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Author(s): Carter T. Atkinson MS, PhD and Dennis A. LaPointe MS, PhD

Source: Journal of Avian Medicine and Surgery, 23(1):53-63. 2009.

Published By: Association of Avian Veterinarians

DOI: <http://dx.doi.org/10.1647/2008-059.1>

URL: <http://www.bioone.org/doi/full/10.1647/2008-059.1>

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Historical Perspective

Introduced Avian Diseases, Climate Change, and the Future of Hawaiian Honeycreepers

Carter T. Atkinson, MS, PhD, and Dennis A. LaPointe, MS, PhD

Introduction

The Hawaiian archipelago is isolated in the central Pacific and consists of 7 large islands and a chain of low coral atolls and small rocky islets that extend in a long arc from Hawaii Island in the southeast to Kure Atoll in the northwest. The archipelago is the most isolated island system in the world, separated from the nearest continental landmass by more than 2000 miles of ocean.¹ The islands range in elevation from just above sea level for atolls in the Northwestern Hawaiian Islands to peaks that exceed 4000 m on Hawaii Island. The interaction of extreme topographic relief, trade winds, and local climatic patterns creates a wide diversity of habitats, ranging from alpine deserts on the highest peaks to montane rain forests with precipitation exceeding 7600 mm per year.

The endemic passerine avifauna of the Hawaiian Islands, particularly the endemic Hawaiian honeycreepers (subfamily Drepanidinae) is often heralded as an outstanding example of adaptive radiation, equal to Darwin's finches from the Galapagos Islands in terms of diversity of bill types and number of species that descended from a common founder.² From an initial colonization by only a few individuals of a single ancestral cardueline finch, this group radiated throughout the diverse habitats on the islands, specializing on a variety of food resources that included nectar, fruits, and insects. Based on recent studies of subfossils, the diversity of this group may have reached 20 genera with more than 50 species prior to human contact with the islands.³ Remarkably, a new genus and species of honeycreeper, the po'ouli (*Melamprosops phaeosoma*), was described in the 1970s from remote rain forests on Maui.⁴

Today, the endemic Hawaiian avifauna faces one of the highest rates of extinction in the world.

Of 41 species and subspecies of honeycreepers known since historic times,⁵ 17 are thought to be extinct and 14 are federally listed as endangered.⁶ Only 3 species and subspecies, Hawaii 'amakihi (*Hemignathus virens virens*), Maui 'amakihi (*Hemignathus virens wilsoni*), and 'apapane (*Himatione sanguinea*) are robust enough in terms of geographic range and population size to be of minimal concern (Table 1). Reasons for these declines are complex and include a suite of interacting factors, including habitat degradation and loss from human activities and invasive species, introduced predators, introduced avian competitors, and introduced avian diseases and disease vectors.

Although the interactions among these various limiting factors makes it difficult to determine their relative impacts on native forest bird populations, it is clear that the abundance, diversity, and geographic distribution of Hawaii's native birds changed significantly after the arrival of mosquitoes, avian malaria, and poxvirus.^{7–10} Other indigenous and introduced pathogens and diseases do not appear to have had the population-level impacts of avian malaria and pox. These include *Toxoplasma gondii* from 'alalâ (*Corvus hawaiiensis*), nêhê (*Branta sandvicensis*), and wild game birds^{11,12}; erysipelas (*Erysipelothrix rhusiopathiae*) from 'alalâ¹³; echinuriasis (*Echinuria uncinata*) from Laysan teal (*Anas laysanensis*)¹⁴; and sporadic outbreaks of avian botulism (*Clostridium botulinum*) from water birds on O'ahu and Hawaii islands and most recently from Laysan teal on Midway Island (National Wildlife Health Center, unpublished data, December 2008).

History and Origins of Avian Malaria and Pox in Hawaii

Avian malaria is a disease caused by intracellular, mosquito-transmitted protozoan parasites in the genus *Plasmodium*. These parasites have a

From the US Geological Survey Pacific Island Ecosystems Research Center, Kilauea Field Station, PO Box 44, Hawaii National Park, HI 96718, USA.

