

Importance of Nest Predation by Alien Rodents and Avian Poxvirus in Conservation of Oahu Elepaio

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ABSTRACT The Oahu elepaio (*Chasiempis sandwichensis ibidis*) is an endangered forest bird endemic to the Hawaiian island of Oahu (USA) and is threatened by nest predation from alien rodents and mosquito-borne diseases. I investigated importance of these threats and evaluated success of conservation efforts from 1995 to 2008. I controlled rodents with snap-traps and bait stations in 3 valleys and switched sites from non-treatment to treatment over time. I mist-netted and color-banded 91 elepaio, inspected them for symptoms of avian poxvirus (*Poxvirus avium*), and estimated survival using multistate mark-recapture models. I determined annual fecundity of each breeding pair and monitored success of 212 nests. The oldest known Oahu elepaio was ≥ 15 years old. Survival of females was higher with rodent control (0.82 ± 0.05) than without (0.55 ± 0.12), but survival of males was not affected by rodent control (0.86 ± 0.02 with vs. 0.84 ± 0.04 without). Survival of elepaio with active or inactive pox-like lesions was 4–10% lower than survival of elepaio with no pox symptoms. Rodent control resulted in higher annual fecundity (0.69 ± 0.05 vs. 0.33 ± 0.06 fledglings/pair) and nest success (62% vs. 33%). Female site-fidelity, mate fidelity, and female encounter probability were lower in the absence of rodent control because more females switched territories and mates after nest failure. Population growth calculated from survival and fecundity estimates was stable with rodent control (1.07 ± 0.04) but declining without rodent control (0.69 ± 0.05). Elepaio numbers have continued to decline despite rodent control, probably because some young birds disperse into adjacent unmanaged areas that act as sinks. The best immediate management strategy for Oahu elepaio is to conduct rodent control over larger areas. Restoration of native forest would benefit elepaio by providing nest sites that are less attractive to rodents. Construction of predator-proof fences and eradication of predators would provide the best long-term protection for elepaio. (JOURNAL OF WILDLIFE MANAGEMENT 73(5):737–746; 2009)

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The elepaio (*Chasiempis sandwichensis*) is a territorial, nonmigratory monarch flycatcher (Monarchidae) endemic to the Hawaiian Islands (VanderWerf 1998). Different forms of elepaio occur on the islands of Kauai, Oahu, and Hawaii (USA) and currently are regarded as subspecies (Pratt et al. 1987, VanderWerf 2007a). The Kauai and Hawaii forms are fairly common (Scott et al. 1986), but the Oahu elepaio (*C. s. ibidis*) has declined severely in the last few decades and now occupies $<4\%$ of its presumed prehistoric range and only 25% of the range occupied in 1975 (VanderWerf et al. 2001). The total population was estimated to be approximately 1,980 birds in the 1990s (VanderWerf et al. 2001). The current range is fragmented into numerous small populations, many of which are isolated by urban and agricultural development (VanderWerf et al. 2001). The Oahu elepaio was listed as endangered under the United States Endangered Species Act in 2000 (United States Fish and Wildlife Service [USFWS] 2000, 2006) and is listed as endangered by the state of Hawaii, and status of the species as a whole was recently elevated to endangered by the International Union for the Conservation of Nature (2007).

Habitat loss has been an important factor in the decline of this forest bird, but the most serious current threats are nest predation by alien black rats (*Rattus rattus*) and diseases transmitted by the alien southern house mosquito (*Culex quinquefasciatus*; VanderWerf et al. 2001, 2006; VanderWerf and Smith 2002, USFWS 2006). Artificial nest experiments revealed that predation rates are high in Oahu elepaio

habitat and that black rats are the most common nest predator (VanderWerf 2001a). A rodent control program using snap-traps and poison bait stations was begun in 1997 and proved to be an effective means of increasing nest success and survival of breeding females (VanderWerf and Smith 2002). Based on the initial success of this management technique, rodent control programs have been implemented in several areas on Oahu by multiple agencies and organizations (United States Army 2006, USFWS 2006, VanderWerf 2007b). Unfortunately, elepaio populations have continued to decline in some areas despite rodent control, and it is unclear whether these continuing declines are due to a decrease in efficacy of rodent control or to some other threat.

Avian malaria (*Plasmodium relictum*) and avian poxvirus (*Poxvirus avium*) are serious threats that cause high mortality in some species of Hawaiian forest birds and limit their distributions (Warner 1968, Atkinson et al. 1995, van Riper et al. 2002), but immunity to these diseases has been discovered in Oahu amakihi (*Hemignathus flavus*; Shehata et al. 2001) and Hawaii amakihi (*H. virens*; Woodworth et al. 2005, Kilpatrick et al. 2006, Foster et al. 2007). Prevalence of malaria and poxvirus is high in Oahu elepaio (VanderWerf et al. 2006), so the impact of these diseases is potentially serious, but their actual effect on wild birds is unknown.

My objectives were to 1) provide an update on effectiveness of rodent control as a management technique for Oahu elepaio using a larger and longer term data set, 2) improve upon previous survival estimates for Oahu elepaio through use of mark-recapture methods, 3) expand upon previous

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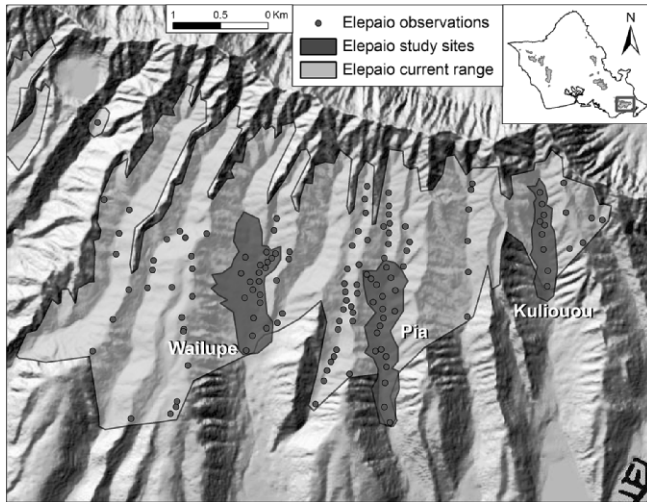


Figure 1. Map showing current distribution of elepaio on Oahu, Hawaiian Islands, USA, and location and area of sites used in this study from 1995 to 2008.

analyses by investigating effects of avian poxvirus on survival, and 4) determine the cause(s) of continuing declines in Oahu elepaio and recommend conservation strategies.

