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# Effects of alien rodent control on demography of the O'ahu 'Elepaio, an endangered Hawaiian forest bird

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The O'ahu 'Elepaio *Chasiempis sandwichensis ibidis* is an endangered monarch flycatcher endemic to the Hawaiian island of O'ahu. Nest predation by alien Black Rats *Rattus rattus* is one of the main causes of the decline of this forest bird. From 1996 to 2000 we monitored demography of the largest remaining O'ahu 'Elepaio population and we controlled rats with snap traps and poison bait stations in an attempt to begin recovery of the species. Nest predation by Black Rats influenced many aspects of 'Elepaio demography. Rat control resulted in a 112% increase in 'Elepaio reproduction, a 66% increase in survival of female 'Elepaio, and restored mate fidelity, site fidelity, female age structure, and female recruitment age to more natural conditions. The 'Elepaio population growth rate ( $\lambda$ ) was 0.76 without rat control and 1.00 with rat control, indicating rat control stabilized 'Elepaio populations, but was not sufficient to cause population increase due to the added threat of alien mosquito-borne diseases. Rat control may facilitate evolution of disease resistance by providing birds that have greater natural immunity an increased chance of reproducing, thereby increasing the proportion of resistant birds in each subsequent generation more quickly.

Key words: *Chasiempis sandwichensis*, Demography, 'Elepaio, Hawai'i, Nest predation, Predator control, *Rattus rattus*.

## INTRODUCTION

THE O'ahu 'Elepaio *Chasiempis sandwichensis ibidis* is a territorial, non-migratory, socially monogamous monarch flycatcher (Monarchidae) endemic to the Hawaiian island of O'ahu. The 'Elepaio has adapted relatively well to disturbed habitats composed of alien plants due to its flexible foraging behaviour, broad diet consisting of diverse arthropods, and variable nest placement (Conant 1977; VanderWerf 1993, 1994, 1998; VanderWerf *et al.* 1997). Despite its adaptability, the O'ahu 'Elepaio has declined severely in the last few decades (Williams 1987), and it now occupies only 25% of the range occupied in 1975 and less than 4% of its presumed prehistoric range (VanderWerf *et al.* 2001). The current population is approximately 1 980 birds, and the distribution is fragmented into numerous subpopulations, many of which are isolated by urban and agricultural development (VanderWerf *et al.* 2001). The O'ahu 'Elepaio was listed as endangered under the United States *Endangered Species Act* in April 2000 (USFWS 2000), and is considered vulnerable by the International Union for the Conservation of Nature (IUCN 2000).

One of the main reasons for the decline of the O'ahu 'Elepaio has been poor reproduction (VanderWerf 1998), and the primary cause of nest failure appears to be predation at nests by the non-native Black, Ship, or Roof Rat *Rattus rattus*. Artificial nest experiments with cameras have shown that Black Rats are the most common nest predator in 'Elepaio habitat, and that rat control can decrease predation

(VanderWerf 2001a). Birds and other animals on oceanic islands like Hawai'i often are naïve with respect to mammalian predators, and predation by humans and other mammals introduced by humans, such as dogs *Canis familiaris*, cats *Felis silvestris*, pigs *Sus scrofa*, rats *Rattus* sp., Stoats *Mustela erminea*, and Small Indian Mongooses *Herpestes auropunctatus* has severely impacted the avifauna of virtually all Pacific islands (Olson and James 1982; Moors *et al.* 1992; Steadman 1995). The Black Rat in particular is thought to have played an important role in the decline of many island birds in the Pacific and elsewhere (Atkinson 1977, 1985; Amarasekare 1993; Robertson *et al.* 1994; McLennan *et al.* 1996; Penloup *et al.* 1997).

Predator control is a commonly used method of attempting to increase bird populations, and though not always effective (Côté and Sutherland 1996), it has been extremely important in the conservation of several endangered Pacific island forest birds, including the Kakerori or Rarotonga Monarch *Pomarea dimidiata* (Robertson *et al.* 1994) and the Yellowhead *Mohoua ochrocephala* of New Zealand (O'Donnell *et al.* 1996). We conducted a rodent control programme from 1997 to 2000 in an attempt to increase reproduction and begin recovery of the O'ahu 'Elepaio. Here we report the effects of rodent control on several demographic parameters of the O'ahu 'Elepaio, including reproduction, survival, age structure, site fidelity, mate fidelity, and population growth, and we discuss the importance of rodent control in the conservation of the Hawaiian avifauna.

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## METHODS

### Study site and population

O'ahu is the third oldest (4 million years) and third largest (1 570 km<sup>2</sup>) of the eight main Hawaiian Islands. It is composed of two roughly parallel mountain ranges, the Wai'anae Range in the west and the Ko'olau Range in the east, separated by the broad Leilehua Plateau. Prevailing north-east trade winds produce high rainfall (up to 7 meters per year) and dense rainforest on the summits and windward slopes, while the leeward slopes support mesic to dry forest. Fifty-six per cent of O'ahu has been developed for urban or agricultural use, and the island contains 73% of the State's human population of 1.2 million, including its largest city, Honolulu.