Table 1. Status of species and subspecies of Hawaiian honeycreepers (Drepanidinae) known from historic times. Compiled from Scott et al,⁵ US Fish and Wildlife Service,⁶ Leonard,⁷² and the IUCN Red List.⁷³

Common name	Scientific name	IUCN status	Federal status
Lāna`i hookbill	<i>Dysmorodrepanis munroi</i>	extinct	extinct
Lesser koa-finch	<i>Rhodacanthis faviceps</i>	extinct	extinct
Greater koa-finch	<i>Rhodacanthis palmeri</i>	extinct	extinct
Kona grosbeak	<i>Chloridops kona</i>	extinct	extinct
Greater `amakihi	<i>Hemignathus sagittirostris</i>	extinct	extinct
Lesser `akialoa	<i>Hemignathus obscurus</i>	extinct	extinct
O`ahu `akialoa	<i>Hemignathus ellisianus ellisianus</i>	extinct	extinct
Lanā i `akialoa	<i>Hemignathus ellisianus lanaiensis</i>	extinct	extinct
O`ahu nukupu`u	<i>Hemignathus lucidus lucidus</i>	extinct	extinct
O`ahu `alauahio	<i>Paroreomyza maculata</i>	critically endangered	extinct
Kākāwahie	<i>Paroreomyza flammea</i>	extinct	extinct
Lana`i `alauahio	<i>Paroreomyza montana montana</i>	nd	extinct
O`ahu `ākepa	<i>Loxops coccineus wolstenholmei</i>	nd	extinct
Ula-`ai-hawane	<i>Ciridops anna</i>	extinct	extinct
Hawaii mamo	<i>Drepanis pacifica</i>	extinct	extinct
Black mamo	<i>Drepanis funerea</i>	extinct	extinct
Laysan honeycreeper	<i>Himatione sanguinea freethii</i>	nd	extinct
`Ōū	<i>Psittirostra psittacea</i>	critically endangered	endangered ^a
Kaua`i `akialoa	<i>Hemignathus ellisianus procerus</i>	extinct	endangered ^a
Kaua`i nukupu`u	<i>Hemignathus lucidus hanapepe</i>	critically endangered	endangered ^a
Maui nukupu`u	<i>Hemignathus lucidus affinis</i>	critically endangered	endangered ^a
Maui `ākepa	<i>Loxops coccineus ochraceus</i>	endangered	endangered ^a
Pōouli	<i>Melanprosops phaeosoma</i>	critically endangered	endangered ^a
Laysan finch	<i>Telespiza cantans</i>	vulnerable	endangered
Nihoa finch	<i>Telespiza ultima</i>	critically endangered	endangered
Palila	<i>Loxioides bailleui</i>	endangered	endangered
Maui parrotbill	<i>Pseudonestor xanthophrys</i>	critically endangered	endangered
`Akiapōlā`au	<i>Hemignathus munroi</i>	endangered	endangered
Hawaii creeper	<i>Oreomystis mana</i>	endangered	endangered
Hawaii `ākepa	<i>Loxops coccineus coccineus</i>	endangered	endangered
`Ākohekohe	<i>Palmeria dolei</i>	critically endangered	endangered
`Akikiki	<i>Oreomystis bairdi</i>	critically endangered	candidate for listing
`Akeke`e	<i>Loxops caeruleirostris</i>	critically endangered	not listed
Hawaii `amakihi	<i>Hemignathus virens virens</i>	least concern	not listed
Maui `amakihi	<i>Hemignathus virens wilsoni</i>	least concern	not listed
O`ahu `amakihi	<i>Hemignathus flavus</i>	vulnerable	not listed
Kaua`i `amakihi	<i>Hemignathus kauaiensis</i>	vulnerable	not listed
`Anianiau	<i>Hemignathus parvus</i>	vulnerable	not listed
Maui `alauahio	<i>Paroreomyza montana newtoni</i>	endangered	not listed
`Iiwi	<i>Vestiaria coccinea</i>	vulnerable	not listed
`Apapane	<i>Himatione sanguinea sanguinea</i>	least concern	not listed

Abbreviations: IUCN indicates International Union for Conservation of Nature and Natural Resources; nd, no data reported.

