Studies in Avian Biology No. 15:103–118, 1994.

AVIFAUNAL CHANGE IN THE HAWAIIAN ISLANDS, 1893–1993

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Abstract. The past century has witnessed more avifanal change in the Hawaiian Islands than in any other part of the United States. Two-thirds of the 68 species present in the main islands in 1893 are now extinct or endangered. Despite some early historical extinctions, a more or less intact native land and freshwater avifauna existed in 1893. The century began with rapid disappearances and declines of forest birds in large tracts of seemingly undisturbed habitat on the larger main islands, with a similar crash on Lanai following its settlement in 1920. A consensus has developed that these disasters resulted from alien bird diseases including avian pox and mosquito-borne avian malaria, although other causes such as the introduction of *Rattus rattus* have been suggested. Today, the presence of vectors of avian malaria is the most significant limiting factor in the distributions of native birds, which are restricted to higher elevations. Slow declines of species that survived the 1890–1910 crash resulted from a variety of factors including habitat alteration by man and feral pigs and predation by introduced mongooses. Kauai retained all of its 1893 species, some in reduced numbers, into the 1960s, but has since experienced still unexplained declines and extinctions. Two recent hurricanes may have wiped out the remnants of several species. Outside the main islands, Laysan lost 3 of its 5 endemic species as a result of the introduction of rabbits.

As a result of human disturbance, nesting seabirds had nearly disappeared from the main islands by 1893. With the decline of egg-gathering and legal protection of offshore islets, many colonies have been re-established. Those that attempt to nest on the main islands, including the endangered Hawaiian Petrel and threatened Newell's Shearwater, still suffer from predation by mongooses and feral pets. Seabird colonies in the Northwestern Hawaiian Islands have recovered from the depredations of feather hunters around the turn of the century and are now protected in a national wildlife refuge.

The Hawaiian Islands now harbor more alien bird species than any other place on earth, most of them introduced since 1893. They represent every zoogeographical realm and include game birds, ornamental species, common cage birds, and others. With the exception of freshwater birds, the lowland Hawaiian avifauna is now entirely artificial. Whether these aliens have a role in the restriction and decline of native birds is not known, but little direct competition has been documented for most species. They primarily inhabit areas no longer available to native birds due to the presence of disease vectors. However, the Japanese White-eye, now the most abundant bird in the islands, is widespread in montane forests and may compete with native birds and provide a disease reservoir.

Key Words: Avian disease; extinction; feral pig; Hawaiian Islands; introduced birds; mongoose.

The Hawaiian Islands have seen more change in their avifauna during the past century than any other part of the United States of America. In virtually every respect, the bird fauna that greets modern observers differs drastically from that described by researchers of the the 1880s and 1890s when the first thorough studies of Hawaiian birds were conducted. Because of the work of such observers as Valdemar Knudsen (Stejneger 1887, 1888, 1889), Scott Wilson (Wilson and Evans 1890–1899), Henry Palmer (Rothschild 1893–1900), R. C. L. Perkins (1903), Henry W. Henshaw (1902), Alvin Seale (1900), W. A. Bryan (1905, 1908), W. K. Fisher (1906), and George C. Munro (1960), we have a surprisingly complete picture of the Hawaiian avifauna as it existed a century ago. The ensuing years saw the extinction of many species, the reduction of others to tiny remnant populations, and the purposeful introduction of more alien birds than in any other place on earth. The willy-nilly destruction of the indigenous avifauna is particularly unfortunate because, as the world's most isolated archipelago, the Hawaiian Islands are singularly important in the study of evolution and island biology. [Note: Scientific nomenclature as given in Tables 1 and 2 follows Pyle (1992b) except for the Hawaiian Coot which follows Pratt (1987), and the akialoas which follow James and Olson (1991). English names follow Pratt et al. (1987) and Pratt (1992b).]

