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DISTRIBUTION AND PREVALENCE OF MOSQUITO-BORNE DISEASES IN O'AHU 'ELEPAIO

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Abstract. The endemic Hawaiian avifauna is one of the most imperiled on earth, and diseases have been one of the most serious causes of species declines. From 1995–2005, we mist-netted and banded 266 endangered O'ahu 'Elepaio (*Chasiempis sandwichensis ibidis*) from 27 sites, examined them for visible symptoms of avian pox virus (*Poxvirus avium*), and screened blood samples for avian malaria (*Plasmodium relictum*). Pox-like lesions and malaria were found in all 'Elepaio populations on O'ahu; no parts of the island were free of these mosquito-borne diseases. Each year, 20% ± 4% of 'Elepaio had active lesions likely caused by pox and an additional 16% ± 4% had deformities and missing toes indicative of healed pox lesions. Prevalence of malaria was 87% over all years combined. Pox prevalence varied among years and was associated with annual rainfall, presumably due to greater abundance of mosquito breeding sites in wet years. Rainfall amounts at least as high as those associated with pox epizootics in 1996 and 2004 have occurred in 13 years since 1947, or once every 4.5 years. Severity of infection varied considerably among birds, and infections involving three or more toes, the feet, or the head were less common in birds with healed lesions than those with active lesions, suggesting such infections resulted in mortality more often. Disease resistance may be evolving in some areas, but 'Elepaio populations on O'ahu are likely to further decline.

Key words: Chasiempis sandwichensis*, disease, 'Elepaio, Hawai'i, malaria, mosquito, pox virus.*

Distribución y Prevalencia de Enfermedades Transmitidas por Mosquitos en *Chasiempis sandwichensis ibidis* de O'ahu

Resumen. La avifauna endémica de Hawai es una de las faunas que está en mayor peligro en el mundo, y las enfermedades han sido una de las causas más importantes de la disminución de especies. Entre 1995 y 2005 capturamos 266 individuos de *Chasiempis sandwichensis ibidis* mediante redes de niebla en 23 sitios. Los individuos capturados fueron examinados para determinar síntomas visibles de viruela aviar (*Poxvirus avium*) y colectamos muestras de sangre para determinar la presencia de malaria aviar (*Plasmodium relictum*). Encontramos lesiones de tipo viruela y malaria en todas las poblaciones de *C. s. ibidis* en O'ahu; ninguna parte de la isla se encontró libre de enfermedades transmitidas por mosquitos. Cada año, el 20% ± 4% de los individuos presentó lesiones activas probablemente causadas por el virus de la viruela aviar y un 16% ± 4% adicional de los individuos presentó deformidades y falta de dedos indicando la presencia de lesiones de viruela que habían sido curadas. La prevalencia de la malaria fue del 87% para todos los años juntos. La prevalencia de la viruela varió entre años y se asoció con la cantidad de precipitación anual, lo que probablemente se debe a la mayor abundancia de sitios de reproducción de mosquitos en años con más lluvia. Niveles de precipitación iguales o mayores a los asociados a la epizootia de viruela en 1996 y 2004 han ocurrido en 13 años desde 1947, o una vez cada 4.5 años. La severidad de la infección varió considerablemente entre aves, y las infecciones que involucran tres o más dedos, las patas o la cabeza fueron menos comunes en aves con lesiones curadas que en aquellas con lesiones activas. Esto sugiere que ese tipo de lesiones causaron mortalidad con mayor frecuencia. La resistencia a la enfermedad puede estar evolucionando en aves de algunas áreas, pero las poblaciones de *C. s. ibidis* en O'ahu probablemente seguirán disminuyendo.

INTRODUCTION

The endemic Hawaiian avifauna is one of the most imperiled on earth, with 33 taxa (species or subspecies) having gone extinct in historical