^a No confirmed sightings in recent years, possibly extinct.

worldwide distribution in multiple avian families but occur primarily in passerine birds.^{15,16} More than 40 species of *Plasmodium* have been described, but they are rarely associated with epidemic disease.^{17,18} Avian pox (*Avipoxvirus* species), by contrast, is a viral infection caused by a large, double-stranded DNA virus that typically causes tumor-like swellings on exposed

skin or diphtheritic lesions on the mouth, trachea, and esophagus of infected birds. It can be transmitted mechanically through contact with infected objects or on the mouth parts of blood-sucking arthropods. The 13 different species currently recognized are defined by host associations ranging from the genus to the family level.^{19,20} Epidemic outbreaks of pox in wild

passerine birds and gallinaceous birds are not uncommon and have also been reported in wild turkeys (*Meleagris gallopavo*),²¹ Galapagos finches,²² and endemic birds in the Canary Islands.²³ The broad host range of both avian pox and avian malaria makes them particularly well suited for invading new areas.

The dates when avian malaria and pox were introduced to the islands remain unknown. However, from the descriptions of tumor-like swellings on dead or moribund forest birds by late 19th-century naturalists²⁴ and the recent polymerase chain reaction (PCR) amplification of poxvirus sequences from museum specimens collected during that period,²⁵ *Avipoxvirus* clearly was well established in native forest bird populations by the late 1800s. Although domestic poultry had long been assumed to be the most likely source of the virus in Hawaii, the 2 or more genetically distinct variants of the virus circulating in native forest birds are distinct from fowlpox and have strong similarities to canarypox.^{25–27}

The most likely opportunity for introduction of avian malaria was in the early 20th century, when local bird clubs introduced nonnative passerine birds from around the world to replace low-elevation native birds that were vanishing from pox infection and other limiting factors. More than 100 documented introductions of passerine birds from Southeast Asia, North and South America, and Africa were made between 1900 and the 1960s, with more than 50 species becoming established here.²⁸ It is unlikely that any of these birds were screened for infectious diseases and the number of avian pathogens that may have been inadvertently introduced remains unknown.^{29,30}

Unlike the externally evident lesions of pox infection, the more cryptic *Plasmodium* infections were first detected in the 1930s by blood smear in a red-billed leiothrix (*Leiothrix lutea*) and a Japanese white-eye (*Zosterops japonica*) collected at Hawaii Volcanoes National Park.^{31,32} Considerable initial confusion existed about which species of *Plasmodium* had been introduced to Hawaii, or whether multiple species were present, because the erythrocytic stages of these parasites have so few distinguishing morphologic features.³³ A detailed study of blood smears from native and nonnative species across the state concluded that only a single species of *Plasmodium* was present and that it was most similar to *Plasmodium relictum capistranoae*.³³ More recently, molecular work has supported identification of *P. relictum* as the sole species of *Plasmodium* in Hawaii. Only a single lineage of this parasite is currently in

Hawaii, with possible origins from birds that were introduced from the Old World.³⁴ In spite of the likely origin of *P. relictum* from one or more of these introduced species, these species no longer appear to be the primary reservoirs of infection. Surveys conducted during the past 30 years have consistently identified the highest prevalence of infection in native, rather than introduced, forest birds.^{8,35–37}

The first epidemiologic studies of avian malaria were conducted in lowland habitats near Līhu'e, Kaua'i in the 1950s.⁷ Laysan finches (*Telespiza cantans*), 'apapane, Kaua'i 'amakihi (*Hemignathus kauaiensis*), and 'anianiau (*Hemignathus parvus*) were exposed to local mosquitoes in unscreened cages and subsequently died from fulminating pox and malarial infections. This simple but convincing demonstration of local disease transmission and pathogenicity became the cornerstone for more detailed ecologic studies in the 1970s, which documented widespread occurrence of malaria in native forest birds on the island of Hawaii.⁸

The Role of Pox and Malaria in the Decline and Extinction of Hawaiian Birds

There is little direct evidence implicating avian pox and malaria in the extinction of any Hawaiian bird, even though it is often cited as a primary factor in the demise of the endemic avifauna. It has been suggested that the major waves of extinction that occurred in the late 1800s and again after 1910 follow the presumed introduction of avian pox and malaria.^{8,9} However, the anecdotal observations by early naturalists and the absence of any comprehensive surveys of native birds or avian disease before the 1970s make this difficult to confirm.