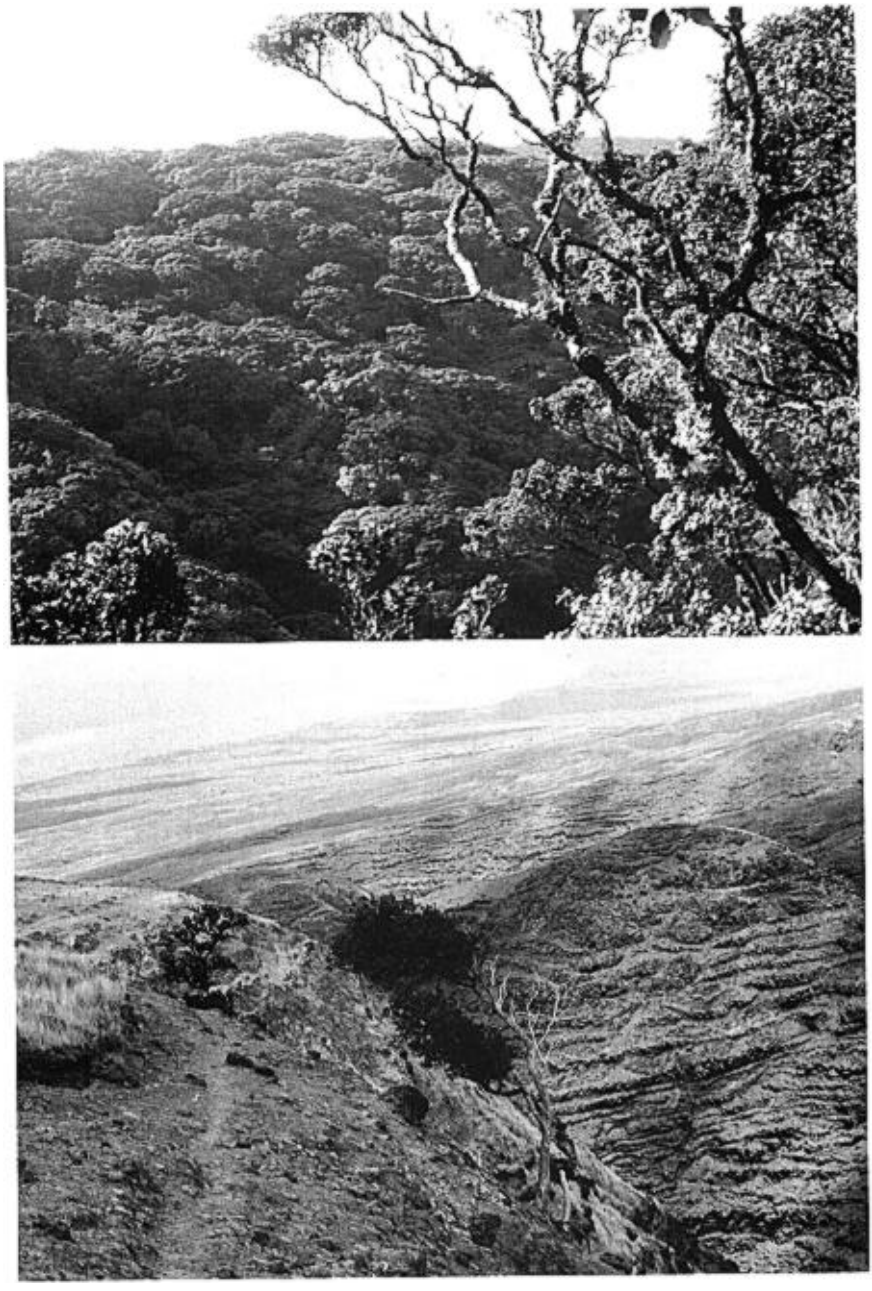

FIGURE 1. Above: Remnant montane ohia (*Metrosideros polymorpha*) rainforest at crest of ridge, eastern Molokai. Below: Lower elevation on south slope of same ridge showing a single ohia tree that has survived damage by feral goats, pigs, and deer.

THE HAWAIIAN AVIFAUNA IN 1893

Land birds

The forest and upland avifauna of the Hawaiian Islands was much degraded even a century ago. Although unknown to observers at the time, well over half of the archipelago's indigenous birds were already extinct. Henshaw (1902) attributed the absence of native forest birds from low elevations to the vagaries of island colonization, but recent fossil discoveries revealed that the first human inhabitants destroyed a rich and varied lowland forest avifauna (Olson and James 1982). New species described from skeletal remains, although undoubtedly an incomplete sample of the prehuman avifauna, more than doubled the recent species list for the islands (Olson and James 1982, 1991; James and Olson 1991). Following the first European contacts in the late 1700s, a new era of avifaunal change ensued, characterized by numerous extinctions on islands with the most contact with the outside world. Oahu, still the islands' political, economic, and population center, lost its oo, thrush, akialoa, and Nukupuu well before 1893 (Wilson and Evans 1890–1899, Henshaw 1901). Maui, site of the first capital of the Kingdom of Hawaii but not explored ornithologically until the 1880s, probably had already lost a thrush and the Black Mamo (James and Olson 1991); its oo and the Poo-uli also had become so rare that their existence was not even known at the time (Wilson and Evans 1890–1899, Henshaw 1902, Casey and Jacobi 1974). Hawaii, the first island to be affected by Europeans, had lost the large meliphagid Kioea and a flightless rail by the 1860s, and the Ula-ai-hawane barely survived in 1893 (Rothschild 1893–1900, Henshaw 1902). Nevertheless, with the exception of Oahu, the historically known terrestrial avifaunas of the Hawaiian Islands were still more or less intact in 1893 (Wilson and Evans 1890–1899, Rothschild 1893–1900). The original montane native forests still existed on most islands, although clearing for agriculture

FIGURE 2. Hawaiian Stilt (*Himantopus mexicanus knudseni*) in taro patch, Hanalei, Kauai.

(Henshaw 1902) and grazing by feral cattle (Tomich 1986) were moving their lower limits inexorably upward (Fig. 1).

Freshwater birds

Freshwater habitats including marshes, taro farms, and fishponds were still an important part of the Hawaiian lowland landscape in 1893, and the native duck, coot, moorhen, and stilt (Fig. 2) were widespread and common (Henshaw 1902). On the other hand, the Nene or Hawaiian Goose, more of an upland bird than a waterfowl, had disappeared from Maui and was steadily declining on Hawaii as it had been since European contact (Baldwin 1945).

Breeding seabirds

Although most Hawaiian seabirds presumably bred throughout the archipelago in prehuman times, only those that nested in protected sites still nested on the larger islands in 1893. Hawaiian Petrels (usually considered a subspecies of *Pterodroma phaeopygia,* but see Tomkins and Milne 1991) nested in the alpine zone on several islands, and Newell's (Townsend's) Shearwaters on forested ridges. Cliff-nesting White-tailed Tropicbirds and Black Noddies still nested commonly throughout the main islands (Henshaw 1902, Perkins 1903). Others bred only on the uninhabited and

still relatively undisturbed Northwestern Hawaiian Islands or on inaccessible offshore islets (Munro 1960).

Introduced birds

By 1893, the indigenous Hawaiian species and the aboriginal Red Junglefowl had been joined by several imported ornamental and "game" species such as Wild Turkey, Common Peafowl, California Quail, Common Pheasant, feral pigeon, and Spotted Dove as well as such passerines as Eurasian Skylark, Common Myna, House Sparrow, House Finch, and Nutmeg Mannikin. Only the junglefowl penetrated far into native forests (Henshaw 1902).

