

FIGURE 319. Generalized diagram of major limiting stresses on native bird populations, typical for area shown in Figure 320.

populations were apparently declining in the 1890s (Perkins 1903). The causes for the declines are unknown, but may include extensive habitat fragmentation due to coffee farming, logging, and grazing, as well as avian disease (discussed below).

Three localized anomalies were identified in our analysis. In the Mauna Kea study area, Elepaio, Palila, and Akiapolaau are nearly absent from the Pohakuloa Flats area, where the habitat is quite similar to that occupied elsewhere. Possible factors, including thermal stress, avian disease, site tenacity, past habitat disturbance, and military activity, were discussed by Scott et al. (1984). A second local anomaly occurs on the north slope of Hualalai, where Akiapolaau are absent from the koa-ohia forest that harbors Hawaiian Crow, Hawaii Creeper, Akepa, and other common native birds. Possibly the area and quality of that "habitat island" is inadequate to sustain indefinitely the Akiapolaau population. A third anomaly is the high density of Akepa near timberline in the middle of the Kau study area, contrasted with the almost complete absence of this species in the south part of that area.

Multidisciplinary approaches may be valuable in unraveling the factors causing some of these

distributional patterns. Additional surveys to document seasonal and annual variation in the geographic distribution of the anomalies may also provide useful insight into their significance and on the role of sampling error in identifying their boundaries. Translocating radio-tagged birds into these areas and following them should provide valuable insight into why a species does not occur there naturally.

LIMITING FACTORS

Numerous factors stress endemic Hawaiian bird populations and propel many species towards extinction. A key principle in wildlife management is the identification and control of those factors that are particularly important in reducing the unimpeded rate of population increase inherent in a species (Leopold 1933, Giles 1978). The limiting factors of Hawaiian forest birds fall into these general categories: habitat modification, predation, disease, interspecific competition, and major environmental perturbations. Aside from these, pesticide contamination from agricultural practices is a potential problem for Hawaiian Hawks, Short-eared Owls, and possibly Hawaiian Crows and waterbirds.

The relative impact of different stresses varies among areas and species, and is conceptually de-

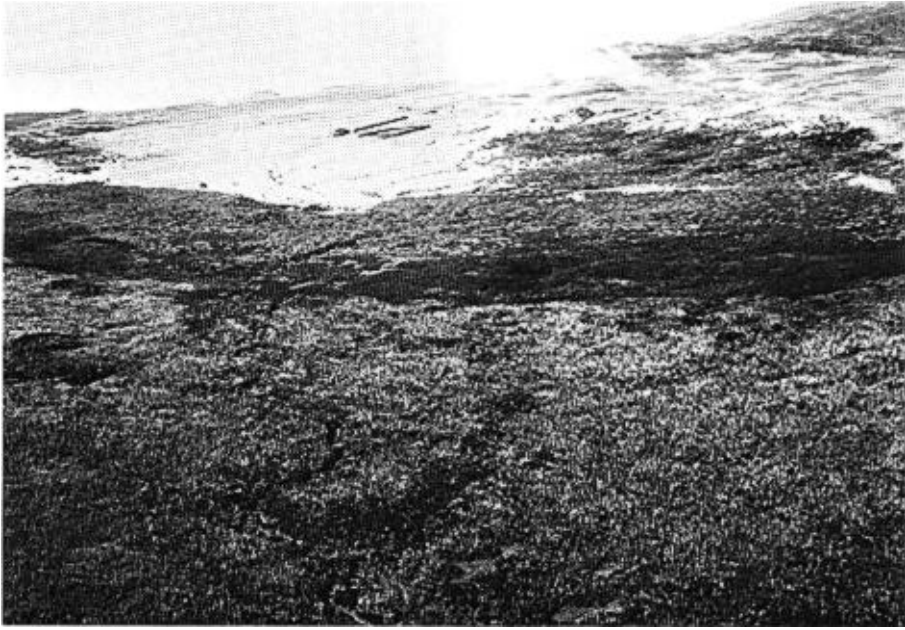


FIGURE 320. Elevational zonation of vegetation on windward Mauna Kea. Lowest zone dominated by dieback of wet ohia forest; next zone (darkest band), by ohia rainforest; top forested zone, by mesic ohia-koa forest. Above this lies open pasture, and still higher lies an indistinctly visible band of mamane woodland (see Figures 49 and 323). Dark triangle in middle of grassland is planted eucalyptus. (Photograph by J. D. Jacobi)

picted in Figure 319 for typical passerines on windward Hawaii (Fig. 320). Where native habitat still remains, disease is believed by many to be the strongest single force below 1500 m elevation (Warner 1968, van Riper et al. 1982). Habitat disturbance is severe in many areas, and large tracts have been converted to introduced vegetation. Pigs, other ungulates, and introduced plants pose a long-term threat to rainforest interiors, especially on steep slopes and in areas already suffering some disturbance. For some ground-dwelling and understory birds, predation may have (or have had) a major effect (Atkinson 1977). Interspecific competition is usually weak but may eventually cause the displacement of some native birds by ecologically similar introduced species. Finally, single cataclysmic events or poor weather conditions attain prominence for perilously low populations.

HABITAT MODIFICATION

Browsers, grazers, and rooters

Goats (*Capra hircus*).—Where domestic goats have been introduced, they almost always create problems for the native flora and fauna—on the Galápagos Islands, the Channel Islands off California, the Hawaiian Islands, New Zealand, and elsewhere throughout the Pacific basin (Baker and Reaser 1972). Goats were abundant by 1850

in the Hawaiian Islands (Marques 1905), but there was little official concern before 1910 (Tomich 1969). Goats cause great damage to drier and more open Hawaiian ecosystems, and usually browse on native plants instead of introduced species. On Haleakala, goats increase erosion by overgrazing, compacting soil, removing cover, and initiating rock slides (Yocom 1967).

Goats were a severe problem in the dry forests of Hawaii Volcanoes National Park (Spatz and Mueller-Dombois 1973), and still are a major problem in Haleakala National Park and adjacent areas where they devastate alpine grassland (Fig. 321) and subalpine scrubland, and also enter high-elevation wet forest below the Kalapawili Ridge, in Kipahulu Valley, and between Kuli Peak and Manawainui Gulch. Overbrowsing is particularly severe in Kahikinui, the dry south slope of East Maui, where formerly extensive koa, ohia, and mamane forests have been reduced to relictual patches in gulches surrounded by barren eroded slopes. On Molokai, goats degrade dry lowland forest, areas along cliff faces, and local areas in the northern valleys. On Kauai, goat damage is evident along the drier perimeter of the Alakai Swamp, and goats invade the wetter, more pristine habitats during drier periods (J. L. Sincock, pers. comm.). On Kahoolawe, where goats have resided for 200 years, almost



FIGURE 321. Severe erosion following overgrazing by goats and rooting by pigs at 2500 m elevation on windward slope of Haleakala, East Maui. (Photograph by C. B. Kepler)



FIGURE 322. Extreme overgrazing and overbrowsing by goats and axis deer have reduced former open to closed canopy native forest to sparse barren grassland on many areas of Lanai. (Photograph by C. B. Kepler)



FIGURE 323. Mamane woodland on west slope of Mauna Kea looking down from timberline at 2800 m elevation. Dead trees in foreground, erosion, heavy browse line, and 200 m elevational retreat of treeline are caused by feral sheep. (Photograph by P. W. Scowcroft)

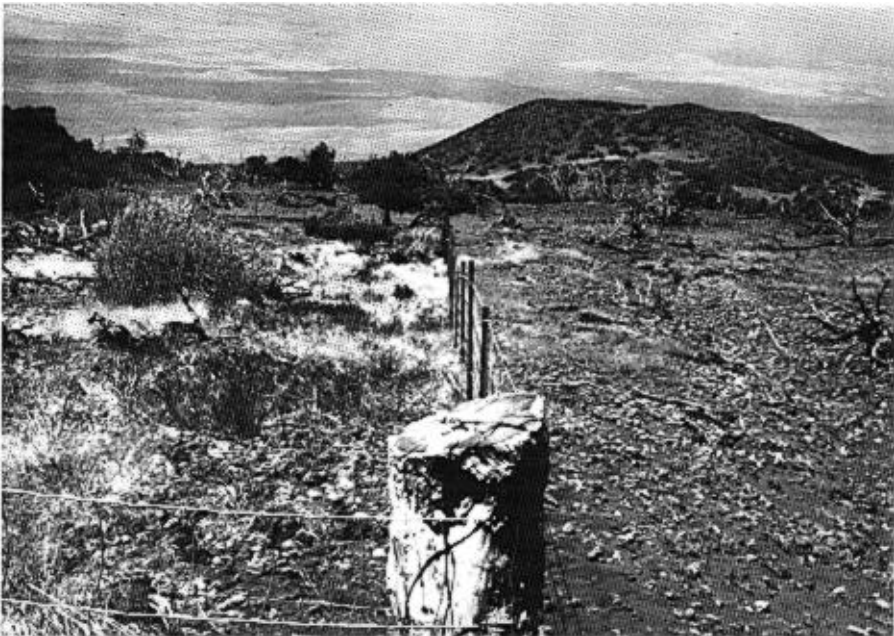


FIGURE 324. Sheep and mouflon enclosure in mamane woodland at 2700 m elevation on Mauna Kea. Regeneration of mamane in enclosure after two years stands in marked contrast to denuded areas outside. (Photograph by P. W. Scowcroft)



