# THE ROLE OF INTRODUCED DISEASES IN THE EXTINCTION OF THE ENDEMIC HAWAIIAN AVIFAUNA

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On the evening of Sunday, 18 January 1778, Captain James Cook first sighted the island of Kauai, thus discovering for the western world the Hawaiian Islands. Since then, that beautiful archipelago has experienced a series of extraordinary biotic changes. In general, the pattern has been one of destruction and replacement of native forms—human, plant, vertebrate and invertebrate animals. The endemic land avifauna, a unique assemblage of forest birds, was not exempt from these effects of "discovery." This avifauna has suffered extinction of nearly half its total species, and restriction of the remainder as remnant populations to a few high-mountain forest sanctuaries.

This report examines first the historical evidence of changes in the indigenous avifauna, especially as related to the effects of introduced diseases. Then it presents experimental evidence clearly demonstrating the high susceptibility of existing drepaniid species to avian malaria and birdpox. Other ecological data are presented that substantiate the theory of extinction and restriction of range by exotic pathogens, which in turn are spread by introduced mosquitoes. Some predictions, based on the evidence derived from field studies and controlled experiments, are offered regarding the future of the Drepaniidae and the endemic Hawaiian avifauna in general.

## PRIMEVAL AND EARLY HISTORICAL CONDITIONS

### DISTRIBUTION

The early record of Hawaii's avifauna is at best fragmentary. At the time of discovery the native forests, together with their bird populations, extended from the high mountain slopes to the ocean. Captain Cook (1785) reported seeing several species of birds in the lowland forests and among the coconut palms lining the ocean shores (see also Stresemann 1950). Other early visitors, such as the English botanist David Douglas who during a visit to Oahu in 1830 recorded large numbers of native birds in the flowered canopies of trees at the edge of Honolulu, substantiated the seashore-to-high-forest distribution of the endemic avifauna.

Sporadic and desultory collecting continued throughout the 19th century. Finally, in 1887 the English ornithologist Scott Wilson began an extended period of field activities that resulted in publication of the definitive work Aves Hawaiienses (Wilson and Evans 1890–1899). This publication was followed shortly by a magnificent two-volume work by Rothschild (1893–1900) containing more data on the distribution of the drepaniids. From these reports, together with the later excellent publications by Perkins (1893, 1903), Henshaw (1902), and Munro (1944), it is possible to estimate the distribution patterns and general abundance of the drepaniids and other endemic bird species before their populations were disrupted.

Some species were very limited in their distribution. For example, the Grosbeak Finch, Psittirostra kona, was restricted to the Kona district of Hawaii where it inhabited an area of a few square miles. In contrast, the Iiwi (Vestiaria coccinea) and the Apapane (Himatione sanguinea) were ubiquitous, ranging from the coastal lowlands to the upper limits of the high forests on all the high islands.

### MOVEMENT PATTERNS

There is considerable historical evidence of seasonal migrations, both altitudinally and from one forest area to another. Prolonged winter storms would apparently induce movement of highland forms into the lower forests and often to the seashore itself. Some of these winter altitudinal movements may, however, have been regular seasonal migrations to the lowlands. Perkins (1893), Henshaw (1902), Munro (1944), and other observers reported extensively on these seasonal altitudinal shifts, which were especially prominent during the early historical period when the native bird populations were still more or less intact.

James Clapper, a long-time resident of Kauai and a student of Hawaiian natural history, has spent many years in and about the native forests of the islands. He reports that these winter movements were common knowledge to the early Hawaiians. During an interview on 6 September 1958 he described one such migration that occurred during a period of winter storms in 1920 that had brought rain to the semi-arid region of Waimea, Kauai. A flock of drepaniids including several species was observed congregating in an introduced *Hibiscus* hedge that was blooming at the side of the road. The birds were feeding on the flowers. Some of the birds were red, others yellow. The flock numbered at least 30. The bills of some were . . . "long and decurved, like that of the curlew, and at least two inches long . . . ," certainly the now rare Kauai Akialoa, *Hemignathus procerus*. First observed in the afternoon, the birds stayed in the area only a few hours and were gone the following morning. Other long-time Kauai residents (*e.g.*, Charles Rice) have reported similar movements during the early part of this century.

More recently, Baldwin (1953) has provided excellent and extensive data on both lateral and vertical seasonal movements of several drepaniid species. While his own observation areas encompassed the elevations of 700 m and 2290 m on the southeastern mountain slopes of the island of Hawaii, he presents additional summarized evidence of both lateral and vertical movement patterns in a variety of drepaniid species in other regions. I believe that these long-established movement patterns had an important role in the decline of the endemic avifauna.

## USE OF INTRODUCED PLANTS

Despite a widely held current view to the contrary, some species of drepaniids were not restricted in their feeding habits to the native flora. For example, the Ou (*Psittirostra psittacea*), which normally fed on the fruit of the native ieíe (*Freycinetia arborea*), mountain apple (*Eugenia malaccensis*), and the berries of the lobelias (family Lobeliaceae), was observed by Munro (1944: 124) to feed on guavas (*Psidium guajava*) on Kauai and on mulberries (*Morus* sp.), both introduced plant species. Henshaw (1902: 44) reported of the Hawaii Amakihi (*Loxops virens*):

It has learned also that the imported nasturtium [*Tropaeolum* sp.] secretes a fine quality of honey and, however close to the house the flowers may grow, it pays them regular morning and evening visits.

He also reported that the Hawaii Amakihi regularly utilized the blossoms of the banana (*Musa* spp.); and Perkins (1893: 106) noted:

The Vestiaria [Iiwi] even comes into the lots in front of the houses [of the Kona region], visiting the peach and rose trees . . . .

On Oahu the Amakihi (*Loxops virens*) was reported during earlier times (Perkins 1903: 409) to be very partial to the nectar of the introduced lantana (*Lantana camara*). The Maui Amakihi was seen in great numbers visiting the flowers of the introduced canna (*Canna indica* and *C. edulis*) in the Iao Valley (*ibid.*); and Baldwin (1953: 362) has reported observations of E. Y. Hosaka wherein:

. . . hundreds of *Vestiaria* and *Himatione* are attracted to the flowering groves of the introduced tree alfalfa in upland pastures of Haleakala, Maui.

Thus the replacement of native plants by exotics did not necessarily leave the drepaniids without food.

## THE PATTERN OF CHANGE AND ITS IMPLICATIONS

By the late 1800's it was apparent that drastic changes were taking place in the endemic bird populations. Cattle, sheep, and goats introduced by Cook, Vancouver, and others at the beginning of the 19th century had multiplied and were causing widespread damage to the native forests. Trees were being cut for commercial purposes, and fires had increased in severity. Suitable lowland areas were being cleared for agricultural purposes, principally sugar cane and, somewhat later, pineapple. Exotic plant species were already spreading in the disturbed areas, and to a lesser extent into the still-intact native forests. In addition, various predators, such as the feral housecat and the introduced mongoose (*Herpestes javanicus auropunctatus*), were well established on several islands. Baldwin and Fagerlund (1943), Warner (1960), and others have described some of the effects of these introductions.

While these factors were important in altering the character of the lowland habitat, many still-undisturbed forests were becoming inexplicably devoid of their bird populations. In 1902 Henshaw (1902: 10) recorded in perplexity:

The author has lived in Hawaii only six years, but 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. One may spend hours in them and not hear the note of a single native bird. Yet a few years ago these same areas were abundantly supplied with native birds, and the notes of the oo, amakihi, iiwi, akakani, omao, elepaio and others might have been heard on all sides. The ohia blossoms as freely as it used to and secretes abundant nectar for the iiwi, akakani and amakihi. The ieie still fruits, and offers its crimson spike of seeds, as of old, to the ou. So far as the human eye can see, their old home offers to the birds practically all that it used to, but the birds themselves are no longer there.
It is more reasonable to conclude that the former inhabitants of such tracts have abandoned them for the more profound solitudes higher up than that they have perished from such slight causes. However, even the abandonment of forest tracts under such circumstances seems inexplicable, and the writer can recall no similar phenomenon among American birds.

The species of *Ciridops* and *Chaetoptila* (a melaphagid) from the island of Hawaii were among the large number of endemics that vanished early and without apparent reason. Neither was hunted by the natives for its plumes. Their habitat had suffered no physical disturbance by man.

The avifauna of Oahu seems to have experienced an especially rapid decline. By 1900, six of the 11 endemic passerine species were believed to be extinct. Indeed, the ornithologist W. A. Bryan (1915) was moved to comment in 1915:

Oahu can make the melancholy boast that it has a greater list of extinct birds, in proportion to the total number of species known from the island, than any other like area in the world.

The Oahu Ou (*Psittirostra olivacea*) was among the species that vanished during this period. It was known to be present on the island in 1893 and 1899, but was practically extinct by 1901. Henshaw (1902: 66) wrote:

The cause of the extinction of the ou upon Oahu seems to be very obscure. The fruit of the ieie vine is the particular food of the bird, and there are considerable tracts of timber on the mountains of the island where this vine still abounds. So too, there are sections where the introduced guava and the mamaki are still plentiful, and the ou is very fond of the fruit and berries. There apparently being no scarcity of food and shelter, why should the ou have disappeared from Oahu, and yet persist upon other islands where the timbered areas are even more restricted?

The changes were no less drastic on the small island of Lanai, although they occurred later than on most other islands. George Munro spent many years on Lanai and was able to watch the process of extinction there. In 1923, according to his reports, the forest birds were at least holding their own, and some species may have been increasing. But by 1932, although the forest was still intact, the native birds were rapidly declining in number. In 1944 he wrote (1944: 102):

I lived on Lanai for 20 years and saw the birds increasing, if anything, till 1923 when the town was built. With the speedy increase of population and greater numbers of domestic fowls the birds began to decrease perceptibly. The native forest is small, of no considerable elevation, and in close proximity to the settlement, offering no protection through isolation.