The most convincing indirect evidence that avian pox and malaria have had a major impact on forest bird populations is their strong negative correlation with extant native birds. Warner was the first to draw a parallel between declines in native bird populations at lower elevations and the presence of mosquitoes and the pathogens they transmit.⁷ He suggested that mosquito populations declined precipitously above 600 m. Later work documented occurrence of the vector as high as 2500 m, but also supported Warner's basic idea by demonstrating a negative association between mosquito numbers and native birds at elevations below 1500 m.^{8,38,39}

The high susceptibility of native honeycreepers to avian malaria and pox also provides strong

circumstantial evidence that these diseases have had substantial impacts on wild populations. Native birds with naturally acquired infection may have parasitemia involving more than 95% of circulating erythrocytes, acute anemia with packed cell volumes as low as 16%, and rapid deterioration of body condition, with mortality rates ranging from 40% to almost 100% between 5 and 15 days after exposure.⁷

More recent studies have conducted experimental malarial infections in native and nonnative birds using single and multiple mosquito bites to mimic natural transmission.⁴⁰⁻⁴³ Declines in food consumption and loss of body mass began approximately 1 week after exposure to single infective mosquito bites in 'i'iwi (*Vestiaria coccinea*),⁴⁰ Hawaii 'amakihi,⁴¹ Maui 'alauahio (*Paroreomyza montana newtoni*),⁴² and 'apapane.⁴³ These declines correlated closely with increases in numbers of erythrocytic parasites in the peripheral circulation. Survivorship was relatively high in infected 'apapane and Hawaii 'amakihi with up to 30% developing low-intensity chronic infections that stimulated immunity to reinfection when challenged with multiple infective mosquito bites. The effects were much more severe in 'i'iwi; individuals of this species had significantly higher mortality (90%) and peak parasitemias at death. Gross and microscopic lesions were also more severe in 'i'iwi. Results of necropsy and histopathologic examination revealed massive enlargement of the liver and spleen with extensive deposition of malarial pigment and diffuse extramedullary erythropoiesis in the liver and kidneys. Mature erythrocytes were replaced almost entirely by immature erythrocytes and precursors that are normally found only in bone marrow. By contrast, it was difficult to infect nonnative species with single infective mosquito bites; parasitemias were low and clinical signs of infection were not evident.

One of 2 extant species of native thrush, 'ōma'ō (*Myadestes obscurus*), also appears to be relatively resistant to malaria. Four birds did not develop clinical signs of disease when exposed to single infectious mosquito bites and birds also recovered from acute infections.⁴² The native monarch flycatchers, Hawaii 'elepaio (*Chasiempis sandwichensis sandwichensis*) and O'ahu 'elepaio (*Chasiempis sandwichensis gayi*), also appear to have some resistance to malaria, based on their current altitudinal distribution and occasionally high abundance in some mid- and low-elevation habitats where disease prevalence is high. This is particularly true on O'ahu, where O'ahu 'elepaio

occur almost exclusively in extensively modified low-elevation forests with high mosquito densities.⁴⁴

Unlike avian malaria, relatively little is known about the pathogenesis of avian poxvirus in Hawaiian forest birds, and the report by Warner still provides some of the best documentation about the course of infection and pathogenicity of the virus in native birds.⁷ Twenty-four Laysan finches were exposed to mosquitoes in downtown Honolulu after keeping their cage wrapped in mosquito-proof cheesecloth for 2 months. Within 2 weeks after the protective cheesecloth was removed, 6 finches developed indurated swellings on the lores and tarsal and wing joints where mosquitoes had access to exposed skin. The swellings increased in size and then erupted into granular, tumor-like lesions that became necrotic with accompanying secondary bacterial infections. As tumors progressed in severity they tended to bleed, particularly from the foot lesions. By the end of 1 month of exposure, every finch had at least one lesion. Death occurred over a variable period of time after birds lost body condition and lesions became necrotic.