FIGURE 325. Aerial view of wet ohia forest in Kohala study area with Maui in background. Heavily grazed grassland on left formerly covered with mesic and dry native forest. Water supply of Lapakahi and other coastal villages failed shortly after forest was cleared. Deep amphitheatre-headed valley barely visible on right. (Photograph by J. D. Jacobi)

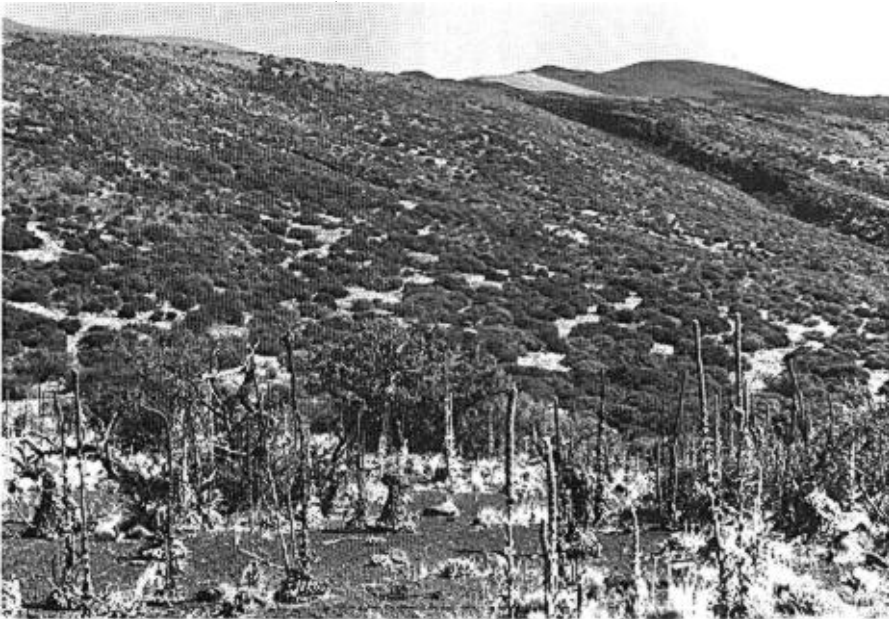


FIGURE 326. Open mamane woodland (dark band) on southeast slopes of Mauna Kea lies between barren alpine desert above and heavily grazed pasture below. Narrowness of this woodland (3 km) appears to strongly limit Palila numbers in this area. (Photograph by J. D. Jacobi)



FIGURE 327. Replacement of native understory by introduced grasses and opening of canopy in koa-ohia forest as a result of grazing by cattle at 1300 m elevation near Puu Waawaa on Hawaii. Hawaiian Crow, Akepa, and Hawaii Creeper are the species most threatened by this type of habitat modification in the north Hualalai area. (Photograph by C. B. Kepler)



FIGURE 328. Extreme overbrowsing and overgrazing by cattle, pigs, and axis deer have reduced a once lush closed canopy ohia forest to a sedge mire punctuated by skeletal tree fern remnants on East Molokai. (Photograph by J. D. Jacobi)



FIGURE 329. Undisturbed ohia rainforest with lush native understory and ground cover at 1150 m elevation on Olokui Plateau, Molokai. Feral ungulates are absent from this inaccessible area because of sheer cliffs. (Photograph by C. B. Kepler)

none of the native flora remains, and the island has largely become a desolate, wind-swept dome of hardpan clay.

Because goats have such a negative impact on dry and mesic habitats, they indirectly place a severe stress on the birds present. On Hawaii, Palila and Akiapolaau have been the most affected endangered bird species. Feral goats have now been virtually eliminated on Mauna Kea by the Hawaii Division of Forestry and Wildlife (R. L. Walker, pers. comm.). On Maui, goats are preventing regrowth in Kahikinui and Manawainui that would regenerate dry koa-mamane-ohia woodland suitable for Maui Parrotbill, Nukupuu, and Akepa. The advance of goats into upper wet forest edges on Maui threatens these birds and other species such as Crested Honeycreeper and Poo-uli. On Lanai, the habitat for Apapane and Common Amakihi (if not yet extirpated) consists of only a small remnant of wet

forest heavily disturbed by goats and deer in the past (Fig. 322). Attempts to eliminate the Lanai goat herd by hunting in the past five years appear to have succeeded. As wet and mesic native forests regenerate, populations of bird species that formerly occurred could be reintroduced to Lanai. On Kauai the incursion of goats into wet forests on the perimeter of the Alakai Swamp results in forest degradation that promotes avenues of invasion for other introduced animals and plants that further degrade the habitat and stress native birds (Sincock et al. 1984).

Several techniques can be used to control goats (Baker and Reeser 1972). The most practical control is a combination of fencing and systematic hunting. Hunting is most effective when continual and supported by trained dogs and helicopters. Because of the high breeding potential of goats, complete eradication is necessary for effective control. The novel "Judas goat" tech-



FIGURE 330. Severe damage to understory from pig rooting in a wet ohia forest at 1500 m elevation, Koolau Forest Reserve, East Maui. Note lack of ground cover and sparse understory; compare with Figure 329. (Photograph by C. B. Kepler)

nique has proven effective at Hawaii Volcanoes National Park for locating the last few head in a large area (D. D. Taylor and L. Katahira, pers. comm.). A captured goat is radio-tagged, color-marked, and released into the control area. This goat eventually joins one of the remaining herds, which can then be radio-located and exterminated. The color-marked Judas goat is spared to find another herd.

Sheep (*Ovis aries*).—When Captain Vancouver brought three sheep to Kealahou Bay, Hawaii, in 1793, he introduced an animal that, because of its fecundity and utility to man, ultimately would be found by the thousands on Hawaii, Molokai, Lanai, Kahoolawe, and Niihau (Kramer 1971). Fortunately Maui and Kauai were spared the stresses imposed by these mammals. Feral sheep have now been eliminated from all islands except Hawaii, where they are well established above 1000 m elevation in many dry

areas, particularly the western slopes of Mauna Loa, where herds of several hundred are frequent. On Mauna Kea they have ranged to the summit region from 1822 to the present; the population was about 40,000 in the 1930s (Bryan 1937).

Sheep are particularly destructive to mamane woodlands (Fig. 323, Giffin 1976, Scowcroft 1983, Scowcroft and Giffin 1983, Scowcroft and Sakai 1983). On Mauna Kea their activities have displaced timberline downward about 200 m (Berger 1981), and with cattle have created a broad gap on the windward slopes between the mamane woodland and the koa forests below. The tendency of sheep to flock and repeatedly use the same trails intensifies their impact on native ecosystems (Giffin 1976).

Four taxa of native birds found in the mamane woodlands on Mauna Kea (Palila, Akiapolaau, the Mauna Kea subspecies of Elepaio, and Com-

mon Amakihi) have been severely threatened by sheep. These four birds reach greatest densities near Puu Laau, an area of large old mamane trees with moderately heavy past browsing pressure. Sheep damage is severe at high elevations in south Kona, and, along with damage caused by other feral and domestic ungulates, may contribute to very low Akiapolaau densities and absence of Palila in the koa and mamane woodlands there. Sheep were nearly eliminated from Mauna Kea in 1982 pursuant to a legal ruling under the Endangered Species Act, but they are still common in south Kona.

Sheep are effectively controlled by fencing and hunting. Fewer than 100 remained on Mauna Kea in 1983 and these will eventually be exterminated (R. L. Walker, pers. comm.). A dramatic increase in new growth of native plants followed sheep control in 1983 (Fig. 324). As the habitat returns to a healthier state, the numbers of birds, including the endangered species, should increase. Although there is at present little interest in removing sheep from Mauna Loa, the dry upper-elevation woodlands of south Kona would regenerate ideal habitat for Palila and Akiapolaau.

Mouflon (*Ovis musimon*).—Mouflon occur on Hawaii at upper elevations on the east slopes of Mauna Kea and in the open subalpine woodland of the Kau study area, and on Lanai. Mouflon were first introduced in 1954 and hybridize freely with feral sheep (Tomich 1969). Like sheep, they prefer dry open habitat and are a great threat to mamane woodland (Fig. 324, Scowcroft and Giffin 1983, Scowcroft and Sakai 1983). On Mauna Kea, mouflon extensively overbrowse mamane, especially at timberline, and have a damaging effect on native vegetation similar to that of feral sheep (Giffin 1982). Palila, Akiapolaau, Elepaio, and Common Amakihi populations on Mauna Kea are thus threatened with an uncertain future until mouflon are controlled, or preferably removed.

In Kau the damage caused to native vegetation near timberline by a growing population of mouflon and other feral ungulates threatens the survival of the Akepa, which reaches its greatest densities in the ecotone between subalpine ohia woodland and alpine scrub. The Hawaiian Goose and Hawaii Creeper may also be adversely affected in this area.

On Lanai, mouflon do not presently penetrate remnant patches of native forest. Mouflon can be controlled by hunting and fencing; there is no systematic control program currently in effect.