As a consequence of his observations, Munro was convinced that introduced diseases were playing a major role in the destruction of the native bird fauna.

Those species of native Hawaiian birds that still persist today are found, with the exception of the Elepaio (an Old World flycatcher: Muscicapinae), only in the upper forests, above elevations of approximately 600–900 m, depending upon local climatic and geographic circumstances, and on the low, isolated, and mosquito-free leeward islands of Nihoa and Laysan. The more ubiquitous species, such as the Iiwi and Apapane, still range over large areas of the high forests of the main islands. Others, such as the Kauai Ou, are for reasons as yet undetermined now confined to quite small portions of the relatively undisturbed high forests.

## INTRODUCTION OF POTENTIAL AVIAN PATHOGENS AND THEIR VECTORS

### AVIAN MALARIA

The potential for avian malaria has probably existed in the Hawaiian Islands for thousands of years. Each autumn over a million migrating shorebirds and ducks pass from Alaska, Siberia, Canada, the United States, and possibly México, to the Hawaiian Islands. Some, such as the Bristle-thighed Curlew (*Numenius tahitiensis*), the Sanderling (*Crocethia alba*), and the Ruddy Turnstone (*Arenaria interpres*), for the most part move on southward, the wintering populations becoming strung out from the Hawaiian Islands to the Tuamotus and other island complexes near the equator. The Pacific Golden Plover (*Pluvialis dominica fulva*), in contrast, winters in large numbers throughout the Hawaiian Islands; and most of the duck species terminate their autumn migratory flights in the ponds and marshes of the main Hawaiian Islands. Medeiros (1958) has reported January census data on waterfowl wintering in the Hawaiian Islands for the period 1950 to 1955. The average yearly wintering population for these years for the islands of Oahu, Molokai, Maui, and Hawaii, computed from his data, was 5195 birds. Before the advent of sport hunting and modification of winter habitat, the number of annual waterfowl migrants was probably five to ten times as high. Indeed, it was the substantial reduction in migratory bird populations through sport hunting that prompted the first legislative attempts to protect these species.

A variety of blood parasites, including the one causing avian malaria, have been reported in North American shorebirds and ducks. Herman (1954) has reported several *Haemoproteus* species in waterfowl; Manwell and Hatheway (1943) and others have demonstrated various species of *Plasmodium* in ducks and shorebirds. It is therefore safe to assume that a reservoir of *Haemoproteus* and *Plasmodium* existed in the Hawaiian Islands

even before the arrival of Europeans. The random introduction of domestic and jungle fowl, domestic ducks, turkeys, game birds, and other avian stock without doubt was important in augmenting and maintaining the reservoir of blood parasites during spring and summer seasons when the migratory birds were absent.

## THE NIGHT-FLYING MOSQUITO

Nevertheless, in the absence of a suitable vector, avian malaria could not be passed on to the native birds; and it is known that Hawaii was free of mosquitoes before the arrival of Europeans. This "deficiency" was satisfied when the tropical and subtropical form of the night-flying mosquito *Culex pipiens fatigans* (= *quinquefasciatus* Say), now known to be the principal vector of avian malaria, was accidentally introduced onto Maui in 1826. Halford (1954: 99) reported the details of the disaster as follows:

Dr. Judd was called upon to treat a hitherto unknown kind of itch, inflicted by a new kind of *nalo* (fly) described as "singing in the ear." The itch had first been reported early in 1827 by Hawaiians who lived near pools of standing water and along streams back of Lahaina [Maui]. To the Reverend William Richards, their descriptions of the flies suggested a pestiferous insect, from which heretofore the Islands were fortunately free. Inspection confirmed his fears. The mosquito had arrived!
Investigation back-tracked the trail to the previous year and the ship *Wellington*, whose watering party had drained dregs alive with wrigglers into a pure stream, and thereby to blot one more blessing from the Hawaii that had been Eden. Apparently no attempt was made to isolate and destroy the hatchery, nor to prevent spread of the pest throughout the archipelago. The pioneer was *Culex quinquefasciatus*, the night mosquito.

The *Wellington* had originally and significantly taken on water on the west coast of México. The night-flying mosquito, *Culex*, has two distinct forms in western America (Barr 1957; Kitzmiller 1959). The tropical and subtropical form, *C. p. fatigans*, is found from the tropics north to near Stockton, California, where it is replaced over a wide belt of intermixing by the temperate subspecies, *C. p. pipiens*. Thus, the Lahaina, Maui, introduction was of the tropical form.

The coastal areas of Hawaii are sufficiently tropical that the species quickly became established, and in time spread to the lowlands of all the major islands. Since *Culex* breeds in ground water and is known to have a flight range of at least 14 miles (Clark 1943), its spread to other habitable parts of an island, once an initial colonization was accomplished, was no doubt very rapid. *Culex* also is able to complete normal development in 30 per cent

sea water (Miller 1945), enabling it to breed in the numerous coral holes along coastlines and thus to penetrate even the drier districts.

While this mosquito has been found breeding sporadically at altitudes higher than 1525 m (Swezy and Williams 1931; Williams 1931), studies by myself and others (*e.g.*, Williams 1935) have demonstrated that population densities drop precipitously when elevations above approximately 600 ± 150 m are reached, the variation being dependent upon local conditions. For example, in the moderately wet mountain country of Kokee, Kauai (elevation approximately 1070 m), an apparently ideal *Culex* habitat, the mosquito is functionally absent—that is, from an epidemiological viewpoint. It is observed on only very rare occasions. This same condition exists in all the upland areas of all the major or high islands.

In contrast, until organized control efforts were instituted relatively recently by the Hawaii Board of Health, the night mosquito was extraordinarily abundant in virtually all lowland areas. It constituted a major pest and was made the subject of a statewide control program. The ecologically determined upper limit of spread of the *Culex* populations was to have a profound effect on the events that followed. Figure 1, which shows the islands in profile, indicates the present general (functional) distribution of *Culex pipiens fatigans* and illustrates the ecological sanctuaries to which the drepaniids are currently confined.

## BIRDPOX VIRUS

The birdpox virus, long a bane of domestic poultry, was without doubt carried to the Hawaiian Islands soon after their discovery by Europeans. The virus (or viruses) has been found in both the Old and New Worlds, and has been reported in a variety of passerines and other bird groups. Birdpox is known to be transmissible by mosquitoes and other biting flies such as the hippoboscids, the virus being carried on the proboscis of the insect after it feeds on an infected bird. It is reported that mosquitoes are able to infect susceptible birds for two months after a single feeding on an infected bird (Stefferud 1956: 465).

## HIPPOBOSCID FLIES

It is likely that hippoboscid flies, known as vectors for several blood parasites including several species of *Haemoproteus*, were introduced at an early date with the domestic fowls. There are no good reports in the early literature substantiating this, although Perkins (1893: 106) reported hippoboscids on an Iiwi
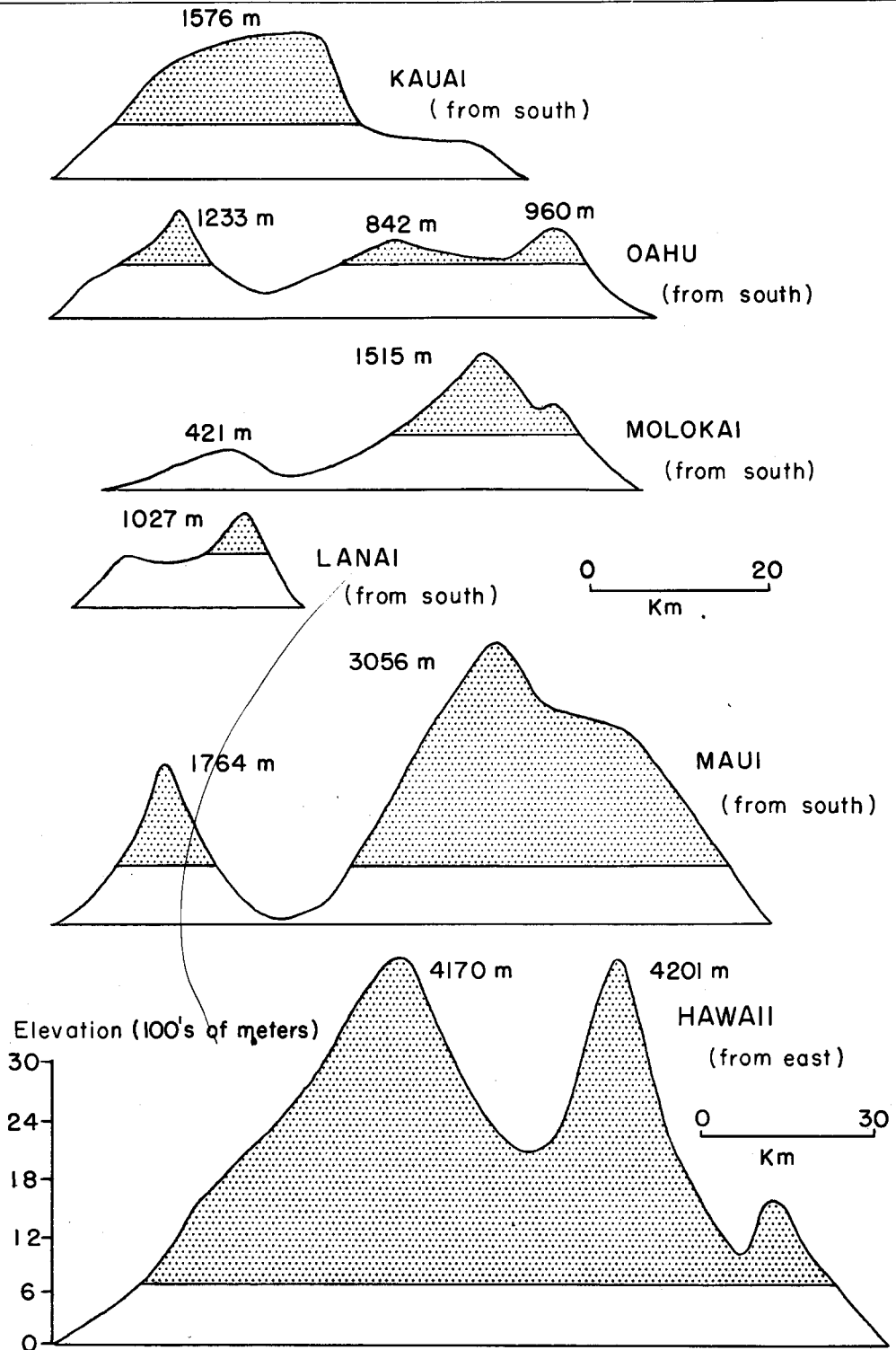
FIGURE 1. Vertical profiles of the Hawaiian Islands showing areas above 600 m altitude (stippled). Below that level (white areas) the native drepaniids are essentially extinct.