STUDY AREA

I conducted this study in Kuliouou, Pia, and Wailupe valleys in the Koolau Mountains of southeastern Oahu at elevations ranging from 100 m to 400 m (Fig. 1). These valleys support part of the largest remaining elepaio population on the island, which was estimated to be 475 birds in the 1990s (VanderWerf et al. 2001). Elepaio were most common in riparian forest on the floor of each valley, but also occurred on adjacent slopes and ridges. Vegetation consisted of mesic forest dominated by alien plants, primarily strawberry guava (*Psidium cattleianum*), mango (*Mangifera indica*), kukui or candlenut (*Aleurites moluccana*), and Christmasberry (*Schinus terebinthifolius*), with smaller numbers of native plants such as papala kepau (*Pisonia umbellifera*), alahee (*Psydrax odoratum*), koa (*Acacia koa*), lama (*Diospyros sandwicensis*), and lonomea (*Sapindus oahuensis*). I began the study in 1995 with marking and monitoring of elepaio in Pia and Kuliouou. Rodent control was initiated by the Hawaii Division of Forestry and Wildlife in Pia Valley in 1997, and I expanded the study over the next several years to include eastern and western Wailupe Valley and additional elepaio territories within each valley. At their largest extents, the study areas in Wailupe, Pia, and Kuliouou encompassed 57 ha, 49 ha, and 24 ha, respectively.

METHODS

Elepaio Monitoring

I captured elepaio with mist nets and marked each bird with an aluminum leg band and a unique combination of 3 plastic colored leg bands. I weighed and measured each bird, inspected them for molt, fat, and symptoms of poxvirus, then released them unharmed at the site of capture within 1

hour. I collected a blood sample <1% of body weight from the brachial vein of each bird for genetic analysis and disease screening.

I monitored elepaio on weekly visits to each territory in the study sites during the breeding season from January to May and occasionally in other months. I identified territories using call-playbacks and spot-mapping (VanderWerf et al. 2001, VanderWerf 2004). I recorded the band combination of all marked birds, whether each marked bird had remained on the same territory between years and, if both members of a pair were marked, whether they had remained with the same mate. I also searched in all directions from each study site for marked birds that might have dispersed, though steep terrain hindered searching in some areas.

I measured elepaio fecundity as the number of fledglings produced per pair each year. I counted pairs as having reproduced only if I observed them feeding fledglings. It is unlikely that I overlooked any fledglings that survived more than a few days out of the nest, because fledglings are fed by their parents for 4–6 weeks, are easy to locate by their persistent begging calls, and may stay on their natal territory for up to 9 months, until evicted by the parents at the start of the next breeding season (VanderWerf 1998).

I attempted to locate all elepaio nests in the study sites each year and determine their fates. I counted nests as successful if they fledged ≥ 1 chick, and I calculated nest success as the successful proportion of total nests, based only on nests in which I observed eggs using a pole-mounted mirror or I observed parents incubating. Some nests were abandoned for unknown reasons before eggs were laid and in some cases before completion, but most pairs that abandoned a nest built another in which they did lay eggs. It is possible that some nests counted as abandoned actually were depredated before I observed incubation, which would cause an overestimate of nest success, but the proportion of abandoned nests did not differ between treatment and control areas (26% vs. 17%, respectively; $\chi^2_1 = 1.45$, $P = 0.23$). In a few cases fledglings were produced from nests I did not find, and it is also likely that I did not find a few nests that failed, but any bias in nest success due to unfound nests is likely to have been similar over time and among study sites, so comparison of nest success with and without rodent control is still meaningful.

I classified each elepaio as male or female and by disease status (i.e., healthy, active pox, or inactive pox). Male Oahu elepaio are about 10% larger than females and have more black on the throat, but there is some overlap (VanderWerf 1998). In a few cases I confirmed sex by behavior (e.g., singing, copulation) or genetically. I regarded elepaio with 1) soft swellings, warty growths, open sores, or crusty scabs on the toes, feet, legs, or face as having active pox-like lesions, 2) missing or deformed toes or feet as having inactive pox-like lesions, and 3) no visible pox-like symptoms as healthy (VanderWerf et al. 2006, van Riper and Forrester 2007). I did not clinically confirm field diagnoses of pox because risk of biopsy was too high in this

Table 1. Rodent control by year in study sites for the Oahu elepaio on Oahu, Hawaiian Islands, USA. += rodent control, -= no rodent control, blank = not included that year.

| Site | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 |
|-----------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Pia | - | - | + | + | + | + | + | - | - | + | + | + | + | + |
| Kuliouou | - | - | - | + | - | + | - | - | - | - | - | - | - | - |
| Wailupe E | | | | - | + | + | + | + | + | + | + | + | + | + |
| Wailupe W | | | | | - | + | + | + | + | + | + | + | + | + |

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 sample of dead birds ($n = 10$) by examination of tissue obtained during necropsy. Although pox is the most likely cause of the lesions observed in elepaio, I refer to them as pox-like lesions or simply lesions because I did not clinically confirm diagnoses. Some individuals were tested for avian malaria (VanderWerf et al. 2006), but most blood samples were not tested so I was not able to examine effects of malaria.