CHANGES IN NATIVE BIRD POPULATIONS 1893–1993

Forest bird crashes

The past century in the Hawaiian Islands has been punctuated by sudden population crashes of native species. Unlike gradual declines that result from progressive events such as habitat alteration, these declines were rapid, obvious, and mysterious to contemporaneous observers (Warner 1968, Atkinson 1977). A wave of such extinctions occurred between 1893 and 1910. The Hawaii Oo was still common in 1893 but was "fast nearing extermination" (Henshaw 1902) a few years later. The Hawaii Akialoa, uncommon but still widespread in the 1890s (Henshaw 1902), was never reliably reported in the 20th century (Greenway 1967). During the same period several species already rare or with restricted distributions on Hawaii, including the Greater Amakihi, Hawaii Mamo, Ula-ai-hawane, both koa-finches, and the Kona Grosbeak disappeared. On Molokai, Bishop's Oo, Akohekohe, and Black Mamo, all of which existed in moderate numbers in the 1890s (Perkins 1903), were either extinct or nearly so by 1907 (Bryan 1908). Lanai lost its akialoa before 1900 and the Lanai Hookbill was last seen in 1918 (Munro 1960). On Maui, the once abundant Ou disappeared before 1900 and the Maui Parrotbill, Nukupuu, and Akohekohe became so rare that they were believed possibly extinct (Richards and Baldwin 1953, Banko 1968). Kauai lost no species, but its oo, akialoa, and Nukupuu were so reduced that their existence was uncertain until 1960 (Richardson and Bowles 1964). Lanai, which had been nearly uninhabited since 1900 experienced a wave of extinctions following the building of Lanai City in 1923. By 1940, seven of Lanai's original eight passerine species were extinct or very rare, with only the Apapane surviving in any numbers (Munro 1960). Table 1 lists species, subspecies, and populations that have become extinct or severely reduced since 1893.

Another aspect of this phenomenon was that huge tracts of seemingly pristine forest became devoid of native birds almost overnight (Henshaw 1902). Eventually, native birds withdrew entirely from forests below 600 m, and some disappeared from mid-elevation forests that even today appear nearly pristine (van Riper et al. 1986, pers. obs.). On eastern Molokai (Scott et al. 1977, pers. obs.), Kohala Mountain (van Riper 1973) and the east flank of Mauna Loa (Conant 1975) on Hawaii, and West Maui (Scott et al. 1986), forests that have experienced little apparent degradation have lost all but the most common native birds, and even those are scarce.

From the outset, disease had been hypothesized as a possible cause of the early 20th century avian disaster (Henshaw 1902, Perkins 1903, Munro 1960). Few other suggested causes could account for the rapidity of the declines. The obvious lesions and swellings of avian pox, a viral disease spread by physical contact, were noticed by every collector in the 1890s, and Henshaw (1902) remarked about the frequency with which dead birds were found in the forest. Nevertheless, evidence for epizootics remained circumstantial until Warner (1968) demonstrated not only that native birds are unusually susceptible to diseases such as pox and avian malaria, but that the distributions

of native forest birds and mosquitoes are mutually exclusive. Both findings have been corroborated by more recent studies (Scott et al. 1986, van Riper et al. 1986). The mosquito *Culex quinquefasciatus,* introduced on Maui in 1826, provided the vector for avian malaria as well as a ready means of transmission of avian pox. Warner (1968) failed to show conclusively that the spread of mosquitoes was correlated with the observed population crashes of birds (Atkinson 1977) except on Lanai, and recent investigations (van Riper et al. 1986) revealed that avian malaria may not have been present in the islands during the turn-of-the-century wave of extinctions. But avian pox, which can spread by physical contact, could account entirely for that phenomenon (van Riper and van Riper 1985). Atkinson (1977) hypothesized that roof rats (*Rattus rattus*) were the main causative agent, but his hypothesis is based entirely on circumstantial evidence and suffers from a lack of contemporaneous observations of any unusual rat plague. In other examples of rat-caused population crashes of island birds, such as the one that occurred on Lord Howe Island, the cause was obvious at the time (McCulloch 1921). Although rats may have contributed to some extinctions, they are not now regarded as a primary cause of the 1890–1910 Hawaiian bird declines (Scott et al. 1986), which remain enigmatic. However, the second wave of extinctions on Lanai as well as the gradual declines of populations such as the Oahu Alauahio, Kakawahie, Maui Akepa, Kamao, Iiwi on Oahu and Molokai, and Ou, which survived the 1890–1910 plague in good numbers but were rare by the 1960s, probably resulted from the presence of avian malaria after 1920 (van Riper et al. 1986). Little doubt remains that avian malaria is today one of the most important limiting factors in the distribution of Hawaiian native birds (Scott et al. 1985, 1986).

The Laysan disaster

The avifaunal history of Laysan in the Northwestern Hawaiian Islands is independent of that of the main islands but equally disastrous. Its sad history has been recounted by numerous authors (for a detailed summary see Berger 1981). Previously undisturbed Laysan was leased to phosphate miners in 1890. The removal of guano was probably not detrimental to the breeding seabirds and five endemic land and freshwater birds, but the introduction of rabbits in 1903–1904 proved the island's undoing. By 1923, when the island was visited by the Tanager Expedition, the rabbits had destroyed all the vegetation; the Millerbird was extinct, and only two individuals of the Laysan Rail and three of the Laysan Apapane could be found (Wetmore 1925). The expedition witnessed the demise of the Apapane in a sandstorm and, even though the rabbits were exterminated, the rails disappeared before the island was visited again. Of the endemics, only the Laysan Finch and Laysan Duck survived. (The story that the latter was reduced to a single gravid female is apparently apocryphal.) Laysan's seabirds had been heavily harvested by Japanese feather collectors 1909–1910, but none were wiped out and these populations recovered following the designation of the Hawaiian Islands Bird Reservation (now National Wildlife Refuge) in 1909.