This study was conducted at 100–400 m (330–1 320 ft) elevation in Pia, Kuli'ou'ou, and Wailupe valleys, which are located on the leeward side of the southern Ko'olau Range in

State Forest Reserves (Fig. 1). These valleys contain about 300 'Elepaio, which comprise over half of the largest remaining subpopulation (VanderWerf *et al.* 2001). In this area 'Elepaio are most common in tall (up to 25 m) closed canopy riparian forest in the bottom of each valley, but they also occur in shorter (5–15 m), drier forest on adjacent slopes and ridges (VanderWerf *et al.* 1997). The riparian forest is dominated by alien plant species, primarily Strawberry Guava *Psidium cattleianum*, Mango *Mangifera indica*, Kukui or Candlenut *Aleurites moluccana*, Christmasberry *Schinus terebinthifolius*, Mountain Apple *Syzygium malaccense*, and Coffee *Coffea arabica*, with smaller numbers of native plants such as Papala Kepau *Pisonia umbellifera*, 'Alahe'e *Psychradax odoratum*, Mamaki *Pipturus albidus*, and Koki'o Ke'oke'o *Hibiscus arnottianus*. Vegetation on the slopes and ridges generally is less disturbed and consists primarily of Strawberry Guava, Christmasberry, and native trees including Koa *Acacia koa*, 'Ohi'a *Metrosideros polymorpha*, Lama *Diospyros sandwicensis*, 'Alahe'e, and Lonomea *Sapindus oahuensis*.