Rodent Control

I controlled rodents using an experimental design that involved spatial or temporal comparison of treatment and non-treatment sites (Table 1). I collected baseline data on elepaio demography in the absence of rodent control at each site for ≥ 1 year, then began a rodent-control program to assess the impact of nest predation by rodents (VanderWerf and Smith 2002). I controlled rodents with a combination of snap-traps and poison bait containing 0.005% diphacinone in the form of either Eaton's bait blocks[®] (J. T. Eaton Inc., Twinsburg, OH) or Ramik minibars[®] (HACCO Inc., Randolph, WI). I placed bait in tamper-resistant plastic bait stations to shield it from rain and reduce risk of poisoning nontarget species. I secured bait stations in trees ≥ 1 m off the ground to restrict access by dogs and feral pigs. I used snap-traps to augment control and allow identification of rodent species present and to provide a measure of relative rodent abundance. I tied traps to trees or rocks to prevent scavengers from removing them. I counted traps as having caught a rodent if hair or tissue was stuck to the trap and cleaned traps with a wire brush after each capture to remove evidence of previous captures. I counted cases in which line used to secure the trap was stretched taut as captures because this likely was the result of scavenging.

I deployed 1–3 snap-traps and 1–3 bait stations in each elepaio territory depending on size of the territory and abundance of rodents, with an average density of 1.5 snap-traps and 1.5 bait stations per hectare. I sometimes deployed additional traps and bait stations if capture rate or bait take did not decline within 2 weeks. I deliberately concentrated traps and bait stations in sections of each territory known to have been used habitually for nesting, thereby increasing efficiency of the control program.

I deployed traps and bait stations for the duration of the elepaio nesting season each year, usually from late January until late May. I checked and rebaited bait stations twice a week for the first 2 weeks when rodent capture rate and take

of bait were high, then weekly or semi-weekly for the rest of the study period. I used capture rate of rodents in traps as a measure of relative abundance, expressed as a percent of the maximum rate recorded during the season. I judged efficacy of the program by the time required to reach 80% and 90% reductions in rodent capture rate. I applied diphacinone bait in compliance with United States Environmental Protection Agency registrations 61282–26 and 56–42 and with special local need registrations HI-940001, HI-960005, and HI-980008.

Statistical Analyses

To estimate survival, I created an encounter history for each bird using the year of initial capture and recaptures and resightings in subsequent years. I included only territorial elepaio; I did not use non-breeding birds without territories because they were not subject to nest predation and their encounter probability was lower. I used multistate models in Program MARK (White and Burnham 1999) to generate maximum-likelihood estimates of survival (ϕ) and encounter probability (p) of elepaio in 2 states representing rodent control (R) and no rodent control (N). Transition probabilities (ψ) between these states varied among years but were predetermined by the sites in which rodent control was conducted, so I included year effects on transition probabilities in all models to allow the transitions to vary properly. In some years no rodent control was conducted (1995 and 1996) and in other years there were no marked birds left in areas without predator control (2006, 2007, 2008), so survival rates for those nonexistent states were fixed at zero. I grouped elepaio by sex (M or F) and disease status (i.e., healthy, inactive pox, active pox), for a total of 6 groups. My study encompassed 14 years (1995–2008) so there were 13 annual intervals. Model notation follows Lebreton et al. (1992), in which subscripts indicate whether parameters differed among groups (e.g., ϕ_{sex}) or years (ϕ_{yr}) or were constant, indicated by a dot (ϕ).

I compared model fit with Akaike's Information Criterion corrected for small sample size (AIC_c), as calculated by Program MARK. I considered the model with the lowest AIC_c value to have the best fit, but I also considered models with AIC_c values that differed (ΔAIC_c) by ≤ 2 to have a reasonable fit (Burnham and Anderson 2002). I used normalized AIC_c weights as a measure of each model's relative likelihood. I conducted a goodness-of-fit test on a global model that included all factors used in any of the candidate models using the median \hat{c} approach of Program MARK to determine if the model adequately fit the data and if assumptions underlying analyses were reasonable

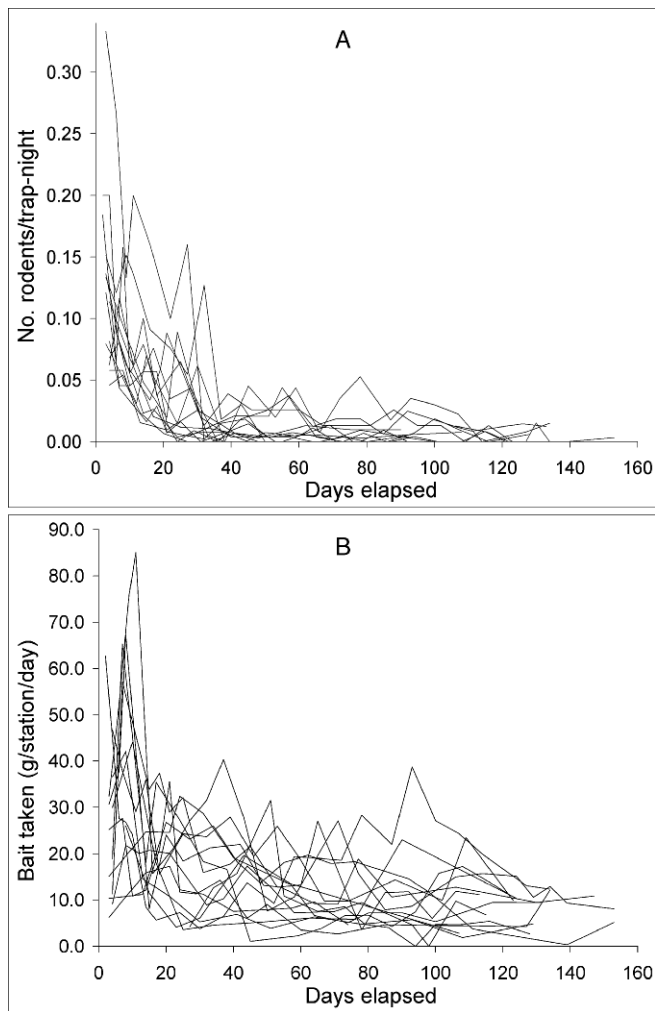


Figure 2. A) Capture rate of rodents in traps, and B) take of bait from stations during predator-control efforts for the Oahu elepaio at 3 sites from 1997 to 2008, on Oahu, Hawaiian Islands, USA. Capture rate and bait take were high at first but declined rapidly and remained low for the remainder of the study period in most years, indicating the control program was effective at reducing rodent abundance. Each line represents a different site and year.

