

A Reassessment of Factors, Particularly *Rattus rattus* L., That Influenced the Decline of Endemic Forest Birds in the Hawaiian Islands¹

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ABSTRACT: Between 1892 and 1930, 58 percent (30 taxa) of Hawaiian endemic forest birds either were greatly reduced or became extinct. The order in which the islands experienced major declines of several forest birds is Oahu (ca. 1873–1887), Hawaii (1892–1900), Molokai (1893–1907), Maui (1894–1901), Kauai (after 1900), and Lanai (1926–1932). Loss of habitat, reduced food supply, introduced avian diseases, as well as predation by man, feral cats, mongooses, and Norway rats (*Rattus norvegicus*) all appear to have reduced some species of birds, but none of these factors adequately explains the accelerated rates of decline of forest birds that occurred after 1892.

Although it has been assumed that roof rats (*Rattus rattus*) reached Hawaii with the first European ships at the end of the 18th century, there is circumstantial evidence, independent of the bird decline data, that indicates that this rat did not arrive until after 1840, probably between 1870 and 1880. The hypothesis is advanced that after its establishment on Oahu in the 1870s, *R. rattus* spread to the remaining large islands in the group, resulting in a stepwise accelerated decline of forest birds on each island in turn. Hawaii thus parallels some other Pacific islands where major reductions of birds have followed the establishment of *R. rattus*. The need for precautions to prevent rats from reaching rat-free islands in the Hawaiian group is emphasized.

During the century following Captain James Cook's discovery of the Hawaiian Islands in 1778, eight endemic forest birds either have become extinct or have been reduced to small numbers. These are the mamoa (*Drepanis pacifica*), kioea (*Chaetoptila angustipluma*), and ula-ai-hawane (*Ciridops anna*) on Hawaii and the omao (*Phaeornis obscurus oahensis*), Oahu oo (*Moho apicalis*), akepa (*Loxops coccinea rufa*), akialoa (*Hemignathus obscurus ellisianus*), and nukupuu (*Hemignathus lucidus lucidus*) on Oahu. The Hawaiian rail (*Pennula sandwichensis*), although not exclu-

sively a forest bird, also became extinct during this period (Perkins 1903). Additional extinctions may have occurred of species unknown. The eight taxa listed make up 15 percent of the 52 species or subspecies of endemic forest birds known to have been present at the time of first European contact.³

Although reductions in the areas occupied by endemic forest birds had occurred on all islands prior to 1890, with the exceptions mentioned above, the avifaunas of the main islands (Figure 1) were still complete so far as species were concerned, many species being abundant. However, during the next 40 years at least 30 species or subspecies (58 percent) of the known endemic forest birds either were greatly reduced or became extinct. If Lanai is excluded, most of these birds declined between 1892 and 1910. This catastrophic change was described by Bryan (1912) as "one of the wonder tales of ornithology." It was a mystery to observers at the time, and no

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³ Included in this total is *Melamprosops phaeosoma*, the new species of honeycreeper recently discovered on Maui (Casey and Jacobi 1974).

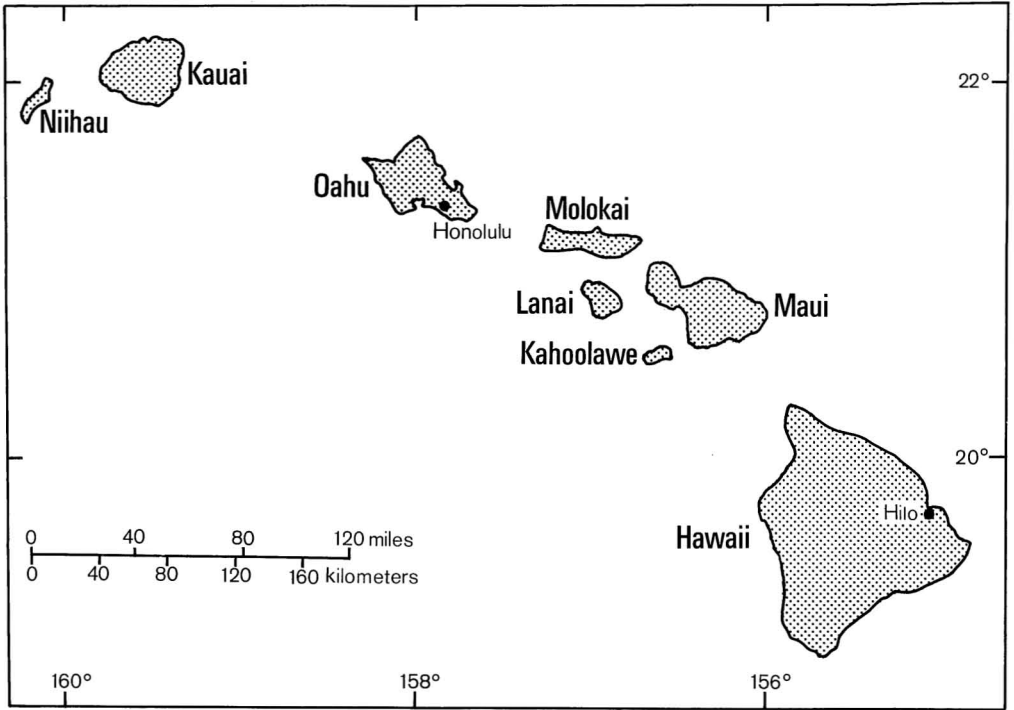


Figure 1. The Hawaiian Islands.

subsequent explanation has proved wholly satisfactory. The present contribution re-examines the historical and biological evidence bearing on the problem and suggests an explanation which, if substantiated, may assist the future conservation of endangered forest birds in Hawaii.

TIMES OF DECLINE IN HAWAIIAN FOREST BIRDS

Published data concerning the timing of declines in the numbers of Hawaiian forest birds are summarized in Table 1. Excluded from the table are species for which there is insufficient evidence of a major decline: the puaiohi (*Phaeornis palmeri*), elepaio (*Chasiempis sandwichensis*), amakihi (*Loxops virens*), anianiau (*Loxops parva*), and apapane (*Himatione sanguinea*).

The dated periods of decline given for each species either have been inferred or were taken directly from the various statements of the observers quoted. These periods are consid-

ered to *include* the times during which major declines of the various species occurred. They are not always exactly coincidental with such declines since the timing of the reports depends on when observers happened to visit each island. A major limitation is the lack of published observations on many islands between 1900 and 1930. Some of the decline periods shown are certainly too long but cannot be shortened unless further information becomes available. Again, the time period shown may not always be the only decline that affected a species. Where no dated period is given, the published evidence is considered insufficient for the species on that particular island. Nomenclature follows that of Amadon (1950). Unless otherwise indicated, information on the current status of each bird is derived from Berger (1972), supplemented by the writer's observations on Kauai (Alakai plateau), Oahu, Maui (Haleakala), and Hawaii (Mauna Loa, Kilauea, and Kona) made between 1966 and 1969.

Time periods during which there were

TABLE 1
ANALYSES OF TIMES OF MAJOR DECLINES IN THE ENDEMIC FOREST BIRDS OF THE HAWAIIAN ISLANDS

SPECIES	OAHU	KAUAI	MOLOKAI	LANAI	MAUI	HAWAII
<i>Corvus tropicus</i> — alala, Hawaiian crow	—	—	—	—	—	“numerous in the eighteen nineties” (11); now rare 1893–1903 (12)
<i>Phaeornis obscurus</i> — omao, Hawaiian thrush	<i>P. o. oahensis</i> : evidently common in 1825; extinct <i>after 1825</i> (11)	<i>P. o. myadestina</i> : extremely common in 1891; numerous in 1899; survives in moderate numbers (13) <i>1900–1928</i> (6, 11)	<i>P. o. rutha</i> : common in the eighteen-nineties (11); survives in very low numbers <i>1907–1923</i> (5, 10)	<i>P. o. lanaiensis</i> : common between 1911 and 1923; not seen since 1931 (11) <i>1928–1931</i> (10)	may have been present (12)	<i>P. o. obscurus</i> : common at 600 m in 1891; still survives <i>1901–1936</i> (8, 11)
<i>Moho</i> spp.—oo	<i>M. apicalis</i> : collected in 1837; extinct <i>after 1837</i> (11)	<i>M. braccatus</i> : common in 1891; survives in low numbers (13) <i>1899–1928</i> (11)	<i>M. bishopi</i> : Munro saw about six birds in 1904 but failed to find it in 1907; probably extinct <i>1893–1902</i> (5, 12, 14)	—	no specimens; one bird seen in 1901 (8)	<i>M. nobilis</i> : originally common (12); presumed extinct W. Hawaii: <i>1892– 1894</i> (11); E. Hawaii: <i>1896–1900</i> (9)
<i>Chaetoptila</i> <i>angustipluma</i> —kioea	—	—	—	—	—	rare in 1840 (Peale 1848); now extinct <i>after 1859</i> (11)
<i>Loxops sagittirostris</i> —greater amakihi	—	—	—	—	—	originally rare and local (12); presumed extinct <i>after 1901</i> (4)

TABLE 1 (Cont.)