Cattle (*Bos taurus*).—Feral cattle are now restricted to forested areas on Hawaii in south Kona, upper Hamakua, and Puna; on Maui in very low numbers west of Waikamoi Stream and

in Waihoi Valley; and on Kauai around Puu Ka Pele (R. L. Walker, pers. comm.). They were formerly very numerous and territorial forester C. S. Judd (1927) labelled 1815–1921 as the “cattle period in Hawaiian forestry.” Overall, cattle have been the single most destructive agent to native Hawaiian ecosystems, particularly to mesic forests. They usually prefer native plants to introduced species. Koa reproduction is completely suppressed by grazing (Baldwin and Fagerlund 1943), and cattle are mostly responsible for converting large tracts of forest to open pasture through suppressing regeneration on south and northwest Haleakala, lower elevations of west Maui and Lanai, much of Molokai, the dry side of Kohala Mountain (Fig. 325), the Waimea plains, the north and east side of Mauna Kea below 2200 m elevation (Fig. 326), the mesic and wet slopes of Hualalai, most of south Kona, and the slopes between Mauna Loa and Kilauea. A consistent pattern of cattle invading wet forests from adjacent mesic areas recurs at ecotones on Maui and Hawaii, and formerly occurred on Kauai before control in the 1920s to 1930s (Sincock et al. 1984).

Domestic stock are a major threat to the 25-km² relictual forest on the north slope of Hualalai that harbors one of the two remaining Hawaiian Crow populations, 74% of the Hawaii Creeper, and 99% of the Akepa on leeward Hawaii (Fig. 327). Initial steps by the Hawaii Board of Land and Natural Resources to create a wildlife sanctuary in the area should lead to recovery of that ecosystem. Fragmentation and modification of mesic koa-ohia forests in Kona is one of several factors responsible for the present grim status of the Hawaiian Crow (Burr et al. 1982, Giffin 1983). Many bird species on Hawaii have gaps in their distribution because of conversion of mesic and dry forests to rangelands and scrublands on the Kapapala Tract, the southern shoulder of Mauna Loa (Kahuku Tract), the south slopes of Hualalai (Puu Lehua area), and between the Mauna Kea mamane woodland and the koa-ohia forests of upper Hamakua. These fragmented populations are more vulnerable to extirpation than would be a single continuous population. This is particularly true on the high eastern slopes of Mauna Kea, where cattle, sheep, and goat activity has reduced the mamane woodland to a 1-km band separated from the lower koa forests by 8–10 km of open pasture. This has resulted in a drastic restriction of the range of Palila, Akiapolaau, Hawaii Creeper, and Akepa in this area, and reforestation of these pasturelands to reconnect the mamane woodland and koa forests is a critical management need on Hawaii for these bird species (Scott et al. 1983).

On Maui a century of ranching has severely

reduced the range of all forest birds, particularly Maui Parrotbill, Nukupuu, Akepa, and Crested Honeycreeper. Large numbers of domestic cattle range freely into the Kahikinui Forest Reserve, where they further degrade the remnant mesic forests.

Feral cattle are no longer the problem they were a century ago, thanks to extensive efforts early in this century by the Hawaii Division of Forestry to fence forest reserves and eliminate feral animals. Unfortunately many of these fences are in disrepair and need maintenance if feral cattle are to be eliminated from forest reserves. In 1983 the Hawaii Department of Forestry and Wildlife began fencing the lower boundary of Kahikinui and removing cattle during extensive drives; legal notice by the State under Hawaii Revised Statutes 183-19 of impending action to remove, without compensation, domestic stock from public conservation lands generated prompt cooperation by ranchers.

Domestic cattle pose a serious threat to the long-term survival of the Hawaiian Crow, Akepa, Hawaii Creeper, Akiapolaau, and Palila on Hawaii, and have restricted the distribution of forest birds on Maui. Rangelands that contain forests essential to the preservation of these species have been identified in the recovery plans (Berger et al. 1977, Burr et al. 1982, Scott et al. 1983, Kepler et al. 1984), and rehabilitation of key segments of these forests is essential to preserve forest birds on Hawaii. Mesic and wet forests important to many species have recently been secured for conservation management by the Nature Conservancy on Hawaii, Maui, and Molokai (Little 1984), but key parcels of mesic koa forest above 1500 m elevation remain unprotected on Hawaii on north Hualalai (for Hawaiian Crow, Akepa, Hawaii Creeper), in central Kona (for Hawaiian Crow, Akiapolaau, Hawaii Creeper), north of Kilauea (for Akiapolaau, Hawaii Creeper, Akepa), and between the Mauna Kea mamane woodland and upper-elevation Hamakua forests (for Akiapolaau, Hawaii Creeper, Akepa). On Maui, the Kahikinui Forest Reserve fences need to be extended and maintained, and all feral ungulates within the reserve removed.

Axis deer (*Axis axis*).—Axis deer were introduced in 1868 on Molokai, in 1920 on Lanai, and in 1960 on Maui (Tomich 1969). Browsing and soil compaction by feral deer, in conjunction with pigs, has converted the vegetation on East Molokai from rainforest to open mire and created a biological disaster (Fig. 328) that extends to the coral reef ecosystem off the south coast of Molokai, now largely smothered in silt and invaded by introduced mangroves. On Lanai, vegetation destruction by deer is believed partly responsible for the probable extirpation of Com-

mon Amakihi and decline of Apapane, and axis deer have replaced goats as the most serious threat to the remnant forests there. Although the numbers of axis deer on Maui are small and confined to disturbed ranchlands, they constitute a major threat to the mesic and wet native forests on Haleakala. Their removal should constitute a high-priority management action (Kepler et al. 1984).

Black-tailed deer (*Odocoileus hemionus*).—This species occurs only on Kauai, where it is a potential threat to essential habitat in the Alakai Swamp. It was released in 1961 (Tomich 1969) and is spreading to many lowland areas. It should be hunted year-round to prevent invasion of the Alakai Swamp.

Pig (*Sus scrofa*).—Feral pigs, first introduced by the Polynesians (Tomich 1969), occur on all the main islands except Lanai and Kahoolawe. Pigs apparently did not establish substantial populations in native forests until after European pigs were introduced (Tomich 1969, Warshauer 1980). The majority of feral pigs live in wet forests, mesic forests, and dry high elevation areas. They feed on tree ferns, grasses, roots, earthworms, and other animal matter (Kramer 1971). The rooting activity of pigs is very destructive to vegetation and soil substrates (Fig. 329 and 330; Ralph and Maxwell 1984), particularly on steep slopes where erosion becomes severe (J. D. Jacobi and F. R. Warshauer, pers. comm.).

Although pig densities may reach 125 animals/km² in some Hawaiian rainforests, these concentrations are exceptional, and the maximum carrying capacity for most areas is probably 50 pigs/km² (Giffin 1978). Densities at this level, however, still cause extensive and severe damage to the ecosystem, and Giffin (1978) recommended a maximum allowable density of 8–10 pigs/km² in Hawaiian rainforests to minimize disturbance to the vegetation and soil. In many forests inhabited by endangered bird or plant species, pigs should be eliminated completely because they radically alter understory composition, hinder forest regeneration, and facilitate the invasion of introduced plants (Mueller-Dombois 1981). Almost all Hawaiian forests have moderate to severe pig damage (J. D. Jacobi and F. R. Warshauer, pers. comm.). Rare exceptions include the outstanding pristine forest on the inaccessible Olokui Plateau on Molokai (Fig. 329) and several isolated peaks of the West Maui Mountains. Control measures for pigs are being developed at Hawaii Volcanoes National Park, and at present it seems possible to eliminate pigs from fenced areas as large as 800 ha (D. D. Taylor and C. P. Stone, pers. comm.).

On Hawaii general habitat degradation by pigs has a negative effect, especially on Elepaio and

Omao, but Akiapolaau, Ou, and Hawaii Creeper are also affected. On Maui, where the threat to the habitat of endangered forest birds by pigs is increased greatly by steep slopes, Poo-uli are strikingly limited to areas of lighter pig disturbance (S. Mountainspring, pers. observ.), and Maui Parrotbill also appear to be sensitive to understory disturbance by pigs (S. Mountainspring, pers. observ.). On Molokai, pigs stress the habitat of Olomao in Kamakou Preserve (Kepler et al. 1984). On Kauai, Kamao, Puaiohi, and Kauai, Oo are probably negatively affected by pig activity (Sincock et al. 1984). The eggs and nestlings of Townsend's (Newell's) Shearwater are occasionally taken by pigs (Telfer 1983); in addition shearwater burrows are trampled and adults eaten (J. L. Sincock, pers. comm.).

Introduced plants

With few exceptions, introduced plant species have become weeds and serious pests on every island that man has visited (Smith 1985). Less than 2% of the 4600 plant species introduced to the Hawaiian Islands have become serious pests in native ecosystems, with lowland areas suffering the greatest disruption by introduced species (Smith 1985). The aboriginal Hawaiians introduced some two dozen species that became naturalized (St. John 1973), but none of these has become a serious pest, except perhaps *Ipomoea congesta*, the status of which as a member of the native flora is uncertain. The present introduced pest flora has thus arrived after Western contact from (1) immigrating peoples from diverse areas who brought plants important in their cultures; (2) agricultural importations of pasture grass and forb seed stock contaminated with weed seeds; (3) foresters who brought trees for reforestation and establishment of a forestry industry; and (4) horticulturists who imported plants of potential interest (Smith 1985). The main impacts of introduced pest plant species on native ecosystems include (1) physical displacement of native species by formation of dense monotypic stands; (2) change of the fire characteristics of communities; (3) alteration of the soil-water regime; (4) modification of the nutrient cycling of ecosystems; and (5) development of synergistic relationships with introduced animals, exemplified by the relation between strawberry guava and pigs in seed bed preparation (Smith 1985).