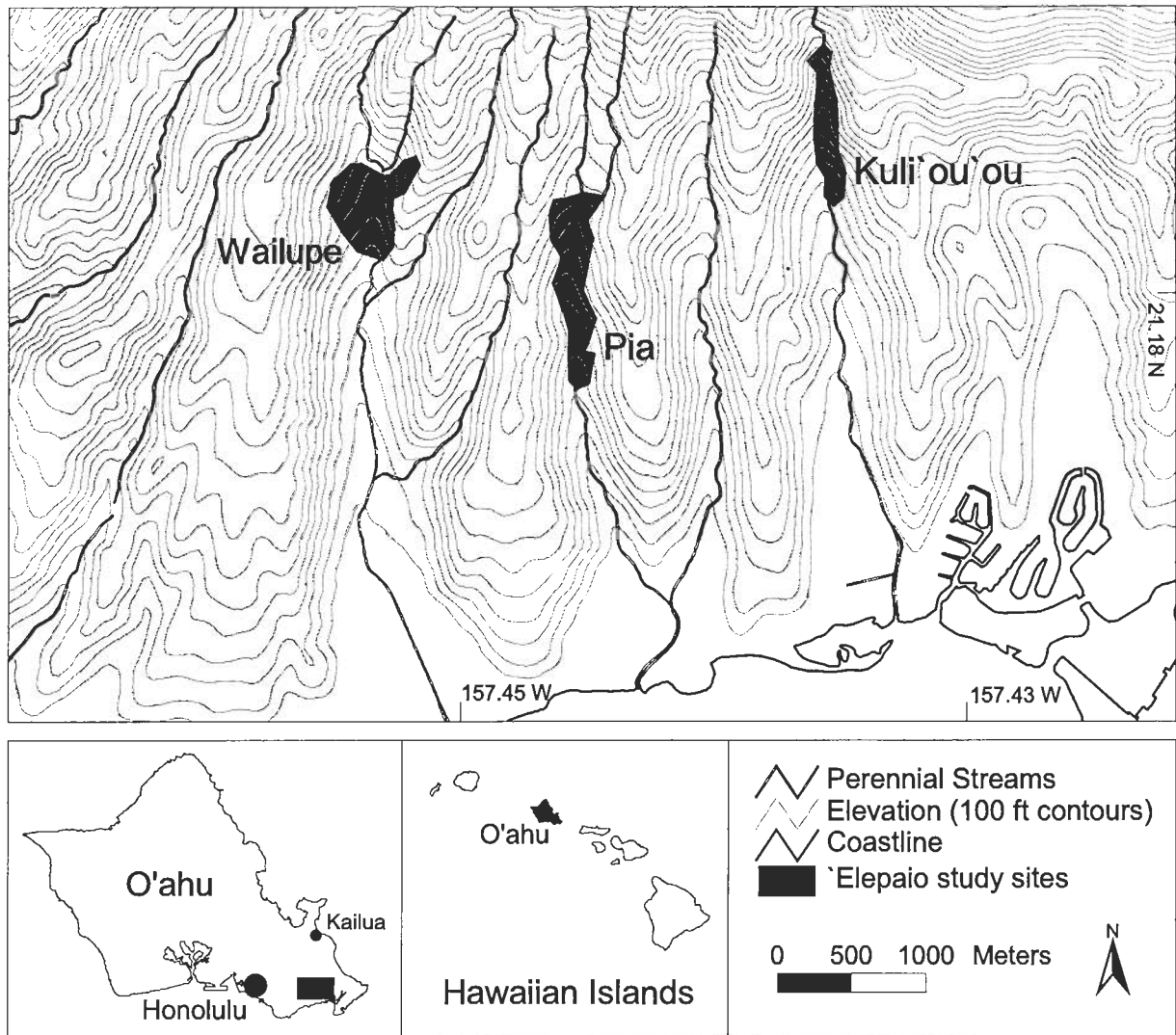


Fig. 1. Locations of O'ahu 'Elepaio study sites, with major cities, latitude and longitude.

This study was conducted from 1996 to 2000, but the number and size of study sites varied among years (Table 1). We attempted to expand the study each year to include additional valleys and more 'Elepaio territories within each valley. The study began in January 1996 with demographic monitoring only of 'Elepaio in two valleys, Pia and Kuli'ou'ou. Rodent control was initiated in Pia Valley in January 1997, with Kuli'ou'ou left as a no treatment site that year for comparison. In 1998 and 1999 the east and west sides of Wailupe Valley were added as third and fourth sites, respectively, each being a no treatment site the first year and a treatment site the second year, and Kuli'ou'ou was switched from a treatment site to no treatment in these years. In 2000 we controlled rodents in all sites to protect as many 'Elepaio as possible, but workload constraints forced us to drop Kuli'ou'ou from the study.

### Rodent control

Rodents were controlled with snap traps and poison bait containing the "first generation" anticoagulant diphacinone in the form of 0.005% two-ounce bait blocks with molasses/peanut butter flavourizer (J. T. Eaton, Twinsburg, Ohio, USA). Bait blocks were placed in durable plastic bait boxes to shield them from rain and to reduce the risk of primary poisoning to non-target species. Bait boxes were tied in trees so they were not accessible to dogs and feral pigs. Snap traps were used to allow identification of rodent species present and to provide a measure of relative rodent abundance. From one to three snap traps and one to three bait stations were deployed in each 'Elepaio territory depending on its size, with an average density of 1.14 snap traps and 1.06 bait stations per hectare (Table 1). Although these densities seem low, traps and bait stations deliberately were concentrated in sections of each territory known to have been

used habitually for nesting, thereby increasing the efficiency of the control programme.

The rodent control programme commenced each year in late January or early February, about three weeks before the usual start of the 'Elepaio nesting season on O'ahu (VanderWerf 1998). Traps and bait stations were checked and rebaited twice a week for the first 2–3 weeks when the catch rate and take of bait were high, then weekly or semi-weekly for the rest of the study period, until the end of the 'Elepaio nesting season in early June. In 1997 and 1998 snap traps were removed to save labour after the mean catch rate fell below 0.01 rodents per trap-day for two consecutive periods (about 50 days). In 1999 and 2000 snap traps were used throughout the season. In 1999 we conducted an experiment to test whether peanut-butter or fish-flavoured bait blocks were more effective. Because take of fish-flavoured blocks was lower and each station initially contained all or half fish-flavoured blocks in 1999, the take of bait is not directly comparable with other years. All baiting procedures were conducted in compliance with U.S. Environmental Protection Agency special local need registration HI-960008 and with regulations of the Hawai'i State Department of Agriculture.

### 'Elepaio demography

To facilitate demographic monitoring, 'Elepaio were captured with mist-nets and marked with a unique combination of an aluminum U.S. Fish and Wildlife Service leg band and three coloured plastic bands. Most birds were lured into a net with playbacks of recorded 'Elepaio songs. Each bird was weighed, measured, inspected for molt, fat, and health, then released unharmed at the site of capture within one hour. A small blood sample was collected from the brachial vein of each bird for genetic analysis and disease screening.

Table 1. Summary of study site sizes, numbers of 'Elepaio pairs monitored, and number of snap traps and bait stations used each year. Number of territories monitored does not always match the number of pairs in Table 2 because some territories contained only a male in some years.