(Cooch and White 2005). I found the overdispersion or variance inflation factor (c) to be 0.999 ± 0.016 for the global model, which was not different from 1.0, so no adjustment of c was necessary and I used the AIC_c to evaluate models instead of the quasi-Akaike Information Criterion ($QAIC_c$; Cooch and White 2005).

I examined variation in fecundity using a General Linear Model, with number of fledglings per pair as the response variable and year and rodent control as independent variables. I compared nest success with and without rodent control using chi-square analysis. I measured site fidelity as the proportion of marked birds that remained on the same territory between years, and mate fidelity as the proportion of marked birds that remained with the same mate between years, based only on cases where both members of a pair were marked and were known to have survived to the next year. I compared site fidelity and mate fidelity with and without rodent control using chi-square analyses.

To determine the overall effect of rodent control on elepaio, I calculated the finite rate of population growth, or lambda (λ), each year using the following equation (Pulliam 1988):

$$\lambda = P_A + P_J\beta$$

where P_A is adult survival, P_J is juvenile survival, and β is mean number of fledglings per pair per year. Values of $\lambda > 1.0$ indicate population increase, those < 1.0 indicate decline, and a value of exactly 1.0 indicates no change. I used annual survival of females for adult survival because it was lower than survival of males and, thus, limited population growth (Kilpatrick 2006). I obtained female survival estimates from a model that contained effects of sex and year on survival. I used a single value of juvenile survival from all years combined because too few juveniles were marked to estimate survival each year. I calculated means and standard errors for λ with and without rodent control from values in each year of the study. I report all values as mean \pm standard error unless otherwise noted. I conducted all analyses with MINITAB Release 12.21 (Minitab Inc., State College, PA).

RESULTS

Rodent Control

A total of 762 rodents were captured in 51,855 trap-nights from 1997 to 2008, an average capture rate of 0.015 rodents/trap-night. Black rats were the most commonly trapped species (46%), followed by house mice (*Mus musculus*; 7%), Polynesian rats (*Rattus exulans*; 1%), and Norway rats (*R. norvegicus*; 1%), with some remains identifiable only to *Rattus* spp. (8%), and the remainder of unknown species due to removal of the carcasses by scavengers (37%). I also caught several nonnative small Indian mongooses (*Herpestes javanicus auro-punctatus*) in snap-traps. A total of 792 kg of bait containing 0.005% diphacinone was taken from bait stations during 58,251 station-nights, an average of 13.6 g/station-night.

The rodent-control program effectively reduced rodent abundance each year. Capture rate and bait consumption were high for the first few weeks, then declined rapidly and remained low for the duration of the season in most years (Fig. 2). The number of days required to achieve 80% and 90% reductions in rodent captures were 25 ± 2 days (range = 15–37 days) and 33 ± 3 days (range = 20–67 days), respectively, and the 90% threshold was reached every year. Lower peaks in capture rate and bait consumption occurred later in the season in some years, probably due to immigration of rodents from surrounding areas.

There was some evidence that the control program caused long-term suppression of rodent abundance. The average capture rate and bait take over the entire season declined during the first 4 years then leveled off without recovering to the initial levels (Fig. 3). Declines across years also occurred in maximum capture rate ($R^2 = 36\%$, $F_{1,14} = 7.87$, $P = 0.014$) and maximum bait take ($R^2 = 31\%$, $F_{1,14} = 6.34$, $P = 0.025$), but there was no decline in the number of days required to achieve 80% ($R^2 = 1\%$, $F_{1,14} = 0.12$, $P = 0.74$)

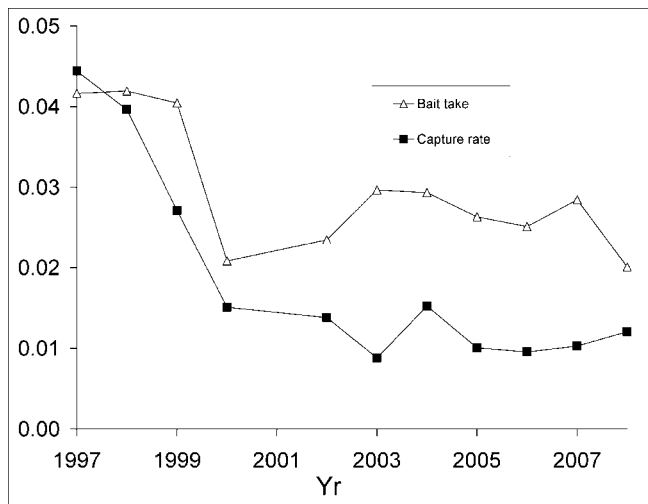


Figure 3. Average rodent trapping rate (rodents/trap-night) and bait consumption (g/station/day) during each year of predator control for the Oahu elepaio at 3 sites combined from 1997 to 2008 on Oahu, Hawaiian Islands, USA. Data were not recorded in 2001. Rodent capture rates did not recover to initial levels, indicating the control program may have caused long-term suppression of rodents.

or 90% reduction in rodent captures ($R^2 = <1\%$, $F_{1,14} = 0.03$, $P = 0.86$).

Elepaio Monitoring

I marked 91 territorial elepaio during the 14 years of this study, with an average of 27.7 ± 1.8 elepaio captured, recaptured, or resighted each year. When first captured, 23 elepaio (25%) had active pox-like lesions, 16 (18%) had apparently inactive pox-like lesions, and 52 (57%) had no visible pox symptoms. The oldest known elepaio was a male captured in adult plumage (and, thus, ≥ 3 yr old; VanderWerf 2001b) in October 1995 and resighted in October 2008, making it ≥ 16 years old. The oldest known female was ≥ 10 years and 1 months old.