For prime forest bird habitat, the worst threat is probably posed by banana poka, a weedy passiflora that infests significant areas of koa-ohia forest on Hawaii and Kauai (La Rosa 1984). Continuous populations of banana poka occur on Hawaii on northeast Mauna Kea, the Olaa Tract near Kilauea Crater, the north and west slopes of Hualalai, and on Kauai in Kokee State

Park (Warshauer et al. 1983). In most areas banana poka infestations become dense enough to smother large tracts of native forest. The regression models indicate that Omao, Elepaio, and Hawaii Creeper have significantly lower densities in infested areas. Biological control (e.g., by heliconiine butterflies) may be feasible (Warshauer et al. 1983) and efforts to this end are currently underway.

Strawberry guava, lemon guava, and several gingers are abundant below 1200 m elevation and crowd out native tree seedlings; these species extend above 1500 m. Numerous species of *Rubus* likewise penetrate forest interiors, and are better defended against browsers than native plants. Fire tree is a weedy pest on windward Hawaii that alters soil nitrogen levels. Fountain grass destabilizes dry forests in the Puna, Kona, and Mauna Kea study areas, including Hawaiian Crow breeding habitat, by promoting wild fire through buildup of dead biomass above ground. In other dry forests, kikuyu grass, broomsedge, and molasses grass smother native tree seedlings; the first two grasses also release allelopathic substances (Rice 1972, Smith 1985). In the koa-ohia forest near Kokee State Park, Kauai, lantana crowds out native herbaceous vegetation (J. L. Sincock, pers. comm.).

Several strategies may mitigate the impact of introduced plants. Perhaps the most cost-effective is to prevent further noxious introductions by a combination of public education (including tourists) on the need for importation control, and greater government effort to enforce existing regulations and prohibit importation of all potential problem species. At present, government efforts focus solely on illegal plants and agricultural pests, and virtually ignore species that pose threats to native ecosystems. Following needed research on the autecology of pest species, development of integrated pest management systems offers considerable hope through use of biological controls, despite many problems associated with this strategy (Smith 1985). Introduced plants can be controlled, or more accurately, prevented from establishing populations, by closely controlling human access to relatively pristine areas, removing feral ungulates that disperse propagules and create seed beds, and quickly eliminating species before they become established. Richardson and Bowles (1964) describe a control plan for the Alakai Swamp, and The Nature Conservancy has a management plan for their Kamakou Preserve on Molokai that has guided the eradication of several species of introduced plants.

Physical habitat disturbance provides the major avenue for introduced plants to invade intact native ecosystems; in Hawaii Volcanoes National Park invasions of introduced plants are directly

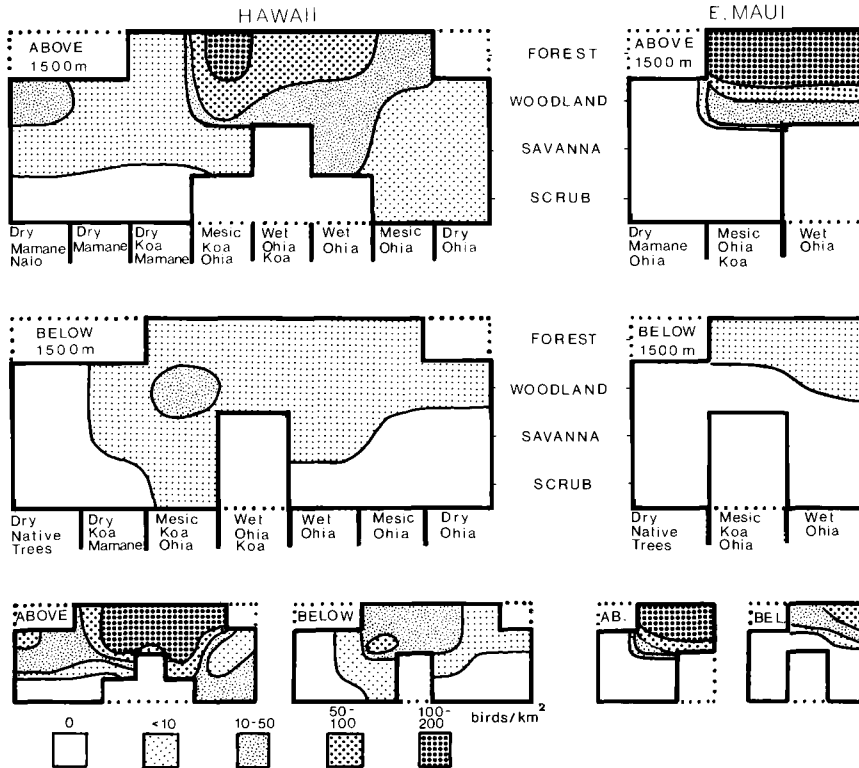


FIGURE 331. Habitat response graphs of endangered passerine species density. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

related to habitat disturbance, particularly by feral pigs (Mueller-Dombois 1981). The Japanese White-eye also facilitates invasion of introduced plants by dispersing their fruit (Guest 1973), as probably do the Red-billed Leiothrix, Melodious Laughing-thrush, Northern Mockingbird, Common Myna, House Finch, and several gallinaceous gamebirds. The most encouraging note, sounded by Egler (1942), Hatheway (1952), and Mueller-Dombois (1981), is that the native biota will frequently hold its own and succeed in the competitive struggle with many introduced plant species, provided disturbance from ungulates and humans is excluded from the system. This point underscores the importance of habitat management as an integral part of conservation strategy for the islands.

Anthropogenic habitat degradation

Logging and clearing.—Early in the 19th century extensive sandalwood harvests probably disrupted bird populations on leeward Hawaii and Maui. Commercial timber harvest on Hawaii threatens some species associated with koa. Prime old-growth koa-ohia forests on Hawaii that should be preserved from logging lie northwest

of Kilauea crater, at 1500–2000 m elevation in Hamakua, in central Kona, and on the north slopes of Hualalai. These forests harbor Hawaiian Hawk, Akiapolaau, Hawaii Creeper, Akepa, and in Kona, Hawaiian Crow, as well as many rare plants and invertebrates. The impact of reduced canopy cover on the endangered passerines is clearly shown in Figure 331. Conservation easements and fee simple acquisition are being sought for these areas, but wider public support is needed. Clearing for subdivision and agricultural development, such as occurred on Kalopa Mauka, Puu Waawaa Ranch, and the Honomalino Tract, particularly threatens Hawaiian Crow.

Ranching.—Cattle ranching is a major economic activity in the Hawaiian Islands, but significant populations of endangered birds presently occur on only a handful of ranches. The impact of cattle was discussed earlier; here, the salient point is that economic incentives are essential in persuading those ranchers who control prime forest bird habitat to manage their land for conservation objectives. Conservation easements, tax write-offs for inactive land, and improved watershed quality are potential benefits

more likely than lawsuits to win the cooperation of landowners. Such procedures have been highly successful on Maui and Molokai, where over 4000 ha of prime habitat has been protected by The Nature Conservancy (Little 1984). For state-lease lands, it is appropriate to withdraw essential habitats areas from the lease and dedicate the land as a sanctuary.

Fire.—Fire is a threat mainly in the mamane-naio woodland on Mauna Kea to Palila, Akiapolaau, Common Amakihi, and the Mauna Kea subspecies of the Elepaio, and to Hawaiian Crow in the lama-ohia woodland and drier koa-ohia forest on the north slopes of Hualalai. Palila and Mauna Kea Elepaio are especially vulnerable because their entire populations lie within dry woodland. Three Townsend's (Newell's) Shearwater colonies on Kauai were recently destroyed by fire (J. L. Sincock, pers. comm.).

PREDATION

Black rat (Rattus rattus).—Black rats are found on all eight main islands. Atkinson (1977) argued from temporal correlations with harbor construction that black rats had a significant negative affect on native birds through nest predation. However, the development of shipping was also correlated with numerous developments other than the probable dates of black rat introduction. Such factors as agricultural expansion and increased importation of domestic fowl, cats, songbirds, etc., may confound Atkinson's argument. It is nonetheless quite possible that during their population explosions black rats were one of many factors in the decline of some native birds, particularly cavity nesters. Black rats caused the extinction of transplanted populations of the Laysan Rail and Laysan Finch on Midway Atoll (Berger 1981), and were no doubt partly responsible for the extinction of the Hawaiian Rail on Hawaii. Black Rat predation also affects the Dark-rumped Petrel (Harris 1970, Simons 1983), and rats may compete for food, especially fruit, with Hawaiian Crow, Omaso, Olomao, Kamao, Puaiohi, and Ou. In the koa-ohia forest north of Kilauea Crater, black rats feed primarily on seasonally abundant fruit but occasionally raid passerine nests. Bird species that have survived to this date in large numbers are unlikely to be annihilated by rats (Tomich 1981), although the rarest forest birds could be severely impacted by rats when subjected to other stresses as well. Rats (this species and/or the next) occasionally damage koa trees by stripping the bark (Scowcroft and Sakai 1984).