Year	Site	Size (ha)	'Elepaio territories monitored	Snap traps used	Bait stations used
1996	Pia	18	10	0	0
	Kuli'ou'ou	12	7	0	0
1997	Pia	20	11	16	16
	Kuli'ou'ou	14	9	0	0
1998	Pia	20	11	23	18
	Kuli'ou'ou	10	5	13	8
	Wailupe east	14	12	0	0
1999	Pia	22	12	24	22
	Kuli'ou'ou	12	7	0	0
	Wailupe east	11	10	19	20
	Wailupe west	12	9	0	0
2000	Pia	22	12	22	18
	Wailupe combined	20	15	25	31

We attempted to locate all 'Elepaio nests in the study areas and determine their fates by regularly visiting each territory throughout the nesting season from January to June. Most nests were built high in trees on thin branches that could not be reached without undue disturbance to the nest. Because one of the primary goals of this study was to measure nest success, we minimized our impacts and did not attempt to determine clutch size or hatching success if it would have been necessary to climb the nest tree to do so. Nest success was based only on nests known to have had eggs laid in them, as determined by observations of incubation or by using a pole-mounted mirror to look inside the nest. Nests were counted as successful if they fledged at least one chick, and nest success was calculated as the successful proportion of total nests. Some nests were abandoned for unknown reasons before eggs were laid. It is possible that some nests counted as abandoned actually were depredated before incubation was observed, which would cause an overestimate of nest success, but the proportion of abandoned nests did not differ between treatment and control sites (26% vs. 17%, respectively; Chi-square = 1.14, df = 1,  $P = 0.29$ ). In a few cases fledglings were produced from nests we did not find, and it is also likely that we did not find a few nests that failed, but it is unlikely that we overlooked any fledglings that survived more than a few days out of the nest. 'Elepaio 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 nine months, until evicted by the parents at the start of the next breeding season (VanderWerf 1998).

'Elepaio are non-migratory and defend their territory all year. The mean size of territories was 1.82 ha in Pia Valley ( $n = 12$ ), 1.71 ha in Kuli'ou'ou Valley ( $n = 9$ ), and 1.24 ha in Wailupe Valley ( $n = 15$ ; Table 1). Annual survival of territory holders was calculated by enumeration, or the proportion of colour-banded birds resighted the following year. We searched surrounding areas for birds that might have moved. Birds that disappeared from their traditional territory and could not be relocated on a new territory were assumed to have died. Site fidelity was calculated as the proportion of colour-banded birds remaining on the same territory between years, and mate fidelity was calculated as the proportion of pairs remaining together between breeding attempts, based only on cases where both birds were banded and were known to have survived.

'Elepaio are sexually mature and capable of breeding when one year old, but they do not acquire adult plumage until three years of age (VanderWerf 2001b). Depending on population density and rate of adult turnover, young

'Elepaio must wait for a breeding opportunity and often do not obtain a territory or mate until their third year (VanderWerf 2001c). Age structure of the breeding population was measured each year by the proportion of territory holders in the first year subadult, second year subadult, and adult (three or more years) age classes.

To determine the overall effect of rodent control on 'Elepaio demography, we calculated the finite rate of population growth, or lambda ( $\lambda$ ), using the following equation (Pulliam 1988):

$$\lambda = P_A + P_J B$$

where  $P_A$  is annual adult survival,  $P_J$  is juvenile survival, and  $B$  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. Annual adult survival was estimated by averaging survival of males and females. For juvenile survival an estimate of 0.33 was taken from work on 'Elepaio at Hakalau Forest National Wildlife Refuge on Hawai'i Island (E. VanderWerf, unpubl. data), because there is not yet enough data to estimate this parameter on O'ahu. Confidence intervals for lambda with and without rodent control were calculated using values from each of the five years of the study.

## RESULTS

### Rodent control

The rodent control programme using snap traps and diphacinone bait stations appeared to be effective at temporarily decreasing the abundance of rodents each year. A total of 313 rodents was caught in snap traps from 1997 to 2000 in all sites combined, of which 44% were Black Rats, 3% were Polynesian Rats *R. exulans*, 2% were Norway Rats *R. norvegicus*, 5% were House Mice *Mus domesticus*, and 46% could not be identified to species because they were too decomposed or had been scavenged. Black Rats comprised 81% of identifiable captures. The catch rate was high during the first 2–3 weeks of the control program each year, then declined over time and remained low for most of the study period (Fig. 2). Catch rate averaged 0.026 rodents per trap per day. Likewise, take of bait from stations was high at first, then declined rapidly and remained low for much of the season in most years (Fig. 3). A total of 4 133 bait blocks was taken in all years combined, and takes averaged 0.26 blocks per station per day.