The best-fitting mark-recapture model included effects of sex on survival with predator control, survival without predator control, and encounter probability with predator control (Table 2, model 1). Models with an effect of sex on encounter probability without rodent control and an effect of pox on survival with rodent control were only slightly less

likely (Table 2, models 2, 3). All models showed that survival was higher with rodent control, indicating a strong treatment effect and justifying the multistate approach. Pox status may have had a similar effect on survival without rodent control (Table 2, model 6), but smaller samples sizes without rodent control hindered estimation. Addition of year effects on survival with and without rodent control did not improve fit (Table 2, models 8, 9) because the differences in survival among years were small (Fig. 4A).

Rodent control had a large effect on survival of female Oahu elepaio (Table 3). Survival of females was 27% higher with rodent control (0.82 ± 0.05) than without rodent control (0.55 ± 0.12) in all pox status groups combined. In contrast, survival of males was not affected by rodent control and was similar in both states (0.86 ± 0.02 with rodent control, 0.84 ± 0.04 without). Elepaio survival was affected to a lesser degree by presence of pox-like lesions. Annual survival of birds with inactive or active lesions was 4–10% lower than survival of healthy birds (Table 3). Survival rates were similar in birds with active and inactive lesions, and the pattern was similar in males and females.

Elepaio fecundity was higher with rodent control (0.69 ± 0.05 fledglings/pair, $n = 186$) than without rodent control (0.33 ± 0.06 fledglings/pair, $n = 55$; $F_{1,240} = 7.17$, $P = 0.008$). Fecundity also varied among years (Fig. 4B; $F_{11,240} = 1.94$, $P = 0.04$). Of 212 nests, 52 were abandoned before eggs were laid. In nests where eggs were laid, success was higher with rodent control (81/130 = 62%) than without rodent control (10/30 = 33%; $\chi^2_1 = 8.34$, $P = 0.004$).

Site fidelity of female elepaio was higher with rodent control (0.88) than without rodent control (0.33; $\chi^2_1 = 12.76$, $P < 0.001$), but site fidelity of males was not affected by rodent control (0.95 with vs. 0.97 without; $\chi^2_1 = 0.39$, $P = 0.53$). Mate fidelity was also higher with rodent control (0.94) than without (0.33; $\chi^2_1 = 15.81$, $P < 0.001$), because most cases of mate switching were caused by a female switching territories. Females had lower encounter probability than males (Table 3), and the difference was larger in the absence of rodent control because more females switched territories after nest failure and more nests failed when rodents were not controlled.

The average elepaio population growth rate with rodent

Table 2. Multistate models used to investigate survival (ϕ) and encounter probability (ρ) of Oahu elepaio from 1995 to 2008 on Oahu, Hawaiian Islands, USA, in 2 states, with rodent control (R) and no rodent control (N). Subscripts indicate whether parameters differed among groups (e.g., ϕ_{sex}) or were constant (ϕ). Transition probabilities (ψ) were predetermined by the sites in which rodent control was conducted each year, so I included year effects on transition probabilities in all models to allow them to vary properly. The ΔAIC_c is the difference from the best (lowest Akaike's Information Criterion adjusted for small sample size) model; AIC_c weight is the relative likelihood of each model.

| Model | ΔAIC_c | AIC_c wt | Likelihood | Parameters |
|---|----------------|------------|------------|------------|
| 1) $\phi R_{sex} \phi N_{sex} \rho R_{sex} \rho N, \psi R_{yr} \psi N_{yr}$ | 0 | 0.29 | 1.0 | 33 |
| 2) $\phi R, \phi N_{sex} \rho R_{sex} \rho N_{sex} \psi R_{yr} \psi N_{yr}$ | 0.41 | 0.24 | 0.82 | 33 |
| 3) $\phi R_{sex+pox} \phi N_{sex} \rho R_{sex} \rho N, \psi R_{yr} \psi N_{yr}$ | 0.79 | 0.20 | 0.67 | 34 |
| 4) $\phi R_{pox} \phi N_{sex} \rho R_{sex} \rho N, \psi R_{yr} \psi N_{yr}$ | 1.51 | 0.14 | 0.47 | 34 |
| 5) $\phi R_{sex} \phi N_{sex} \rho R_{sex+pox} \rho N, \psi R_{yr} \psi N_{yr}$ | 3.26 | 0.06 | 0.20 | 35 |
| 6) $\phi R_{sex} \phi N_{sex+pox} \rho R_{sex} \rho N, \psi R_{yr} \psi N_{yr}$ | 3.53 | 0.05 | 0.17 | 35 |
| 7) $\phi R, \phi N, \rho R, \rho N, \psi R_{yr} \psi N_{yr}$ | 4.84 | 0.03 | 0.09 | 30 |
| 8) $\phi R_{sex+yr} \phi N_{sex} \rho R_{sex} \rho N, \psi R_{yr} \psi N_{yr}$ | 21.93 | <0.01 | 0.00 | 45 |
| 9) $\phi R_{sex} \phi N_{sex+yr} \rho R_{sex} \rho N, \psi R_{yr} \psi N_{yr}$ | 25.47 | <0.01 | 0.00 | 45 |