An interesting but tragic twist to the story is that the Laysan Rail might have been saved except for events associated with World War II. The rails had been introduced to Midway and became numerous there even as the parent population was disappearing. However, no attempt was made to reintroduce them to Laysan after its vegetation had recovered, and they succumbed quickly after rats got ashore at Midway in 1943. The last one was probably seen in June 1944 (Fisher and Baldwin 1946). The Laysan Rail is the only Hawaiian bird whose final demise can be unequivocally attributed to rat predation.

Effects of the mongoose

Small Indian mongooses (*Herpestes auropunctatus*) were introduced by sugar

TABLE 1. EXTINCTIONS, NEAR EXTINCTIONS, AND EXTIRPATIONS OF HAWAIIAN BIRDS 1893–1993

Species	Range[1]	1893 status[2]	Last reported	1993 population estimate[4]
Laysan Rail				
Porzana palmeri	Ly/Md[3]	A	1923/1944[3]	0
Hawaiian Duck (populations)				
Anas wyvilliana	Mo	C	?	0
	Ma	C	?	0
Common Moorhen (populations)				
Gallinula chloropus sandvicensis	Mo	C	<1950	0
	Ma	C	<1950	0
	H	C	>1900	0
Hawaiian Crow				
Corvus hawaiiensis	Ko	C	1993	12[5]
Laysan Millerbird				
Acrocephalus f. familiaris	Ly	C	1912	0
Kamao				
Myadestes myadestinus	Ka	A	1989	<5
Lanai Olomao				
Myadestes l. lanaiensis	La	C	1931	0
Molokai Olomao				
Myadestes l. rutha	Mo	C	1988	<5
Puaiohi				
Myadestes palmeri	Ka	R	1991	<10
Hawaii Oo				
Moho nobilis	H	C	>1900	0
Bishop's Oo				
Moho bishopi	Mo	C	1904	0
	Ma	R	1980	<5
Ooaa (Kauai Oo)				
Moho braccatus	Ka	C	1987	0
Kona Grosbeak				
Chloridops kona	Ko	U	1896	0
Greater Koa-Finch				
Rhodacanthis palmeri	Ko	C	1896	0
Lesser Koa-Finch				
Rhodacanthis flaviceps	Ko	R	1891	0
Ou				
Psittirostra psittacea	Ka	A	1992?	<5
	La	C	ca. 1931	0
	Ma	C	ca. 1900	0
	H	A	1983	<10
Lanai Hookbill				
Dysmorodrepanis munroi	La	R	1918	0
Kakawahie				
Paroreomyza flammea	Mo	C	1963	0
Lanai Alauahio				
Paroreomyza m. montana	La	A	1937	0
Oahu Alauahio				
Paroreomyza maculata	O	C	1985	<5
Kauai Nakupuu				
Hemignathus lucidus hanapepe	Ka	U	1991?	<5
Maui Nakupuu				
Hemignathus l. affinis	Ma	U	1990[6]	<10
Kauai Akialoa				
Hemignathus stejnegeri	Ka	C	1969	0
Lanai Akialoa				
Hemignathus lanaiensis	La	U	1902	0
Hawaii Akialoa				
Hemignathus obscurus	H	C	>1900	0
Common Amakihi on Lanai				
Hemignathus virens	La	C	1976	0
Greater Amakihi				
Hemignathus sagittirostris	H	U	1901	0

TABLE 1. CONTINUED

Species	Range[1]	1893 status[2]	Last reported	1993 population estimate[4]
Maui Akepa				
Loxops coccineus ochraceus	Ma	R	1988	<10
Oahu Akepa				
Loxops c. wolstenholmei	O	R	1976?	0
Ula-ai-hawane				
Ciridops anna	H	R	1892	0
Laysan Apapane				
Himatione sanguinea freethii	Ly	A	1923	0
Akohekohe on Molokai				
Palmeria dolei	Mo	C	1907	0
Iiwi (populations)				
Vestiaria coccinea	La	A	1929	0
	Mo	A	1988	<50
Hawaii Mamo				
Drepanis pacifica	H	U	1898	0
Hoa (Black Mamo)				
Drepanis funerea	Mo	U	1907	0
Poo-uli				
Melamprosops phaeosoma	Ma	no data	1992?[6]	<5

[1] Abbreviations: H = Hawaii (whole island), Ka = Kauai, Ko = Kona Region of Hawaii, La = Lanai, Ly = Laysan, Ma = Maui, Md = Midway, Mo = Molokai, O = Oahu.
[2] Abbreviations: A = abundant, C = common, U = uncommon, R = rare. Sources: Berger (1981), Henshaw (1902), Munro (1960), Perkins (1903).
[3] Introduced population.
[4] Estimates based on Berger (1981); Scott et al. (1986); R. E. David, R. L. Pyle, pers. comm.; pers. obs., and recent publicity of various environmental organizations.
[5] Plus 11 in captivity.
[6] *Fide* R. L. Pyle.

planters during the 1880s on Hawaii, Maui, Molokai, and Oahu (Tomich 1986) and spread quickly throughout these islands. As a result, ground-nesting birds such as the Hawaiian Duck, Newell's Shearwater (King and Gould 1967), and Red Junglefowl disappeared except on Kauai. Mongooses were probably an important factor in the decline of the Nene (Baldwin 1945), and continue to be a limiting factor that may ultimately preclude the successful recovery of that species on Hawaii and Maui (Scott et al. 1986, Tomich 1986). Mongoose predation (along with that of feral cats) also has a significant negative impact on the nesting of Hawaiian Petrels on Maui (Simons 1985). Mongooses may also be one of several inimical factors contributing to the current plight of the Hawaiian Crow, the young of which spend several days on the ground after fledging (Johnston and Banko 1992).