Catch rate in snap traps occasionally fell to zero, but always increased again (Fig. 2), indicating complete eradication was not achieved, probably because rats continually were immigrating from surrounding areas. In some

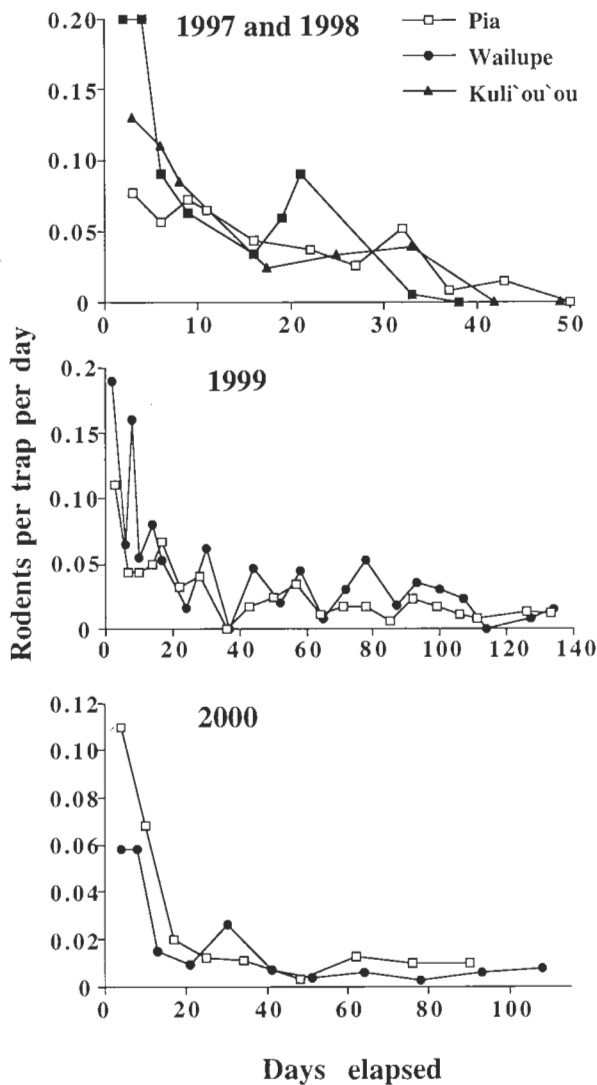


Fig. 2. Daily capture rate of rodents in snap traps in Pia, Wailupe and Kuli'ou'ou valleys from 1997 to 2000.

years there were several progressively lower peaks in bait take later in the season (Fig. 3; 1998), possibly caused by immigration of rats from increasingly distant areas. When the control programme recommenced each subsequent year the catch rate in traps and take of bait were again high for the first few weeks, indicating there was no long-term reduction in rodent abundance.

#### 'Elepaio reproduction

'Elepaio reproduction was very poor before implementation of the rodent control programme. In 1996, only 24% of pairs monitored fledged any offspring.

Beginning in 1997, rodent control resulted in a dramatic increase in 'Elepaio reproduction. Both nest success (Chi-square = 4.90,  $df = 1$ ,  $p = 0.027$ ) and number of fledglings per pair (Mann-Whitney test,  $p = 0.001$ ) were higher in areas with rodent control than in areas without

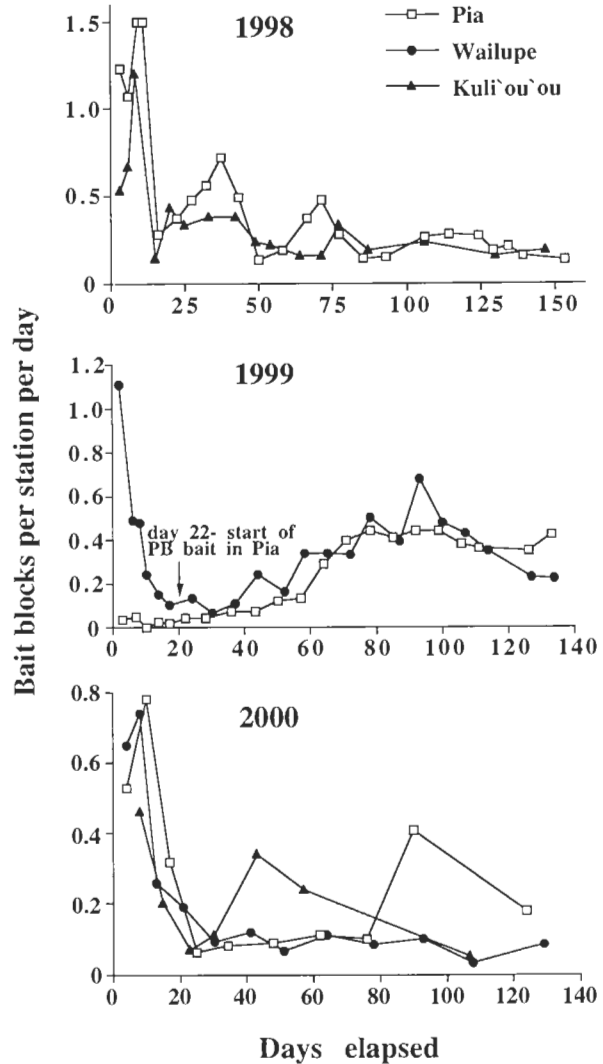


Fig. 3. Daily take of diphacinone bait blocks from stations in Pia, Wailupe and Kuli'ou'ou valleys from 1998 to 2000. Baiting was conducted in Pia Valley in 1997, but daily take was not recorded.

rodent control, based on data from 1996 to 2000 combined (Table 2). Reproduction of 'Elepaio at each site increased the first year rodent control was conducted (Fig. 4), and dropped again if rodent control was discontinued (e.g., Kuli'ou'ou in 1999).