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times, 22 currently listed as endangered or threatened under the U.S. Endangered Species Act, and eight of 13 other extant taxa considered at least vulnerable (Scott et al. 2001, International Union for the Conservation of Nature 2003). One of the most serious causes of the decline of Hawaiian birds has been alien diseases, particularly avian malaria (*Plasmodium relictum*) and avian pox virus (*Poxvirus avium*), which in Hawai'i are transmitted primarily by the introduced southern house mosquito (*Culex quinquefasciatus*; Warner 1968, van Riper et al. 1986, 2002, Atkinson et al. 1995). The role of avian malaria and avian pox in limiting the distribution of Hawaiian birds is widely recognized (Scott et al. 1986, van Riper et al. 1986, Scott et al. 2001), but additional information is needed to fully understand the long-term threat from disease and to evaluate the continuing potential impact of disease on Hawaiian birds (Benning et al. 2002, U.S. Fish and Wildlife Service 2003). For example, there is little information on annual variation in infection rates or frequencies of disease epizootics, and no information is available for some avian taxa or areas. Obtaining long-term data on the distribution and prevalence of alien diseases in Hawai'i and their impacts on the demography of wild bird populations is a high priority conservation need (U.S. Fish and Wildlife Service 2003).

The O'ahu 'Elepaio (*Chasiempis sandwichensis ibidis*) is an endangered, insectivorous, nonmigratory monarch flycatcher (Monarchidae) endemic to the Hawaiian island of O'ahu (Conant 1977, VanderWerf 1998, 2004). Habitat loss has been an important factor in the decline of this forest bird, which now occupies less than 4% of its presumed prehistoric range (VanderWerf et al. 2001), but the primary factors that currently limit O'ahu 'Elepaio populations are presumed to be nest predation by alien black rats (*Rattus rattus*) and mosquito-borne diseases (VanderWerf 1998, VanderWerf and Smith 2002). There is very little information about avian diseases on O'ahu (Shehata et al. 2001), and no information on prevalence of diseases in the O'ahu 'Elepaio, which survives entirely at low elevations where mosquitoes are abundant (VanderWerf et al. 2001).

In this paper we present data from 1995–2005 on the spatial and temporal distribution of avian pox and malaria from the entire current range of the O'ahu 'Elepaio. This information is useful for understanding the potential for disease to further affect 'Elepaio populations, and will be valuable for conducting population viability analyses and determining whether the current recovery strategy is likely to be effective.

METHODS

FIELD TECHNIQUES

We mist-netted, banded, and inspected 266 'Elepaio from 27 sites on O'ahu for visible symptoms of avian pox (Fig. 1). This sample represented >10% of the extant population of about 2000 birds, and these sites encompassed all major populations (VanderWerf et al. 2001), although sample sizes from some areas were small. Sampling sites ranged in elevation from 100 m to 900 m. Birds were captured in every month, but sampling effort per month varied among years. A blood sample not exceeding 1% of body weight was collected from the brachial vein of each bird to screen for malaria and for genetic studies.

Avian pox occurs in two forms: cutaneous pox, which is characterized by wart-like growths and swellings usually on unfeathered areas, and diptheritic or wet pox, which causes soft yellowish cankers and lesions on membranes of the upper respiratory and digestive tracts (Hansen 1987, Tripathy 1993; van Riper and Forrester, in press). We regarded 'Elepaio with soft swellings, warty growths, open sores, or crusty scabs as having active cutaneous pox-like lesions, and those with missing toes or other deformities on the toes, feet, or head as having healed or inactive pox-like lesions. We observed only the cutaneous form of pox in this study, and regarded 'Elepaio with no visible symptoms as healthy. We categorized the severity of infection based on the number and location of lesions. We did not clinically confirm field diagnoses of pox in 'Elepaio because the risk of biopsy and exacerbation of lesions or deformities was judged to be too high for this endangered bird. Atkinson et al. (2005) and van Riper et al. (2002) similarly did not biopsy birds to confirm field diagnoses of pox, but van Riper et al. (2002) confirmed field diagnoses in a subsample of birds ($n = 10$) by histopathologic and chorioallantoic membrane examination of tissue ob-