captured near Kona in the 1890's. I found heavy infestations of hippoboscids on lowland Kauai populations of the introduced House Finch, *Carpodacus mexicanus*, which were being trapped during my investigations there in 1961. We may thus conclude that the vector is well established today.

## EARLY EVIDENCE OF DISEASE IN THE NATIVE AVIFAUNA

### BIRDPOX

Numerous descriptions of birdpox or "bumble-foot" in lowland populations of the endemic avifauna are found in the early literature. The observations of Perkins (1903: 425) are typical and quite indicative.

. . . Like many other Drepanididae [*sic*] 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. One individual of *H. procerus* affected in all parts I picked up on the ground, it being quite unable to fly. Quite recently (Feb. 1902) two individuals of *Oreomyza flammea* were examined, one of which was crouched on the ground at the foot of a bush, the other in the middle of a dense shrub. Both of these birds were affected on the head, and neither would move until they were actually poked up. 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. It not only affects the smaller birds but the crow, the buzzard, the introduced pheasant and even the Californian quail are sometimes attacked, and a similar disease is very disastrous to tame poultry. It is quite probable that the disease was introduced with the latter.

Henshaw (1902), Munro (1944), and others have provided similar descriptions of what appears to be birdpox virus infections in wild populations of drepaniids. In 1891 Munro collected several specimens of the Kauai Akialoa. His observations (1944: 117) of this population suggest the presence of not only birdpox, but other avian maladies as well.

. . . Although these birds were quite numerous, it was evident that they were susceptible to disease. Their habit of coming to the forest's edge and to low elevations exposed them to introduced diseases. One was so disabled with lumps on legs and bill that it could scarcely fly. Another had a tumor a quarter of an inch thick in its throat full of small worms, and a tumor on its ovaries contained a brown paste.

Amadon (1950) examined a specimen of Apapane found by Baldwin in the Hawaii National Park that had a mild case of "bumble-foot." In 1958 I found a dead Iiwi hanging by its foot in a Mamane (*Sophora crysophylla*) tree growing on the east slope of Mauna Kea

at an elevation of 2450 m. The right foot was badly swollen at the tarsal joint from "bumble-foot" and apparently had become inextricably lodged in a branch fork. Since this population of Iiwi is known to migrate with the tree-flowering seasons, the disease was probably contracted elsewhere.

Specimens of the House Finch referred to earlier that were trapped in lowland areas near Lihue, Kauai (elevation 30 m), in August 1961, showed considerable signs of current and past birdpox infections. Several specimens lacked one or more toes, and nearly half of all trapped specimens exhibited the characteristic primary lesions on exposed body parts such as the bend of wing, lores, and tarsal joint. In most cases these lesions were not severe, having the indurated swelling but no necrosis or granulation typical of highly susceptible forms. It is probable that the House Finch, having been exposed to the disease during the course of centuries on the North American continent, has become resistant to the virus.

In summary, available evidence indicates that in the second half of the 19th century the lowland populations of the native avifauna on all the major islands experienced severe infestations by birdpox. These epizootics were so numerous and extreme that large numbers of diseased and badly debilitated birds could be observed in the field. The epizootics were heaviest in the wetter portions of the lowland forests and increased in severity during the rainy season. The disease is present to some extent today both in introduced and endemic bird species.

### AVIAN MALARIA

There is no direct historical evidence of the effects of avian malaria on the endemic avifauna, principally owing to ignorance of the nature of the disease and its causative organism during the early period. The etiology of avian malaria was established long after the Hawaiian birds suffered their decline. There is, however, considerable circumstantial evidence suggesting that this pathogen was of profound importance in the extinction of the endemics.

In this regard the report of Henshaw (1902: 20) is of great significance.

. . . I am not aware that the birds of the Hawaiian Islands are more subject to fatal diseases than those of other lands. Dead birds are, however, found rather frequently in the woods on the island of Hawaii, especially the iiwi and akakani [Apapane].
There is no doubt that sudden and marked changes of temperature affect Hawaiian birds unfavorably, especially the two species just mentioned and, after

heavy and prolonged storms, many individuals of both species are driven into sheltered valleys and even along the sea-shore far from their woodland haunts. Under such circumstances scores of the above named species are picked up dead or dying, and the mortality among other birds is, perhaps, unusually great.

Henshaw was, of course, unaware of the possible presence of avian malaria in the lowlands. I am convinced that the mass mortality of birds driven into the lowland areas by winter storms or other causes and exhibiting no birdpox lesions can be directly attributed to massive infections of one or more species of *Plasmodium,* the organism causing avian malaria. Evidence to be presented beyond establishes the extreme susceptibility of the drepaniids to avian malaria. What had been in primeval times a retreat from inclement weather had become, with the advent of the *Culex* mosquito, a death trap for the native birds.

*Plasmodium* has to date not been reported in wild drepaniids, and I searched in vain for it in these birds on both Kauai and Hawaii. Fourteen specimens representing two drepaniid species (*Himatione sanguinea, Loxops virens*) were collected in the Pohakuloa Flat area of Hawaii (elevation about 1700 m), and examined for blood parasites in November 1959, with negative results. In the summers of 1959 and 1961, 18 drepaniids representing three species (*H. sanguinea, L. virens* and *L. parva*) were collected in the Kokee-Alakai mountain country (elevation about 1200 m) of Kauai, with similar negative results.

However, Baldwin (1941) and Fisher and Baldwin (1947) reported *Plasmodium* in the introduced Pekin Nightingale (*Leiothrix lutea*) and the White-eye (*Zosterops japonica*) in the Hawaii National Park area of Hawaii. In addition, Alicata (1947) and Kartman (1949) have demonstrated *Haemoproteus columbae* in pigeons from the Honolulu area. I found several species of *Plasmodium* and another blood parasite, possibly *Haemoproteus*, in lowland Kauai populations of the introduced White-eye and House Finch in August 1961. Of seven White-eyes examined, all had mild infections of avian malaria; of 10 House Finches examined, all had avian malaria, and three possibly contained *Haemoproteus.*

There is little doubt that other introduced passerines will eventually be found to carry the disease. Das Gupta and Siddons (1941) found *Plasmodium* in the Malay Chestnut-bellied Munia (*Munia atricapilla atricapilla*); Doré (1920a, 1920b) has reported it in two species of birds introduced into New Zealand:

the Groundlark *Anthus novazealandiae,* and the Songthrush *Turdus ericitorum;* and Laird (1953, 1962) has found a variety of blood parasites including *Plasmodium* in passerines, including *Zosterops,* from the Solomons, New Hebrides, and elsewhere. In view of the above and other similar evidence, it is probably a legitimate deduction that passerines in general are subject to the disease when the epidemiological factors are propitious.

Nevertheless, major responsibility for establishment and spread of avian malaria and other debilitating diseases cannot be assigned to the introduced passerines of the Hawaiian Islands. The migratory shorebirds and waterfowl, the numerous domestic fowl, and the introduced upland game birds such as the Ringneck Pheasant (*Phasianus colchicus*) and California Quail (*Lophortyx californicus*) all without doubt played, and continue to play, significant roles in the spreading of these pathogens.

## EXPERIMENTAL EVIDENCE OF DREPANIID SUSCEPTIBILITY TO BIRDPOX AND MALARIA

### GENERAL PLAN OF EXPERIMENTATION

In 1958 a series of studies on disease susceptibility in the Drepaniidae was begun. Although at the outset the general approach was purely exploratory, the problem ultimately resolved itself into four partially independent components including: (1) susceptibility of the Laysan Finch (*Psittirostra cantans*) to birdpox virus; (2) susceptibility of the Laysan Finch to avian malaria; (3) susceptibility of the high-forest drepaniid populations to birdpox virus; and (4) susceptibility of the high-forest drepaniid populations to avian malaria.

### BIRDPOX INDUCED IN THE LAYSAN FINCH

My field studies and a later thorough investigation by Butler (1962) had established that *Culex* was absent from the remote and isolated leeward Hawaiian island of Laysan. This small sand island hosts one species of drepaniid, the Laysan Finch, which is present in considerable numbers and is easily captured. I estimated the population from transect census data in 1959 at 15,000. In June 1958, 24 specimens of the Laysan Finch were procured during an expedition (Warner 1958a, b) to the island and transferred to Honolulu via a U.S. Coast Guard vessel in cages tightly wrapped with several layers of cheesecloth. Upon arrival they were placed in a large cage in the basement of the Board of Agriculture and Forestry Building in downtown Honolulu. The cage remained swathed in cheesecloth to

prevent entry of insects, especially mosquitoes.