ANALYSES OF TIMES OF MAJOR DECLINES IN THE ENDEMIC FOREST BIRDS OF THE HAWAIIAN ISLANDS

SPECIES	OAHU	KAUAI	MOLOKAI	LANAI	MAUI	HAWAII
<i>Loxops maculata</i> — creeper	<i>L. m. maculata</i> : fairly common in the eighteen-nineties; now rare <i>after 1900</i> (11)	<i>L. m. bairdi</i> : abundant in the eighteen-nineties (12); now relatively common	<i>L. m. flammea</i> : abundant in the eighteen-nineties (12); now rare <i>1907–1923</i> (10, 11)	<i>L. m. montana</i> : abundant in the eighteen-nineties (12); presumed extinct <i>1928–1932</i> (10)	<i>L. m. newtoni</i> : abundant in the eighteen-nineties (12); now relatively common	<i>L. m. mana</i> : very abundant in the eighteen-nineties (12); now rare <i>1896–1936</i> (8, 11, 12)
<i>Loxops coccinea</i> — akepa	<i>L. c. rufa</i> : one shot in 1893; possibly extinct <i>before 1893</i> (11)	<i>L. c. caeruleirostris</i> : fairly common	—	—	<i>L. c. ochracea</i> : abundant in some localities in the early eighteen-nineties; now very rare <i>1894–1928</i> (11, 12)	<i>L. c. coccinea</i> : common and widely distributed in 1891; now rare W. Hawaii: <i>after</i> <i>1891</i> (12); E. Hawaii: <i>after 1896</i> (7)
<i>Hemignathus obscurus</i> and <i>H. procerus</i> — akialoa	<i>H. o. ellisianus</i> : possibly seen in 1888 (16); pair seen in 1892 (12); extinct <i>after 1834</i> (11)	<i>H. procerus</i> : common in the eighteen- nineties (11, 12, 14); surviving in very low numbers (13) <i>1900–1920</i> (6, 11)	—	<i>H. o. lanaiensis</i> : very rare in 1892 (8); extinct <i>after 1892</i> but major decline may have begun earlier	—	<i>H. o. obscurus</i> : common in the eighteen-nineties (11, 12, 14); presumed extinct W. Hawaii: <i>1894–</i> <i>1936</i> (11, 12); E. Hawaii: <i>1896–1936</i> (7, 8, 11)
<i>Hemignathus lucidus</i> —nukupuu, and <i>H.</i> <i>wilsoni</i> —akiapolau	<i>H. l. lucidus</i> : moderately common in 1860 (12); extinct <i>1860–ca. 1890</i> (11, 12)	<i>H. l. hanapepe</i> : “very scarce” as early as 1888 (16); not common in the eighteen-nineties (11, 12); survives in very low numbers (13) <i>after 1899</i> (11, 12) but major decline may have begun earlier	—	—	<i>H. l. affinis</i> : un- common in the eighteen-nineties; rediscovered in 1967 (2) <i>after ca. 1895</i> (12)	<i>H. wilsoni</i> : abundant in the eighteen-nine- ties (11, 12, 14); survives locally in low numbers W. Hawaii: <i>after</i> <i>1894</i> (12); E. Hawaii: <i>after 1896</i> (7)

TABLE 1 (Cont.)

SPECIES	OAHU	KAUAI	MOLOKAI	LANAI	MAUI	HAWAII
<i>Pseudonestor xanthophrys</i> —Maui parrotbill	—	—	—	—	rather rare in the eighteen-nineties (9, 12); survives in very low numbers (2) <i>ca. 1900–1928</i> (11, 12)	—
<i>Psittirostra psittacea</i> —ou	formerly not uncommon (14); nearly disappeared by 1893 (12); last seen in 1899 (9) <i>1846–1887</i> (14, 16)	extremely common in the eighteen-nineties (11); now rare <i>1892–1928</i> (10, 12)	widespread in 1907; presumed extinct <i>1907–1923</i> (5, 10)	extremely common in the eighteen-nineties and up till 1923 (11); probably extinct <i>1928–1931</i> (10)	extremely common in the eighteen-nineties (11); last recorded in 1901 (3) <i>1892–1901</i> (3, 12)	“countless numbers” at Kona in 1892 (12); now rare W. Hawaii: <i>after 1896</i> (12); E. Hawaii: <i>after 1900</i> (7)
<i>Psittirostra bailleui</i> —palila	—	—	—	—	—	originally “extremely numerous” in upper parts of Kona and Hamakua districts (12); now very local <i>1892–1902</i> (11, 12)
<i>Psittirostra palmeri</i> —greater koa finch	—	—	—	—	—	originally “by no means rare” in upper forests (14); probably extinct W. Hawaii: <i>1892–1896</i> (4, 14)
<i>Psittirostra flaviceps</i> —lesser koa finch	—	—	—	—	—	several specimens collected in 1891; presumed extinct W. Hawaii: <i>1891–1892</i> (4, 11, 12)

TABLE 1 (Cont.)

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SPECIES	OAHU	KAUAI	MOLOKAI	LANAI	MAUI	HAWAII
<i>Psittirostra kona</i> — grosbeak finch	—	—	—	—	—	local but not rare in the early eighteen-nineties; probably extinct W. Hawaii: 1892–1896 (4, 14)
<i>Palmeria dolei</i> — crested honeycreeper	—	—	“locally abundant” in the eighteen-nineties (12); five birds seen in 1907 (5); not seen since 1907 (11) 1893–1907 (5, 12)	—	“locally abundant” in the eighteen-nineties; now common in restricted areas after 1892 (12)	—
<i>Ciridops anna</i> — ula-ai-hawane	—	—	—	—	—	formerly widely distributed (12); now extinct after 1859 (11)
<i>Vestiaria coccinea</i> — <i>iiwi</i>	“once so common on the island is now very scarce” (15); now rare before 1899 (15)	numerous in 1891 but since reduced; now fairly common 1891–1928 (10, 11)	“most commonly met with after apapane and amakihi” in 1907 (5); close to extinction 1907–1923 (5, 10)	fairly common in 1923; probably extinct 1926–1928 (10)	very common originally (12); now fairly common after 1892 (10)	very common originally (12); now fairly common after 1892 (10)
<i>Drepanis pacifica</i> — mamo	—	—	—	—	—	formerly widespread; still in some numbers in the Hilo district up to 1880; none seen since 1898 1880–1898 (8, 12) but decline began earlier

TABLE 1 (Cont.)

SPECIES	OAHU	KAUAI	MOLOKAI	LANAI	MAUI	HAWAII
<i>Drepanis funerea</i> — Perkins' mamo	—	—	rare in the early eighteen-nineties but Perkins saw as many as seven in a day during 1893 (12); none seen since 1907 <i>1893–1907</i> (1, 5, 12)	—	—	—
Most probable periods of major decline affecting several species	1873 (14)–1887	1900–1920	1893–1907 and 1907–1923	1926–1932	1894–1901	1892–1896 (western Hawaii) and 1896– 1900–? (eastern Hawaii)

REFERENCES CITED: 1, Amadon 1950; 2, Banko 1968; 3, Banko 1971; 4, Berger 1972; 5, Bryan 1908; 6, Bryan and Seale 1901; 7, Henshaw 1901; 8, Henshaw 1902; 9, Henshaw 1903; 10, Munro 1921–1935; 11, Munro 1944; 12, Perkins 1903; 13, Richardson and Bowles 1964; 14, Rothschild 1893–1900; 15, Seale 1900; 16, Wilson and Evans 1890–1899.

coincidental declines in the numbers of several forest birds on the same island are summarized in the last row of Table 1. These are inferred from a consideration of all the dates given for individual species.