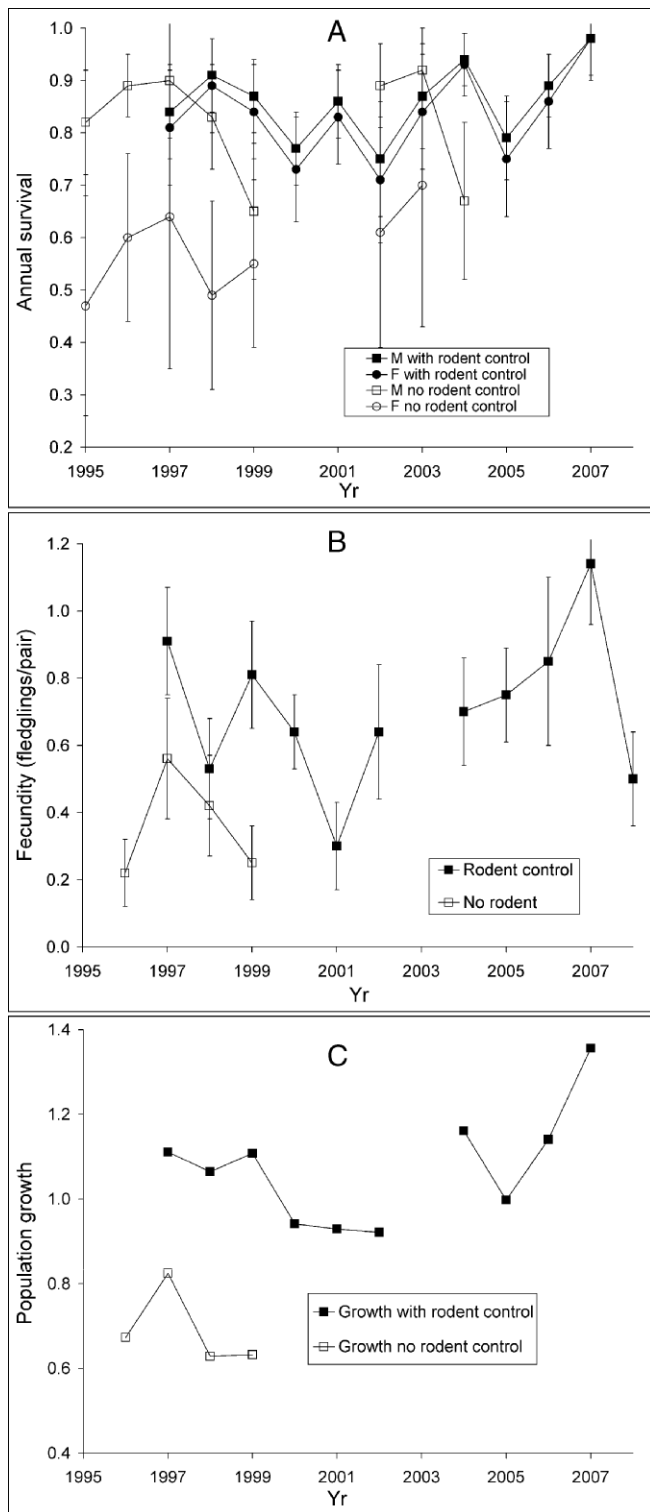


Figure 4. A) Survival, B) fecundity, and C) population growth of Oahu elepaio at 3 sites on Oahu, Hawaiian Islands, USA, in years with and without rodent control. Rodent control increased fecundity and survival of females but did not affect survival of males. Population growth was higher with rodent control, and >1.0 in 6 of 10 years in which rodents were controlled, indicating potential increase.

control was 1.07 ± 0.04 , and population growth was positive in 6 of the 10 years in which rodents were controlled (Fig. 4C), indicating potential for elepaio numbers to at least stabilize or possibly increase. Without

rodent control, the average population growth rate was lower, 0.69 ± 0.05 ($t_8 = 6.2$, $P < 0.001$), indicating rapid decline. However, the actual number of elepaio breeding pairs in each study site declined during the study period despite rodent control (Fig. 5), indicating the potential population growth calculated from demographic values was not being realized.

DISCUSSION

Rodent control continues to be an effective method of reducing predation on Oahu elepaio nests. Several demographic parameters were substantially higher with rodent control than without, including female survival (0.82 ± 0.05 vs. 0.55 ± 0.12), fecundity (0.69 ± 0.05 vs. 0.33 ± 0.07), and nest success (62% vs. 33%). Effectiveness of rodent control has not declined since 1996 to 2000, when these parameters were found to be 0.83%, 0.70%, and 58%, respectively (VanderWerf and Smith 2002). Alien mammalian predators are widely recognized as one of the most serious threats to island birds, and predator control has been shown to aid in conservation of many island bird species (Côté and Sutherland 1997, Penloup et al. 1997, Parkes and Murphy 2003). Benefits of predator control to Oahu elepaio are particularly similar to those for the Rarotonga monarch (*Pomarea dimidiata*; Robertson et al. 1994) and the North Island robin (*Petroica longipes*; Armstrong et al. 2006). Robertson et al. (1994) and Armstrong et al. (2006) also found that control of predators, primarily black rats, resulted in improvements in reproduction and survival of females but that survival of males was not affected by rodent control.

When rodents were controlled, demography of Oahu elepaio was remarkably similar to demography of a large, stable population of Hawaii elepaio at Hakalau Forest National Wildlife Refuge (Table 4). The main difference was slightly higher fecundity on Oahu, which may be related to higher ecosystem productivity and food availability in the Oahu study areas, which were at lower elevations. Rodents are known to be abundant at Hakalau (Nelson et al. 2002), yet nest predation at Hakalau was low, and this difference in nest predation between the 2 areas probably is related to the species of trees used for nesting. On Oahu, elepaio nest primarily in alien trees that bear fruit or nuts, which provide abundant food for rats and may attract rats into the forest canopy (VanderWerf and Smith 2002). At Hakalau, elepaio nest primarily in native ohia (*Metrosideros polymorpha*) trees, which have tiny, wind-dispersed seeds that do not provide food for rats (VanderWerf 2004). However, predominant use of alien trees for nesting by Oahu elepaio does not necessarily imply a preference for these species and may simply reflect the abundance of alien plants in the riparian habitats where most remaining Oahu elepaio occur (VanderWerf et al. 2001). Vegetation in most valleys on Oahu is dominated by alien species, and in some areas there are no native trees left in which elepaio could nest (VanderWerf et al. 1997). Although elepaio are adaptable and are able to use a variety of trees for nesting, replacement of native plants by invasive alien fruit-bearing trees may