The rationale for such an approach lay largely in the fragmentary and incomplete knowledge of avian diseases and their etiology in the Hawaiian Islands. Paul Breese, then Director of the Honolulu Zoo and a keen student of the native avifauna, reported (personal communication) that Laysan Finches had been brought to Honolulu in the past either to be sold as cage birds or for the zoo. In every case they lived only a short time and then died of unknown causes.

Hence, this first experimental effort was an attempt: (1) to maintain the species in an apparently hostile environment by eliminating potential contact with possible arthropod disease vectors, and (2) subsequently to induce and then to diagnose any avian disease that might manifest itself in the caged Laysan Finches.

The caged finches were fed mixed bird seed, abundant greens, and fruit. Raw eggs and chopped hard-boiled eggs were occasionally provided. A supply of coral sand had been obtained from Laysan Island, and was available *ad libitum*. The birds consumed substantial quantities of this, much more than the usual gravel consumption by seed-eating birds. Standard canary gravel and water were also supplied *ad libitum*. The finches remained very partial to raw eggs, a taste acquired during their more predatory, egg-eating days on Laysan.

The birds were maintained in the tightly screened cage for two months, with no mortality and no evidence of any disease. There was much singing, molted feathers were properly replaced, and a minimal amount of agonistic behavior was exhibited. Interesting elements of their Laysan-adapted behavior were observed regularly, for example, their proclivity to bathe among wet spinach greens placed in the cage as food (Laysan has no standing fresh water supplies). The general impression obtained from the captive group was of a hardy and gregarious finch, capable of living comfortably in crowded conditions.

After two months of this cloistered existence, the cheesecloth cover was removed from the cage. The windows of the unscreened room were opened wide to permit entry by mosquitoes and other insects. All other conditions, including diet, remained unchanged. It is important to note that the mosquito population in Honolulu had, largely through the continued vigorous efforts of the then Territorial Board of Health, been reduced to the merest fraction of its earlier size. This was especially true in the downtown Honolulu area where the experiment was being conducted; in the peripheral and mauka (upland) regions of the city adjacent to forested areas, mosquito populations remained relatively high.

Within two weeks after removal of the protecting cheesecloth, indurated swellings typical of the first stage of birdpox virus infection had appeared on lores, tarsal, and wing joints (bend of wing) of six of the finches. These swellings increased in size, then erupted as granular, tumorlike lesions, and finally became necrotic with accompanying secondary
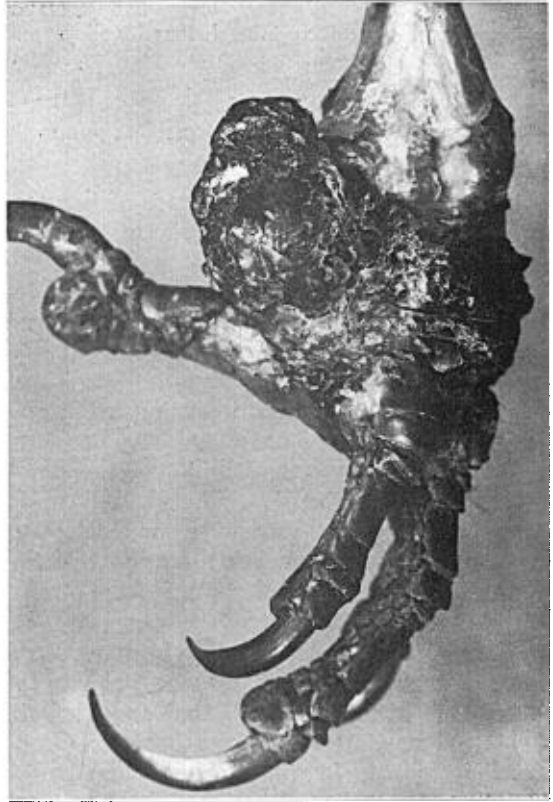


FIGURE 2.   Birdpox lesion on the foot of a Laysan Finch.

bacterial infections. A bacterial examination was made on one of the more severe foot lesions with the assistance of G. W. Chu, Professor of Bacteriology, University of Hawaii. The tumorous foot was thoroughly washed with Zepharin, rinsed with sterile water, and sectioned. Smears and cultures were made, which subsequently demonstrated cocci of mixed types typical of secondary infection with necrosis.

By the end of one month virtually every finch had at least one lesion, and several had as many as three or four at different exposed points, such as the corner of the mouth, forehead, eyelid, or foot. As the tumors progressed in severity bleeding occurred, particularly from the foot lesions. The afflicted birds gradually weakened, and death occurred after a variable period, generally after the lesions had become granular and necrotic. Figure 2 illustrates the crippling nature of a birdpox lesion on the foot. The characteristics of the lesions matched the descriptions provided by Worth (1956) and Burnet (1933) for birdpox in passerine species.

It is well known that domestic fowl and many passerines have genetically inherited

FIGURE 3.   Birdpox tumor on the eye of a Laysan Finch.

immunological capacities against the pox virus (Worth 1956; Stefferud 1956). Indeed, a standard practice among poultry growers is to induce a pox virus lesion in some noncritical spot, such as the wing membrane, permitting the bird to develop an immune reaction while sparing vital regions like the mouth and feet. To test whether the Laysan Finch, despite its long isolation from the virus, had some degree of immunogenetic capacity that was being masked by death due to secondary bacterial infections, three birds suffering from acutely severe tumors were treated with the antibiotic Auromycin. These birds remained active after all others had succumbed, despite an increase in tumor size to grotesque proportions. Figure 3 illustrates one of these antibiotic-treated finches. The initial pox lesion was above the right eye; the tumor had become very large and was physically debilitating. At the termination of the experiment there was no sign whatsoever of regression in any of the lesions.

On this basis I conclude that the Laysan Finch has altogether lost—or never acquired during its evolutionary history—a functional immunogenetic capacity against the birdpox virus.

## BIRDPOX INDUCED IN HIGH-ISLAND DREPANIIDS

In 1961, in the course of experiments with wild-trapped drepaniids from the mountain forests of Kauai, additional evidence of susceptibility to the birdpox virus was obtained. Eight specimens of the Amakihi (*Loxops virens*), Lesser Amakihi (*Loxops parva*), and Apapane from the Kokee region of Kauai (elevation approximately 1100 m) were trapped alive and transferred to the lowlands near Lihue, Kauai. While under observation for residual effects of avian malaria, which all eight had contracted during an experimental exposure to the lowland mosquitoes (details of which are presented beyond), the mosquito-bitten legs, feet, and lores of these birds developed large numbers of the indurated swellings typical of the first stage of birdpox. Unfortunately, the study had to be terminated before the possibility of immunogenetic resistance to the virus was determined. However, it is quite clear that the extant drepaniid populations of the high forests of Kauai are still susceptible to the birdpox virus. Future studies must determine whether exposure to the pathogen over the last century and a half has conferred on the high-island drepaniids some measure of resistance not currently shared by the isolated Laysan Finch.

## AVIAN MALARIA INDUCED IN THE LAYSAN FINCH

It was evident that the experiment conducted in 1958, while establishing beyond doubt the pathogenicity of birdpox virus to the Drepaniidae, had contributed nothing to the question of susceptibility to avian malaria. The Honolulu *Culex* population was extremely low, rendering unlikely any prompt and massive cases of malaria. Several of the Laysan Finches did develop symptoms suggesting moderate malarial infections, but as a result of an accident the blood smears taken during the study were lost before being examined.

To answer this question in a definitive way, 36 Laysan Finches were trapped alive on Laysan Island in July 1959. The birds were brought to Lihue, Kauai, again in cages tightly shrouded with several layers of cheesecloth, and then placed in hardware cloth cages in a mosquitoproof room for one month before the start of the exposure experiment. During this interval only one bird died; no specific cause of death could be determined at autopsy. The bird was fat and in (apparently) excellent condition. As with the Honolulu group in 1958, the birds in general were hardy and adaptable to the cage situation.

On 22 September 1959 the birds were separated into three groups, consisting of two lots of 13 birds each for experimental and control groups, and the remainder for other studies. Peripheral blood smears made from all birds before the start of the experiment
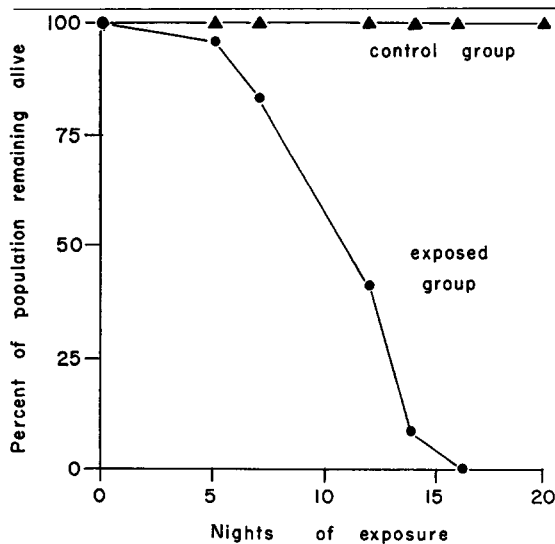
FIGURE 4. Cumulative mortality curves in Laysan Finches exposed to lowland mosquitoes or kept in a mosquitoproof enclosure (control group) at Lihue, Kauai.

were negative for malaria or other blood parasites. One group of 13 birds was then transferred to a cage constructed of 1.25 × 2.5 cm mesh hardware cloth and placed outside but under a sheltering canopy to protect it from inclement weather and direct sun. The other group remained in the mosquitoproof room as a control.

