O'ahu and Hawai'i, including the 'Apapane, Lesser 'Akialoa (*H. obscurus*), 'Elepaio, Palila, and Kona Grosbeak (*Chloridops kona*) with extensive swellings on their legs and feet. Rothschild (1893–1900) and Wilson and Evans (1890–1899) also mention numerous birds that they encountered with lesions on their legs, feet, and heads. Avian pox was first confirmed in an 'Ākepa on Hawai'i by Henshaw (1902a). Munro (1944) associated the increasing numbers of domestic poultry with the spread of avian pox throughout the islands. In any event, by the late 1800s, it is clear that avian pox was widespread in the islands. It is, therefore, probable that it played a role in the massive extinctions of the native birds at the turn of the century. Today, this disease is still impacting native forest birds (Jenkins et al. 1989, VanderWerf *this volume*, van Riper et al. in press).

Malaria, a parasitic disease caused by blood protozoan infections (*Plasmodium* spp.), was the second important disease introduction, probably brought in with caged passerine birds in the early 1920s (Laird and van Riper 1981, van Riper and van Riper 1985). The mosquito vector for malaria, *Culex quinquefasciatus*, was present on all the main islands at that time, and then spread the parasite to previously unexposed native avian species. This mosquito is present up to 1650 m elevation, the highest reaches of the extant wet forests on Hawai'i Islands, but its abundance is quite low at the upper elevations (Goff and van Riper 1980). Despite this, infected birds are found at all elevations, and malaria transmission in Hawai'i does occur quite successfully at relatively low vector densities. The key ob-

servation of van Riper et al. (1986) is that the altitudinal distribution of the parasite is not a direct reflection of vector densities. At lower elevations, *C. quinquefasciatus* is numerous, and the avian malarial parasite level low. At the mid-elevation ranges (about 800–1,300 m), malarial parasite levels increase disproportionately to the number of vectors. These are also the lowest elevations at which native birds are normally present. It thus appears that a directional selection pressure, exerted by the pathogenicity of the malarial parasite, is presently forcing the native avifauna into higher forest areas. It affects young birds, as in Hawai'i where first-year birds have up to six times greater parasitemia levels than do adults, particularly in native species. Laysan Finches from mosquito-free Laysan Island have been shown to be very susceptible to *Plasmodium* infections (Warner 1968), with 100% mortality in test birds (van Riper and van Riper 1985). In other Hawaiian birds, there are varying degrees of susceptibility to malaria (Atkinson et al. 1995, 2000; Jarvi et al. *this volume*, Shehata et al. *this volume*, Yorinks and Atkinson 2000), and these differences are observed even between populations of the same species, depending upon their length of historical exposure to mosquitoes (van Riper et al. 1986).

Because the endemic avifauna apparently evolved in the absence of many disease factors, it is probable that the native birds have lost some immunogenetic mechanisms. So, when confronted with newly encountered diseases, naive native birds are more susceptible than their introduced counterparts with a long history of exposure and natural selection. This situation has been documented in North America birds, for example, where introduced birds succumb more readily to native eastern equine encephalitis (Karstad 1971b). In Hawai'i, avian pox and malaria, the two introduced diseases which have probably had the greatest negative impact on native birds, appear to have an attenuated pathology when compared to continental strains (C. van Riper, pers. obs.). In addition, populations of some species (e.g., Hawai'i 'Amakihi) seem to have developed some resistance to the present *Plasmodium* parasite. Recently, there have been some preliminary indications that genetic resistance to some introduced diseases may be evolving (Shehata et al. *this volume*, Atkinson et al. 2000, S. Jarvi pers. comm.).