Table 3. Annual survival (ϕ) and encounter probability (p) of male and female Oahu elepaio with and without rodent control and by disease status from 1995 to 2008 on Oahu, Hawaiian Islands, USA, estimated with Program MARK.

| Rodent control? | Sex | Pox status | ϕ | ϕ SE | p | p SE |
|-----------------|-----|--------------|--------|-----------|------|--------|
| Yes | M | Healthy | 0.88 | 0.03 | 0.94 | 0.02 |
| | | Inactive pox | 0.80 | 0.07 | 0.94 | 0.02 |
| | | Active pox | 0.84 | 0.05 | 0.94 | 0.02 |
| | F | Healthy | 0.84 | 0.05 | 0.83 | 0.06 |
| | | Inactive pox | 0.74 | 0.10 | 0.83 | 0.06 |
| | | Active pox | 0.79 | 0.08 | 0.83 | 0.06 |
| No | M | Healthy | 0.84 | 0.04 | 1.00 | 0.00 |
| | | Inactive pox | 0.84 | 0.04 | 1.00 | 0.00 |
| | | Active pox | 0.84 | 0.04 | 1.00 | 0.00 |
| | F | Healthy | 0.55 | 0.12 | 0.58 | 0.32 |
| | | Inactive pox | 0.55 | 0.12 | 0.58 | 0.32 |
| | | Active pox | 0.55 | 0.12 | 0.58 | 0.32 |

have greatly contributed to the decline of Oahu elepaio by increasing nest predation.

Elepaio with pox-like lesions had lower survival than healthy elepaio, but the difference was small. This result supports the idea that elepaio have relatively strong immunity to introduced diseases and are less vulnerable to them than many endemic Hawaiian birds (Warner 1968, Atkinson et al. 1995, van Riper et al. 2002, VanderWerf 2006). Survival of elepaio with pox-like lesions was 4–10% lower than survival of healthy birds, but because only $20 \pm 4\%$ and $16 \pm 4\%$ of elepaio had active or inactive lesions each year, respectively (VanderWerf et al. 2006), the population-level effect of pox on elepaio survival was a reduction of only 2%. Nevertheless, if there were no mortality from disease and the survival rate of healthy females (0.84) is substituted for average survival of females in all pox categories (0.82), the population growth rate with rodent control would be 1.09 ± 0.04 , allowing for more rapid increase. It is possible that pox prevalence will decrease over time as susceptible birds disappear from the population

(VanderWerf et al. 2006) and that the evolution of disease tolerance may be accelerated by rodent control (Kilpatrick 2006), so it is conceivable that this higher survival rate may be attained in the future. Mortality from pox appears to be higher during epizootic years when higher rainfall leads to increased mosquito abundance, such as occurred in 1995–1996 and 2003–2004 (VanderWerf et al. 2006), and indeed some of the larger declines in elepaio numbers occurred during those periods (Fig. 5).

Survival of elepaio with active and inactive lesions was surprisingly similar, indicating that either some birds categorized as having healed lesions actually were still infected or that some inactive lesions became active again, or recrudesced (Olsen and Dolphin 1978). VanderWerf (2001c) found that survival and reproduction of Hawaii elepaio did not differ between birds with healed lesions and those without any pox symptoms, but there was no known pox transmission at that site during the study period. Genetic screening of birds for viral DNA would provide a more accurate means of determining whether lesions observed were in fact caused by pox and whether infections were still active (Thiel et al. 2005, Jarvi et al. 2008). The difference in survival of males and females cannot be attributed to pox, because prevalence of lesions did not differ between sexes and if anything was lower in females (16%) than in males (21%; VanderWerf et al. 2006). The lower survival of females was likely due to a cost of reproduction, as has been shown in Hawaii elepaio (VanderWerf 2008).

Effects of poxvirus are often reported in captive birds, and laboratory challenge experiments have been used to inves-

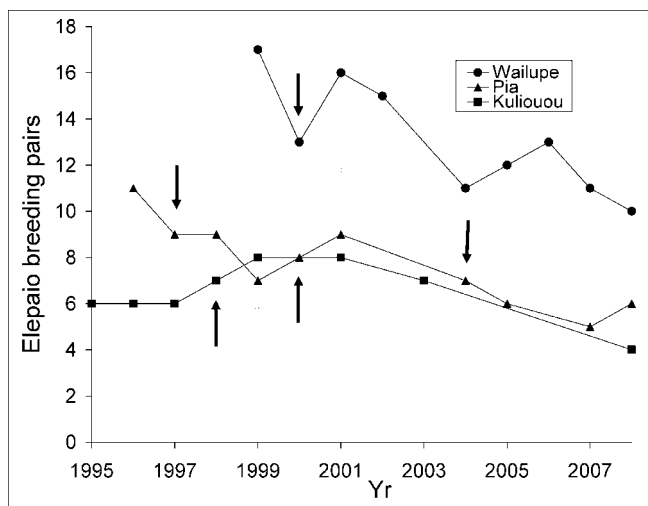


Figure 5. Number of Oahu elepaio breeding pairs in 3 study sites from 1995 to 2008 on Oahu, Hawaiian Islands, USA. Numbers of pairs declined gradually even though estimates of survival and reproduction indicated populations should have remained stable or increased slowly once rodents were controlled. Black arrows indicate start of rodent control. Gray arrows indicate cessation of rodent control.