More recently, molecular characterization and experimental infections have revealed 2 genetically distinct variants of poxvirus that differ significantly in virulence.²⁵ Both variants caused lesions when inoculated into the foot pads of Hawaii 'amakihi, but size and severity of the lesions differed. Lesions associated with variant 1 were relatively small and self-limiting, whereas those associated with variant 2 were large, bloody, proliferative, and ultimately fatal in 4 experimentally infected birds. Both variants were isolated from Hawaii 'amakihi from Kilauea Volcano, but phylogenetic analyses based on sequence of the virus 4b core protein grouped variant 1 closely with canarypox whereas variant 2 clustered in a different, but closely related clade. Hawaii 'amakihi that recovered from infection with variant 1 were not immune to subsequent challenge with variant 2. This agrees well with field observations of recurring pox infections in some recaptured birds that have healed lesions. These findings also raise questions about the temporal and spatial dynamics of virus transmission in wild birds and suggest that interactions between genetically and biologically distinct poxviruses, their susceptible hosts, and concurrent malarial infections may play important roles in determining severity of epidemics.

Other than these limited experimental studies, information about the potential impact of poxvi-

rus on Hawaiian forest bird populations is based on observations of pox-like lesions on captured wild birds. Although these studies are limited by the presumptive nature of the diagnosis, it has been argued that most pox-like lesions are likely to be caused by poxvirus. In one study, virus was recovered from 20 of 22 pox-like lesions from wild Hawaiian birds.⁹ Using a presumptive diagnosis based on presence or absence of tumor-like swellings or missing digits, results of another study found declines in numbers of some breeding Hawaii `elepaio that were correlated with the occurrence of pox epidemics.⁴⁵ Preliminary observations of O`ahu `elepaio suggest that annual mortality of birds with active lesions is up to 40%, whereas birds with mild infections involving only one or more toes frequently recover.^{45,46}

Recent work also indicates that prevalence of malaria in O`ahu `elepaio is extremely high with an average infection rate of 87% in birds that were sampled between 1995 and 2005.⁴⁴ Pox and malaria infection appeared to be independent of each other in this study, whereas in other field studies in Hawaii, birds with pox-like lesions are infected with concurrent malarial infections more frequently than expected by chance.^{8,36} Although this suggests that the 2 diseases interact with each other, we know little about whether this apparent interaction is caused by simultaneous transmission of the diseases by the vector or by differential mortality among pox-infected, malaria-infected, or coinfecting birds or whether it is simply a reflection of the longer exposure that birds with chronic malaria would have to potential pox infections. The high frequency of concurrent pox and malaria infections makes it extremely difficult to identify demographic effects of either agent alone.

Vector Abundance and Transmission Across Altitudinal Gradients

A model has been proposed that depicts transmission of avian pox and malaria across an altitudinal gradient on Mauna Loa and Kilauea volcanoes.^{8,9} This model places the highest rates of malaria and pox transmission in midelevation (1200 m) forests where the declining numbers of mosquitoes between sea level and tree line overlaps with increasing numbers of native forest birds at elevations above 1000 m.⁸ Disease transmission disappears at elevations above 1500 m when mosquito populations fall to low levels, creating high elevation "refugia" from avian malaria.

The presence or absence of mosquitoes and their relationships to native bird distribution was first quantified by Scott et al³⁸ who found that threatened and endangered passerine birds were less abundant in areas with detectable mosquito populations and reached their greatest densities at altitudes higher than 1500 m. These observations are consistent with the uncommon occurrence of Maui `alauahio and `i`iwi below elevations of 1500 m; these are 2 species in which mortality exceeded 75% after exposure to single infective mosquito bites.^{40,42} These findings are also consistent with laboratory studies that demonstrate thermal constraints on sporogonic development of *P. relictum* in experimentally infected *Culex quinquefasciatus*.⁴⁷ Sporogonic development of the parasite dramatically slows at 15°C and ceases at 13°C. The 15°C isotherm in Hawaii closely follows the 1500-m contour line and high-elevation refugia may also be maintained by thermal limits on malarial development.

At elevations below 1500 m, the key factor driving epizootics of pox and malaria is the seasonal and altitudinal distribution and density of *C. quinquefasciatus*. The important role of this mosquito species in the epidemiology of malaria transmission has been supported by identification of infected individuals in the wild during periods of peak disease transmission and by laboratory experiments that have demonstrated that *C. quinquefasciatus* is several orders of magnitude more susceptible to the parasite than other introduced mosquito species.^{8,48,49} The dynamics of vector populations on the east flank of Mauna Loa and Kilauea volcanoes has been recently modeled, illustrating the dependence of vector populations on both temperature and rainfall and the seasonal fluctuations of vector populations across altitudinal gradients.⁵⁰ Peak mosquito populations occur at elevations between 1200 and 1500 m during the warmer fall months of September to December.⁴⁷ It is during this time of the year that seasonal epidemics of malaria and pox transmission are common (C. T. A., unpublished data, 1991–1998).