Variation between observers' citations as well as seasonal changes can affect assessments of the abundance of species. Much of the decline data of Table 1 are based on repeated observations by the same observers. In many cases, no matter whether a bird was originally recorded as abundant or scarce, it has not been seen since the beginning of the century. Thus, the declines under discussion are not simply fluctuations in numbers.

Differences in decline times between islands are quite marked in some cases, a point stressed by Palmer in Rothschild (1893–1900) and Munro (1944). Writing of Molokai in May 1893, Perkins (1913:xxxiii) said: "All animal life seemed abundant after my experience on Oahu. Common species of birds were plentiful, though not in the extraordinary numbers observed on Hawaii. . . ." Palmer, referring to Kauai in June 1893, wrote: "What a striking contrast from Oahu! Everywhere here the trees appear to be alive with birds." An earlier remark by Rothschild in the same text indicates that the major decline of forest birds on Oahu was almost certainly after 1873, a date that cannot be derived from the published data relating to individual species. This is consistent with the report given to Perkins (1903) that the Oahu nukupuu (*Hemignathus l. lucidus*) was still moderately common in 1860. Another bird that may throw light on the Oahu decline is the ou (*Psittirostra psittacea*), described by Rothschild (1893–1900) as originally being not uncommon on the island. In listing its habitat, Dole (1879) mentioned only "Hawaii," while describing the apapane, iiwi (*Vestiaria coccinea*), and amakihi as being present in the whole group. Some of Dole's distribution information is clearly in error, but his failure to list the ou for Oahu, where he lived, could mean that the species had largely disappeared from the island by 1879.

On Hawaii, Henshaw (1902) discussed the 1896–1901 period when he lived in the Hilo District and remarked: ". . . within this time

large areas of forest, which are yet scarcely touched by the axe save on the edges and except for a few trails, have become almost absolute solitude. . . . Yet a few years ago these same areas were abundantly supplied with native birds. . . ." If these comments are compared with those of Perkins (1893, 1903) for the western (Kona) district, it seems clear that the major decline of forest birds was not synchronous over the whole island. The limited data suggest this was also true of Molokai.

To summarize: a major decline of forest birds occurred on most of the larger Hawaiian islands during the 1892–1910 period, although the 1910 date is somewhat arbitrary. The decline on Oahu was earlier (but probably occurred after 1873) and that on Lanai, later (1926–1932). No large island escaped a major decline in its birdlife. No extinctions of forest birds are known on the larger islands since 1932.

The analysis which follows attempts to explain the accelerated decline of the Hawaiian avifauna that occurred after 1892.

LOSS OF HABITAT

Forest clearing was continual in the Hawaiian Islands throughout the last century. Perkins (1901, 1903) considered that destruction of the native forest, particularly that part between sea level and 460 m (1500 ft) which comprised the lowest belt, was a major cause of the decline in birds, although he acknowledged that other factors were involved. He cited the downward movement of birds to the lower edge of the then-existing forest (460 m) during winter storms as evidence and pointed out that birds such as the ou, apapane, and anianiau were present near the coast in Cook's time.

The lowland forest of the drier parts of the Hawaiian Islands was considered by Rock (1913) to have been the most diverse of all Hawaiian forests. It is possible that endemic birds specifically adapted to these dryland forests became extinct as a result of the destruction of the lowland forest during the Polynesian period. Perkins' argument may

also be true of some Oahu birds, such as the Oahu nukupuu, that are considered to have been dependent on the now-vanished koa (*Acacia koa*) forest (Perkins 1903).

As a general explanation of the accelerated decline of the 1890s, however, the idea of lowland forest destruction is inadequate. The major decline at the end of the last century affected birds throughout forests that were apparently little modified, at least so far as their structure and composition were concerned, and considerable areas of such forests were still present on all the main islands except Lanai. Henshaw's (1902) remarks concerning the disappearance of birds from unmodified forest on Hawaii have been quoted above. Palmer, in commenting on the rarity of native birds on Oahu in 1893, specifically mentioned the fact that extensive forests with tall trees still remained (Rothschild 1893–1900).

Destruction of the lower forest belt was already far advanced on some islands, e.g., Kauai, Oahu, and Hawaii, by the time European settlement had begun (cf. Cook 1785, Bingham 1847). Destruction of this zone continued during the sandalwood trade, which reached its height between 1810 and 1825 and was practically finished by 1830 (Bryan 1915). On Hawaii, Wilson (1890) referred to certain districts being "entirely denuded of wood." As pointed out by Berger (1972), a large reduction in the numbers of forest birds must have accompanied this clearing. But birds were still abundant in the remaining forests on all major islands excepting Oahu up until the 1890s. Twenty years later extensive forests still remained but the numbers of birds had declined.

INTRODUCED BROWSING MAMMALS AND OTHER FACTORS AFFECTING FOOD SUPPLY

Cattle, horses, sheep, goats, and English pigs were all released in the Hawaiian Islands from 1778 to 1803 (Tomich 1969). Of these, cattle and goats have had the greatest influence on the Hawaiian forest, and an adverse effect on the food supply of forest birds might be expected. Perkins (1903) apparently rated

cattle and goats second in importance to forest destruction as a factor contributing to avian extinction.

On Hawaii, cattle increased so rapidly that by 1822 herds numbering in the thousands were present on Mauna Kea (Hartt and Neal 1940). Numbers remained high until well into this century (Judd 1927). In writing of cattle damage on Hawaii in 1887, Wilson (1890) referred to "giant tracts of mighty giants which, in certain districts, are dying by hundreds." Cattle also became abundant during the last century on Kauai, Oahu, Molokai, and Maui (Tomich 1969). Goats increased to large numbers on several islands, particularly Hawaii and Maui, and Hillebrand warned about goat damage as early as 1856 (Tinker 1938).

The effects of sheep, horses, and English pigs have been more localized. Sheep continue to affect the mamane (*Sophora chrysophylla*) forests on Mauna Kea since cattle were excluded from the area; however, sheep are less able than cattle to survive in wet forest (Tomich 1969). Damage to the forest by English pigs, which are widely distributed in upland forests, has occurred but pigs are not a new influence, English pigs having absorbed or replaced earlier Asian pigs introduced by the Polynesians (Tomich 1969).

Axis deer were introduced to Molokai in 1868 and to Lanai in 1920 (Tomich 1969). On Molokai, Perkins (1903) commented on an area of forest which between 1896 and 1902 lost "two-thirds or more" of all its trees as a result of destruction by cattle and axis deer.

It is clear that cattle and goats were an early factor in the Hawaiian Islands and had already modified extensive areas of forest on most of the main islands (possibly excepting Molokai) prior to 1890. Therefore, they cannot be used to explain the sudden and widespread decrease in species of birds that occurred after 1892, especially as much forest relatively unmodified by browsing animals still remained. Munro (1944) actually referred to open forests thinned by the encroachment of cattle and pigs as having been a "collector's paradise" for forest birds in the 1890s. In view of Perkins' comments, Molokai may appear to be an exception, but as late as 1923

Munro (1923–1935) was able to spend 5 days on Molokai in “dense native forest” between 490 and 1070 m, where he found no trace of “ground animals” except mice. He wrote (1944): “In fact large areas of forest on Molokai have never been entered by cattle and the birds are practically all gone.”

Introduced forest birds, introduced European rats, and decreases in endemic insect populations may also have adversely affected the food supply of endemic forest birds. Introduced passerine birds that have become widely distributed in forest are the Japanese white-eye (*Zosterops japonica*), the red-billed leiothrix (*Leiothrix lutea*), and the melodious laughing-thrush (*Garrulax canorus*). Introduction times occurred mostly from 1918 onwards (Caum 1933), too late to implicate these birds in major declines of the endemic birds. On Oahu, Caum reported that laughing-thrushes did escape from captivity in 1900, after which there were releases on Molokai, Maui, and Hawaii. Major declines of endemic birds had begun on all these islands before this time.

At least two of the three species of rats in Hawaii were present during most of the 19th century. The last species to arrive may have been the roof rat, *Rattus rattus*, but whether this had any effect on the food supply of forest birds in addition to or different from those resulting from the introduction of the Polynesian rat, *Rattus exulans*, by the Polynesians is not clear. Competition for food between *R. rattus* and some honeycreepers such as the ou is certainly possible. Norway rats, *Rattus norvegicus* are not common in native forests (Tomich 1969) and, therefore, are less likely to be a food competitor.