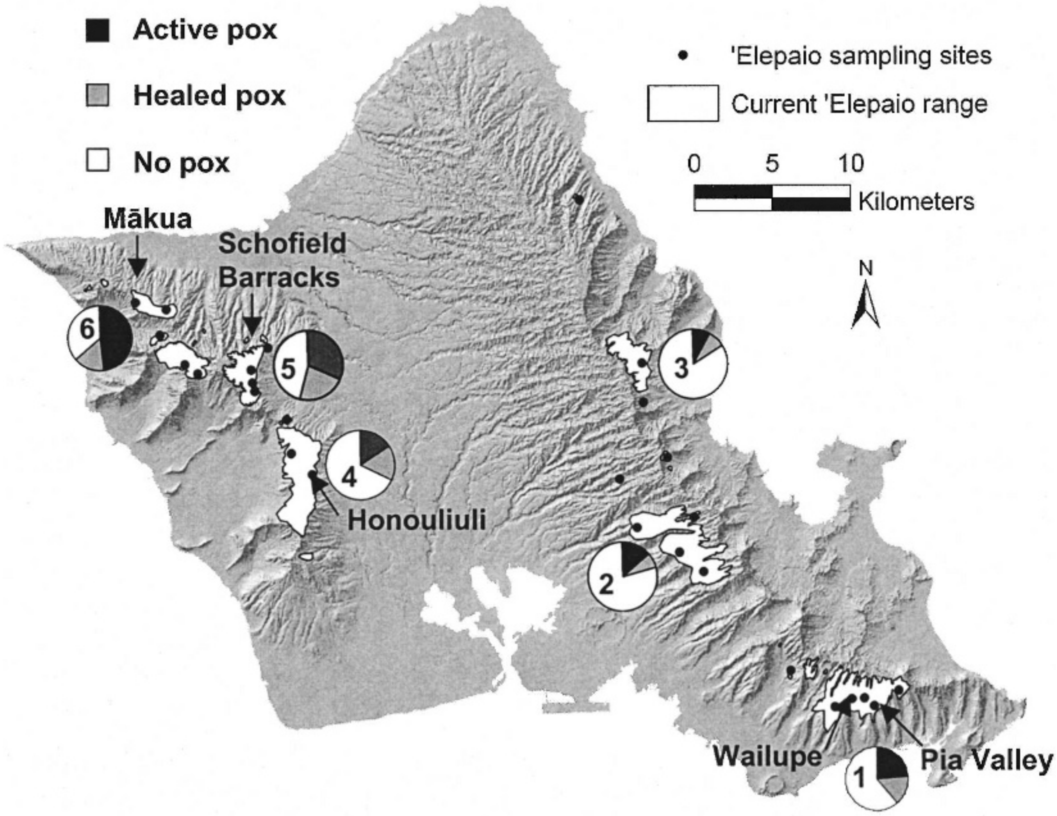

FIGURE 1. Current range of the O'ahu 'Elepaio (modified from VanderWerf et al. 2001), disease sampling locations from 1995 to 2005, and prevalence of avian pox in 'Elepaio populations: 1 = southeastern Ko'olau (n = 113); 2 = central Ko'olau (n = 28); 3 = windward Ko'olau (n = 12); 4 = southern Wai'anae (n = 31); 5 = Schofield Barracks West Range (n = 63); 6 = northwestern Wai'anae (n = 19).

tained during necropsy. Although pox is the most likely cause of the active and healed lesions observed in 'Elepaio, we refer to them as "pox-like lesions" or simply "lesions" because we did not clinically confirm diagnoses.

Fifty of the blood samples collected were screened for avian malaria, 20 using an immunoblot test for malarial antibodies (Atkinson et al. 2005), and 30 using a PCR-based test for malarial DNA (Feldman et al. 1995). There was no difference between the two tests in the proportion of positive results ($\chi^2_1 = 2.0$, $P = 0.16$).

STATISTICAL ANALYSES

We defined pox prevalence as the proportion of birds that had active pox lesions. Birds with healed pox lesions were counted separately because one of the primary goals of this study was to determine how many 'Elepaio are affected by pox each year, and 'Elepaio with healed pox lesions have the same survival and reproduction as healthy 'Elepaio (VanderWerf 2001). We calculated pox prevalence in each year of the study to provide a measure of annual variation, and within seasons (January–March, April–June, July–September, and October–December) across all years combined. Infection severity was examined by chi-squared analysis of the numbers of birds with active versus healed lesions by body region. Chi-squared analyses were also used to assess seasonal variation in pox prevalence, and to test for differences in pox prevalence between males and females and between subadults ($\leq$2 years old) and adults ($\geq$3 years old).