Polynesian rat (Rattus exulans).—Polynesian rats arrived with the Polynesians and occupy all forested Hawaiian islands. Predation by Polynesian rats has been observed on adult Laysan Al-

batross (*Diomedea immutabilis*) and other seabirds (Kepler 1967, Tomich 1969). Like the black rat, this species is an agile climber (Atkinson 1973), but its impact on forest birds is unknown. Presumably bird populations had reached an equilibrium with predation from Polynesian rats by the time of Western contact. Above 1500 m elevation, Polynesian rats are much less common than black rats (Tomich 1981; C. P. Stone, pers. comm.). Feathers have been found in the stomachs of both black and Polynesian rats, but it is not known whether rats actually prey on live birds (Stone 1985).

House cat (Felis catus).—Cats have been present in the Hawaiian Islands since Western contact and were abundant by the 1860s (Twain 1872:Chap. 63). Feral populations occur on all the main islands. Cats are most common at lower elevations but are also frequent in the mamane-naio woodland on Mauna Kea and have been observed in high-elevation rainforests on Hawaii and Maui. In a single ravine on Lanai, Perkins (1903:393, 433) found 22 native birds killed by cats over a two-day period and twice witnessed them feeding on Ou. Cats appear to exert a modest but continued pressure on bird populations (George 1974) that is probably most severe for birds that forage mostly in the understorey, including the Elepaio, Omaso, Olomao, Kamao, Puaiohi, Maui Parrotbill, and Poo-uli. Cats probably contributed significantly to the extinction of Hawaiian Rail, and probably feed on young Hawaiian Geese. Cats may also compete with Hawaiian Hawks and Short-eared Owls for rodent prey (George 1974). On Kauai, cats caused mortality at about 75% of the nesting Newell's Shearwater burrows at one colony in 1982 (T. Telfer, pers. comm.), and are a source of predation on Dark-rumped Petrels above 3000 m elevation on Maui (Simons 1983).

Without detailed study it is difficult to quantify the effect that feral cats have upon native birds, particularly insular species that have evolved without mammalian predators. Feral cats were present for many years on Little Barrier Island, New Zealand, and were known to be serious predators of nesting procellariids. Within two years of the eradication of cats from the island, the population of Stitchbird (*Notiomystis cincta*), a very rare nectarivorous meliphagid, increased between three- and six-fold, much to the surprise of the New Zealand Wildlife Service, as cats had not previously been suspected as predators of this species (C. R. Veitch, R. Hay, pers. comm.). Cats may exert a similarly significant but as yet unknown pressure on the Hawaiian avifauna.

Small Indian mongoose (Herpestes auropunctatus).—This species was introduced to the Hawaiian Islands in 1883 and occurs on Oahu,

Molokai, Maui, and Hawaii from sea level to the upper limits of vegetation (Baldwin et al. 1952). No population is known from Kauai, although one lactating female was found dead on a highway in 1976 (but had no internal or external injuries, and may have been a hoax), and the general public has reported several dozen possible sightings (J. L. Sincock, pers. comm.). The mongoose is a generalized carnivore that feeds mainly on rodents and insects (Kramer 1971). Birds constitute about 4% of the diet, with Zebra Dove and other gamebirds most frequently taken (Baldwin et al. 1952).

Among native forest birds, the mongoose constitutes a persistent threat, probably of generally small magnitude, and as with cats, understory birds will be most affected. The mongoose is a predator at Hawaiian Goose nest sites and is considered an important factor in reducing nesting success (Walker 1966, Banko 1982, Banko and Manuwal 1982, Stone et al. 1983). Mongoose predation on Hawaiian Crows occurs during the first two weeks after the young leave the nest, when the fledglings cannot sustain upward flight and often perch on the ground for extended periods (Giffin 1983). Local control of mongooses around nest sites may effectively reduce crow mortality from this source. The mongoose is also implicated in seabird predation in the Hawaiian Islands, and probably was a key factor in reducing Townsend's (Newell's) Shearwater populations to near zero levels on Oahu, Molokai, Maui, and Hawaii (King and Gould 1967). Bryan (1908) found mongooses occupying Dark-rumped Petrel burrows on Molokai, and mongooses are a major source of predation at the petrel colony in Haleakala, where an active trapping program has led to increased nesting success (Simons 1983).

Common Barn-Owl (*Tyto alba*).—Common Barn-Owls were introduced to the Hawaiian Islands in 1958 and occur on all of the larger islands in most habitats (Berger 1981). Although they feed primarily on rodents, they have been observed taking numerous seabirds on Kauai (Byrd and Telfer 1980) and are known to take passerines in small numbers (Bent 1938).

Common Myna (*Acridotheres tristis*).—In the 1890s Common Mynas "increased prodigiously," occurred deep into native forests, and were observed feeding on the young and eggs of native birds (Perkins 1903:394). Our survey showed that they prefer disturbed habitat and are generally not found in association with the rarer native species. Nonetheless, during their population explosions, Common Mynas and other introduced birds may stress native bird populations directly through predation and indirectly through competition for nesting cavities and food, and may

have had significant impacts on some species in the past.

Man (*Homo sapiens*).—Illegal taking, usually by shooting, primarily affects the larger native birds. Poaching of Hawaiian Geese was a problem especially in the past, although incidents still occur (Baldwin 1945a, Stone et al. 1983). Hawaiian Hawks are probably occasionally shot in some hunting areas. Indirect evidence suggests that shooting is a factor in the decline of the Hawaiian Crow on the north slopes of Hualalai (Burr et al. 1982, Giffin 1983). Public education, establishment of limited-access sanctuaries, and strict enforcement of protective statutes are measures that would reduce the impact of shooting. In earlier times, Hawaiians took Dark-rumped Petrel and Townsend's (Newell's) Shearwater nestlings for food (Munro 1944).

DISEASE

Because the endemic Hawaiian avifauna evolved in the absence of many diseases common in continental areas, a reduction in the effectiveness of immunogenetic mechanisms has probably occurred (van Riper and van Riper 1985). When native birds encounter introduced pathogens, they may thus be more strongly affected than introduced birds from continental areas. The role of disease in reducing native Hawaiian bird populations was first suspected by Perkins (1893, 1903) and Henshaw (1902), but a long time passed as evidence was amassed and techniques were developed that substantiated this hypothesis. Compelling evidence of the debilitating role that malaria appears to play was presented by Warner (1968) and van Riper et al. (1982). In New Zealand, Myers (1923) suggested that population reductions in some native species were due to high susceptibility to malaria. Declines of endemic insular birds due to introduced diseases seem to parallel the decrease of Polynesians and other island peoples due to diseases (e.g., measles, common colds) caught from Westerners in whom their effects were much less severe (Lack 1954:168–169).

Native passerines, particularly Hawaiian honeycreepers, have experimentally shown great susceptibility to and mortality from avian malaria (Warner 1968, van Riper et al. 1982). After reviewing previous studies, Laird and van Riper (1981) concluded that only one species of avian malaria occurred in Hawaii, *Plasmodium relicitum capistranoae*, but found unusual morphological forms of this species at high levels of parasitemia. The ornithophilous night-biting mosquito *Culex quinquefasciatus* (= *C. pipiens fatigans*) is the primary vector (van Riper et al. 1982). Although van Riper was not successful in transmitting malaria with *Aedes albopictus*, his

sample sizes were small and he also had difficulty in completing the sexual stage of malaria in the primary vector; Boyd (1949) reported that *A. albopictus* was a vector of secondary importance for malaria. Malaria was probably introduced to the Hawaiian Islands via introduced birds, with candidates including the Common Myna (first introduced in 1865), Nutmeg Mannikin (1865), House Finch (1870), and House Sparrow (1871), although van Riper et al. (1982) speculated that the date was later.

Malaria has been identified in blood smears from wild Townsend's (Newell's) Shearwater, Hawaiian Crow, Elepaio, Omao, Common Amakihi, Iiwi, and Apapane, as well as in wild Rock Dove, Red-billed Leiothrix, Japanese White-eye, Northern Cardinal, House Finch, House Sparrow, and Nutmeg Mannikin (for primary references see review by van Riper and van Riper 1985). In inoculation experiments, introduced species have far higher survival rates than native species (100% vs. 42%); native species whose range does not include mosquito-infected areas (Laysan Finch, Palila) have 0% survival after malarial inoculation (van Riper et al. 1982). In North America, isodiagnosis (the inoculation of blood from wild birds into susceptible captive hosts) revealed prevalences of over 60% for malaria in wild bird populations, apparently representing a high degree of immunity to fatal disease in populations that evolved in the presence of malaria (Herman 1968). Similarly in North America, native birds are less susceptible to the native eastern equine encephalitis than introduced birds that evolved in its absence (Karstad 1971).

The role of avian pox in regulating native bird populations is not fully understood at present. Avian pox is caused by several strains of the virus *Poxvirus avium*, and recovery usually confers immunity, at least to the infecting strain. Avian pox has two manifestations, wet pox leading to lesions in the mouth and upper respiratory tract, and dry pox leading to integumentary lesions (Cavill 1982). It is transmitted directly by contact with an infected individual, by secondary contact with infected objects, or mechanically by vectors (Cavill 1982). Mosquitoes of all species are ideal vectors, because the virus needs a small break in the integument for infection (van Riper and van Riper 1985). In the Hawaiian Islands pox virus was first isolated from a Red-tailed Tropicbird (*Phaethon rubricauda*) (Locke et al. 1965), and not until 1984 was the virus isolated from a main island passerine (C. B. Kepler, pers. observ.).