Large reductions of some species of native insects have been discussed by Zimmerman (1948), and it can be argued that these reductions have affected the food supply of forest birds (Banko and Banko, unpublished). The argument is difficult to refute without detailed studies of the foods consumed by particular bird species. It must be pointed out, however, that the major declines under discussion have affected a range of birds with very diverse feeding habits including some that are not insectivorous.

A further point in relation to changes in the food supply of forest birds has been stressed by Warner (1968), who mentioned observations of endemic forest birds seen feeding from introduced plants in earlier times; thus, replacement of native by introduced plants did not necessarily leave forest birds without food.

Factors affecting food supply within standing forest may have resulted in slow declines of forest birds in some areas, but they do not appear sufficient as a general explanation for the accelerated declines of the 1892–1910 period under discussion.

INTRODUCED AVIAN DISEASES

Introduced diseases, including avian malaria and birdpox, were considered by Munro (1944) to have been the main reason for the reduction of forest birds in Hawaii; some experimental evidence in support of this view has been provided by Warner (1968). Munro associated increased human population and greater numbers of domestic poultry with the decline. As examples, he mentioned Kona, Hawaii, where a large reduction of birds occurred between 1892 and 1894 at the time of an increase in human population; and Lanai, where the increase in human population after 1923 seemed to parallel the decline in forest birds.

Confirmation that birdpox was present among Hawaiian endemic birds was first obtained from a specimen of *Loxops coccinea* sent to Washington in 1902 by Henshaw (1902). The disease had been observed earlier, however, for Perkins (1893) wrote: “As on Oahu, many of the birds in Kona had swellings on the legs and feet; in some cases they had even lost one or more claws and parts of the toes. The species affected were *Himatione*, *Hemignathus*, *Chasiempsis*, *Loxioides*, and *Rhodocanthis*.” In view of the rather specific nature of birdpox viruses (Austin, Bull, and Chaudry 1973), it is of interest to note the range of genera mentioned as being affected by this disease.

The timing of any disease effect is critical to the present discussion. Perkins’ observa-

tions referred to above were made during the 1890–1892 period. With similar observations by Munro (1944) made in the 1890s and those of Rothschild (1893–1900), it is clear that birdpox was already widespread in the Hawaiian Islands by the *early* 1890s. Perkins (1903:425) wrote: “Like many other Drepnididae the species of *Hemignathus* are grievously affected by a disease, which is probably contagious, and causes swellings on the legs and feet, as well as on the head at the base of the bill, and on the skin around the eyes. . . . In other cases birds, on which these growths are largely developed, appear not to suffer very serious inconvenience. Sickly birds generally retire to dense cover to die, so that it is difficult to estimate whether the disease causes much mortality. I have no doubt it is sometimes fatal.” Perkins mentioned the occurrence of the disease in introduced birds and thought it quite probable that it had been introduced with poultry. Henshaw (1902) stated “. . . frequently such tumors have serious consequences. . . . Often, however, the tumors slough away with little or no damage, save to leave the integument rough and thickened.” Munro (1944) recorded that he noticed birdpox in the Kauai akialoa (*Hemignathus procerus*) in 1891 and thought it likely that decline of this bird began at that time. However, there is nothing to indicate from his remarks that a major decline had affected this species by 1898 or 1899 when he was again working on Kauai. Bryan and Seale (1901) were able to obtain four specimens of this species as late as 1900.

Unlike Munro, neither Perkins nor Henshaw suggest in any of their writings that disease was a major factor responsible for forest bird declines in Hawaii. Their observations suggest that not only was birdpox widespread among Hawaiian forest birds by the 1890s but that at least some species had developed a degree of resistance to it. This would be expected if forest birds had been exposed to the disease for some time.

Malaria was found in pigeons at Honolulu by Alicata (1938) and subsequently the presence of *Plasmodium* species (agent of avian malaria) and of *Haemoproteus* species has been demonstrated in other introduced birds

(Fisher and Baldwin 1947, Alicata 1947, Warner 1968, Navvab Gojrati 1970). Malaria has seldom been demonstrated among endemic forest birds in the wild, and we know little about the frequency with which such diseases prove fatal (Berger 1975*a, b*).

Warner (1968) transferred two groups of Laysan finches (*Psittirostra cantans cantans*) from Laysan Island to Oahu and Kauai in 1958 and 1959. He found that both birdpox and avian malaria developed in the birds following their exposure to potential disease vectors such as mosquitoes and hippoboscids flies. All but three birds, treated with Aureomycin, had died by the end of the experiment. In a further trial, eight honeycreepers including amakihi, anianiau, and one apapane were captured at 1200 m on Kauai and then exposed to disease vectors in a lowland environment on the same island. All birds developed acute malaria within 10 days of exposure and subsequently developed birdpox as well.

Further evidence that the honeycreepers may be susceptible to mosquito-borne malaria is provided by the fact that attempts to keep honeycreepers at Paradise Park, Manoa Valley, Oahu, have failed (Mr. J. Throp, personal communication). The mosquito population is extremely high in this area. On the other hand, at Honolulu zoo, Waikiki, where mosquitoes are few, Mr. Throp kept two amakihi for a year in an aviary open to mosquitoes. He reported (personal communication, 1975): “When the first died, the post-mortem report by Dr. Fred Lynd, State Veterinarian, showed malaria in the blood. But the virus had not been the terminal factor in the bird’s death. The bird actually died of cranial trauma probably caused by a cat. The second bird died shortly after the first, of the same cause. But, and this is interesting, malaria was not found.”

Although Warner’s (1968) experiments do not fully separate the effects of birdpox, malaria, and direct loss of blood induced by high numbers of mosquitoes, they do suggest that malaria could adversely affect honeycreeper populations. The question is, “When did this effect begin?” As pointed out by Warner, a reservoir of *Haemoproteus* and

Plasmodium, associated with waterfowl and shorebirds, probably existed in the Hawaiian Islands before the arrival of Europeans. This would have been augmented by the early introduction of domestic fowl. Further influxes of diseases probably arrived with introduced game birds, a trend which began before 1855 (Caum 1933).

At first, the absence of suitable vectors may have prevented the spread of bird diseases. Warner considered that the chief vector in Hawaii was probably the night-flying mosquito (*Culex quinquefasciatus*). This species was apparently introduced to the islands at Lahaina, Maui, about 1826 (Osten-Sacken 1884, Hardy 1960). Warner pointed out that the numbers of these mosquitoes were greatly reduced at altitudes above 600 ± 150 m, the variation depending on local conditions. As most surviving honeycreeper populations occur above this altitude, Warner argued that forest areas on each of the islands above 600 m had functioned as disease-free refuges. Supporting evidence was his failure to find blood parasites in the sample of honeycreepers collected from 1200 m on Kauai and the low resistance of these birds to avian malaria when they were transferred to low altitudes.

Whatever the role of the night-flying mosquito has been in transferring diseases in Hawaii, mosquitoes could not have been a new factor in the 1890s. They were a pest species in the Hawaiian Islands by 1857 when Dr. Hillebrand is reported to have imported frogs for mosquito control (anonymous 1903). If the 1826 date for the introduction of night-flying mosquitoes is correct, it was at least another 47 years before the major decline of birds under discussion occurred on Oahu and 66 or more years before a similar decline occurred on other islands including Maui itself. The time lapse appears too great for mosquitoes to be implicated.

A second argument against night-flying mosquitoes being involved is that a number of endemic forest birds that have become extinct or greatly reduced have never been recorded at altitudes as low as 600 m. These are the Maui nukupuu (*Hemignathus lucidus affinis*) recorded between 1225 and 2050 m,

the Maui parrotbill (*Pseudonestor xanthophrys*) between 1225 and 2000 m, the palila (*Psittirostra baileui*) between 1220 and 2845 m, the greater koa finch (*P. palmeri*), and lesser koa finch (*P. flaviceps*) both between 1530 and 1835 m, the grosbeak finch (*P. kona*) between 1070 and 1680 m, and the crested honeycreeper (*Palmeria dolei*) between 1530 and 2050 m (Munro 1944, Banko 1968, Berger 1972).

Furthermore, if mosquitoes or any other disease vector are largely restricted in their effects to altitudes below 600 m, it is difficult to explain why areas above 600 m on Oahu, Molokai, and Lanai have not been more effective as refuges. It is not a matter of large size, for in the smallest of these potential refuges, Lanai, forest birds persisted until the 1926–1932 period, later than on any of the larger islands.