The pattern of historical decline in native Hawaiian birds is bimodal. The initial reduction of native birds was in the mid- and late 1800s and was unlikely due to disease. However, the second phase of extinctions in the early 1900s was the most likely the result of a number of factors, including introduced predators and habitat loss,

but avian pox and malaria were likely the primary causes. Other than avian pox and malaria, the majority of avian diseases present in Hawai'i are relatively non-pathogenic. Harm to infected individuals varies with the parasite, and some parasites typically produce more negative effects on their hosts than others. *Ascaridia* larvae, for example, migrate through and damage various organs in route to their final destination, whereas for other parasites (e.g., acanthocephalans and cestodes), only the localized sites of parasite attachment may become inflamed. Many parasites, such as *Dispharynx* and *Capillaria*, feed only on intestinal contents, rarely disrupting their host's condition. The greatest threat of most maladies is the lowering of the host's resistance so that other stresses can cause death. For example, *Histomonas meleagridis* infections become more severe when certain types of intestinal bacteria are present (Kemp and Springer 1978), and the severity of *Ascaridia galli* infections is influenced by levels of coccidia and some viruses (Levine 1980).

Many parasites require intermediate hosts, while others facultatively rely upon them for increased success of transmission. The gapeworm (*Syngamus trachea*) does not require an intermediate host, but birds that feed on earthworms are more severely infected (Levine 1980). The eyeworm (*Oxyspirura mansoni*) is the most widespread helminth infecting avian hosts in Hawai'i. This parasite is probably found in all birds that regularly eat the intermediate host, the burrowing cockroach (*Pycnoscelus surinamensis*). There are a number of other examples where intermediate hosts limit the types of birds infected in Hawai'i. Because of their influence on parasite and disease transmission, intermediate hosts could be important targets in a parasite control program. Alicata (1947) reported success in controlling the poultry eyeworm by the introduction of toads to poultry yards in Hawai'i. Mosquito eradication is well documented as a successful means of malaria control.

Other disease pathogens might have a similar influence in the future; it is vital that no new diseases and parasites or their vectors be introduced to the islands (Loope et al. *this volume*). Arboviruses, Newcastle disease, and possibly avian influenza, are absent, based on preliminary surveys by Quisenberry and Wallace (1959), Wallace et al. (1964), and Okamoto (1975). The obvious solution is careful control in the importation of birds, including the monitoring and clearing of all parasites in these birds.

Species being reintroduced into the wild from captive populations, such as the Nēnē, in particular, should be monitored for diseases and parasites (Griffith et al. 1989, Snyder et al. 1996).

Care should be taken to insure that released birds do not carry diseases or parasites that are absent in wild populations. For instance, *Cyathostoma*, a gapeworm infecting geese, has never been reported in Hawai'i, but Avery (1966) reported it from captive Nēnē at a rearing facility in Slimbridge, England. Life cycles of this parasite are similar to *Syngamus trachea*, and disease symptoms can be quite severe (Levine 1980). Avery (1966) also reported tuberculosis and two species of tapeworms, *Menatoparataiena southwelli* and *Fimbiaria fasciolaris*, from captive Nēnē in England. It is not known if these parasites have reached Hawai'i in captive birds that have been released in the past from Slimbridge, but great care should be taken to prevent their introduction.

In summary, there is compelling evidence today that a few diseases are presently playing a major role in influencing the numbers and distribution of native birds (Daszak et al. 2000). In order to preserve and properly protect these birds, it is imperative that the importance of diseases and parasites be recognized as limiting factors for endemic birds and that efforts be made to reduce breeding sites for known vectors and to conduct research on development of disease-resistant populations for repopulating historical range (Fancy and Ralph 1997, Cann and Douglas 1999, Jarvi et al. *this volume*, Shehata et al. *this volume*).