Perkins (1893) noted the occurrence at lower elevations in Kona of apparent pox lesions on Elepaio, Greater Koa-Finch, Palila, and Apapane, and noted that a similar phenomenon occurred on Oahu. Pox-like lesions have also been

found on Hawaiian Goose (Banko and Manuwal 1982), Hawaiian Hawk (Perkins 1903), Hawaiian Crow (Perkins 1903, Giffin 1983), races of Elepaio on Hawaii (van Riper et al. 1982) and Kauai (J. L. Sincock, pers. comm.), Omao (van Riper and van Riper 1985), Kamao (S. Mountainspring, pers. observ.), Kauai Akialoa, Molokai Creeper (Perkins 1903), Nukupuu (S. Mountainspring, pers. observ.), Akiapolaau (J. M. Scott, pers. observ.), Common Amakihi, Iiwi, and Apapane (van Riper et al. 1982), as well as on the introduced Ring-necked Pheasant, California Quail, Japanese White-eye, Northern Cardinal, House Finch, House Sparrow (van Riper and van Riper 1985), and Red Junglefowl (J. L. Sincock, pers. comm.). Birds with pox-like lesions are more likely to have malaria than unblemished birds (van Riper et al. 1982), and mortality apparently from pox has been observed on several occasions for wild native birds (Perkins 1903; C. van Riper III, pers. comm.; C. B. Kepler, pers. observ.).

Although numerous records of integumentary pox-like lesions have been reported, infections by *Aspergillus*, *Trichomonas*, or bacteria may also cause such lesions (Karstad 1971). *Aspergillus* and *Trichomonas* are apparently quite rare in wild Hawaiian passerine populations, and although integumentary lesions of bacterial origin have not yet been diagnosed from wild populations of Hawaiian birds, the record is too fragmentary to be definitive (van Riper and van Riper 1985). Recently W. R. Hansen and C. van Riper III (in van Riper and van Riper 1985) have isolated and clinically diagnosed pox virus from pox-like lesions on five native and four introduced Hawaiian passerine species, suggesting that the large number of pox-like lesions reported may be a true reflection of the prevalence of pox infection in the Hawaiian Islands. A high prevalence of pox in the islands is also suggested by the necessity of vaccinating poultry against pox in commercial operations (Bice 1933; J. L. Sincock, pers. comm.).

Because of the important role that mosquitoes play in transmitting avian disease, it is instructive to examine the relations between the distributions of mosquitoes and native birds. Mosquitoes were first released in the Hawaiian Islands in 1826 by sailors who dumped water casks containing larvae into a stream on Maui (Hardy 1960). The species with the widest elevational range, *Culex quinquefasciatus*, occurs year-round as high as 1500 m in many areas, while *Aedes albopictus* occurs as high as 1200 m seasonally (Goff and van Riper 1980). Mosquitoes need to occur only seasonally or during irregular intervals to inoculate native bird populations in an area; pathogen reservoirs in these areas would

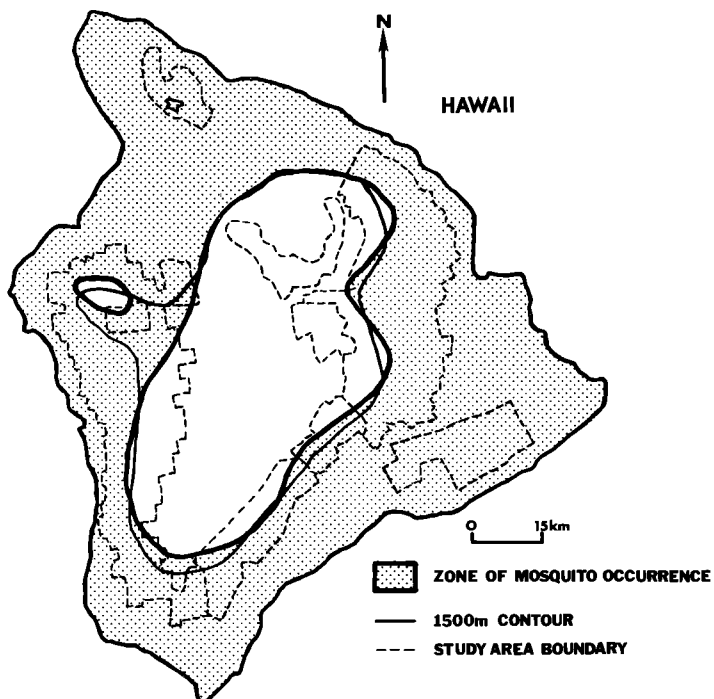


FIGURE 332. Approximate distributional limits of mosquitoes (chiefly *Culex quinquefasciatus*) on Hawaii.

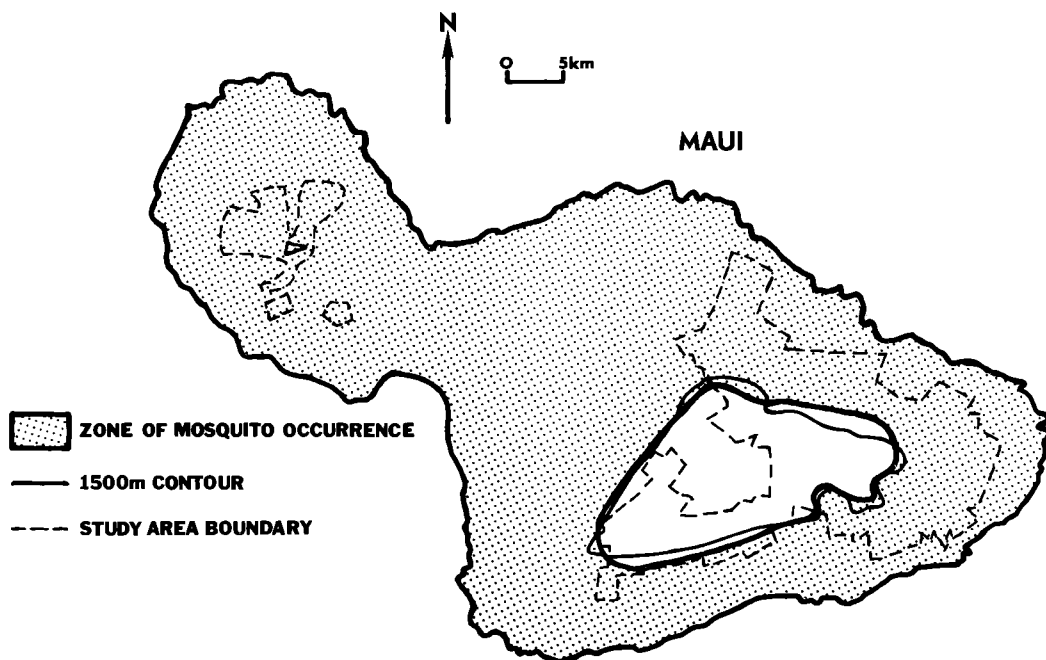


FIGURE 333. Approximate distributional limits of mosquitoes (chiefly *Culex quinquefasciatus*) on Maui.

TABLE 72
RESPONSE OF NATIVE BIRDS TO MOSQUITO PRESENCE^a

Species	Study area				
	Kau	Hamakua	Kipukas	Kona	Maui
Hawaiian Crow	X	X	X	-6.1*	X
Elepaio	-4.5*	-3.0	...	-9.6*	X
Omao	-2.1	X	X
Ou	X	-5.8*	X	X	X
Maui Parrotbill	X	X	X	X	-8.2*
Akiapolaau	...	-2.4	X	-2.9	X
Common Amakihi	-2.8	...	2.8	...	-5.9*
Hawaii Creeper	X	-5.6*	X
Maui Creeper	X	X	X	X	-21.0*
Akepa	...	-8.1*	X	-9.2*	X
Iiwi	-2.4	-2.1	...	-4.4*	-7.2*
Crested Honeycreeper	X	X	X	X	-20.3*
Apapane	-6.8*	-4.1*

^a Entries are *t* statistics for including the variable of mosquito presence in the regression models in Tables 14–32; all *t* statistics are significant at $P < 0.05$; * indicates $P < 0.001$; ... indicates no significant response; X indicates no model for that entry.

probably be introduced species, or less susceptible native species (e.g., Apapane) that migrate daily to lower elevation areas where vectors are common.

To quantify the potential role of mosquitoes on native bird distribution, we constructed maps of mosquito distribution for Hawaii and Maui (Figs. 332 and 333) from over 200 campsite records and literature records, taking into account human activities, local variation in wind patterns, water sources, and forest edge. These maps reflect the occurrence of *Culex quinquefasciatus* and *Aedes albopictus*, both of which are proven vectors of malaria and strongly suspected vectors of pox. Although these maps are admittedly less accurate than our bird distribution maps, we include them for their heuristic value. The zones of mosquito presence on these maps indicate regions where we predict that mosquitoes are present for at least several weeks each year at densities sufficiently high to infect native bird populations and be detectable by human observers. In some montane areas, mosquitoes occur only seasonally during certain prevailing wind regimes (e.g., weak trades, Kona storms) (Goff and van Riper 1980).

Each census station was scored as 0 if it fell outside the zone of mosquito occurrence, and 1 if it fell within. We then took the final equations (regression models) for the habitat response of native species in those study areas where both mosquito presence and absence zones occur, and offered the new variable "mosquito presence" to these models. This procedure partials out the potentially confounding effect of the habitat variables.