The first death occurred in the experimental group after five nights of exposure to the lowland Kauai environment. After 12 nights of exposure five more birds of the experimental group were dead, and the remainder were showing signs of severe debility. By the end of the 16th night of exposure the last of the outside group had died. The control group remained in excellent condition throughout, with no deaths or visible signs of debility. Figure 4, presenting the cumulative mortality curves for the experimental and control groups, clearly demonstrates the lethality of the disease to the drepaniids. Peripheral blood smears from several debilitated birds of the experimental group contained massive infections of *Plasmodium*; in one specimen, 97 per cent of the erythrocytes contained schizonts in various stages of maturation.

It is likely that anemia resulting from direct loss of blood to the feeding mosquitoes also played a role in debilitating the exposed finches. Evidence obtained in subsequent experiments and presented later in this report has established that the drepaniids are more likely to be bitten by mosquitoes than are other, better-adapted passerine groups. Thus, the combined action of mosquito attack per se and malaria-induced erythrocyte destruction

with toxaemia was fatal to the susceptible birds. Hill (1942) and Marvin and Rigdon (1945) have also reported on death due to malaria-induced anemia and toxic hypoglycaemia in birds.

Having established that the lowland malaria potential was great enough to cause mass mortality in the Laysan Finch, further tests were conducted to determine the minimum exposure necessary to induce a severe malarial infection. It should be noted that the *Culex* population near Lihue, Kauai, was very high at this time, although, because of some mosquito control efforts, it was no doubt lower than it had been in past years. Five of the previous control birds were transferred to a new cage having a mesh size of 1.2 × 2.5 cm. The cage was then placed outside on the evening of 22 October, and moved in at sunrise. This procedure was followed for three nights only, the group thereafter being held in the mosquitoproof room and checked at frequent intervals for symptoms of malaria. On 3 November, 11 days after first exposure to the night mosquito, one bird was seriously debilitated and the others were listless. Packed cell volumes (PCV or hematocrit) were determined for three of the birds, blood being collected in heparinized capillary tubes from the pectoral vein. Table 1 summarizes the results of these and other tests and observations. The weakest bird had a PCV of 16 per cent as compared with a normal PCV (control group) of 53 per cent, and its blood was very pale and watery; clotting time was excessively long. Within four hours this bird was dead from avian malaria.

Two days later, on 5 November, PCV was measured in two birds of the exposed group, and blood smears were made for all birds. The sickest of the four remaining birds in the exposed group had a PCV of 27 per cent and was suffering from an acute malarial infection. Its blood was pale and watery in appearance; clotting time was greatly increased. A less debilitated bird had a PCV of 44 per cent.

The experiment was terminated after 17 days. Three birds of the night-exposure group were dead; the remaining two were listless and suffering from moderately severe malaria infections. Examination of blood smears substantiated the other observations. All birds in the exposed group had heavy infections of avian malaria. Smears from birds in the terminal stages of the disease showed that 85 to 90 per cent of erythrocytes were infected with schizonts of at least two species of *Plasmodium* in various stages of development.

It is therefore clear that (1) the Laysan

TABLE 1.  Laysan Finch response to three nights of exposure to lowland Kauai conditions, October 1959.

| Bird no. | Test day | PCV (%) | Malaria infected | Observations |
|---|---|---|---|---|
| 76 | 1 | 54 | No | Lively; normal. |
| 77 | 1 | 51 | No | Lively; normal. |
| 81 | 1 | 53 | No | Lively; normal. |
| 97 | 1 | 53 | No | Lively; normal. |
| 98 | 1 | 54 | No | Lively; normal. |
| 76 | 11 | 43 | Yes | Lively, some loss of vigor. |
| 77 | 11 | — | Yes | Lively, some loss of vigor. |
| 81 | 11 | — | Yes | Lively, some loss of vigor. |
| 97 | 11 | 16 | Yes | Very weak. Blood thin. Died with symptoms of severe malariaemia. |
| 98 | 11 | 24 | Yes | Weak, listless. |
| 76 | 13 | 44 | Yes | Lively; swellings developing on legs. |
| 77 | 13 | — | Yes | Lively; swellings developing on legs. |
| 81 | 13 | — | Yes | Lively; swellings developing on legs. |
| 97 | 13 | a | a | Dead on day 11. |
| 98 | 13 | 27 | Yes | Very weak, blood thin. |
| 76 | 17 | a | a | Died on day 17 with symptoms of severe malariaemia. |
| 77 | 17 | — | Yes | Listless but still feeding. |
| 81 | 17 | — | Yes | Listless but still feeding. |
| 97 | 17 | a | a | Dead on day 11. |
| 98 | 17 | a | a | Died on day 17 with symptoms of severe malariaemia. |

a Bird dead in course of experiment.

Finch, and probably the Drepaniidae in general, are extremely susceptible to avian malaria; and (2) three nights of exposure to the night mosquito were sufficient to produce lethal infections of *Plasmodium*, given the *Culex* density present at that time. In all likelihood, lethal infection of malaria could have been achieved with but one night of exposure in earlier times, before the advent of mosquito-control programs.

## AVIAN MALARIA INDUCED IN HIGH-ISLAND DREPANIIDS

An opportunity arose in 1961 to pursue further the question of susceptibility of the high-island remnant populations of drepaniids to *Plasmodium*. A month was spent on the island of Kauai during July and August of that year conducting the necessary experiment.

Eight individuals of three species of drepaniids, the Amakihi, Lesser Amakihi, and Apapane, were caught in mist nets in the high forests near Alakai Swamp at an elevation of approximately 1200 m. A total of 22 White-eyes, cohabitants of the high-mountain forests, were also caught.

The birds were transported to the lowland near Lihue and placed in tightly screened compartments of a cage built especially for the experiment. The cage, which was 2.1 m high by 3 m long by 30 cm deep, was divided into four horizontal sections or tiers. Each section was 45 cm high. The top two sections were equipped with mosquitoproof screening, the bottom two with 1.2 × 1.2 cm hardware cloth. The birds were then held for one week in the fine mesh compartments on a diet consisting of papaya, fruit flies, termites, a syrup of diluted honey containing hydrolysed protein and peanut butter, and a "softbill" mix of high-protein baby food, wheat germ, milk, and multiple vitamins.

An examination of the mosquito larvae dip-count records for 1961, provided through the courtesy of the Territorial Board of Health for the Lihue District, indicated that the *Culex* population in the experimental area had been reduced to considerably less than 50 per cent of its former level as a result of an emergency mosquito-control program that had been instituted in July 1960. These dip counts consist of samplings of *Culex* larvae habitats to determine the population density of the aquatic larval stage of the mosquito. Thus the epidemiological factors bearing on the 1961 experiment were markedly different than those of the 1959 Laysan Finch exposure experiment. Figure 5 presents larvae dip-count data and clearly demonstrates the population density changes from July 1960, to August 1961.

This marked reduction in the *Culex* population density had two immediate consequences in the study: (1) it rendered impossible a statement of comparative susceptibility of the Laysan Finch and the major (high) island drepaniids because of the drastic reduction in the vector population between 1959 and 1961; and (2) the 1961 high-island drepaniid malaria-susceptibility experiment was rendered conservative.

Blood smears taken from all birds after one week of confinement in the fine-mesh cages were negative for blood parasites. PCV values for the drepaniids averaged 53 per cent. On 6 August, after the week of adjustment, the White-eyes were split into two groups of 11 birds each, one group being placed in a large-mesh cage, the remaining 11 left in the fine-mesh cage. Because of the small total number of drepaniids, no control group was established. Rather, all eight were moved to the second large-mesh cage for exposure to the night mosquito. While this was not optimal experimental design, it was felt that (1) the week of adjustment-holding in the small-mesh cage provided what might be considered a pre-exposure control; and (2) the exposure group would now be large enough to justify a firm statement of pathogenicity of *Plasmodium* to the high-forest birds.

By the evening of 11 August, five days after transfer to the large-mesh cage, symptoms of acute malaria were observed in two of the drepaniids. One Lesser Amakihi was very weak; when checked at midnight it was hang-
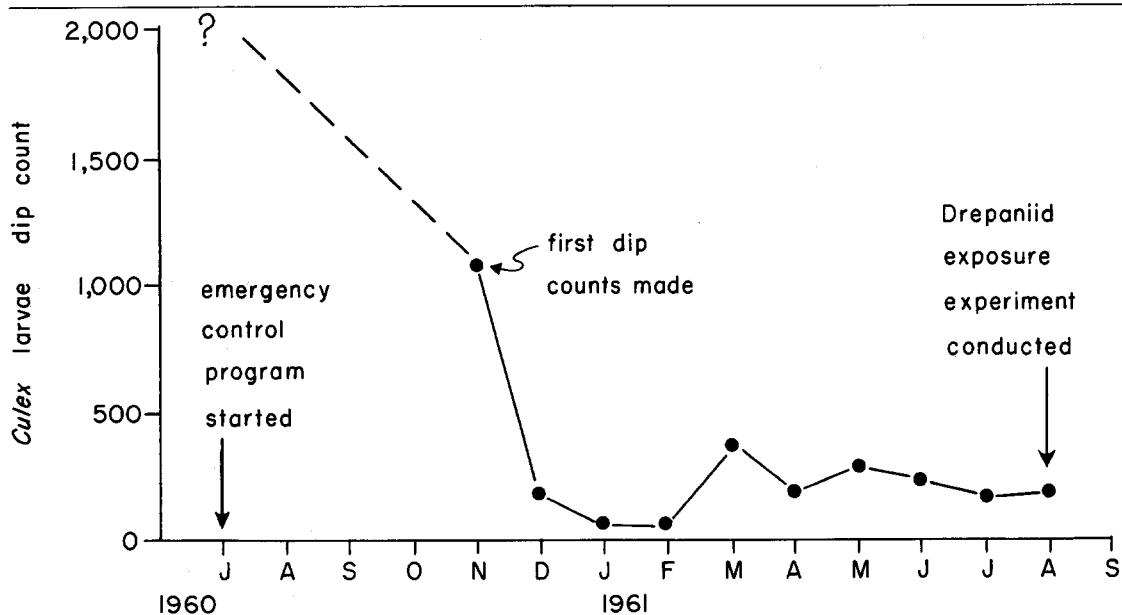
FIGURE 5.    Dip counts of *Culex* larvae in the Lihue District, Kauai.

ing upside down from the cage wire against which it had been roosting, having fallen over backward while sleeping. Earlier in the day it had appeared weak and listless, although it had eaten regularly and had normal feces. When placed on the perch it remained there, with feathers fluffed out. A blood smear revealed a heavy infection by at least two species of *Plasmodium*; developing erythrocytic schizonts were abundant, occupying an estimated 45 per cent of the RBCs.