Changes wrought by feral pigs

Pigs (*Sus scrofa*) arrived in the Hawaiian Islands with the first Polynesians. Aboriginal pigs were small and apparently did not penetrate far into native forests. Much larger and therefore more ecologically damaging pigs were introduced in historic times (Tomich 1986). Feral pigs are now the most significant modifiers of native forests (Scott et al. 1985). Their rooting destroys the shrub layer (Tomich 1986), spreads alien weeds into new areas (Scott et al. 1985), and facilitates the spread of mosquitoes (Scott et al. 1986). For reasons that are not entirely clear, feral pigs have within the past two decades penetrated into remote native rainforests not previously occupied where they may reach plague proportions locally (Lamoureux and Stemmermann 1976). As a result of one such ongoing plague, the Poo-uli, an understory bird of unknown affinities (Pratt 1992a) discovered in East Maui in 1973 (Casey and Jacobi 1974), by 1990 had disappeared from the type locality and survived only in a small portion of its original range not yet devastated by pigs (Engilis 1990). A thorough survey in August 1992 failed to find any Poo-uli (R. David, pers. comm.).

FIGURE 3. The recently-extinct Kauai Oo; Alakai Swamp, Kauai, July 1975.

The fall and rise of the Nene

The history of Hawaii's State Bird has been largely independent of that of other native land and freshwater birds because of its unique ecology. In historic times Nene were definitely known only from Hawaii but probably also lived on Maui before it was explored ornithologically. Fossil remains show that Nene once inhabited all the main Hawaiian Islands (Olson and James 1991). It was long a popular food item on Hawaii and was often hunted. In 1893, although it still existed "in fair numbers" in the remote upper lava flows of Kona, Wilson considered it "clearly doomed to extinction before many years are past" (Wilson and Evans 1890–1899).

Baldwin (1945) estimated a late 19th century population of 25,000 birds which dropped precipitously around the turn of the century. The Nene has been rare throughout the 20th century (Baldwin 1945). By 1951, the wild population may have been as low as 30 (Smith 1952). Fortunately, several flocks had been maintained in captivity, and a program of reintroduction of captive-reared birds was begun on Hawaii in 1960 and on Maui in 1963 (Kear and Berger 1980). Although successful in saving the species from extinction, this program has had only limited success in re-establishing self-sustaining Nene populations (Stone et al. 1983). Populations on Hawaii depend on continued release of captive-reared birds to maintain their numbers (Scott et al. 1985), but an apparently stable population of under 150 birds has been established in Haleakala National Park, Maui (Hodges 1991). Nene that escaped from captivity on mongoose-free Kauai in 1982 did so well that a second flock was purposely released at Kilauea Point National Wildlife Refuge in 1991 (Telfer 1991). The Kauai population now numbers over 100 and appears to be thriving even in totally artificial habitats (Telfer 1992). Reintroduction to the mongoose-free islands of Kauai and Lanai may be the key to long-term survival of the Nene.

Collapse of Kauai's avifauna

One of the most dismaying recent avifaunal events in the Hawaiian Islands is the ongoing collapse of the endemic avifauna of Kauai. Although several species had become greatly reduced in numbers and range at the turn of the century, Richardson and Bowles (1964) found that all of the island's historically known birds survived in 1960 and that, at least on the Alakai Plateau, an essentially intact native avifauna still existed. Thus Kauai was the only one of the main Hawaiian Islands not to have lost any bird species in historic times. It was not to remain so. The ensuing years witnessed a progressive withdrawal of native birds into the highest reaches of the Alakai (Scott et al. 1986). The Kauai Akialoa was last reliably reported in 1969 (P. L. Bruner, pers. comm.). The Kauai Oo, which had crashed shortly after 1900 but maintained a small population in the Alakai into the early 1970s, was reduced to a single known pair by 1981 (Scott et al. 1986). The female disappeared after Hurricane Iwa in 1982 (Pyle 1983b) and the male was last seen in 1985. Except for an unconfirmed voice-only report in 1987, subsequent searches have failed to find the oo (Pyle 1989b). Because its vocalizations

are distinctive and audible at great distance (pers. obs.), the Kauai Oo must be presumed extinct (Fig. 3). The Kamao, once Kauai's most abundant bird and still common in the Alakai in 1960 (Richardson and Bowles 1964), declined to a few hundred individuals by 1973 (Sincock et al. 1984) and to about two dozen in 1981 (Scott et al. 1986). A 1989 survey in the heart of the bird's 1981 range located only a few individuals (Engilis and Pratt 1989, Pyle 1989b). The Ou maintained a population in the low hundreds in the heart of the Alakai into the mid-1970s (pers. obs.), but 1981 surveys estimated that fewer than ten remained (Scott et al. 1986). The 1989 survey observed only three. The Akikiki was still common to abundant in 1960, but declines were apparent by the mid-1970s (Scott et al. 1986, pers. obs.). Thousands remained in the heart of the Alakai in 1981 (Scott et al. 1986), but the species had disappeared from the Kokee area, where it could be found as recently as 1978 (pers. obs.). In the 1980s, it became increasingly difficult to find in the fringes of the Alakai region, and it is now uncommon to rare within it (pers. obs.). In contrast to these dismal trends, the Puaiohi, always considered rare (Richardson and Bowles 1964), still existed in 1989 at approximately its 1960 levels (Scott et al. 1986, Engilis and Pratt 1989). Likewise, the Nukupuu, very rare in 1960, continued to be reported occasionally (Pyle 1992a), and the more common species seemed to be holding their own into mid-1992 (pers. obs.).