In 42% of the native passerine models, a negative response to mosquito presence is registered

at the 0.1% significance level (Table 72); no positive responses appear at this level, but a weak positive term occurs in a Common Amakihi model, a species with populations that are more resistant to avian malaria than are many other native species (van Riper et al. 1982). Virtually all the rare passerines—Ou, Maui Parrotbill, Akiapolaau, Hawaii Creeper, and Akepa—are much rarer in mosquito-infested areas, as are some populations of more common species such as Elepaio, Omao, Common Amakihi, and Apapane. Staggering drop-offs of densities in mosquito-infested areas occur for Maui Creeper (94% fewer than in identical mosquito-free habitat), Crested Honeycreeper (82% fewer), and Iiwi (75% fewer). The distributional patterns on Maui for Nukupuu, Akepa, and Poo-uli, and on Kauai for Kamao, Puaiohi, Kauai Oo, Ou, Kauai Akialoa, Nukupuu, Kauai Creeper, and Akepa strongly suggest that mosquito-borne diseases currently restrict the ranges of these species too, although we are unable to analyze quantitatively the effect of mosquito presence on density.

The assumed mosquito-free refugia harbor the best remnants of the original avifauna and are relatively few and small: the dry Mauna Kea woodland and the upper wet and mesic forests of Hamakua, Kau, central Kona, north Hualalai, East Maui, and the Alakai Swamp on Kauai. Range truncation is strongly suggested for species that have their highest densities at the lowest elevations of mosquito-free areas; Hawaiian Crow, Ou, and possibly Nukupuu fall into this category. These are the species that may be the most vulnerable to extinction due to avian disease, because nearby mosquito-infested habitat is similar in physiognomy and resources to mosquito-free habitat, and may be more attractive

because of fewer conspecifics. The species restricted to the Alakai Swamp may be particularly vulnerable because the absence of high elevations on Kauai might preclude a permanent refugium from mosquitoes.

Resistance to malaria and pox has developed or may have originally been present in some native bird populations, and would seem to explain high densities of some species in mosquito-infested areas. Resistance can vary among the populations of a species; Common Amakihi from mosquito-free areas on Hawaii are quite susceptible to malaria, but those from mosquito-infested areas are resistant (van Riper et al. 1982). The peculiar present-day distribution of Omao may reflect early extinction of susceptible populations in Kohala and Kona due to mosquito-borne disease as well as development of resistance and subsequent dispersal of populations in Hamakua and Puna. Some of the uncommon native birds (Liwi, Hawaii Creeper) have distributions suggesting that they are slowly developing resistance, but densities are still quite low in mosquito-infested areas.

Although we have interpreted the existing, largely circumstantial evidence as indicating a major role for avian disease in limiting present native bird populations, restricting their ranges to high elevations, and causing the extinction of several forms, further study is needed on the seasonal and annual variation in mosquito distribution and abundance, the identity of pox vectors, the biology of disease transmission, the prevalence of disease in wild populations, and the physiological effects of avian disease, before conclusive statements can be made regarding the exact role of disease in limiting native birds.

Maintaining unbroken forest where possible may slow mosquito advances into prime forest bird habitat. Habitat fragmentation and forest edges are important modifiers of the flight and dispersal pattern of mosquitoes (Kennedy 1975). Wide-ranging flights over poorly defined areas are typical of mosquitoes in savannas and cultivated areas; restricted flights over sharply defined areas are typical in forests and unbroken woodlands (Gillies 1972). In Kona the extinction of many native bird species at the end of the 19th century, and the near absence of endangered passerines now over most of the area, may reflect early habitat fragmentation below 1000 m elevation due to coffee farming (Munro 1944), and to strong sea breezes that blow mosquitoes to higher elevations during the day. Significantly the north Hualalai refugium, where most endangered birds in Kona occur, lies in a relatively windless area protected from trade winds, winter Kona storms, and sea breezes (J. C. Giffin, pers. comm.). In the distributional anomalies section,

we tentatively attribute a number of species responses on windward Hawaii and Maui to trade wind patterns that blow mosquitoes into unbroken forests.

Options for controlling mosquitoes over large wilderness areas seem few, although genetically engineered strains of mosquitoes may have management potential, and biological controls and sterile male releases offer a distant hope. In intensively managed areas, elimination of mosquito breeding sites would be helpful in reducing vector densities. Mosquitoes often breed in wallows and tree fern sites created by feral pig activity, and mosquito densities appear significantly lower in pig-free kipukas (forest habitat-islands) than in nearby pig-damaged ones (L. Katahira, pers. comm.). Control of pigs in endangered species habitat may reduce disease transmission rates. Adding larvicides innocuous to vertebrates to high-elevation ponds and water tanks would also reduce breeding sites. It may be possible to develop pox and malaria vaccinations that confer lifetime immunity, a technique that would have use for intensively managed species. For species in captive propagation, it may be possible to develop genetic resistance to disease by selective breeding. Further introductions of birds that are liable to host pathogens and that enter montane rainforests (e.g., Kalij Pheasant to Maui and Kauai) should be banned. Strengthening quarantine and importation controls to monitor and clear parasites on introduced birds and to prevent establishment of other mosquito species would prevent introduction of disease problems not yet present; papers in Laird (1984) discuss control measures for curbing the spread of disease vectors by commercial activity. Introductions of native species bred elsewhere must also be carefully examined; for example several potentially serious parasites that are not yet present in the Hawaiian Islands have been found on captive Hawaiian Geese in Slimbridge, England (van Riper and van Riper 1985).

INTERSPECIFIC COMPETITION

The role of interspecific competition in modifying avian habitat response has been widely studied (Svärdson 1949, Cody 1974). Abbott et al. (1977) suggested that interspecific competition interacted with floristic diversity in determining the occurrence, morphology, and foraging behavior of Galápagos finch species. Noon (1981) identified competition as a major factor in differentiating the ecological patterns of sympatric forest thrushes in eastern North America. Williams and Batzli (1979) showed that competition affected woodpecker behavior by experimental removal of the dominant species. Pearson (1975) suggested that competition with

monkeys affected bird community structure in the Amazon basin. Diamond (1973, 1975, 1978), Terborgh (1971), and Terborgh and Weske (1975) inferred that competition was responsible for many patterns of elevational distribution among congeneric species. Others have suggested a minor role for competition. Rotenberry and Wiens (1980b) found very little evidence of close biological coupling between bird species in their shrubsteppe sites, partly because of unpredictable climate. Landres and MacMahon (1983) also found only weak evidence of competition among fly-catching birds in oak woodlands.

To evaluate the role of interspecific competition from other bird species in modifying the habitat response of Hawaiian forest birds, we conducted an analysis of the correlation between various pairs of species after all the habitat variables had been partialled out (Mountainspring and Scott 1985). A total of 170 partial correlations were examined among 14 species in seven study areas (Table 73). Only 6% of the partial correlations are significantly negative, but 67% of them are significantly positive. The correlations between very similar species, where competition is most likely to operate, are mostly positive (e.g., omnivorous introduced species such as Melodious Laughing-thrush, Red-billed Leiothrix, and Japanese White-eye; insectivorous natives such as Elepaio, Common Amakihi, Kauai Creeper, and Akepa; nectarivorous natives such as Iwi and Apapane). The pattern of positive association rather than avoidance dominates every data set.

Wiens (1977) suggested that competition is a rare phenomenon in a varying environment because populations are seldom at the carrying capacity, and resources are often superabundant. We might thus expect to see few negative correlations within our data set.

The average negative correlation is low ($r = 0.06$), which indicates that the small-scale geographic displacement (or depression of population density) between native and introduced species is rather minor (the area involved would be on the order of 1% of the species' range for total displacement but larger if low densities co-existed). This is a measure of the displacement occurring at a given instant, however, and if the negative association is sustained over time, the net effect would be competitive displacement of the less successful species over a region as displacements accumulate over time.

Two species-pairs show a consistent pattern of negative partial correlations over several adjacent study areas—Japanese White-eye/Elepaio in windward Hawaii (Hamakua, Puna, Kohala, and Kau study areas; $P = 0.06$), and Japanese White-eye/Iwi in montane Hawaii (Hamakua, Kau, and

TABLE 73
DISTRIBUTION OF NEGATIVE AND POSITIVE PARTIAL CORRELATIONS ACROSS STUDY AREAS BY NATIVE OR INTRODUCED STATUS OF THE MEMBERS OF EACH SPECIES PAIR

Study area	Intro./ intro.		Native/ native		P^a
	-	+	-	+	
Kau	0-1		0-10		.003
Hamakua	0-3		0-10		.075
Puna	0-3		0-6		.034
Kona	0-3		0-6		.063
Kohala	0-3		0-3		.250
East Maui	0-3		0-10		.230
Kauai	0-1		5-16		.234
Overall	0-17		5-61		$\ll .001$

^a Probabilities are for the two-tailed test that native/introduced species pairs have a greater proportion of negative correlations than do native/native pairs.

Kona study areas; $P < 10^{-7}$). The Japanese White-eye/Elepaio relation probably reflects a response to interspecific competition because both species depend on insects in the understory and the subcanopy; moreover, Elepaio frequently defend their territory from Japanese White-eye, particularly on Hawaii (Conant 1977).

The Japanese White-eye/Iwi relation probably reflects interspecific competition for limited nectar resources, because both species frequently take nectar from understory trees and shrubs. Iwi are specialized to exploit high-quality resources and probably have difficulty exploiting poor resources (Pimm and Pimm 1982). When ohia or mamane flowers are locally unavailable, Iwi rely heavily on alternate nectar sources that may be in short supply, unlike Apapane or Common Amakihi, which switch to insects and fruit. This specialization may thus make Iwi particularly vulnerable to the negative impact of the omnivorous foraging behavior of Japanese White-eyes.