Table 4. Comparison of demographic parameters in Oahu elepaio with rodent control from 1995 to 2008 on Oahu, Hawaiian Islands, USA, and in Hawaii elepaio at Hakalau Forest National Wildlife Refuge on Hawaii, Hawaiian Islands, USA, from 1991 to 2000. Data on Hawaii elepaio from VanderWerf (2004) and VanderWerf (2008).

| Parameter | Oahu elepaio with rodent control | Hawaii elepaio |
|-----------------------------|----------------------------------|----------------|
| Annual survival M | 0.86 | 0.87 |
| Annual survival F | 0.82 | 0.81 |
| Nest success | 62% | 65% |
| Fecundity (fledglings/pair) | 0.69 | 0.56 |

tigate susceptibility to poxvirus in several species (Warner 1968, van Riper et al. 2002, van Riper and Forrester 2007), but this study provides one of the few estimates of effects of pox on a population of wild birds. In Galápagos mockingbirds (*Nesomimus parvulus*), survival of adults on Genovesa during an El Niño event from 1982 to 1983 was 39% in birds with pox-like lesions and 56% in asymptomatic individuals (Curry and Grant 1989), and the resighting rate of fledglings on Santa Cruz during a 2-month period was 72% (13 of 18) in healthy fledglings but zero (0 of 14) in birds with pox lesions (Vargas 1987). Male small ground finches (*Geospiza fuliginosa*) from Santa Cruz Island, Galápagos, with evidence of pox were less likely to have a mate (17%) compared to males without pox (77%), indicating fitness costs associated with poxvirus infection (Kleindorfer and Dudaniec 2006). In Laysan albatross (*Phoebastria immutabilis*), fledging rate of chicks with pox lesions (82%) was not different from fledging rate of chicks with no pox symptoms (80%; Young and VanderWerf 2008). Avian pox is often more prevalent and has more serious consequences in island-endemic birds than in widespread continental species and seabirds (Atkinson et al. 2005, Smits et al. 2005, Wikelski et al. 2005, van Riper and Forrester 2007), but some island birds do have strong immunity, particularly amakihi and to a lesser degree elepaio and omao (Atkinson et al. 2001, Kilpatrick et al. 2006, Foster et al. 2007).

Survival estimates derived by mark–recapture methods in this study (0.86 ± 0.02 and 0.84 ± 0.04 for males with and without rodent control and 0.82 ± 0.05 and 0.56 ± 0.12 for females with and without rodent control) were similar to but slightly higher than previous estimates obtained by enumeration (0.79, 0.76, 0.83, 0.50, respectively; VanderWerf and Smith 2002). Enumeration produced fairly accurate estimates of survival in this case, and in Hawaii elepaio (VanderWerf 2008), because both study populations had high site fidelity and high encounter probability. However, application of mark–recapture methods resulted in more precise survival estimates, which allowed better evaluation of population growth rates.

Demographic calculations indicated that increases in survival and reproduction resulting from rodent control should have been sufficient to allow elepaio numbers to stabilize or increase slowly, but field observations indicated this did not occur. Continuing declines were not likely to be due to low adult survival or reproduction, because estimates of these parameters were robust when rodents were controlled. Failure of elepaio numbers to stabilize in response to rodent control must be due to poor local recruitment, which could be caused by either low juvenile survival or emigration. Survival of juvenile Oahu elepaio may be lower than the estimate from the limited data available (0.33), but it is similar to an estimate of juvenile survival in Hawaii elepaio (0.32) that was based on mark–recapture analysis of a larger sample (VanderWerf 2008). Juvenile survival might be lower on Oahu due to the higher prevalence of diseases in the low-elevation forests where

elepaio occur on that island (VanderWerf et al. 2006) but also could be higher due to lack of competition and increased opportunities for young birds to establish territories in the small populations remaining on Oahu (VanderWerf 2004), so the evidence is equivocal.

Emigration is a more likely cause of poor local recruitment because the study sites were small (Fig. 1) and natal dispersal in elepaio is driven by the distance required to find a vacant territory, which is often 300–500 m (VanderWerf 2008). More vacancies occur, at least for females, in areas where rodents are not controlled due to higher mortality of nesting females. Vacancies also occur within the study sites, but at a lower rate, and there is more competition for these vacancies because population density is higher. It has been shown that young elepaio are subordinate and usually unable to challenge an older bird (VanderWerf and Freed 2003) and also that young birds establish territories and acquire mates more often in areas with lower population density (VanderWerf 2004). Unmanaged areas adjacent to the study sites on Oahu likely have low female survival and reproduction due to nest predation and, therefore, act as sinks that attract more birds than they produce. The study sites may act as sources of emigrants, but they are too small to support the adjacent sinks. The study sites are in effect pseudo-sources, areas from which emigrants are produced even though there is no surplus, meaning they cannot withstand emigration in the long-term.

MANAGEMENT IMPLICATIONS

The best immediate recovery strategy for the Oahu elepaio is to conduct rodent control over a larger area, which would allow more young birds to settle in managed areas where they receive protection from nest predators. If rodents are controlled over sufficiently large areas, elepaio numbers should increase. Restoration of native trees that are less attractive to rodents also would benefit elepaio by providing safer nest sites and may be a means of reducing the need for rodent control. If alien trees are removed, simultaneous reforestation with native species would minimize any disruption of nest-site availability and foraging habitat. The spatial scale of rodent control could be greatly increased through aerial broadcast of rodenticide, which was recently approved in the State of Hawaii. The scale of rodent control also could be expanded with ground-based methods, but this would be labor-intensive using the diphacinone bait currently available for conservation use. It might be possible to improve the performance of ground-based rodent control by increasing the density of traps and bait stations or the frequency of their maintenance, but the reduction in rodent abundance is already high and occurs rapidly in most years and responses in elepaio survival and reproduction are already sufficient to allow recovery, so such extra effort seems unwarranted (Choquenot and Parkes 2001, Armstrong et al. 2006).

The best long-term management option would be construction of predator-proof fences and permanent eradication of rodents and other predators instead of

perpetual control. In New Zealand, large-scale predator control programs and creation of predator-free “mainland islands” are now widely accepted means of reversing declines in many native species and maintaining their populations (Innes et al. 1999, Clout 2001, Saunders and Norton 2001, Dilks et al. 2003, Parkes and Murphy 2003). Large-scale predator fencing and eradication projects require a large initial investment, and funding for endangered species management in the Hawaiian Islands has been especially difficult to obtain (Leonard 2008), but would provide the best protection and may prove more cost-effective and environmentally sound in the long-term.

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