In summary, it is possible that avian disease organisms and their vectors have been present in the Hawaiian Islands since the 1820s. If so, such diseases could have reduced the numbers of Hawaiian forest birds during the first two-thirds of last century, particularly at lower altitudes, and could possibly have been implicated in some of the early declines such as that of the kioea or of the Kauai nukupuu (*Hemignathus lucidus hanapepe*). But any hypothesis that relates the post-1892 accelerated decline of forest birds to disease requires evidence that either a new disease lethal to passerine birds or a new disease vector reached the Hawaiian Islands in the latter third of the last century.

INTRODUCED MAMMALIAN PREDATORS

Man

Several forest birds were hunted for their feathers by the early Hawaiians including the oo (*Moho* spp.), mamo, iiwi, apapane, and ou (Brigham 1899). However, there is nothing to suggest that hunting of birds suddenly increased in the 1890s when many major declines occurred. Some species that declined, e.g. the greater and lesser koa finches and the grosbeak finch were never hunted.

There was increased shooting of the Hawaiian crow (*Corvus tropicus*) in the 1890s (Berger 1972) but otherwise the only increased hunting at this time was associated with collectors. These people took specimens from particular areas but, because of topography, could have covered only a small fraction of the total range of species that declined.

Feral Cats

Cats (*Felis catus*) were introduced to the Hawaiian Islands with the first Europeans and quickly became feral (Perkins 1903, Bryan 1915). Tomich (1969) gave records of cats occurring to altitudes exceeding 2000 m and, in pointing out the versatility of the cat's feeding habits, mentioned mice, small birds when available, lizards, and arthropods as serving as food. There are several records of cats preying on forest birds in Hawaii. Wilson and Evans (1890–1899) quoted a letter from a Mr. von Tempsky of Kula, Maui, written in 1890, in which he recorded that cats had killed plenty of birds during the winter. Both Palmer in Rothschild (1893–1900:15) and Perkins (1901) mentioned high levels of cat predation on Lanai in the 1890s. Later remarks by Perkins (1903) show that one of the species preyed upon was the ou, which he considered to be easily caught by cats. However, on Lanai the major decline of forest birds including the ou did not occur until more than 25 years later (Munro 1921–1935).

Some Hawaiian forest birds, rare by the early 1890s, may have been exceptionally vulnerable to cats because of their fearless behavior. For example, Perkins (1895) mentions the very tame behavior and curiosity of Perkins' mamo (*Drepanis funerea*).

Because cats have been present in Hawaii since the early days of European settlement, they do not at first sight appear to be involved in the accelerated forest bird decline of the late 19th century. However, if any marked change in the food available to cats occurred at this time, as, for example, an unusual increase in the numbers of rats or mice, then increased cat numbers and, therefore, in-

creased predation on forest birds might have been expected.

Mongoose

The small Indian mongoose (*Herpestes auropunctatus*) was introduced into the Hawaiian Islands in 1883 when a group of 72 animals was released along the Hilo-Hamaku coast of Hawaii to control rats (Bryan 1938). Subsequently mongooses were released on Maui, Molokai, and Oahu but Kauai and Lanai remained free of this predator. Baldwin, Schwartz, and Schwartz (1952) found the animal from sea level to over 1200 m on Molokai and Oahu, and to over 3000 m on Maui and Hawaii.

There is evidence that mongooses are predators of ground-nesting birds (Schwartz and Schwartz 1950, 1951), of burrow-nesting seabirds (King and Gould 1967), and occasionally of small passerines such as house sparrows or house finches which feed on or near the ground (La Rivers 1948). Studies of the foods taken by mongooses in forests do not appear to have been made so that the high proportion of rodents and insect remains found in the droppings collected from canefields (e.g. Kami 1964) give no indication of what birds may be taken in forest.

It has been pointed out that Kauai, which lacks mongooses, is the only island to have retained all the endemic birds known to have been there. Even so, a major decline in forest birds occurred there between 1900 and 1920. Furthermore, the endemic bird fauna of Lanai, where mongooses are also absent, suffered a similar major decline in the 1920s.

That mongooses could have contributed in any major way to the forest bird decline under discussion seems unlikely. Their tree-climbing ability is weak (Baldwin, Schwartz, and Schwartz 1952), so that their predation on passerines would be significant only on the few species that feed on or nest near the ground.

Rats and Mice

Although Perkins (1903:465) suggested that mice may have been present in Hawaii

prior to Cook's arrival, the limited evidence makes it more probable, as concluded by Tomich (1969), that the early Hawaiians introduced only the Polynesian rat. House mice (*Mus musculus*) had reached the Hawaiian Islands by 1816 (Kotzebue 1821) so that they, like the Polynesian rat, cannot be considered a new factor that caused the declines of forest birds at the end of the 19th century. Both the Norway rat and the roof rat were introduced by Europeans although in neither case is the exact date known.

Several probable instances have been recorded of predation on forest birds by rats in Hawaii (e.g., Tomich 1971, Frings in Berger 1972) and if rats were not largely nocturnal, many more instances might be known. The Norway rat, because of its relatively poor climbing ability, is a much less effective predator of passerine birds than is the roof rat. Berger (1972:9) stated that the roof rat eats both eggs and nestlings of honeycreepers on the main islands but noted that direct evidence is very difficult to obtain. The only known case of rats exterminating a passerine bird in Hawaii occurred on the Midway Islands in 1943 when roof rats escaped from ships and established on these islands. Within 18 months of the rats being first noticed, populations both of the Laysan finch and of the Laysan rail (*Porzanula palmeri*) had been exterminated (Johnson 1945, Baldwin 1945, Fisher and Baldwin 1946).

Implication of either species of European rat as a cause for the accelerated decline of endemic forest birds at the end of last century would require evidence that one or both species had arrived at that time. It has usually been assumed that both the Norway rat and the roof rat reached Hawaii with the first sailing ships that visited the islands (e.g., Tinker 1938). However, the evidence discussed below suggests that this was not the case.

Evidence of a Late Entry by the Roof Rat (Rattus rattus) to Hawaii

The earliest record of rats in the Hawaiian Islands is that of Cook (1785: vol. 2:228) who made his first landing at Kauai in 1778

and wrote "There were . . . some rats resembling those seen at every island at which we had yet touched." These were presumably the Polynesian rat, *R. exulans*, the *iolo* of the Hawaiians; no other rodents were mentioned.

The next record known to me is that of Kotzebue (1821) who commanded a Russian naval expedition that visited Hawaii in 1816. He wrote (III:237): "The only original quadrupeds of the Sandwich Islands are a small bat and the rat. To these is added our common mouse, besides the flea, some species of *Blatta* and other noxious parasites."

This observation may have been obtained from J. F. Eschscholtz, the naturalist of the expedition. It implies that the Norway rat had not established in Hawaii as late as 1816, for otherwise the size difference between it and the smaller Polynesian rat is likely to have made the presence of the European species known.

The naturalist Andrew Bloxam, who accompanied Lord Byron during his 10-week visit to the Hawaiian Islands in 1825, wrote (Byron 1826:253): "As to the quadrupeds of the Sandwich Islands, the three natives, i.e. the hog, dog, and rat, need no description; those now introduced are the cow, horse, sheep, goat, rabbit, and mouse."

Judged by this comment, European rats still had not established in Hawaii. This may not be surprising in view of the fact that the first wharf was not constructed at Honolulu until 1825 (anonymous 1890). Prior to that time, vessels were anchored offshore and people and supplies were taken ashore in small boats, thus reducing the chances of rats getting ashore.

By 1835 the Hawaiians had recognized the presence of a rat larger than the Polynesian rat, for at that time Malo (1903) wrote of the animals that had been imported since the time of King Kamehameha I: "The following are things that crawl: the rabbit, or *iole-lapaki*, which makes excellent food, the rat or *iolo-nui*, the mouse or *iolo-liilii*, the centipede. . . . These things are late importations; the number of such things will doubtless increase in the future."

Only one type of introduced rat, presumably the Norway rat, is mentioned here. Had

the roof rat been present, its brown phenotypes might have been misidentified as the Polynesian rat. This is not likely to have happened with the black phenotype, however, as black phenotypes of the Polynesian rat have not been recorded in Hawaii (P. Quentin Tomich, personal communication). The absence of any mention of "black rats" by Kotzebue, Bloxam, or Malo is probably indicative of the absence at the time of the roof rat.