The causes of Kauai's post-1960 bird declines are unknown. Pratt et al. (1987) speculatively attributed them to penetration of the Alakai by disease-bearing mosquitoes. Engilis and Pratt (1989) note that the Ou had disappeared from areas with high pig damage. By the 1980s, the severely stressed populations had become particularly vulnerable to natural disasters such as hurricanes. Montane forest birds in the islands historically moved to the lowlands in great numbers to ride out storms. Henshaw (1902) reported finding "scores" of forest birds dead or dying in the lowlands of Hawaii after severe weather. Now, however, lowland valleys that once were safe havens have become pestilential death traps. Hurricane Iwa in November 1982 may have delivered the *coup-de-grace* to the Kauai Oo (Pyle 1983a, b). The Ou and Kamao, though still extant after the storm, never regained even their modest numbers of the previous decade. Class 5 Hurricane Iniki in September 1992 caused even more serious island-wide devastation (Fig. 4). Populations of the common species appeared greatly reduced six weeks afterward (pers. obs.), and Apapane and Iiwi were reported from several low-elevation sites where they would not normally have been found. Surveys by state and federal biologists in the heart of the Alakai Plateau in early 1993 found much more serious damage to the habitat than had been apparent from aerial inspections. *All* remaining habitat for native birds was damaged more or less severely and none of the critically endangered species were found in 40 man-days of search (R. L. Pyle, pers. comm.). Only time will tell whether the Kamao, Puaiohi, Ou, and Nukupuu survived the ravages of Iniki. The prognosis is not hopeful.

Other native bird declines

In historic times, the Hawaiian Crow had an enigmatically restricted distribution in the Kona region and was absent from seemingly ideal habitats elsewhere on the island of Hawaii (Berger 1981). Crows were still common in 1892 (Perkins 1903) but declined thereafter at least partly as a result of active persecution by ranchers (Munro 1960). The population had reached dangerously low levels by the mid-1970s (Scott et al. 1986). A small captive flock established in the early 1970s is now highly inbred and has produced few young in the past decade. As of this writing, only 12 birds remain in the wild (Engbring 1992) and 11 in captivity (Duvall 1992). The Hawaiian Crow has recently been the center of considerable sometimes heated controversy with regard to how

FIGURE 4. Former closed-canopy montane koa (*Acacia koa*) forest badly damaged by Hurricane Iniki: Kokee, Kauai, October 1992.

best to aid its recovery. A study by the National Research Council (1992) may bring some rationality to the effort, but prospects for the crow's survival are not good.

The Oahu Alauahio (= Oahu Creeper) is probably nearing extinction. Though common at the turn of the century (Bryan 1905), it has been regarded as rare ever since (Munro 1960, Berger 1981) and has received scant attention from ornithologists. The last reliable sighting was in 1985 (Bremer 1986), though one may have been seen in Halawa Valley in 1989 (Saito 1989). Surveys throughout the remaining habitat on Oahu in 1991 (Conry 1991) failed to find the alauahio, and also confirmed the recently suspected (Pyle 1990b, 1991, 1992a) near disappearance of the Oahu Elepaio, once the commonest native bird on the island (Henshaw 1902). The Elepaio was still widely distributed and relatively abundant in the 1960s (Conant 1977) and common in the 1970s (Berger 1981) but had been in a slow decline since the 1940s (Williams 1987). Its reduction is particularly troubling because the Elepaio had long been regarded as almost extinction-proof. Henshaw (1902) thought that it would survive in "scarcely diminished numbers" long after most Hawaiian birds were extinct "so long as any woodland at all is left." Berger (1981:103) stated that the Oahu Elepaio had adapted to man-made environmental changes "as no other endemic land bird has been able to do." Apparently even adaptable species can take only so much abuse. Because the Elepaio's decline on Oahu only recently received much notice, its specific causes have not even been hypothesized. The decline coincided with the spread into native forests and increase of several potentially competitive alien species (Williams 1987, pers. obs.), most noticeably the Japanese White-eye, Japanese Bush-Warbler, and Red-vented Bulbul, but whether these events are related is not known.

New natural arrivals

Successful natural colonizations of remote islands are exceedingly rare and few have been observed in historic times. However, in one of the few positive changes in

the indigenous Hawaiian avifauna, two new freshwater birds have arrived in the last decade apparently unaided by man. Pied-billed Grebes (*Podilymbus podiceps*) were long regarded as only occasional stragglers to the islands (Berger 1981), but in the early 1980s at least one pair began breeding at Aimakapa Pond in Kona on the island of Hawaii. By 1989, 12 grebes were present on the pond and five active nests were recorded (Pyle 1989a). In a similar development, a small group of Fulvous Whistling-Ducks (*Dendrocygna bicolor*) appeared at James Campbell National Wildlife Refuge on Oahu in 1982. Although the operators of a nearby aquafarm have released a variety of ornamental waterfowl, they claim not to have brought in the whistling-ducks (R. L. Pyle, pers. comm.). This species has undergone recent "explosive" expansions in North America and the West Indies (Palmer 1976) so a natural colonization is plausible. In February 1990, ten adults and ten juveniles were seen at the aquafarm and an adult with 12 small chicks was found on the refuge (Pyle 1990a).