Other than the early mosquito exposure experiments by Warner,⁷ little research has been conducted on the prevalence and transmission of these diseases in habitats below 600 m. Shehata et al⁵¹ and VanderWerf⁴⁶ measured prevalence of malarial and pox infections in lowland bird communities on O`ahu but did not study vector populations or measure transmission rates. Prevalence of malarial infections in O`ahu `amakihi captured in Mānoa Valley were surprisingly low,

with only 1 of 16 (6.3%) birds positive for malaria by serologic methods and none of 42 individuals positive by PCR.⁵¹ Prevalence in a sample of 268 nonnative birds from the same area was 11.6% by PCR, suggesting that the O'ahu 'amakihi may have some refractoriness to infection. Without information about vector populations or transmission rates, however, it is difficult to rule out alternative explanations, including whether the birds were immune survivors of a previous infection with parasitemias too low to be detected by PCR, or whether they were simply not exposed to infective mosquito bites.^{51,52}

On Hawaii Island, recently emergent populations of Hawaii 'amakihi have been found in remnant patches of 'ôhi'a (*Metrosideros polymorpha*) forest in the Puna district at elevations below 300 m.^{49,53} These populations are expanding in range at densities that exceed those of Hawaii 'amakihi at elevations above 1500 m on Mauna Loa Volcano. These populations are increasing in spite of prevalences of infection that range from 55% to 83% by serologic methods.⁴⁹ Unlike the apparently *Plasmodium*-refractory O'ahu 'amakihi, these lowland Hawaii 'amakihi appear to be more resistant to the pathologic effects of malarial infection and have unique nuclear and mitochondrial haplotypes that are not found in 'amakihi from high elevation.⁵⁴ Analysis of museum specimens of low-elevation 'amakihi collected between 1898 and 1948, just before the presumed introduction of malaria to Hawaii, identified the same unique haplotypes present today, suggesting that the recent resurgence of these birds originated from pockets of surviving individuals with some natural disease resistance, rather than recolonization of the lowlands by high elevation birds.⁵⁴ Low-elevation Hawaii 'amakihi have also been recognized in areas of East Maui at 300 m elevation and almost at sea level in Pelekunu Valley on Moloka'i (C. T. A., unpublished data, 2003). Similar to Hawaii Island, prevalence of infection in low-elevation 'amakihi on Moloka'i exceeds 75% (C. T. A., unpublished data, 2003), suggesting that selection for disease resistance has occurred on other islands as well.

Dynamics of Epidemic Outbreaks

When highly virulent pathogens are introduced into naïve populations, epizootics can spread rapidly and have major demographic impacts over wide geographic areas. Based on what we know about the high susceptibility of honeycreepers to malaria from both laboratory and field

studies, it seems likely that malaria swept rapidly across all of the lower Hawaiian Islands after it was introduced, leaving few survivors. The cool, high-elevation mountains of Kaua'i, Maui, and Hawaii not only provided the only refugia from the diseases, but also fueled high rates of disease transmission at middle elevations by providing a continuous source of highly susceptible native birds. Disease transmission at middle elevations is fueled every fall by increasing mosquito populations and a seasonal influx of dispersing, susceptible birds from higher elevations.

The recent emergence of low-elevation 'amakihi populations suggest that the system is evolving at different rates because of variation in selective pressure across the altitudinal gradient.^{49,54} With transmission occurring year round at lower elevations, and low-elevation populations not being continually diluted by emigrating, highly susceptible juvenile birds from high elevations, it might be predicted that disease resistance would first appear here. This suggests that disease resistance may subsequently spread over the next few decades, with eventual recovery of midelevation populations of the more resistant species. Although this predicted scenario is encouraging for the more common native species that currently have the widest distribution, there is concern that threatened and endangered species may not have sufficient genetic variability to adapt to these diseases.