In 1840 the Wilkes Exploring Expedition visited the Hawaiian Islands including Oahu, Kauai, Hawaii, and Maui. With them was the naturalist Peale who had made the original description of the Polynesian rat in Tahiti. Peale (1848:47) wrote under *Mus decumanus*: "The common Brown or Norway Rat, was observed at the Hawaiian, and some other islands in the Pacific Ocean, where it has been introduced by commercial intercourse with Europe and America. It was observed to retain its partiality for the habitations of mankind, with all its burrowing and destructive habits, but does not seem to multiply so rapidly as it does in those countries where the cereal grains are grown. . . ." The only other rodent Peale mentions in the Hawaiian Islands is the house mouse (*Mus musculus*).

The Wilkes Expedition was present in Hawaii for over 6 months, so that it seems very unlikely that the roof rat had reached the Hawaiian Islands in 1840. Any confusion of the roof rat with the Polynesian rat can be ruled out in this case since Peale specifically stated that the only "high" island where *Mus exulans* (= *R. exulans*) was encountered was Tahiti. Whether the invasion of Hawaii by the Norway rat and the house mouse had resulted in a temporary decline of the Polynesian rat (as may have occurred in New Zealand) is a matter for conjecture.

Most significant perhaps of Peale's observations was that he did not record the roof rat on any island in the Pacific visited by the expedition nor at places where the expedition collected along the Pacific coast of North America: Nisqually in Puget Sound, the Willamette River at Portland, the Columbia River as far inland as Fort Okanagan, the

Umpqua River in Oregon, and San Francisco Bay and the Sacramento River in California. Cassin's (1858) reprinting of volume VIII of the U.S. Exploring Expedition's account (mammalogy and ornithology) incorporated notes made on the voyage by Pickering but again there was no mention of *R. rattus*.

The apparent absence of the roof rat at points visited by the expedition along the western coast of North America is consistent with other records of rats along this coast. The roof or black rat had reached the North American continent as early as 1544 (Palmer 1898) and became abundant in settled areas (Silva 1927). Following the invasion of North America by the Norway rat about 1775, the roof rat gradually disappeared from most parts of the United States and Canada, becoming extinct in many localities (Lantz 1909, 1910). This decline in America paralleled the disappearance of the roof rat from northern Europe after 1725 when the Norway rat was spreading rapidly (Barrett-Hamilton and Hinton 1912). Lantz, in common with many other writers of the time, thought that the roof rat and the black rat were distinct species, and much of the recorded history of the roof rat in the United States refers to the black phenotype, the history of the white-bellied form being unknown (cf. Lantz 1910). However, it is apparent that the Norway rat never completely replaced the roof rat in the warmer southeastern states of North America (Ecke 1954, Mallis 1954). Mallis considered that in the West, high altitudes and extensive arid regions had impeded the spread of the roof rat so that it did not reach California until 1851.

There is disagreement concerning the time of arrival of the Norway rat in California, for Lantz (1910) quoted Audubon as saying that the species was unknown on the Pacific coast in 1851 but also quoted Newberry as thinking it had arrived at a much earlier date. By 1855, the Norway rat was certainly abundant at several points along the Pacific coast, including San Francisco, Astoria, and Fort Steilacoom (Palmer 1898). Palmer made no specific mention of what had happened to the roof rat along this coast but stated as a generalization that "since the introduction

of the brown rat, the black rat has become comparatively rare in most places where the former is abundant." Of the white-bellied phenotype, Palmer stated that it was common in the southern United States.

The roof rat in Hawaii probably originated from European-type stocks moving in a westerly direction across the Pacific (Tomich 1969), so that the most likely source is the Pacific coast of North America or Europe. The data assembled by Judd (1974) show that practically all the shipping visiting Hawaii between 1840 and 1860 originated in North America (where San Francisco was the main port), Britain, or France. The rat records from North America and Europe discussed above suggest that during this period, when rats were present, the Norway rat was the dominant species and often the only species present. Thus, the Norway rat was also the most likely rat to board ships departing from North American or European ports.

Partial confirmation for the above supposition can be obtained from the historical analysis of Atkinson (1973), who found no evidence of roof rats aboard ships visiting New Zealand prior to the late 1850s and early 1860s when the roof rat appears to have begun its spread through New Zealand. In Hawaii there is apparently nothing in the literature to suggest that the roof rat reached the islands between 1840 and 1870.

From 1860 onward, the chances of Hawaii being invaded by the roof rat were increased, because at some time during the succeeding 30 years there appears to have been an unexplained change in the species of rat commonly carried by European ships, a change that resulted in the roof rat becoming the common shipboard species (Atkinson 1973). An example of one ship of the 1870s that probably had roof rats aboard when it visited Hawaii was the research vessel H.M.S. *Challenger*. Writing of the ship's visit to Bermuda in 1872, Moseley (1892:515) said: "When the ship was moored at Bermuda, alongside the wharf in the dockyard, boards were placed on all the mooring chains as a fence against rats. Rats nevertheless appeared in the ship, and were all curiously enough of

the old species, the Black Rat (*Mus rattus*). . . ." The *Challenger* subsequently visited Honolulu for 16 days in 1875, although it is not clear from the narrative of Tizard et al. (1885) that the ship was moored directly to the wharf at Honolulu. From here the *Challenger* sailed for the island of Hawaii where it stayed a week, anchored in Hilo Bay.

One would expect that the first Hawaiian island to be invaded by the roof rat would have been Oahu, as the port of Honolulu was then the only port of call for overseas trading vessels. At present we have no firm evidence of exactly when the roof rat first reached the Hawaiian Islands although outside limits for the time period can be set by Peale's failure to record the species in 1840 and by what appear to be the earliest authenticated specimens of *R. rattus* collected in the Hawaiian Islands in 1899 and held by the National Museum at Washington (D. E. Wilson, personal communication). However, there are six separate indications, some only of anecdotal character, which taken together do throw light on the timing of the spread of the roof rat through the islands.

One indication of the arrival in Hawaii of an arboreal rat in the latter part of last century concerns the ieie vine (*Freycinetia arborea*), the fruit of which is readily eaten by rats. Perkins (1903) wrote: "Why the ou should have become extinct on Oahu and remain abundant in far more restricted forests on Molokai and Lanai is by no means clear, but with regard to the former island it may be noted that now over extensive areas it is often difficult to find a single red IeIe fruit, which the foreign rats have not more or less eaten and befouled, and they may thus have indirectly brought about the extinction of the Ou, even if in times of scarcity of the fruit they do not actually prey on the bird itself."

Perkins' use of the word "now" when referring to extensive areas that had been denuded of fruit implies a change on Oahu that had occurred only recently. As the Norway rat is a relatively poor climber, the "foreign rat" referred to would be either the roof rat or the Polynesian rat.

A second indication of the arrival of a new arboreal rat is the observation of Baldwin

(1887) when discussing the land mollusks of the Hawaiian Islands, mainly those of Oahu. He wrote: "The agencies now threatening the wholesale destruction of these little gems of the forest are the rats and mice, which have become very abundant in mountain forests, particularly where there are no cattle. Their ravages are not confined to the shells whose habitats are on the ground, but extend to those found on trees. It is not uncommon to find around the charnel cells of these noxious little animals hundreds of empty mutilated shells."

The use of the phrase "now threatening" implies a new factor that had reduced the land snail population in the years immediately prior to 1887, namely, from about 1870 to 1886. The effect noted on arboreal species of land snail again implies a climbing rodent and since the initial effects on snails of the house mouse and the Polynesian rat occurred either at the beginning of the 19th century or centuries earlier, the presence of the roof rat is implied as a new influence.

A third indication of a comparatively recent influx of an arboreal rat late last century arises from the remarks of Bryan (1915:235): "Of late years the tree rat has become a great pest in the coconut trees and does great damage to the young nuts by gnawing holes in them. They readily pass from one tree to another along the leaves, and when a colony of rats becomes established in a grove the tin sheaths so commonly placed about the trunk of the tree do but little good, unless the tops of the trees are kept clear of the neighboring foliage." In another statement in the same work Bryan (1915:291) said: "The black rat, or one of its numerous varieties, is our common tree rat... they prefer the treetops. There they make their nests, usually in the crowns of coconut palms, and feed upon the fruit of these useful trees, often doing much damage by gnawing the young fruits."