King (1977) and Berger (1981) suggested that introduced birds may compete for food resources with native birds. To examine this hypothesis, we divided the species-pairs into three groups according to the native or introduced status of the two species in the pair. We then tallied the positive and negative partial correlations for native/native, native/introduced, and introduced/introduced species pairs.

Interactions of native/native and introduced/introduced species-pairs have virtually no negative associations (Table 73). The five negative native/native post-habitat correlations from Kauai are negligible, with $r = -0.08$ for the greatest magnitude among the five. More important is the substantial proportion of negative correlations among native/introduced species-pairs.

TABLE 74
PERCENTAGES OF NEGATIVE PARTIAL CORRELATIONS
AMONG PRIMARY AND SECONDARY POTENTIAL
COMPETITORS IN NATIVE/INTRODUCED SPECIES PAIRS

Study area	Primary potential competitors	Secondary potential competitors
Kau	67	50
Hamakua	33	20
Puna	67	33
Kona	60	29
Kohala	33	33
East Maui	40	0
Kauai	50	33
Overall	47	25

Native/introduced pairs have significantly higher proportions of negative correlations than either native/native (Chi-square test, $P < 10^{-4}$) or introduced/introduced pairs (Chi-square test, $P < 0.003$). In each area native/introduced pairs have a higher proportion of negative correlations than native/native pairs. Among the native/introduced species-pairs in each study area (Table 74), the interactions between primary potential competitors (those species that feed on similar foods) account for more negative associations than do interactions between secondary potential competitors (species that have little overlap in diet) (Chi-square test, $P < 0.04$). This suggests that competitive interactions between species for food are one cause of negative interspecific correlations. Our results show that a broad and diffuse "front" of competition occurs between the native and introduced avifaunas, affecting about one-half (47% in Table 74) of the primary potential competitors among native/introduced species pairs in a forest. Competition with introduced species may be one of several factors causing the decline of the native Hawaiian avifauna in this century.

Japanese White-eyes are the most abundant, widespread, and omnivorous forest passerines, and their negative correlations with Elepaio, Iiwi, Common Amakihi, and Kauai Creepers indicate that Japanese White-eyes are a focus of the native/introduced encounter. If we restrict the scope to primary competitors, native/introduced pairs involving Japanese White-eyes have a significantly greater proportion (62% vs. 32%) of negative correlations (8+, 13-) than all other native/introduced pairs (17+, 8-; $Z = 2.03$, $P = 0.04$). To see whether it is reasonable to conclude that Japanese White-eyes were partly responsible for the decline of Hawaii Creepers in the 1940s as Dunmire (1961) suggested, we calculated the partial correlation between the two species for

the Hamakua study area, where over 70% of the Hawaii Creeper population occurs. Despite the rarity of Hawaii Creepers, the post-habitat correlation is significantly negative ($r = -0.064$, $P < 0.003$), thus supporting the hypothesis. Because Japanese White-eyes were introduced relatively recently (1929-1937) and may have arrived in some remote areas only in the past 15 years or so, it is very likely that in many areas native bird populations have not yet adjusted to their presence. Japanese White-eyes are the most abundant bird in many areas, and their high densities, coupled with their facultative omnivory, suggest that the effect of this species on native birds is much greater than the effect of native species on it, further indicating the potent role that Japanese White-eyes play in depressing native bird populations.

Another phenomenon relevant to the native/introduced species pairs competition is the explosive expansion of range and numbers that introduced species sometimes undergo soon after introduction, only to decline in later years as other factors come into play. This is documented for the Red-billed Leiothrix on Oahu by annual Christmas bird counts (Anonymous 1974). Common Mynas experienced a population explosion into heavily forested areas in the 1890s, possibly adversely affecting the survival of some now-extinct species (Perkins 1903). Since then, Common Mynas have declined and are not found in dense forests. Interspecific competition for resources was possibly more severe during these population explosions. As most introduced birds occur in disturbed areas and forest edges, native birds may be buffered from violent fluctuations in introduced bird populations by dwelling in refugia of undisturbed native forests. Diamond and Veitch (1981) also noted the propensity of introduced birds to associate with disturbed vegetation in New Zealand. In view of this, management of rare insectivorous species such as the Hawaii Creeper, Nukupuu, or Poo-uli, should include a policy to preserve unbroken blocks of forest and reduce forest edges where feasible.

The prospects are poor for controlling introduced species. A more realistic strategy is to restrict importation of bird species not yet present in the islands and to restore the integrity of native ecosystems, because disturbed areas provide the chief avenues of introduced bird dispersal.

Interspecific competition doubtless occurs from introduced species other than birds (Banko and Banko 1976). Numerous predatory insects have been introduced, such as the notorious yellowjacket wasp (*Vespa pensylvanica*). The introduced carnivorous snail *Euglandina rosea* decimates native land snail populations (see Clarke et al. 1984). Another introduced snail

(*Oxychilus alliarius*) suspected of preying on native snails, is abundant within the range of the Poo-uli, and may contribute to the declining numbers of that species. Data are presently too meager to assess fully the impacts of introduced invertebrates on the native biota, but effects include reduction not only of native invertebrate populations by predators and parasites (thereby seriously depleting the food resources of native birds), but also of native plant populations by herbivores, pathogens, and pathogen vectors (Howarth 1985). Although biomass trends of canopy arthropods along an elevational transect in Hawaii Volcanoes National Park (Gagné 1979) show little resemblance to elevational trends in native bird density (particularly in the drop-off below 1300 m elevation), more extensive studies are needed on the diets of native birds and the impact of introduced species on resource levels. The most cost-effective strategy to reduce problems caused by introduced invertebrates is (1) prevention of further introductions by strengthening quarantine procedures, (2) fumigation of imported biological material (e.g., Christmas trees, cut flowers), and (3) improvement of the surveillance of importations (Howarth 1985). Minimizing disturbances of native ecosystems (e.g., land clearing, grazing, pig rooting, invading weeds) that favor introduced invertebrates will also lessen their impact.

DISASTERS

Usually enough individuals survive hurricanes and heavy storms to perpetuate the population, but unfavorable events are potentially important when populations are extremely low. Laysan Island, 1500 km northwest of Honolulu, originally supported an endemic subspecies of Apapane, the Laysan Honeycreeper (*Himatione sanguinea freethii*). Laysan Honeycreepers frequented tall grass and low bushes (Fisher 1906). Unfortunately, rabbits were introduced in 1903 and by 1911 had destroyed most of the vegetation (Dill and Bryan 1912). By 1923 the rabbits had removed the last vestiges of vegetation, and members of the 1923 Tanager Expedition found only three Laysan Honeycreepers. These birds "perished during a three-day gale that enveloped everything in a cloud of swirling sand" (Wetmore 1925).

A severe tropical storm is thought to have been responsible for eliminating the Puerto Rican Bullfinch (*Loxigilla portoricensis grandis*) from the island of St. Kitts (Raffaele 1977). Cataclysmic storms could adversely affect other precariously low populations. Particularly vulnerable are those species having very small ranges. Broadside hits on the Alakai Swamp or the

northeast slope of Haleakala could eliminate several species.

The island of Hawaii is the site of frequent volcanic eruptions and massive lava flows moving from volcano summits to the ocean. These flows are as wide as 1 km, destroy large tracts of native forest, and fragment the range of forest birds (see Fig. 48). Presently the greatest threat may be to nesting areas of the Hawaiian Crow; the 1984 Mauna Loa lava flow covered part of the area where Ou were most numerous in the 1977 survey. It has been 200 years since an eruption on Maui, but renewed eruptions are possible; the small range of Poo-uli could be demolished by a major eruption along the east rift zone of Haleakala, but this is quite unlikely. Fires resulting from volcanic activity are an additional threat in dry and mesic habitats.

CONSERVATION

HISTORY OF HUMAN DISTURBANCE

The recent history of the Hawaiian biota may be divided into three cultural periods: the pristine period before Polynesian contact (ca. 400 A.D.); the Polynesian period before Western contact (1778); and the modern period to the present. The series of changes that Polynesians initiated drastically altered pristine ecosystems that had evolved in isolation for millions of years and were in fact older than the main islands themselves. The main Hawaiian islands are geologically young (0–6 million years) and transient, formed in succession as the Pacific Plate slowly slides northwest over a hot spot in the earth's mantle. In 8 to 10 million years, each island in turn moves over and past the hot spot to erode away, while the native birds colonize new islands emerging to the southeast. From Kure Atoll in the Northwestern Hawaiian Islands, a line of seamounts continues north until subducted near the Aleutians, with the northernmost over 70 million years old. Based on DNA hybridization studies, Sibley and Ahlquist (1982) inferred that the ancestral Hawaiian honeycreeper may have colonized the archipelago 15–20 million years ago on forested high islands that have since become low islands or seamounts. Thus the fauna and flora that Polynesians found on the young main islands may have had their origins back millions of years on now submerged islands. Existing in isolation for eons, free of many stresses faced by their continental ancestors, many species lost their defensive biochemistry, morphology, and behavior. Plants lost their alkaloids and thorns (Carlquist 1970), birds lost some of the immunity they had to disease, some birds became flightless (James and Olson 1983), and many insects lost their wings altogether (Zimmerman