The relationship between pox and rainfall was investigated with a regression of annual pox prevalence on annual rainfall. A single measure of annual rainfall was calculated by averaging rainfall from the five National Weather Service gauges (Niu Valley, Pālolo Fire Station, Kunia Substation, Schofield Barracks, and Mākua Ridge; National Weather Service 2005) that were closest to the five sites where the majority of 'Elepaio were caught each year (Pia Valley, Wailupe Valley, Honouliuli Preserve, U.S. Army Schofield Barracks West Range, and Mākua Military Reservation). Annual rainfall was summed each year from July through June, rather than by calendar year, because the majority of rainfall in Hawai'i occurs in the winter season (Giambelluca et al. 1986).

Overall prevalence of malaria was calculated for the entire 10-year study and was not examined annually or seasonally because of small sample sizes. Chi-squared analysis was used to test for coincidence of malaria and pox. Values presented are means ± SE unless otherwise noted.

RESULTS

The average annual prevalence of active pox-like lesions in O'ahu 'Elepaio from 1995–2005 was 20% ± 4% (range = 0%–45%). Prevalence of deformities and missing digits indicative of healed pox lesions averaged an additional 16% ± 4% per year. Prevalence of active lesions did not differ between males (21%) and females (16%; χ^2_1 = 1.3, P = 0.26), or between adults (26%) and subadults (18%; χ^2_1 = 1.5, P = 0.22), so data from all ages and sexes were combined.

Pox-like lesions occurred in all 'Elepaio populations on O'ahu, and at all elevations from 100 m to 900 m (Fig. 1). Prevalence of active lesions differed among 'Elepaio populations (χ^2_5 = 11.5, P = 0.04), with higher prevalence in the northern Wai'anae Mountains, which are relatively dry, and lower values in the central and windward Ko'olau Mountains, which are quite wet.

Variation in annual prevalence of pox-like lesions was associated with annual rainfall (R^2 = 0.44, $F_{1,8}$ = 8.1, P = 0.02; Fig. 2). Prevalence was higher in years with more rain, and there were two peaks of exceptionally high prevalence, 1995–1996 and 2003–2004, each associated with a year of high rainfall. Prevalence also varied seasonally, with more birds than expected having active infections from July to September (χ^2_3 = 8.5, P = 0.04; Fig. 3).

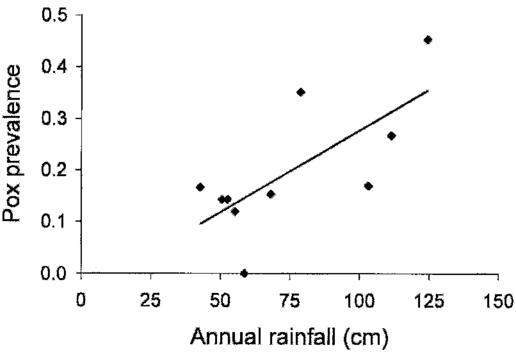

FIGURE 2. Avian pox prevalence in O'ahu 'Elepaio (proportion of individuals with active lesions) was positively related to annual rainfall from 1995–2005. Rainfall values are averages from the five National Weather Service gauges closest to the five sites where most 'Elepaio were captured.

Severity of infection varied among birds, with lesions present on one to five toes, one or both feet, the bill, and the body. Infection severity was greater in 'Elepaio with active lesions than in those with healed lesions (χ^2_5 = 21.9, P < 0.001; Fig. 4). Lesions on one or two toes were common in birds with active and inactive infections, but very few birds had healed lesions on three or more toes, the feet, or the head.

Fifteen 'Elepaio were captured on at least two occasions, of which eight had active or healed lesions on at least one occasion and six had changed status between captures. Two birds that were healthy on initial capture had active lesions when recaptured. One bird that

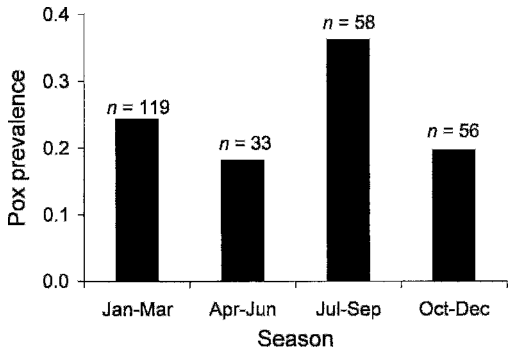

FIGURE 3. Avian pox was most prevalent (proportion of individuals with active lesions) in O'ahu 'Elepaio from July to September. Sample sizes indicated above bars.