Global Warming and Its Impact on Hawaiian Disease Ecology

The ecology of pox and malaria transmission in Hawaii depends on climatic conditions—primarily seasonal changes in temperature and rainfall that drive vector populations.⁴⁹ These environmental factors may be responsible for persistence of high-elevation refugia on the higher islands. The effects of a 2°C warming on the altitudinal location of the 13°C and 17°C isotherms have been modeled. These isotherms delineate a high-risk zone for malaria transmission (below the 17°C isotherm), a transition zone with seasonal epizootic transmission (between the 17°C and 13°C isotherms), and a low-risk zone for transmission (above the 13°C isotherm) where thermal constraints inhibit complete development of the parasite in the mosquito vector. Given habitat limitations by current land use and following a projected 2°C temperature rise, available high-elevation forest habitat in the low-risk zone is predicted to decline by 57% at Hanawâ Natural



Figure 1. Aerial photograph of the windward, eastern slope of Mauna Kea Volcano on the island of Hawaii. Native forest below 600 m has mostly been lost to intensive agricultural development. Although extensive tracts of native forest persist between 600 m and tree line at approximately 2000 m, they are threatened by invasive species. High-elevation disease refugia on Mauna Kea are limited on the eastern side of the mountain to a narrow band of forest above 1500 m that is capped by both the inversion layer and by degradation and loss of forest cover by ranching. High-elevation refugia provide a safe haven from disease transmission for threatened and endangered species such as the *ʻakiapōlāʻau*, Hawaii creeper, and Hawaii *ʻākepa*, but also provide a source of uninfected juvenile and adult honeycreepers that help to maintain seasonal epidemics of malaria and pox at elevations below 1500 m. In a warming climate, high-elevation populations of Hawaii's most endangered birds may be threatened by expanding disease transmission, particularly if upward expansion of critical forest habitat is capped by a stable inversion layer or land-use practices such as cattle ranching.

Area Reserve on Maui Island to as much as 96% at Hakalau Forest National Wildlife Refuge on Hawaii Island. The Alaka'i Wilderness Preserve on Kaua'i Island currently has no areas in the low-risk zone for malaria transmission because the highest elevation is less than 1800 m, but it would experience an 85% loss of forested habitat where transmission is highly seasonal to conditions where transmission could occur throughout most of the year.

If climatic changes occur slowly, the tree line and forest bird habitat might be able to keep pace with warming temperatures, slowly moving up the

sides of the high volcanoes on Hawaii and Maui and allowing the lower limits of high-elevation refugia to continue to remain above disease transmission.⁵⁵ Recent analyses of climatic data from Hawaii indicate that temperatures have shown a significant upward trend over the past 80 years, but disease transmission may be influenced by more than a general warming trend.

The tropical inversion layer may play a more significant role than temperature in determining tree line and the upper extent of forest bird habitat in the Hawaiian Islands.⁵⁶ Often visible as a thin layer of clouds around higher peaks, the inversion layer forms as cool, dry air descends and meets warm, moist air that is driven upward by convection currents, prevailing trade winds, and topographic relief.⁵⁷ As these air masses meet, they form an inversion layer that caps moisture and cloud development between 1800 and 2400 m. The inversion layer has remained relatively stable in height but has increased in frequency of occurrence during the past 25 years.^{56,58} Although it is difficult to predict whether this trend will continue, it suggests that changes in the base height of the inversion layer may ultimately have a substantial impact on the persistence of high-elevation disease refugia. If a stable inversion layer and its effect on rainfall prevents expansion of forest bird habitat into higher elevations, remaining high-elevation forest bird populations may be squeezed between expanding disease transmission from lower elevations and the upper limits of suitable habitat (Fig 1). These changes would likely push remaining populations of threatened and endangered honeycreepers to extinction, and cause severe declines in nonendangered species such as *ʻiʻiwi* and Maui *ʻalauahio* that exhibit high susceptibility to avian malaria.