The single Apapane was also showing signs of listlessness and general debility, as was one Amakihi. The latter remained fluffed up on a perch when not feeding, but flew readily when disturbed.

On 15 August, after nine days of exposure, all drepaniids had symptoms of malaria in varying degrees. The Lesser Amakihi that had first shown signs of debility on 11 August was now in the final stages of the disease. One Amakihi was panting heavily and in apparent extreme discomfort. The remaining birds were listless, with occasional bouts of shivering and panting.

Blood smears taken from all drepaniids on 16 August, 10 days after the start of exposure, confirmed that all birds were suffering from acute avian malaria. The Lesser Amakihi in the terminal stage of malariaemia was sacrificed and blood was drawn by heart puncture, to provide enough for PCV determination. It had been impossible to obtain enough by pectoral vein tap. The PCV for this specimen was 21 per cent; an estimated 97 per cent of

the RBCs were invaded by schizonts, and there were many free schizonts in the blood. The course of the disease is clearly shown in the photomicrographs (Figs. 6, 7, and 8). Other data for the blood of the specimen shown in figure 8 are given in table 2, together with the normal values for chicken blood for comparative purposes.

Packed-cell volumes in four of the other exposed drepaniids were as follows: Apapane, 30 per cent; Amakihi, 32 per cent; Amakihi, 35 per cent; Amakihi, 47 per cent. It will be recalled that the normal value for control drepaniids averaged 53 per cent. Several blood smears were subsequently submitted for evaluation by malariologist P. C. C. Garnham of the London School of Hygiene and Tropical Medicine. He offered the following tentative identifications (personal communication): (1) the Apapane harbored both *Plasmodium relictum* and *Haemoproteus*; (2) a Lesser Amakihi contained *P. elongatum*; and (3) an Amakihi contained *P. elongatum*. Owing to the faint staining and lack of appropriate biological tests such as inoculation into canaries, positive identification of the species of *Plasmodium* was not possible. Relative to the pathogenicity, Garnham commented:

The infection in P1.2 [Lesser Amakihi] is excessively severe, but is like that seen in abnormal hosts with *P. elongatum*. Several of the others are also unusually heavy, and would denote severe or acute infections.

A postexposure examination of blood in the control and exposure groups of the White-eyes revealed no blood forms of *Plasmodium* in the
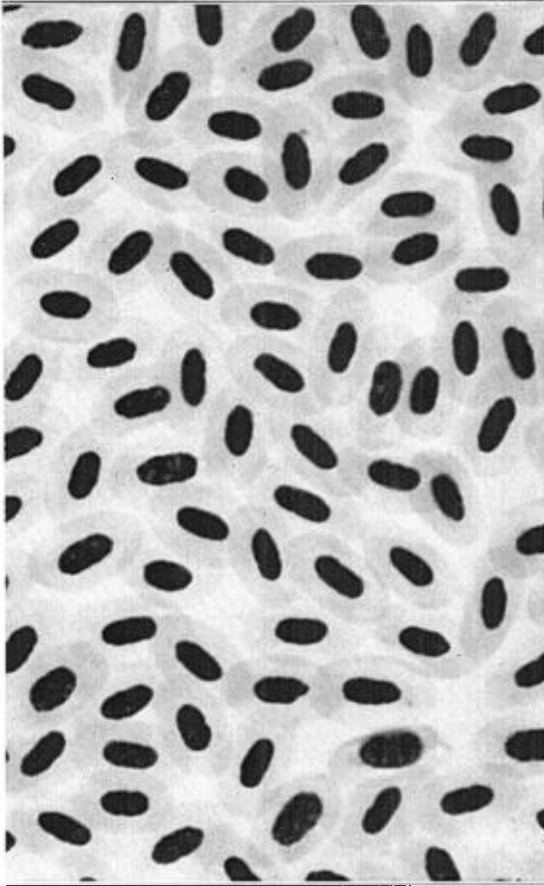
FIGURE 6.   Normal drepaniid blood (oil immersion, 1545×).
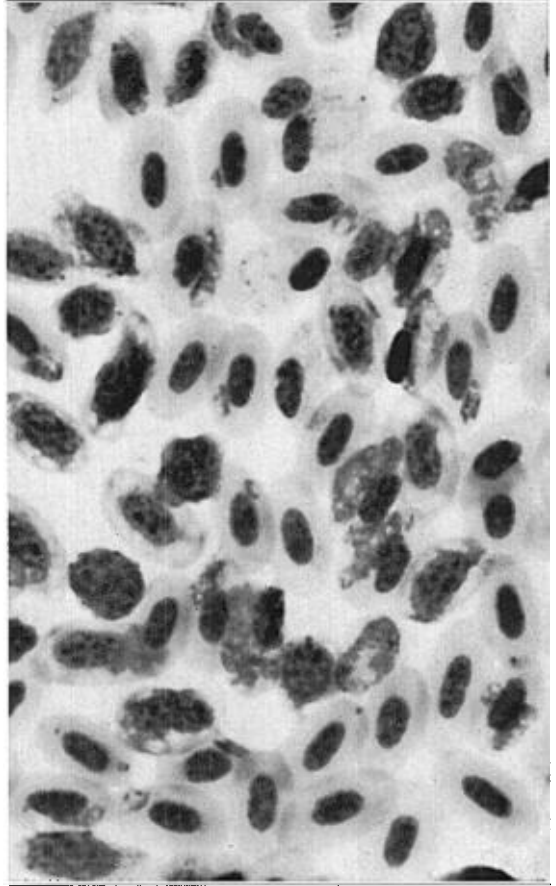


FIGURE 7.   Blood of *Loxops parva* in an early stage of malaria. About 70 per cent of the RBCs contain developing *Plasmodium* schizonts (oil immersion, 1545×).

control group, and a light infection (1.5 per cent) in one member of the exposed group. This particular bird had been showing occasional panting and moderate listlessness. It is clear that (1) avian malaria is not present in the Kauai high-forest drepaniids or in populations of White-eyes with which they are in contact; (2) the drepaniids exhibit a far greater susceptibility to avian malaria than do the White-eyes; and (3) under the conditions of this cage experiment the pathogenicity of *Plasmodium* to the drepaniids is still great enough to be potentially lethal, despite exposure of at least the lower fringes of the drepaniid populations to the pathogen for perhaps 100 years (the exact date of the *Culex* introduction onto Kauai is unknown).

## NONIMMUNOGENETIC FACTORS INFLUENCING SUSCEPTIBILITY

Observations of the birds sleeping at night yielded several significant points. (1) The sleeping posture of the White-eye differs in important ways from that of the drepaniids. The White-eye would almost invariably tuck bill and face into the fluffed back feathers. It also fluffed the breast feathers, and crouched down with belly nearly touching the perch. These actions materially reduced the ability of *Culex* to find exposed soft parts to bite. None of the drepaniids, including the Laysan Finches observed in 1959, slept in this posture. As a consequence the corner of the bill, the

TABLE 2.   Hematology data for Lesser Amakihi in terminal stages of malariaemia.

|  | Lesser Amakihi[a] | Chicken (Averaged)[b] |
|---|---|---|
| Hemoglobin | 1.9 gm/ 100 ml blood | 11.6 mg/100 ml blood |
| Red Blood Cells | 1280 × 10³/mm³ blood | 3400 × 10³/mm³ blood |
| White Blood Cells | 313,000 × 10³/mm³ blood | 25,000 × 10³/mm³ blood |

[a] Tests courtesy of Wilcox Hospital, Lihue, Kauai.
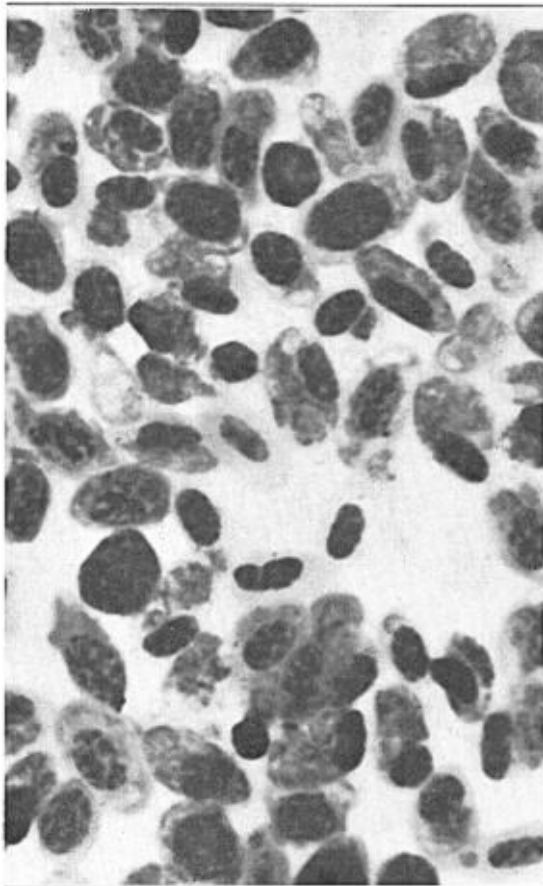[b] Lucas and Jamroz 1961.