LIMITING FACTOR VI: ABIOTIC FACTORS

PRE-HUMAN CONTACT

Hurricanes, fires, floods, volcanic eruptions, and other short-duration high-energy abiotic events cause infrequent environmental perturbations that often greatly impact species and ecosystems. These phenomena can be so large as to influence all or a significant portion of an endangered species range, as seen in other areas of North America. For example, Hurricane Hugo in 1989 resulted in the loss of half of the population of the endangered Puerto Rican Parrot (*Amazona vittata*). Hugo had similar devastating effects on Red-cockaded Woodpecker (*Picoides borealis*) when it destroyed 95% of the suitable nesting trees at the Francis Marion National Forest in South Carolina, home to 20% of the known Red-cockaded Woodpecker population (USFWS 1989). The Short-tailed Albatross (*Phoebastria albatrus*) was thought to be extinct, the result of volcanic eruptions on its nesting grounds (Hasegawa 1984). However, birds that were apparently at sea during the eruptions later recolonized the former nesting colonies, and the species is making a slow recovery. Abiotic influences were most likely the major lim-

iting factor to Hawaiian birds prior to human arrival. Not only did the extensive lava flows destroy habitat, but they also created partial dispersal barriers to birds, especially flightless species. Extreme weather events such as hurricanes, floods, and El Niño oscillations all influenced avian survival in pre-human Hawai'i as did massive landslides, subsidence, changes in sea level, and tsunamis (Stearns 1966, Carson and Clague 1995).

POST-POLYNESIAN CONTACT

As the lowland native vegetation was eliminated by Polynesians, habitat patch size concomitantly decreased. These smaller patches were much more susceptible to abiotic perturbations. Strong winds would have felled solitary trees, while hurricanes could have potentially destroyed many of the smaller lowland habitat patches. Assuming that the upland forests were still somewhat intact, hurricanes would not have had as great an impact, in fact probably providing openings for forest regeneration.

Volcanic eruptions and subsequent lava flows would have had a greater impact on the post-Polynesian contact native birds because habitat patch in the lower forests was continually being reduced. As the lowland patches became further apart, any destruction of remaining patches by lava flows would have increased barriers to dispersal and ultimately resulted in less habitat for birds.

El Niño oscillations would have continued to influence avian resources, but with smaller habitat patches spaced further apart, ultimately the variable weather conditions would have had a greater negative impact on food resources and ultimately upon avian populations.

POST-EUROPEAN CONTACT

As Europeans further reduced available avian habitat through agricultural and residential clearing, and the activities of their introduced ungulates, abiotic factors would have escalated their impact on the native birds. In Hawai'i the current ranges of many of the endangered species are extremely small, frequently less than 10,000 ha (Scott et al. 1986). Small distributional areas make endangered Hawaiian species extremely vulnerable to stochastic abiotic perturbations of their environment. For example, Scott et al. (1986) estimated the 'Ō'ū population on the island of Hawai'i to number 300 individuals and have a distributional of less than 5,000 ha. In 1984 a flank eruption of Mauna Loa resulted in lava flows and subsequent fires that eliminated all habitat where the greatest number of 'Ō'ū had been observed (Reynolds and Snetsinger *this volume*). This habitat loss, due to an abiotic

event, undoubtedly hastened the decline of this species in that it has not been reliably reported from Hawai'i since 1987 (Pyle 1992, Reynolds and Snetsinger *this volume*). The impact on low-land populations of the 'Ōma'ō, Hawai'i 'Amakihi, and 'Elepaio went undocumented.

Probably the most significant example of recent abiotic impacts on native birds occurred on the island of Kaua'i, and is summarized by Pratt (1994). The historic avifauna, although confined to the Alaka'i Plateau with some populations very reduced, still retained all species through 1960 (Richardson and Bowles 1964). Montane forest birds on Kaua'i and other islands formerly moved to lower elevations in great numbers during storms (Henshaw 1902a). Beginning in 1980s, a series of hurricanes destroyed a large portion of the remaining Alaka'i Plateau habitat, and many individuals were driven to lower elevations, thus exposing them to introduced diseases; thus followed the extinction of many native species. Following Hurricane Iwa, the 'Ō'ō'ā'ā (*Moho braccatus*) population was reduced to a single male, and no individuals have been reported since 1987 (Pyle 1989). The 'Ō'ū, common to the 1980s (Scott et al. 1986), was reduced to a few birds by the 1990s (Pratt 1994). The Kāma'ō (*M. myadestinus*), once one of Kaua'i's most abundant native birds, declined to several hundred individuals by 1973 (Sincock et al. 1984), to several dozen in 1981 (Scott et al. 1986), and to only several individuals by 1989 (Pyle 1989). In 1992 Hurricane Iniki caused even more devastation to the small remnant of existing native bird habitat on the Alaka'i Plateau. Pratt (1994) questions if the Kāma'ō, Puaiohi (*Myadestes palmeri*), 'Ō'ū, and Nukupu'u (*H. lucidus hanapepe*) will survive the ravages of Iniki. To make matters even worse, Atkinson et al. (1995) have now found avian malaria in the Alaka'i birds, where prior to recent hurricanes, they demonstrated that this parasite was absent from these forests.