Resurgence of seabirds

In contrast to the dismal trends in native land birds, seabirds breeding in the Hawaiian Islands have rebounded from centuries of persecution and appear to be in better condition today than in 1893. Ancient Hawaiians and their commensals undoubtedly eliminated all but cliff-nesting seabirds from the lowlands of the main islands, and also raided offshore islets to capture birds for food (Harrison 1990). Since the turn of the century, several species have recolonized the main islands and colonies on islets have largely recovered (Berger 1981). Red-footed Boobies returned to mainland Kauai and Oahu in the 1940s (Berger 1981), Laysan Albatrosses (*Diomedea immutabilis*) recently established a now thriving (pers. obs.) colony at Kilauea Point National Wildlife Refuge on Kauai (Byrd and Telfer 1979), and Wedge-tailed Shearwaters (*Puffinus pacificus*) have established scattered colonies on Kauai (Byrd and Boynton 1979). Relatively accessible Manana Island off Oahu had no seabird colonies by 1893 (Harrison 1990), but thousands of birds of five species nested there by the 1970s (Berger 1981). The Common Fairy-Tern (*Gygis alba*) was not known to have nested on the main islands in historic times (Munro 1960), but in 1961 colonized Koko Head, Oahu (Ord 1961) and subsequently expanded its range into the Honolulu area (Berger 1981) where it is now a common sight in urban parks (pers. obs.). Seabirds on Midway Atoll suffered greatly during the Second World War (Fisher and Baldwin 1946) and in subsequent years as a result of military activities. However, following destruction of antennas that killed many birds, the albatross colonies have recovered to previous levels (Berger 1981).

INTRODUCTIONS OF ALIEN BIRDS

The relatively few species of introduced birds present in the Hawaiian Islands a century ago have been joined by a vast array of additional alien species (Table 2). These fall into three basic categories: accidental escapes from captivity; birds purposely introduced by private individuals for a variety of reasons; and game birds introduced by government agencies. Most of those in the second category were brought in by the Hui Manu ("Bird Club"), an organization founded in 1930 for the sole purpose of introducing alien birds to the islands. Many introductions, such as those of bulbuls and estrildids in the 1960s, were illicit, but regulations were rarely enforced with any vigor until very recently. The enthusiasm for introduced birds in the Hawaiian Islands is difficult for mainlanders to understand, but can be appreciated in light of the near total absence of native birds from the lowland areas where most people live. Perhaps introduced birds are better than no birds at all. Fortunately, most species that have become established have filled unoccupied niches and, except as potential disease reservoirs, are probably of relatively benign

TABLE 2. BIRDS INTRODUCED AND ESTABLISHED IN THE HAWAIIAN ISLANDS 1893–1993[1]

Species	First introduced	Introduction site(s)[2]	Distribution 1992	In native forest?[3]
Cattle Egret				
Bubulcus ibis	1959	Ka, O, Mo, Ma, H	all main islands	no
Black Francolin				
Francolinus francolinus	1959	Ka, Mo, Ma, H	Ka, Mo, Ma, H	no
Gray Francolin				
Francolinus pondicerianus	1958	all main islands	O, Mo, Ma, H	no
Erckel's Francolin				
Francolinus erckelii	1957	all main islands	Ka, O, Mo, La, H	yes
Chukar				
Alectoris chukar	1923	all main islands	Mo, Ma, La, H	no
Japanese Quail				
Coturnix japonica	1921	all main islands	Ka, Ma, H	no
Kalij Pheasant				
Lophura leucomelana	1962	H	H	yes
Gambel's Quail				
Callipepla gambelii	1928	La, Kw, H	La, Kw, H	no
Chestnut-bellied Sandgrouse				
Pterocles exustus	1961	H	H	no
Zebra Dove				
Geopelia striata	1922	O	all main islands	no
Mourning Dove				
Zenaida macroura	1964	H	H	no
Rose-ringed Parakeet				
Psittacula krameri	?	Ka, O, H	Ka, O, H	no
Barn Owl				
Tyto alba	1958	Ka, O, Mo, H	all main islands	no
Island Swiftlet				
Aerodramus vanikorensis	1962	O	O	no
Red-vented Bulbul				
Pycnonotus cafer	1965	O	O	yes
Red-whiskered Bulbul				
Pycnonotus jocosus	1966	O	O	yes
Japanese Bush-Warbler				
Cettia diphone	1929	O	Ka, O, Mo, Ma, La	yes
White-rumped Shama				
Copsychus malabaricus	1931, 1940	Ka, O	Ka, O	yes
Greater Necklaced Laughing-thrush				
Garrulax pectoralis	1919[4]	Ka	Ka	no
Gray-sided Laughing-thrush				
Garrulax caerulatus	1947	O	O	yes
Melodious Laughing-thrush				
Garrulax canorus	1900	Ka, O, Mo, Ma, H	Ka, O, Mo, Ma, H	yes
Red-billed Leiothrix				
Leiothrix lutea	1918	Ka, O, Mo, Ma, H	Ka, O, Mo, Ma, H	yes
Northern Mockingbird				
Mimus polyglottos	1928	O, Ma	all main islands	no
Japanese White-eye				
Zosterops japonicus	1929	Ka, O, Ma, H	all main islands	yes
Northern Cardinal				
Cardinalis cardinalis	1929	Ka, O, H	all main islands	yes
Red-crested Cardinal				
Paroaria coronata	1928	O	Ka, O, Mo, Ma, La	no
Yellow-billed Cardinal				
Paroaria capitata	ca. 1930	H	H	no
Yellow-faced Grassquit				
Tiaris olivacea	ca. 1970	O	O	no
Saffron Finch				
Sicalis flaveola	>1960	O, H	O, H	no
Western Meadowlark				
Sturnella neglecta	1931	Ka, O	Ka	no