Nests were found in nine different species of trees (Table 3), but nest success was not related to tree species (Chi-square = 2.95,  $df = 4$ ,  $p = 0.57$ ). Nest height ranged from 2 to 19 meters above the ground, but height of failed nests ( $9.0 \pm 0.6$  m,  $n = 41$ , range 2–19 m) did not differ from height of successful nests ( $9.9 \pm 0.6$  m,  $n = 45$ , range 3.9–18 m;  $t = 1.10$ ,  $df = 83$ ,  $p = 0.27$ ).

Even with rodent control, fecundity of O'ahu 'Elepaio was low. The average clutch size was 1.83 (range 1–3,  $n = 12$ ), the mean number of fledglings per successful nest was 1.11 (range 1–2,  $n = 63$ ), and the mean number of broods per successful pair was 1.05 (range 1–2,  $n = 63$ ).

Table 2. Comparison of 'Elepaio reproduction with and without rodent control. Total values for nest success and fledglings per pair are summed over all years. No rodent control was conducted in 1996, and all sites received rodent control in 2000.

Year	Rodent control?	% Nest success (n)	Fledglings per pair (n)
1996	No	43 (7)	0.24 (17)
1997	Yes	64 (11)	0.91 (11)
	No	50 (2)	0.56 (9)
1998	Yes	57 (14)	0.63 (16)
	No	38 (8)	0.42 (12)
1999	Yes	62 (21)	0.76 (21)
	No	23 (13)	0.25 (16)
2000	Yes	50 (18)	0.62 (26)
Total	Yes	58 (64)	0.70 (74)
	No	33 (30)	0.33 (54)

Table 3. Number of successful and failed O'ahu 'Elepaio nests by tree species, 1996–2000 combined. "Other" consists of uncommonly used species that were lumped for statistical tests due to small sample sizes, including Mountain Apple *Syzygium malaccense*, Lonomea *Sapindus oahuensis*, Quinine *Cinchona pubescens*, Papala Kepau *Pisonia umbellifera*, and Chinese Banyan *Ficus microcarpa*. Of all these species used for nesting only Lonomea and Papala Kepau are native to Hawai'i.

Nest tree species	Number of successful nests	Number of failed nests
Strawberry Guava <i>Psidium cattleianum</i>	19	17
Mango <i>Mangifera indica</i>	11	13
Kukui <i>Aleurites moluccana</i>	8	7
Christmasberry <i>Schinus terebinthifolius</i>	5	1
Other	4	5

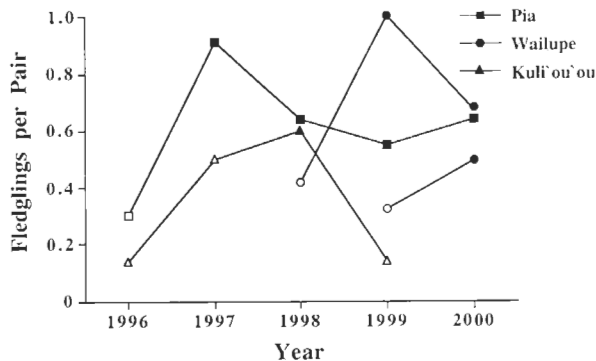


Fig. 4. Annual reproductive success of 'Elepaio pairs in Pia, Wailupe and Kuli'ou'ou valleys with (filled symbols) and without (open symbols) rodent control from 1996 to 2000.

'Elepaio renested after failure, producing up to three clutches in a season.

Other than presumed predation, storms appeared to be the most common cause of nest failure. Nineteen of the 47 known nest failures

occurred during periods with heavy rain and strong winds in late March and early April.

### Survival

Survival of female 'Elepaio was higher with rodent control (0.83,  $n = 18$ ) than without rodent control (0.50,  $n = 14$ ; Chi-square = 4.07,  $df = 1$ ,  $P = 0.04$ ), but survival of male 'Elepaio was not affected by rodent control (0.79,  $n = 78$  with vs. 0.76,  $n = 50$  without; Chi-square = 0.22,  $df = 1$ ,  $P = 0.64$ ). Without rodent control survival of females was lower than survival of males (Chi-square = 3.54,  $df = 1$ ,  $P = 0.06$ ), but with rodent control survival of males and females was similar (Chi-square = 0.14,  $df = 1$ ,  $P = 0.71$ ).