The last individuals of the Laysan Honeyeater were seen just prior to a severe three-day windstorm in 1923 (Wetmore 1925, Baily 1956). The Palila, known only from 13,900 ha of māmane forest on the island of Hawai'i, is at great risk from loss of habitat due to fire. Two hundred ha were lost to fire in 1979. A similar size fire in the māmane forest with highest densities of Palila could remove habitat for 800 birds, 12% to 40% of population estimates for the species (Scott et al. 1984).

Clearly, abiotic disturbances can have a major impact on species with small populations and restricted distributions. However, it is important to note that in all the cases we have cited, the abiotic events were able to impact significant

portions of species' ranges only because they had been decreased by other factors. In the case of the Short-tailed Albatross, the birds had been eliminated from all but one of their nesting islands by individuals killing birds for their feathers, and to habitat loss as the result of grazing by cattle. In the case of the Laysan Honeycreeper, its habitat had been destroyed by rabbits that had been introduced to provide meat to guano workers. Loss of vegetation may have also contributed to the severity of the windstorm. The 'Ō'ū occurred in less than 5% of its historical range as the result of introduced predators and disease (Scott et al. 1988).

Restoring species to all or a significant portion of their historic range is the surest way to guard against loss of species to abiotic threats. In Hawai'i, this will require that recovery actions be put in place over much larger areas than in the past. Current populations of several of Hawai'i's endangered species (e.g., three Po'ouli [*Melampus phaeosoma*]) are so small that lack of genetic diversity may be contributing to their decline. However, this remains one of many unstudied questions.

CONCLUSIONS

The composition of the flora and fauna of Hawai'i has been shaped by a number of biotic and abiotic factors. Prior to the arrival of Polynesians about 400–500 AD, all these factors were natural; new diseases, parasites, and new competitors arrived on their own and all evolved in the absence of the hand of humans. The arrival of the first Polynesians' voyages changed all that, for with them came the dog, Polynesian rat, and pig, all known predators on a very vulnerable avifauna. The nature of introduced diseases on plants and animals remains unknown. But the record of species lost directly at the hand of humans—directly, through hunting and habitat modification, or indirectly, as the result of predation and habitat modification of our commensals—while incomplete, is well documented. At least 50% of the known species were lost. The arrival of Europeans and later other ethnic groups brought new and more powerful tools for habitat modification and hunting as well as large ungulate browsers and grazers that were capable of inflicting unprecedented habitat change on the Hawaiian landscape. With the Polynesians, conversion of landscapes to anthropogenic cover types was largely restricted to elevation below about 1,600 m. After 1778 there were no elevational limits, and loss of habitat extended to the tree line at 3,000 m on Mauna Kea. With this increase in loss and modifications of habitat, and the introduction and continuing introduction of a host of alien species and diseases, the Ha-

waiian avifauna experienced its second extinction spasm, one that continues to this day. Efforts to save species have largely failed, in large part because of the failure of recovery actions to match the scale of the threat. Recovery actions, with the exception of those on the smaller islands in the leeward chain, have not been conducted over all or a significant part of threatened and endangered species' ranges. As a result, species responses have been at the level of increases in survival or reproduction for individual animals, not at the population, subspecies, or species level required for recovery. Perhaps the best example is the Nēnē. Efforts to save this species date back to at least 1950 (Kear and Berger 1980); captive breeding efforts resulted in release of thousands of birds on Hawai'i and Maui. Efforts to control predators focused on small predator-free exclosures or in the immediate vicinity of nesting pairs. However, these efforts have been over but a very small fraction of the Nēnē's range.