Prospects for Intervention

Without question, the one factor that prevented widespread and rapid extinction of virtually all of Hawaii's endemic and highly susceptible honeycreepers after the introduction of these diseases was the presence of significant altitudinal gradients on Kaua'i, Maui, and Hawaii, where susceptible native birds could maintain high populations in relatively disease-free refugia. While providing havens where rarer species can still persist, these high-elevation refugia also set up conditions for maintaining high rates of epidemic transmission of the parasite in adjacent midelevation habitats, through seasonal move-

ment of susceptible, dispersing juvenile birds and through altitudinal movement of susceptible adults as they follow nectar resources.⁵⁹

Given the likelihood of global warming, management of midelevation habitats to try to reduce disease transmission is becoming increasingly important. The best opportunities for doing this will probably come through reduction of mosquito larval habitat. Feral pigs and other ungulates can create larval habitat in forest habitats and their removal through fencing and control programs may significantly reduce mosquito habitat, particularly on Kilauea and Mauna Loa Volcanoes on the Island of Hawaii, where volcanic soils are porous and streams and natural bodies of water are rare (C. T. A., unpublished data, 1995).⁴⁷ Management of man-made water sources on ranch lands and agricultural operations and elimination of standing water sources that provide habitats for mosquitoes in residential areas adjacent to natural areas are also practical things that can be done to reduce mosquito numbers.^{60,61} One key factor to consider when determining the scale of these efforts is the ability of *C. quinquefasciatus* to disperse up to 3 km through closed-canopy forests,⁶² making it essential to control mosquitoes in buffer zones around critical mid- and high-elevation habitats. The formation of conservation or watershed partnerships, such as the Three Mountain Alliance on Hawaii Island⁶³ and the West Maui Mountains Watershed Partnership,⁶⁴ has brought together tracts of public and private land under a unified resource management that may allow for effective landscape level control of avian disease.

There will likely be an important place for vaccines and chemotherapy for management of avian pox and malaria during translocation or release of captive birds or management of small populations of critically endangered forest birds,⁶⁵ but there is currently no effective technology for delivering them to large numbers of wild birds to interrupt disease transmission. Although experimental DNA vaccines have been developed for avian malaria and canarypox vaccines are commercially available, these tools have not yet been applied in Hawaii and their safety and efficacy in Hawaiian forest birds need to be determined.⁶⁶ Similarly, the recent interest in development of transgenic mosquitoes to reduce their competency as vectors of *Plasmodium* may eventually have important applications in Hawaii, but there are still significant technical and regulatory issues that need to be overcome before this becomes a reality.⁶⁷

Preservation of remaining low-elevation forests may be one of the most cost-effective strategies for long-term sustainability of more common endemic species, but this will do little or no good for rare species that may be on the verge of losing uncommon genetic haplotypes that may be needed for disease resistance. Given the threat of global climate change, it will become increasingly important to ensure that threatened and endangered species have the inherent genetic variability to allow selection for disease resistance under natural conditions. This requires continued protection and management of existing populations to prevent further loss of rare alleles and use of captive propagation and translocations to help manage remaining genetic diversity.

The recent increase in watershed partnerships in the Hawaiian Islands to manage and restore increasingly large areas of mid- and high-elevation habitats for native species,⁶⁸ the investment during the past decade in captive propagation facilities and expertise for some of the rarest species in Hawaii,⁶⁹ the development of methods for translocating and releasing endemic forest birds,⁷⁰ and the steady movement toward development and application of predator control strategies for large areas of native forest⁷¹ are all important developments during the past decade that will help to prevent further extinctions of Hawaii's endemic avifauna.

Conclusion

The effects of avian malaria and poxvirus on native Hawaiian birds have become a classic example of the potential impacts of introduced diseases on naïve wildlife populations. These diseases continue to be an important example of what can go wrong when pathogens and vectors are moved outside of their natural ranges. Although the road to recovery for some species will be long and challenging, some of the more common species such as 'amakihi and 'apapane have proven to be remarkably adaptable to change. Their survival into the next century may ultimately depend on our ability to remove or mitigate introduced threats and restore native forests from sea level to tree line.⁷²

Acknowledgments: We thank the US Geological Survey Wildlife and Invasive Species programs, the US Geological Survey-Natural Resource Protection Program and the National Science Foundation (DEB0083944) for the financial support that made this research possible. The collection of data for various

studies described here would not have been possible without the assistance and support of numerous technical staff, coworkers, and student interns who spent many long days in the field and laboratory under often-difficult living and working conditions.

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