### Site and mate fidelity

Site fidelity of female 'Elepaio was much higher with rodent control (0.93,  $n = 14$ ) than without rodent control (0.33,  $n = 9$ ; Chi-square = 9.17,  $df = 1$ ,  $P = 0.002$ ). In contrast, site fidelity of male 'Elepaio was not affected by rodent control (0.97,  $n = 63$  with vs. 0.95,  $n = 37$  without; Chi-square = 0.30,  $df = 1$ ,  $P = 0.58$ ). Without rodent control site fidelity was much lower in females than in males (Chi-square = 18.91,  $df = 1$ ,  $P < 0.001$ ), but with rodent control site fidelity was similar in males and females (Chi-square = 0.48,  $df = 1$ ,  $P = 0.45$ ). Mate fidelity also was much higher with rodent control (1.0,  $n = 9$ ) than without rodent control (0.33,  $n = 9$ ; Chi-square = 9.0,  $df = 1$ ,  $P = 0.003$ ).

### Age structure and recruitment

Rodent control resulted in an increase in female recruitment age and an upward shift in the age structure of breeding females, but rodent control did not affect recruitment and age structure of males (Fig. 5). Without rodent control 34% of breeding females were subadult (less than three years old), but with rodent control only 15% of breeding females were subadult (Chi-square = 8.35,  $df = 1$ ,  $P = 0.004$ ). In males, the proportion of breeding males that were subadult was 9% both with and without rodent control (Chi-square = 0.01,  $df = 1$ ,  $P = 0.98$ ).

### Population growth

The average (95% C.I.) rate of population growth without rodent control for all years combined was 0.76 (0.64–0.88), indicating a rapid 26% decline per year (Table 4). With

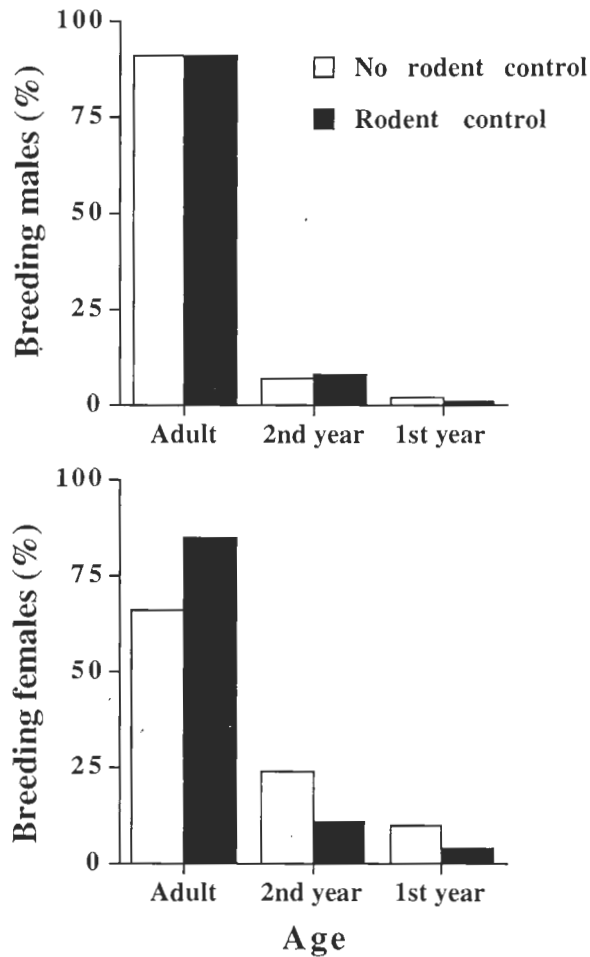


Fig. 5. Age structure of breeding 'Elepaio with and without rodent control, for males and females separately. Adults were at least three years old.

Table 4. 'Elepaio population growth rate (lambda) each year with and without rodent control. Values for all years are averages. No rodent control was conducted in 1996 and all sites received rodent control in 2000.

Year	Lambda without rodent control	Lambda with rodent control
1996	0.79	—
1997	0.85	1.09
1998	0.73	0.96
1999	0.67	1.06
2000	—	0.87
All years	0.76	1.00

rodent control the average rate of population growth was 1.00 (0.84–1.15), indicating a stable population.

## DISCUSSION

Control of alien rodents, primarily Black Rats, resulted in dramatic increases in reproduction and survival of female O'ahu 'Elepaio. These results are not surprising considering the widespread effect of predation by Black Rats on

island birds worldwide (Atkinson 1977; Moors *et al.* 1992; Robertson *et al.* 1994). However, this study also revealed that rat predation had cascading effects that influenced many other aspects of 'Elepaio demography, including, female site fidelity, mate fidelity, and age structure and recruitment of females. Moreover, results of this study demonstrate that rodent control can restore each of these parameters to conditions that allow for population stability and help to maintain naturally evolved behaviours. Control of alien rodents is crucial to the conservation of this endangered forest bird.