At this time the Polynesian rat was generally considered to have disappeared from Hawaii (Perkins 1903, Bryan 1915, Stone 1917), although later recognition of its widespread distribution and abundance in the islands (Illingworth in Gregory 1931, Svihla

1936) must throw some doubt on whether the earlier supposition was entirely correct. As pointed out by Tomich (1969), the lack of good observational evidence at the time makes it difficult to learn what happened to the numbers of Polynesian rats. Nevertheless, studies have shown that where the Polynesian rat and the roof rat occur together in coconut plantations, the roof rat causes by far the greater damage to coconuts (Nicholson and Warner 1953, Morrison 1954, Strecker 1962). Thus, Bryan's identification of the rat concerned as the "tree rat" or "black rat" is almost certainly correct and his statement beginning "Of late years..." shows that he is referring to new damage on coconuts resulting from the roof rat.

A fourth indication of a late entry of the roof rat to Hawaii concerns the frequency in which some of the early observers encountered rats in trees during the 1890s. Thus, Rothschild (1893-1900) wrote: "Even in considerable heights in the mountains Palmer saw a great number of rats and on one day killed three up in the trees. There can be no doubt, he thinks, that these, too, are very destructive to bird life." Perkins (1903:398, 465) twice referred to the arboreal habits of rats and conveyed the impression that he also encountered numerous rats in trees, e.g., "The imported rats now abound in many parts of the forest and lead largely an arboreal life, feeding on such fruits as are to be had, especially that of the iei-e (*Freycinetia*) and the mountain apple (*Eugenia*) and on the brightly coloured molluscs of the genus *Achatinella* and the duller ground-frequenting *Amastra*."

The impression given by these observers is that rat numbers were unusually high in the 1890s, at least on some islands, and that rats were seen during daytime. That their numbers remained high for some years is shown by the remarks of Lantz (1909): "During the present attempts to abate the rat nuisance in Honolulu, Hawaii, about one-third of the rats taken have been shot from trees. While all four of the cosmopolitan species of *Mus* are common in Hawaii, those shot are chiefly the roof rat and the black rat." A few years later Bryan (1915), dis-

cussing black rats, stated: "... seldom seen during the day, but at night they become very active. ..."

The high numbers of rats seen in trees during daytime in the 1890s can be contrasted against the situation today when they are seldom seen. Thus, Mr. W. Banko, a biologist with much experience in Hawaii, reported (personal communication, 1975) seeing "a rat in a tree only twice during ten years of intermittent field work in Hawaii." One of these incidents was of a rat which ran up a tree after escaping from a live trap. In both cases he identified the species as almost certainly having been *R. rattus*.

Frequent daylight sightings of rats usually accompany rat irruptions. Thus, it seems very probable that observers of the 1890s experienced an irruption of the roof rat such as often occurs when a species invades a new habitat (Elton 1958). The peak of the irruption presumably had passed by the time Bryan's (1915) remarks were written, and evidence of subsequent irruptions of the roof rat in Hawaiian forests is lacking.

A fifth indication of a late entry of the roof rat to Hawaii is the anecdote relating to rats being driven into trees by mongooses (e.g., Nelson 1917). There is no basis for believing that the climbing ability of a rat species could be changed through predation by mongooses over the short span of a few years (cf. Baldwin, Schwartz, and Schwartz 1952). The likely explanation for the origin of the story is that rats were not noticed in trees until after the introduction of mongooses to Hawaii in 1883. Presumably the story originated on Hawaii or Maui for, as indicated earlier, Oahu may have been invaded by the roof rat in the 1870s, before mongooses were released.

A sixth indication concerning the spread of the roof rat involves the effects of the mongoose on the rat population of sugarcane fields. Following their introduction in 1883, mongooses appear to have been at first very effective against rats. Walker (1945) quoted a Hilo planter, Mr. Austin, as saying in 1884: "These fields as well as the rest were infested with rats a year ago. Now there is not a stick of rat-eaten cane to be found, or a rat." The very large fraction of the cane crop destroyed

by rats in earlier years is indicated in the statement (anonymous 1888): "Now a field is harvested clean and not a stalk of cane is damaged." After 1888 some writers turned against the mongoose (Tomich 1969), but whether this was because it was no longer effective against rats is not clear.

There was thus a period of at least 5 years when rat damage to cane fields on Hawaii was at a very low level. This would be understandable if at that time the chief damager of cane was the Norway rat. If either the Polynesian rat or the roof rat had been present during the 1883-1888 period much more damage to the cane crop might have been expected. These two rats now cause considerable damage to cane in the presence of mongooses, the proportions of each rat species varying with distance from the coast (Doty 1945; Hood, Nass, and Lindsey 1970). On Kauai and Lanai, where mongooses are absent, the Norway rat predominated as late as the 1940s (Walker 1945). On Kauai this species remained the most destructive rat, causing more acute and widespread damage than on other islands, until prebaiting control methods were introduced in 1938 (Doty 1945).

The early effectiveness of the mongoose against rats in cane fields on Hawaii suggests that the spread of the roof rat did not take place on this particular island until some date after 1888. It would be of great interest to find comments relating to the early effectiveness of mongooses against rats on Oahu.

Specimens held by the United States National Museum, Washington, D.C., include *R. rattus* from Oahu dated 1905 and *R. rattus* from Maui and Hawaii dated 1899 (E. Wilson, personal communication). The Hawaii specimen labelled no. 99674 Kau and dated 4 July 1899 may be the specimen referred to by McGregor (1902) who, when speaking of Maui, stated: "Several rats were seen and a specimen shot was identified by Dr Merriam as the common *Mus rattus* which he says has been previously known from Hilo."

Too much weight cannot be placed on the absence from museums of pre-1899 specimens of the roof rat collected in Hawaii. It is likely that little systematic collecting and identification of rats was carried out in the

islands until after the appearance of plague in Honolulu in 1899.

The circumstantial evidence discussed for the timing of the entry of the roof rat into the Hawaiian Islands is not dependent in any way on inferences that might be made from the bird decline data. Considered separately, none of the above six "indications" could be accepted as unequivocal evidence of a late entry of the roof rat. Taken together, however, they suggest either that the roof rat did not reach the Hawaiian Islands until the 1870–1890 period or that there was a large but temporary increase in a preexisting but small population of the roof rat. In support of the second idea one might argue that the presence of the Norway rat in Hawaii may have prevented the spread of the roof rat by mechanisms similar to those apparently operative in northern Europe and North America during parts of the 18th and 19th centuries. A reduction in the Norway rat population, such as may have occurred when mongooses were introduced, might then have allowed an upsurge in the roof rat population.

The second hypothesis seems rather unlikely in view of the known ability of the roof rat to thrive in warmer climates, whether the Norway rat is present or not (e.g., Tinker 1938, Mallis 1954). The Hawaiian Islands have extensive areas of forest suitable as habitat for the roof rat. Judged by rates of spread in New Zealand (Atkinson 1973), this rat would have spread through such forest within 10 years of its establishment on a particular island. Thus, in my view, the hypothesis of a late invasion and spread of the roof rat through the Hawaiian Islands is by far the more probable explanation of the various observations discussed above. The critical question is whether this late invasion of the roof rat could account for the catastrophic decline of endemic forest birds that occurred during the latter part of the 19th century.

SPREAD OF THE ROOF RAT AND THE DECLINE OF FOREST BIRDS

There are at least two partially documented examples of islands in the Pacific region where major declines of forest birds followed

the invasion and spread of the roof rat. The best known is that of Lord Howe Island in the southwestern Pacific Ocean, about 724 km northeast of Sydney, Australia. The roof rat first appeared on this island in 1918 following the grounding of the S.S. *Makambo* (Hindwood 1940). Data from Hindwood (1940) and Recher and Clark (1974) show that between 1919 and 1938, five species (33 percent) of the indigenous land bird fauna became extinct. Most if not all of these extinctions occurred within 2 years after the roof rat had gained a foothold, for McCulloch (1921) wrote: "But two short years ago the forests of Lord Howe Island were joyous with the notes of myriads of birds, large and small and of many kinds. . . . Today, however, the ravages of rats, the worst enemy of mankind, which have been accidentally introduced, have made the note of a bird rare, and the sight of one, save the strong-billed Magpie and the Kingfisher (*Halcyon*), even rarer. Within two years this paradise of birds has become a wilderness, and the quietness of death reigns where all was melody."

Judged from the observations of Bell (in Hindwood 1940), both cats and the Polynesian rat were present on Lord Howe Island at the time of the roof rat's invasion but, unlike in Hawaii, the Norway rat was absent.