Contrast these recovery efforts with those on behalf of the congeneric Aleutian Canada Goose (*Branta canadensis leucopareia*). The factors associated with the decline of these species are similar: hunting and introduced predators. While hunting of both species was largely eliminated, the story with respect to introduced predators is quite different. The introduced Arctic Fox (*Alopex lagopus*) was eliminated from entire islands on which the Aleutian Canada Goose bred. The population has increased from 790 in 1975 to more than 24,000 in 1998 (V. Byrd, pers. comm.). The number of Nēnē continues to decline (USFWS 1996a, c). This demonstrates clearly that the management response has to match the scale of the threat to a species.

The islands of Hawai'i are so large that elimination of known predators on native birds will be extremely difficult. Cats have been eliminated from areas as large as 2,180 ha (Veitch 1985). Norway rats have been eliminated from islands only as large as 100 ha, while it has been suggested that 100 ha are the largest area from which elimination of rats is possible. The recent elimination of rats over 1,000 ha on Midway Island (R. Shallenberger, pers. comm.) gives hope for effective removal of rats over areas at least that large on the major islands. The māmane forest on Mauna Kea and 'Akiapōlā'au (*H. munroi*) habitat in Hakalau Forest National Wildlife Refuge would make excellent areas to demonstrate that rats could be removed from biologically significantly sized areas in structurally complex habitats. Removal of feral ungulates, as

demonstrated by the successful removal of pigs and goats from Hawai'i Volcanoes National Park, appears to be limited only by our desire to do so.

If we fail to eliminate or control nonnative predators and ungulates from all or a significant part of the range of Hawai'i's endangered bird species, we will continue to catalog the demise of an avifauna. Since the completion of the Hawai'i Forest Bird Survey (Scott et al. 1986), the 'Ō'ū, 'Ō'ō'ā'ā, Kāma'o, and Moloka'i Oloma'o (*Myadestes lanaiensis rutha*) are presumably extinct, and the Po'ouli (*Melamprosops phaeosoma*), with only three individuals known, is functionally extinct. Despite this record of loss, current efforts to save the species are conducted at scales (individual animals) inappropriate to the challenge (species ranges). Unless we act now to eliminate introduced mammals from all or a significant part of the ranges of these species, all is lost.

While additional biological reserves are needed, the current "system" of biological reserves (national parks, national wildlife refuges, Nature Conservancy reserves, and Hawai'i Department of Natural Resources wildlife management areas) provides a framework to initiate an aggressive habitat restoration initiative (Holt and Fox 1985). Much of what has to be done was documented fifteen years ago in a detailed summary of threats, their impacts, and actions till then (Stone 1985). Not much has changed. More areas have been dedicated to long-term conservation of native species. The Hakalau Forest National Wildlife Refuge, Kona Forest National Wildlife Refuge, and The Nature Conservancy's Waikamoi Preserve on Moloka'i are but three examples (see Holt and Fox 1985 for a listing of extant reserves in 1985). Nonetheless, with few exceptions (Katahira et al. 1993) we have consistently failed to act on available information and use existing methods to eliminate sheep, goats, mouflon, rats, and cats over biological significant areas. A similar conclusion was made 11 years ago (Stone and Stone 1989).

A lot has been accomplished. Much more could be accomplished by working cooperatively and using currently available methods. Economies of scale in cost and efficiency will be gained as new techniques become available. The biological impact on birds, their habitats, and other endemic plants and animals is well documented (see citations in this article; Stone 1985, Stone and Stone 1989). We will be judged poorly by future generations of conservationists if we fail to act aggressively on that information.