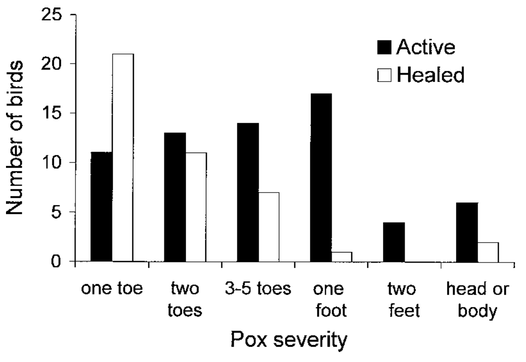

FIGURE 4. Severity of pox infections in O'ahu 'Elepaio with active and inactive lesions from 1995 to 2005. Birds with healed lesions exhibited less severe infections, presumably due to higher mortality of birds with more severe infections.

was captured three times had an active lesion on one toe in May 1998, active lesions on one foot and two toes in March 2000, and healed lesions on four toes in February 2001. At the final time of capture this bird was unable to use one foot for perching, and it apparently died in 2001. Another bird was captured with active lesions in September 1996 and January 2000. One bird was captured with apparently healed lesions on three toes in June 1997 and January 2000, but the portion of each toe that was missing or deformed had increased over time. Two birds that had small active lesions on initial capture were recorded as healthy at the time of recapture, demonstrating that some birds heal without noticeable deformities.

Prevalence of avian malaria in the 50 'Elepaio blood samples screened was 87%. Eighteen of the 44 birds (41%) that were positive for malaria also had active or healed pox lesions, while two of six birds (33%) that were negative for malaria had active or healed pox lesions. Coincidence of pox and malaria did not occur more often than expected by chance ($\chi^2_1 = 0.1$, $P = 0.72$). None of the 15 recaptured birds was tested twice for malaria.

DISCUSSION

The prevalence of avian pox-like lesions and avian malaria found in O'ahu 'Elepaio during this study was high compared to that found in other studies. On Hawai'i, which has higher mountains than O'ahu, mosquito-borne diseases are relatively common up to about 1500 m in elevation (Goff and van Riper 1980, van Riper et al. 2002), with the upper limit to this distribution determined by thermal inhibition of development of mosquito larvae and of the malarial parasite within the mosquito host (LaPointe 2000, Benning et al. 2002). Even if comparisons are restricted to elevations below 1500 m, prevalence of pox-like lesions was higher in O'ahu 'Elepaio (20% active and 16% healed) than in 'Elepaio on windward Hawai'i (9% active and 10% healed; van Riper et al. 2002) or leeward Hawai'i (13% active and healed combined; Atkinson et al. 2005). Similarly, the prevalence of malaria in O'ahu 'Elepaio (87%) was higher than that found in Hawai'i 'Elepaio (*C. s. sandwichensis*) by Atkinson et al. (2005; 43%) or van Riper et al. (1986; 6%). Compared to other Hawaiian forest birds, only 'Apapane (*Himatione sanguinea*) at 710 m elevation on leeward Hawai'i exhibited frequencies of pox (36%) and malaria (100%) infection similar to those in O'ahu 'Elepaio (Atkinson et al. 2005). On O'ahu, Shehata et al. (2001) found that overall prevalence of avian malaria at a low-elevation site was 10% in 13 alien and two native bird species, with no species having higher than 28% prevalence. The persistence of 'Elepaio populations at low elevations on O'ahu despite high levels of pox and malaria infection indicates immunological resistance to these diseases (VanderWerf et al. 2001), although this has not been clinically demonstrated as it has been with the 'Ōma'o (*Myadestes obscurus*; Atkinson et al. 2001) and Hawai'i 'Amakihi (*Hemignathus virens*; van Riper et al. 1986).

Variation in prevalence of pox in O'ahu 'Elepaio was related to annual rainfall. The primary vector of avian pox in Hawai'i is the southern house mosquito, which breeds primarily in small pools of organically rich water (Goff and van Riper 1980, LaPointe 2000). A geographical association of high mosquito abundance and high rainfall was demonstrated on Hawai'i (Goff and van Riper 1980), so the temporal association of rainfall and pox prevalence observed in this study is not surprising.