A second example of a major decline of forest birds following introduction of the roof rat is that of Big South Cape Island, 1.6 km southwest of Stewart Island, New Zealand. An irruption of the roof rat began on this forest- and scrub-covered island in 1962 and by 1965, when rats had reached very high numbers, at least eight species (42 percent) of the indigenous land bird fauna had been either greatly reduced (four spp.) or eliminated (four spp.) (Blackburn 1965, Atkinson and Bell 1973). In this case cats were not present and the island was without rats until the 1950s.

These examples show that in some circumstances a population of roof rats invading and irrupting on an island for the first time can bring about dramatic changes in the island's bird fauna. I suggest that the stepwise decline of endemic forest birds that occurred island by island in the Hawaiian group between 1870 and 1930 was also the

result of a series of roof rat irruptions that followed the invasion and establishment of this rat on each island in turn. The invasion and irruption of roof rats on the Midway Islands in 1943, which was followed by the loss of the Laysan rail and a population of Laysan finches, can be seen as the most recent step in the spread of the roof rat throughout the Hawaiian Islands.

In Hawaii, as in the examples quoted above, there appears to be no evidence of resurgence in the numbers of bird species greatly reduced but not eliminated at the time of the rat invasion. However, this may not mean that on larger islands such as New Zealand, some recovery of bird numbers would not occur after rat numbers had fallen below their irruptive peaks.

As discussed earlier, it seems most probable that the roof rat reached Honolulu and, thus, Oahu in the 1870s or early 1880s, following which another 10 or 15 years elapsed until it invaded Hawaii. An explanation is needed for this apparent time lag in the spread of the roof rat from Oahu to other islands.

Elsewhere in the world a frequent means of roof rat dispersal has been from rat-infested ships moored to wharves. However in the Hawaiian Islands, wharf facilities outside Honolulu were very restricted prior to 1897. Most places visited regularly by the interisland steamers were open roadsteads where ships anchored and produce and people were ferried to landings or small wharves by lighters and longboats. A small wharf was built at Hilo about 1897 (Stacker 1912), but the first substantial wharf at this port was not completed until December 1903 (Thurston 1913). At this time Thrum (1903) wrote that Hilo was "the only port outside of Honolulu with any wharf accommodation for even the coasting vessels of the islands." On Maui, when the breakwater at Kahului Harbor was completed in 1908, vessels were able to anchor closer to the wharf (Thrum 1908), but the old whaling port at Lahaina remained as an open roadstead until 1922 when a new wharf was completed (Thrum 1922). Similarly, wharf facilities at Molokai and Kauai remained rudimentary until well

into this century. On Lanai the harbor and wharf for deepwater ships at Kaunalapau was not completed until 1926 (Wentworth 1925; H. Munro, personal communication, 1975) a date that coincides with the onset of the bird decline on the island (Table 1).

Thus, the early lack of wharves suitable for mooring deepwater ships, except at Honolulu, would have restricted dispersal of the roof rat either to its being carried in packaged stores or escaping from shipwrecks. This restriction could well account for the comparatively slow rate at which the roof rat appears to have spread through the islands after its arrival on Oahu.

DISCUSSION

How was it that observers of the last century did not associate the decline of forest birds with an influx of rats at the time it occurred? In the first instance, the indigenous birds of settlements had long since disappeared by the time the major changes occurred in the forest. Secondly, only a minority of naturalists were familiar with Hawaiian forests and their birds. Thirdly, many observers treated all species of rats alike without realizing that the effects of roof rats on passerine birds are generally very much greater than the effects of the other two species.

In spite of these considerations and the lack of documentation, it appears that a few persons did recognize during the last century that rats were affecting endemic birds. For example, in a popular account of the mongoose, Walker (1945) wrote: "Most of the endemic birds disappeared with the clearing of wooded areas and the accidental introduction of tree-climbing rats. Many birds were acknowledged to be extinct before 1883." If this statement is restricted to Oahu it appears to be an accurate description of what happened.

It is important to recognize that current rates of predation by the roof rat on forest birds in Hawaii probably bear little relation to the rates that would have occurred during an irruption of this rat. Furthermore, the

only bird species now preyed on are those that survived the initial invasion and irruption of the roof rat. It is also important to recognize that the roof rat is not an equally effective predator of forest birds and seabirds. For example Norman (1970) studied an island off Tasmania where *R. rattus* coexisted with an extensive colony of short-tailed shearwaters (*Puffinus tenuirostris*) and found little evidence of active predation on the shearwaters by the rat. This study may have influenced Norman (1975) in his review of predation by *R. rattus*, *R. exulans*, and *R. norvegicus* to conclude that "the rat's role as an avian predator has been overestimated." Certainly one can agree with Norman that there are few direct observations "to implicate rats as causative agents in localized population declines," but this is scarcely surprising in view of the nocturnal habits of rats. On an island, in the absence of direct observations of rat predation, circumstantial evidence for an effect of rats can still be gained by examining the degree to which the time of a rat invasion coincides with the time of a bird decline and then by checking that no other factor (e.g., another predator such as cats) has been introduced to the system at the same time. In the Hawaiian Islands, the spread of the roof rat appears to have overlapped the spread of the mongoose. However, there is little to suggest that the mongoose is an effective predator of passerine birds, whereas the adverse effects of the roof rat on such birds are known.

Both food competition and predation could be considered as possible mechanisms through which the roof rat could reduce the numbers of forest birds. Many Hawaiian forest birds depend mainly on nectar or insects for food. Many insects taken as food are unavailable to rats, either because they are too small for rats to use profitably or because their position in foliage, beneath the bark, or in crevices of trees makes them impossible for rats to reach. Thus, it seems likely that the chief effect of the roof rat on passerine birds is through predation on eggs, nestlings, and sometimes adult birds.

The Hawaiian avifauna evolved in an environment entirely lacking in mammalian

predators (until the arrival of the Polynesian rat), so that behavioral adaptations to such predation were probably poorly developed. One factor that may have made the honeycreeper family (Drepanididae) more vulnerable to predation is its characteristic odor, which apparently is shared by all members of the family (Perkins 1901, 1903; Henshaw 1901). This smell is so strong that Perkins (1893) was able to state: "Certain nests I could readily recognize as belonging to *Himatione* by the overpowering scent that still clung to them after the young had flown."

Other factors besides smell must have affected the vulnerability of Hawaiian forest birds to predation, since some honeycreepers showed little sign of a major decline and members of other families lacking this smell (e.g., the Meliphagidae) did decline. Such factors may be the height above ground or accessibility of nest sites and roosting sites, the length of the incubation and fledging periods, and the number of broods that a species could raise in a single season. Berger (1972:127) has noted how the amakihi, one of the species apparently little affected by the decline of last century, "often build their nests so near the tips of small and brittle branches that it is impossible to reach the nests. . . ." He recorded that the apapane, another honeycreeper that apparently escaped any major decline, build many nests that are inaccessible. What is inaccessible to a human may not always be so to a rat; still, these observations indicate a nesting behavior that may have increased the chances of a population surviving a period of heavy predation by rats.

Berger (1972: 124) commented also on the long nestling periods of members of the honeycreeper family (17–22 days) relative to those of other passerine families. Long nestling periods would increase the chances of predation.

A further point to be noted in Hawaii is that the numbers of *R. rattus* present appear to have remained at a high level for some years, at least on Oahu (cf. Perkins 1903, Lantz 1909). Long periods with high levels of *R. rattus* may have allowed cats to increase their numbers above their original level, thus

further increasing predation on forest birds for a period.

I am not suggesting that all declines of forest birds in Hawaii subsequent to 1892 were a result of predation by the roof rat. The greater amakihi (*Loxops sagittirostris*) and the Maui parrotbill for example, neither of which was abundant in 1892, may have declined as a result of other changes. On the other hand, some of the 1873–1887 declines of birds on Oahu may well have been the result of the initial invasion and establishment of the roof rat there.

There may even now be some relationship between the distribution of the roof rat in Hawaiian forests and the occurrence of some of the rarer forest birds. For reasons of food supply, rat numbers may remain low in some parts of the forest at times when the habitat is favorable for such birds. Further distributional studies of *R. rattus* are needed. Perhaps the most important practical conclusion that can be drawn from this analysis, however, is that precautions must be strengthened against the spread of all species of rats to further islands in the Hawaiian archipelago.

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