Before rodent control was implemented reproduction of 'Elepaio was very low, too low to allow long-term persistence of a population. Nest success was not related to nest height or tree species, indicating rats are ubiquitous throughout the forest and reach even the top of the canopy. Rat predation may be especially frequent in the disturbed habitat occupied by 'Elepaio in this study because the dominant tree species, Strawberry Guava, Mango, Kukui, Christmasberry, and Mountain Apple, all bear fruits or nuts that may help to support large rat populations and attract rats into the canopy in search of food, where they encounter 'Elepaio nests. The effectiveness of rodent control at increasing 'Elepaio population growth varied among years, with larger differences between treatment and control sites in wet years with high fruit abundance, such as 1999, than in dry "El Niño" years with little fruit, such as 1998 and 2000 (E. VanderWerf, unpubl. data).

Adult 'Elepaio have few predators. Nocturnal predation at nests by Black Rats appeared to be the primary cause of mortality for female 'Elepaio. After rat predation was managed, annual survival of males and females was similarly high. Rat control likely influenced survival of females and not males due to the incubation behaviour of 'Elepaio; male and female 'Elepaio share incubation in alternating shifts during the day, but only the female incubates at night (VanderWerf 1998), making females potentially more vulnerable than males to nocturnal predators like rats. Feral Cats and Small Indian Mongooses also were present in the study areas, but most 'Elepaio nests were built on thin branches that probably were not accessible to these larger predators. In an experiment using artificial nests with electronic cameras, all predation events occurred at night and a Black Rat was the predator in every case (VanderWerf 2001a).

The shift in female recruitment and age structure was a direct result of the decline in mortality of breeding females. As mortality of breeding females declined due to rodent control, fewer breeding opportunities became available



for young females, and more females were forced to delay recruitment and wait for a vacancy. Because male 'Elepaio apparently were not preyed upon by rats and survival of males was not affected by rodent control, there were no changes in breeding opportunities or recruitment of males associated with rodent control.

Although we did not anticipate the increases in mate fidelity and female site fidelity caused by rodent control, these patterns are not surprising. It has been shown in several bird species that breeding dispersal and mate switching are more frequent after reproductive failure, especially when caused by predation (Payne and Payne 1993; Gowaty and Plissner 1997; Haas 1998). Management techniques like predator control that increase reproductive success therefore can be expected to result in increased mate and site fidelity. In this study, all cases of mate switching occurred after failure the previous year, and all but one case of female breeding dispersal occurred after failure. Only once did a female switch territories after reproducing the previous year, and that occurred when the original male had died and the territory was taken over by a young male. Mate fidelity and philopatry in birds are thought to lead to enhanced reproduction through greater familiarity, more efficient pairing and mating, and earlier nesting (Choudhury 1995; Black 1996). Predator control not only caused an immediate increase in nest success of 'Elepaio, but also may lead to long-term improvements in reproductive performance through increased mate and site fidelity.

Although the rodent control programme was effective in the short term, there was no long-term reduction in rodent abundance and the control programme started from scratch each year. It is worth investigating whether year-round control that would depress rodent numbers indefinitely is more cost and labour effective than the seasonal methods employed in this study.

This study is similar in many respects to a study by Robertson *et al.* (1994) on the effects of rodent control on the Kakerori or Rarotonga Monarch. In both studies control of rodents, primarily Black Rats, resulted in a large increase in the reproductive rate, a decline in mortality of females, and an upward shift in the age structure of the breeding population. Population size of Kakerori initially was extremely low (29 birds) and rodent control led to a rapid increase in the number of birds. In this study the immediate goal of rodent control was to stabilize core populations of 'Elepaio while they were still relatively large. The long-term recovery strategy

for 'Elepaio is for these core populations, once stabilized, to serve as sources of colonists to support smaller populations and perhaps recolonize areas where 'Elepaio have disappeared.

However, even with rodent control the mean rate of population growth was 1.0, indicating the population was stable, but not increasing. In addition to predation by rats, the 'Elepaio and other Hawaiian forest birds are threatened by diseases carried by the alien Southern House Mosquito *Culex quinquefasciatus*, particularly Avian Malaria *Plasmodium relictum* and avian poxvirus (*Avipoxvirus* sp.) (Warner 1968; van Riper *et al.* 1986; Atkinson *et al.* 1995; VanderWerf 2001c). Recovery of the O'ahu 'Elepaio likely will require management of these diseases in addition to rodent control. Currently there is no practical and environmentally sound method of controlling mosquitoes or disease transmission in the forests occupied by the O'ahu 'Elepaio. However, if there is natural, heritable variation in immunity to these diseases, rodent control may facilitate the evolution of disease-resistance by providing birds that have greater natural immunity an increased chance of reproducing, thereby increasing the proportion of resistant birds in each subsequent generation more quickly.

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