The 10-year time period encompassed by this study was relatively dry overall, with below average rainfall in eight years, but was punctuated by two years with high rainfall (1996 and 2004), each of which apparently produced an epizootic of avian pox. Historical rainfall data from the Honolulu International Airport beginning in 1947 indicate that annual rainfall as high as that associated with the severe epizootic in 1996 (>90 cm) has occurred six times, or once every 9.7 years, and that rainfall as high as that associated with the minor epizootic in 2004 (>75 cm) has occurred in seven other years, or once every 8.3 years. The 1960s were an exceptionally wet period on O‘ahu, with several consecutive years of over 75 cm of rain, and the number of ‘Elepaio recorded on the Honolulu Christmas Bird Count declined most rapidly during that time (VanderWerf et al. 2001), suggesting increased levels of mosquito-borne diseases likely played a role in their decline.

The geographical distribution of pox prevalence, with higher proportions of infected birds in the drier northern Wai‘anae Mountains and lower proportions in the wetter central and windward Ko‘olau Mountains, seems counterintuitive given rainfall patterns on O‘ahu. However, laboratory experiments by van Riper et al. (1986) demonstrated that Hawai‘i ‘Amakihi from dry areas were more susceptible to avian malaria than ‘Amakihi from wet areas. The current distribution of O‘ahu ‘Elepaio consists of population remnants that reflect historical patterns of disease and survival. ‘Elepaio have already disappeared from the wettest areas on O‘ahu in the northern Ko‘olau Range and the northern slope of the Wai‘anae Range (VanderWerf et al. 2001). ‘Elepaio populations in moderately wet areas of the central Ko‘olau Mountains likely consist primarily of “survivors” that have been subjected to frequent epizootics and strong selection for disease resistance, causing them to exhibit fewer and less severe infections currently. ‘Elepaio populations in drier areas of the Wai‘anae Mountains have experienced fewer epizootics and infrequent selection for resistance, and thus contain a larger proportion of birds that still exhibit serious infections. The number of ‘Elepaio in Schofield Barracks West Range and Mākua Valley has declined since surveys were first conducted in 1996, with the greatest drop occurring immediately after the severe pox epizootic in 1996 (U.S. Army, unpubl. data), and it may be that susceptible birds are still being removed from the population by disease.

The apparent seasonality of pox prevalence, with higher values from July–September and January–March, was at least partly caused by a sampling bias. Many samples from March and September were collected in 1996, which was a wet year, and many were collected from Schofield Barracks, where prevalence was high. On Hawai‘i, mosquito abundance and disease transmission are highest in the late summer and fall when temperatures are highest and development of mosquito larvae and the malaria parasite are least inhibited (Goff and van Riper 1980, van Riper et al. 1986). Temperatures are relatively warm year-round at the lower elevations on O‘ahu, so no such thermal seasonality would be expected.

Whether a bird survives pox is largely determined by its immune system (Jarvi et al. 2001) and the virulence of the pox (Tripathy 1993), but also may be affected by the number and location of mosquito bites that result in infection. Many ‘Elepaio survived infection and subsequent loss or deformation of one or two toes, and such injuries do not affect their subsequent survival or reproduction (VanderWerf 2001). In contrast, ‘Elepaio with infections on three or more toes, the feet, or the head apparently survive at a much lower rate. Birds that survive pox infection are thought to have increased immunity to subsequent infections (Tripathy 1993), although stress can trigger a recrudescence (Olsen and Dolphin 1978), and it is not clear how long a host remains infected. In this study, birds were captured with active lesions up to 3.5 years apart.

There is presently no practical method of controlling transmission of mosquito-borne avian diseases in forested environments in Hawai‘i. Vaccines against some strains of pox have been developed, primarily for use in the poultry industry (Tripathy 1993; van Riper and Forrester, in press), and utility of these vaccines for treating individual Hawaiian forest birds should be investigated, but they would not provide a long-term solution to the threat from pox in wild bird populations because immunity produced by vaccination would not be heritable. The most effective method of reducing the threat from disease in ‘Elepaio may be rodent control. The increased reproductive success resulting from rodent control may facilitate the evolution of disease resistance by providing birds that have greater natural immunity a better chance of reproducing, thereby increasing the proportion of resistant birds more quickly (VanderWerf and Smith 2002). The potential evolutionary acceleration of disease resistance through rodent control was demonstrated quantitatively by Kilpatrick (2006), and appears promising. Whether any natural increase in disease resistance is sufficient to allow recovery of O'ahu 'Elepaio without additional management remains to be seen.

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