FIGURE 8. Blood of *Loxops parva* in the terminal stage of malaria. About 97 per cent of RBCs contain developing *Plasmodium* forms (oil immersion, 1545×).

forehead, and the tarsi were exposed to mosquito attack when the birds were asleep. Mosquitoes could be observed regularly feeding at these exposed points on the drepaniids throughout the night hours. It will be recalled that birdpox lesions were most common in these places in the Laysan Finches studied at Honolulu in 1958. (2) The number of mosquitoes attracted to the sleeping drepaniids was markedly greater than for the White-eyes. Counts of *Culex* resting on the body feathers, perched near the birds' feet, or actually feeding on the drepaniids were five to ten times greater than in White-eyes. On rare occasions a mosquito would be observed feeding on a White-eye, usually on the foot. The mechanism responsible for this substantial difference in attractiveness has not been determined.

## MALARIA IN INTRODUCED BIRD SPECIES IN THE LOWLANDS

While the drepaniid lowland exposure experiment was in progress (August 1961) some lowland passerine forms were sampled for blood parasites. Birds captured in nets near Lihue, Kauai, were bled for peripheral blood smears, examined for ectoparasites and evidence of birdpox lesions, banded, and then released.

Seven White-eyes and 10 House Finches were taken. All had light infections (ca. 1 per cent) of *Plasmodium*. Three House Finches exhibited blood forms suggestive of *Haemoproteus*. These same finches were found to be carrying numbers of parasitic pupiparous flies of the family Hippoboscidae. It has been noted already that these same birds exhibited considerable evidence of present and former birdpox lesions. Toes were missing, and primary indurated swellings were found on feet, legs, bend-of-wings, and head.

## MALARIA IN AN ENDEMIC NONPASSERINE SPECIES

During the summer of 1961 large numbers of the endemic Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*) were observed and reported grounded along the windward beaches of Kauai. Birds were frequently seen along the roadways, usually dead but on occasion alive yet unable to fly. It was at first presumed that occasional birds were being attracted into collision with automobiles at night by the glare of headlamps. However, the number of dead birds found off the roadways and along beaches defied explanation. Thelma Hadley (1961) also reported a similar phenomenon occurring in October 1960.

I made blood smears from a fledged juvenile Dark-rumped Petrel and found a serious case of avian malaria. The bird, although alert, was unable to fly, even when launched into the air by hand.

The Dark-rumped Petrel is endemic to the Hawaiian Islands, and during earlier times nested on all the major islands. It is now known to nest only locally on the higher volcanic slopes of Maui and Hawaii, and probably on Kauai. It is possible that this species and the endemic Newell's Shearwater (*Puffinus newelli*), which is also believed to be virtually extinct, have suffered the same fate as the drepaniids. The Newell's Shearwater, once abundant, was known to nest in burrows on the lower slopes of most or all of the high islands. Thus those portions of the shearwater and petrel populations that had nesting burrows within the "mosquito belt" were in locations eminently suited for exposure to the introduced night mosquito and its various pathogens. The nestlings would be especially vulnerable to mosquito

attack owing to their lack of a dense feather covering and their sedentary behavior. It remains, however, for further studies to clarify the role, if any, of mosquitoes in the reduction of petrel populations.

## PRESENT DISTRIBUTION OF THE DREPANIIDS

Surveys conducted in recent years by myself, Amadon (1950), Baldwin (1953), Richardson and Bowles (1961, 1964), and others have definitely established that the Drepaniidae are now confined to regions above 600 m, and in some instances considerably higher elevations. To date, the causes of the contemporary restriction of drepaniid distribution have been sought primarily in the great modifications undergone by the lowland flora in historic times. As pointed out earlier, most of the native lowland forests have been drastically altered. At middle elevations the forests have been invaded to varying degrees by introduced plants such as the lantana and guava. Even the high forests were virtually all subjected at times to overgrazing and destruction of the understory. Thus it has seemed logical to assume that drepaniids are now limited in their distribution to the intact, or relatively intact, native forests.

However, as noted earlier, some drepaniids were not limited in early historic times to strictly native forest areas or plants. The Ou, the Iiwi, and others were commonly associated with non-native vegetation before 1900. Munro (1944) watched the drepaniid populations of Lanai become progressively more restricted to the high areas even though the lower forest remained intact and virtually undisturbed, a clear indication of distributional changes independent of the vegetation. And recently Richardson and Bowles (1964: 43) reported that several species of endemics on Kauai, including the Elepaio, Amakihi, Lesser Amakihi, Akepa (*Loxops coccinea*), Apapane, and Iiwi:

. . . occur in extensive areas of much-changed native forest, as for example near growths of blackberries, introduced acacias, or karaka (*Corynocarpus*) in the Kokee region; near growths of guava as in the Ka Loko Reservoir area; or in such areas as the upper Wailua River drainage, where the fern *Dicronopteris* has supplanted much of the native plant cover.

In considering this, they were led to comment further:

Perhaps the continued occurrence of numbers of [native] koa or ohia trees in these regions is sufficient to enable these native birds to survive, or even to prosper, as in the case of the apapane particularly.

It is my conclusion, in view of the recent evidence, that the principal reason that the more ubiquitous drepaniids remain strictly in the regions above 600 m is to be found in their continued susceptibility to introduced diseases, principally avian malaria and birdpox. Any protracted visit to the lowland mosquito belt would mean immediate death from infections of *Plasmodium*. Even if some survived the malaria, onset of birdpox would complete the extermination.

There may be unidentified pathogens being transmitted by *Culex* in addition to the two mentioned above. *Culex* is known to be a vector of Japanese B encephalitis (Hodes 1946), St. Louis encephalitis, Western equine encephalitis, and Murray Valley encephalitis, all serious virus diseases of humans that are known to infect birds as well (Chandler 1955). While these viruses are presently not believed to be established in the Hawaiian Islands, their introduction is possible.

Quisenberry and Wallace (1959), in a study of the arthropod-borne virus potentials for Hawaii, have discussed in some detail the possibilities and dangers of such introductions. Dog filariasis, or heartworm, now common in the Hawaiian Islands (Anon. 1953), is also transmitted by *Culex*. Its effects on the drepaniids, if any, are unknown.

A preliminary survey of drepaniid distribution in those few bits of intact native forest that still exist below the 600-m level was made during October and November 1959. One such area is found near Hilo, Hawaii; a second is on the eastern slopes of Haleakela on Maui. Transects up the slopes of these areas demonstrated a rather abrupt lower edge of drepaniid distribution, at about the 600-m level, even though to the eye the character of the forest did not appreciably change. While more study of these interfaces is needed, the pattern of drepaniid distribution in intact near-native forests and its cessation at the upper edge of the *Culex* belt is highly suggestive.

## SELECTION PRESSURES TOWARD IMMUNOGENETIC CAPACITIES IN THE REMNANT AVIFAUNA

Given the conditions of a high-mountain sanctuary, an interface of host-disease interaction at about 600-m elevation, and occasional forays by the host species into the lowlands, it is significant to ask if some degree of immunogenetic capacity might be developing in the remnant populations. The susceptibility experiment using high-forest Kauai birds previously described does not answer this question, primarily because the lowland Kauai

*Culex* population had been reduced by more than 50 per cent in the intervening years since the Laysan Finch susceptibility experiment was conducted. This reduction grossly altered the epidemiological factors of the test situation. Assuming that the remote and isolated Laysan Finch does indeed represent the pre-European immunogenetic capacity of the Drepaniidae, well-controlled quantitative studies could be conducted to evaluate the relative susceptibility of high-island drepaniids and the Laysan Finch to selected pathogens. This has not yet been done.

There is, however, on record one significant observation made in 1961 by Blanche Pedley, a competent amateur ornithologist living in the mauka or upper part of Honolulu. The area under study contains guava, Christmas berry (*Schinus terebinthifolius*), iron woods (*Casuarina* spp.), brassica (*Brassica campestris*), mango, and other introduced plants. The introduced Pekin Nightingale and the endemic Elepaio (Muscicapinae; *Chasiempis sandwichensis*) regularly inhabit the area; less often the introduced Chinese and Shama Thrushes, *Garrulax canorus* and *Copsychus malabaricus*, are present. She reported (Pedley 1961):

About a month ago I began hearing bird calls which I had not heard in these parts before. In a few days I was able to catch fleeting glimpses of small plump greenish birds, some quite yellow. Although I was never able to see white eye-rings, I was sure I must be seeing mejiro [*Zosterops japonicus*]—the birds could not possibly be amakihi! A few days later I saw four or five feeding on the blossoms of thunbergia [*Thunbergia* sp.] vines growing over guava trees within a few feet of our house. Two were also searching for food around clusters of ironwood cones on the tree beside our garage. I was no longer in doubt. They were amakihi.

Since then a day has not passed when I could not see or hear them. They seem to particularly enjoy the thunbergia blossoms. This morning I was delighted to see a flock of at least twenty scolding at each other among the guavas along our driveway and this afternoon, as I sit at my desk writing, I can hear several in the trees just outside my window.