TABLE 2. CONTINUED

Species	First introduced	Introduction site(s)[2]	Distribution 1992	In native forest?[3]
Yellow-fronted Canary *Serinus mozambicus*	<1965	O, H	O, H	yes
Common Canary *Serinus canaria*	1910	Md	Md	no
Red-cheeked Cordonbleu *Uraeginthus bengalus*	<1965	O, H	H	no
Lavender Waxbill *Estrilda caerulescens*	<1965	O, H	H	no
Orange-cheeked Waxbill *Estrilda melpoda*	<1965	O, Ma, H	O, Ma	no
Black-rumped Waxbill *Estrilda troglodytes*	<1965	O, H	H	no
Common Waxbill *Estrilda astrild*	<1965	O	O	no
Red Avadavat *Amandava amandava*	1900	O, H	Ka, O, Ma, H	no
Warbling Silverbill *Lonchura malabarica*	>1960	H	all main islands	no
Chestnut Mannikin *Lonchura malacca*	1936	O	Ka, O	no
Java Sparrow *Padda oryzivora*	<1965	O	Ka, O, Ma, H	no

[1] Sources: Berger (1981), Hawai'i Audubon Society (1989), Moulton and Pimm (1983), Pyle (1992a, b), Williams (1983).
[2] Abbreviations as for Table 1 plus Kw = Kahoolawe.
[3] Sources: Berger (1981), Scott et al. (1986), Pratt et al. (1987).
[4] Probably misidentified at the time as *G. albogularis*.

influence on native ecosystems (Moulton and Pimm 1983). A few, however, have spread deep into native forests and may be competing with native birds or contributing to habitat degradation. The Japanese White-eye is now the most abundant bird in the Hawaiian Islands and is found at all elevations and in all habitats (Scott et al. 1986). White-eyes compete for food with several native species (Mountainspring and Scott 1985). The Red-billed Leiothrix and Melodious Laughing-thrush also are found throughout native rainforests at least on Maui and Hawaii, but they are understory birds that appear not to compete with any native species (Scott et al. 1986). The leiothrix and the Kalij Pheasant probably contribute to habitat degradation by spreading seeds of banana poka (*Passiflora mollisima,*), an aggressive vine that has overgrown large areas of native forest on Hawaii (Lewin and Lewin 1984, Scott et al. 1986). The Northern Cardinal occurs in a wide variety of habitats, including native rainforest, on the main Hawaiian Islands but is more common in disturbed areas (Scott et al. 1986). The Red-vented Bulbul has become ubiquitous on Oahu (Williams and Giddings 1984), including forests at the highest elevations (pers. obs.), and the Japanese Bush-Warbler, now abundant in Oahu forests, is also increasing on Molokai, Lanai, Maui, and Kauai (Scott et al. 1986, pers. obs.). The effects, if any, of cardinals, bulbuls, and bush-warblers on native birds are as yet undetermined.

THE MODERN HAWAIIAN AVIFAUNA

Today, the avifauna of the Hawaiian Islands includes only tattered remnants of the avian community present a century ago. Of the 68 native land and freshwater species or subspecies known to have been present in 1893, 29 are now extinct or nearly so (Table 1), and a further 17 are Endangered Species but not in immediate danger of extinction. Ongoing threats to endangered forest birds

include habitat damage by feral pigs, upward expansion of the range of disease-bearing mosquitoes, and natural disasters. Some species (Olomao, Kamao, Bishop's Oo, Ou, Nukupuu, Oahu Alauahio, and Poo-uli), if still extant, may not survive the 20th century. The surviving indigenous birds have been joined by a host of alien species, several of which are now significant elements of forest bird communities. The Hawaiian lowlands now have an entirely artificial land avifauna.

The endemic freshwater birds are all Endangered Species that survive primarily in a few small refuges maintained for their benefit. The Hawaiian Duck has been successfully reintroduced on Oahu and Hawaii but interbreeding with feral Mallards (*Anas platyrhynchos*) poses a new threat to the species, at least on Oahu (Engilis and Pratt 1993). The Hawaiian moorhen no longer inhabits Maui or Hawaii, and 1983 reintroductions on Molokai apparently were not successful (Engilis and Pratt 1993). The Nene, although saved from imminent extinction, still depends on release of captive-reared birds to maintain its population, at least on Hawaii. On the positive side, the freshwater bird community has recently been augmented by two natural colonizations, and populations of the endemics appear to be more or less stable (Engilis and Pratt 1993).

Hawaiian seabirds have largely recovered from a series of challenges and have reoccupied a few nesting sites abandoned since ancient times. Laysan Albatrosses and Common Fairy-Terns now nest successfully on Kauai and Oahu respectively. Newell's Shearwaters and Hawaiian Petrels, though still imperiled, appear to be maintaining stable populations that benefit from protected nesting areas and active public programs to mitigate artificial losses. And nesting colonies in the Northwestern Hawaiian Islands are once again as large as they were in 1893. Seabirds provide the one bright spot in the rather pitiful present condition of the Hawaiian avifauna.

ACKNOWLEDGMENTS

I am grateful to P. L. Bruner, R. E. David, A. Engilis, D. Kuhn, and particularly R. L. Pyle, Regional Editor for *American Birds*, who shared unpublished information with me. D. Kuhn provided onsite information on Kauai forest birds immediately following Hurricane Iniki. J. V. Remsen and R. L. Pyle made helpful comments on the manuscript.

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