There is at present no unequivocal interpretation of this observation. The Honolulu *Culex* population has been greatly suppressed in recent years. Perhaps this suppression is of enough magnitude that the lower critical level for disease transmission has been reached. It would also not be surprising to find that a degree of historically acquired immunogenetic capacity against avian malaria and birdpox has developed in the Oahu Amakihi. It is an intriguing hypothesis that these two factors may have combined to tip the balance sufficiently to permit recolonization of parts of the lowland habitat. The report additionally corroborates the ability of drepaniids to use introduced plants as food sources.

## DISCUSSION AND CONCLUSIONS

### THE CASE FOR EXTINCTION BY DISEASE

I have reviewed the evidence implicating introduced disease pathogens, principally avian malaria and birdpox, transmitted by the introduced night mosquito *Culex pipiens fatigans* and possibly hippoboscid flies, as major forces in the decline of the endemic Hawaiian avifauna. Consideration of this evidence leads to the following conclusions.

1. For a period of years following discovery of the Hawaiian Islands and the Drepaniidae by Europeans, these birds were observed utilizing habitats from the upper edge of vegetation to the seashores. Certain drepaniids were able to use plant species introduced by the early colonists as food sources. Many drepaniid species exhibited strong altitudinal and regional migrations, both in response to food needs and because of climatological factors.

2. The latent threat of avian malaria and birdpox, sustained by migrating shorebirds and waterfowl that had been infected in their summer habitats, and by domestic avian stock brought in by the colonists, was made active with the accidental introduction of the night-flying mosquito in 1826. The subspecies introduced, *Culex pipiens fatigans*, was the tropical form, and is limited in its distribution to areas below approximately 600 m, creating a mosquito-free sanctuary on those "high" islands having mountain peaks above this elevation.

3. As a consequence of the introduced vector the lowland populations of drepaniids and possibly other endemic bird species suffered recurrent epizootics of malaria, birdpox, and probably other diseases. High-elevation drepaniid populations also contacted the vector during their seasonal migrations to the lowland habitats. The more vulnerable species were swept to extinction by a combination of these epizootics and other changes in their habitats. The extant remnant populations of drepaniids are today limited to regions above the "mosquito belt," which extends to approximately 600–700 m depending upon local topography.

4. Neither malaria nor birdpox is normally present today in the high-elevation drepaniid populations, or in the cohabiting introduced bird species. However, the drepaniids remain highly susceptible to these diseases, dying of

malaria after brief experimental exposure to the lowland environment, even though there has been a drastic reduction in the lowland *Culex* population density as a result of recent control efforts. The drepaniid species examined still lack adequate immunogenetic capacities against either malaria or birdpox, eventually succumbing to the latter if not immediately felled by the former. Evidence indicates that even brief excursions into the lowland habitat would be fatal.

5. The drepaniids lack certain behavioral and possibly physiological nonimmunogenetic defenses against mosquito attack that are possessed by the introduced White-eye.

6. Preliminary evidence suggests that other elements of the native avifauna, especially the ground-nesting shearwaters and petrels, are being adversely affected by malaria. This and other introduced diseases may have played a significant role in the decimation and near-extinction of the endemic Dark-rumped Petrel and Newell's Shearwater.

7. There is some indication that the Oahu Amakihi may be recolonizing certain lowland habitats. However, the present lack of evidence makes it impossible to tell whether this extension of range is resulting from an historically developed immunogenetic capacity against introduced diseases, a reduction in arthropod disease vectors to subcritical densities, or both.

While certain aspects of the general problem will no doubt remain obscure, many of the specifics can now be explained. The hitherto enigmatic abandonment of intact lowland forests and the concomitant extinction of forms having strong altitudinal migration patterns or fixed lowland habitats is clarified. The early and exceptionally rapid extinction of most of the endemic avifauna of Oahu, when viewed in this light, also is explained. This island has extensive areas of low elevations suitable for propagation of *Culex*, a situation compounded by the lack of adequate high-forest sanctuary areas. According to a survey conducted by the Territorial Board of Health (Anon. 1953), Oahu has the greatest acreage of major actual breeding sites of *Culex* of any of the islands. Despite continued control efforts, parts of the island are still plagued with enormous numbers of *Culex*.

As regards the critical high-forest sanctuary areas, Oahu has only one mountain over 1000 m (Mt. Kaala, elevation 1228 m), and but two over 900 m (Palika Peak, elevation 945 m, and an unnamed point of ridge near Puu Konahaunui, elevation 946 m). This ecological vulnerability was compounded by the early

establishment of domestic fowl populations associated with a large and widespread human population. It is therefore not surprising that so few of Oahu's endemic forms survived the onslaught.

PORTENTS OF THE FUTURE

There is nothing man can do to re-establish a species, once it is extinct. The loss of many drepaniid and other endemic forms is irrevocable. Hope persists for those species that now exist as remnant populations in the sanctuaries of the high forests. Neglecting the ill-understood problems consequent to modification of the lowland flora, as selection toward disease-resistant forms continues (as it undoubtedly is at present), the remnant populations will become progressively more able to penetrate into the pestilent lowlands. We may thus witness, within a few decades, the return of more endemic species into the disturbed but potentially habitable lowland forests. Many such potential habitats exist on all the islands, especially in the 150- to 600-m zone at the bases of the mountains.

Unfortunately, this possibility is clouded by the continued introduction of exotic game-birds and other disease carriers into Hawaii. In 1960 alone, 1969 exotic gamebirds of seven different species were imported by the Hawaii Bureau of Game and released into the uplands of the Hawaiian Islands. Several esoteric pathogens have already been brought in by wild turkeys, francolins, and pheasants, including a gapeworm (probably *Syngamus trachea*) and a coccidium. The degree of pathogenicity of such parasites to the endemic avifauna is unknown, although Goble and Kuntz (1945) have demonstrated that many passerines can serve as carriers of gapeworm. In addition, passerines are known to be susceptible to the coccidial *Isospora*. Boughton (in Chandler 1955) has reported references to its occurrence in 173 species of birds, mostly passerines. Judging from the extreme susceptibility of the Drepaniidae to known exotic avian diseases such as malaria and birdpox, the danger is probably very great.

With a few notable exceptions, the Hawaii Department of Fish and Game has in recent years tried to minimize establishment of exotic pathogens through quarantine and prerelease checks. However, current knowledge of avian diseases is rudimentary; adequate diagnostic procedures for many pathogens have yet to be developed. Occult forms of the viral diseases are especially hard to detect. New diseases are continually being found in gamebirds. For example, Rosen and Mathey (1955)

reported five previously unsuspected diseases in California pheasants. They included avian encephalomyelitis, spirochaetosis, Asiatic Newcastle disease, botulism, and visceral lymphomatosis. The first two were found in game farm birds, the third in an imported shipment, and the last two in wild birds. Thus a truly effective quarantine and prerelease checking program is not possible at present. This problem is further amplified by the flow of commercial avian stock into the islands.

The other major latent threat to the remnant endemic avifauna is believed to be the temperate-zone subspecies of the night mosquito, *Culex pipiens pipiens.* This form, while not yet established in the Hawaiian Islands, is abundant in the lowlands of coastal California from Stockton northward. Should it be accidentally introduced into Hawaii before the development in the existing populations of a sufficient immunogenetic capacity against malaria and birdpox, then the high forests will no longer be the ecological sanctuaries they now are. *Culex pipiens pipiens* would very likely be able to invade and reproduce in all but the very highest portions of the wetter forest regions, carrying the seeds of debility and death. Such an event could very well herald the extinction of one of the world's most extraordinary avifaunas.

## SUMMARY

When the Hawaiian Islands were first discovered by Captain James Cook in 1778 the endemic avifauna inhabited all parts of the islands, from the seashore to the upper limits of vegetation. In 1826 the tropical subspecies of the night mosquito, *Culex pipiens fatigans,* was accidentally introduced at Lahaina, Maui. The mosquito rapidly spread to the lowland areas of all the high islands. Epizootics of birdpox and of unidentified debilitating diseases subsequently swept through the lowland bird populations, causing a widespread disappearance of birds from even those forests whose vegetation had not been disturbed by man. Many species became extinct, and the remainder became restricted to elevations above approximately 600 m.

Investigations were begun in 1958 to determine the nature and distribution of these diseases, and to measure the present susceptibility of the Drepaniidae to them. It was found that:

1. Distribution of epidemiologically significant numbers of *Culex p. fatigans* is limited to elevations below about 600 m.

2. The extant drepaniid species are restricted to elevations above 600 m, despite apparently habitable areas at lower elevations.

3. Lowland populations of introduced passerines are regularly infected with birdpox virus, *Plasmodium* (avian malaria), and probably *Haemoproteus.*

4. The remnant drepaniid populations are free of these pathogens, for all practical purposes, due to their isolation in the ecological (mosquito-free) sanctuary of the higher elevations.

5. Four species of drepaniids, three from the high mountain area of Kauai and one from Laysan Island, died immediately from avian malaria and birdpox when experimentally exposed to the lowland environment.

6. Three nights of exposure to the lowland Kauai environment produced lethal cases of avian malaria in the Laysan Finch.

7. The drepaniids exhibited no appreciable immunogenetic capacity against either avian malaria or birdpox, although such resistance may now be developing.

Some considerations of the future of the Drepaniidae are offered. These focus attention on the development of resistance to present diseases and the possible effects of the introduction of new pathogens and new vectors.

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I would like to dedicate this report to the Hawaii Audubon Society, in acknowledgment of its consistent efforts toward preservation of Hawaii's remarkable avian heritage.

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