

DEMOGRAPHY OF HAWAII‘I ‘ELEPAIO: VARIATION WITH HABITAT DISTURBANCE AND POPULATION DENSITY

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Abstract. From 1994 to 1997, I monitored ‘Elepaio (*Chasiempis sandwichensis*), a forest bird endemic to Hawaii, in three sites that differed in either degree of habitat disturbance or population density. The goal was to determine whether areas with disturbed forest and reduced population density due to disease were lower-quality habitats that acted as population sinks. Sites where the forest had been disturbed by cattle grazing and timber harvesting contained larger ‘Elepaio territories, supported less dense ‘Elepaio populations, and had a higher proportion of subadult birds in the breeding population and, thus, can be considered lower-quality habitat for ‘Elepaio. However, ‘Elepaio populations in disturbed sites did not have lower survival, reproduction, or site fidelity than a population in denser forest, and they were self-sustaining. Disturbed sites were not population sinks maintained by immigration; they simply had a lower carrying capacity. Annual survival of territory-holders was high and was slightly higher in males (0.86 ± 0.04 [mean ± 1 SE]) than in females (0.79 ± 0.05). Fecundity was low, with pairs producing 0.56 ± 0.06 fledglings per year. Site fidelity was high in males (0.98) and females (0.93), and most birds remained on the same territory for the duration of the study or until their presumed death. Population growth was stable at two sites ($\lambda = 0.96 \pm 0.03$, 1.02 ± 0.04) and increasing (1.12 ± 0.04) at a site recovering from an epizootic of avian poxvirus. Young, subadult-plumaged males defended smaller territories and produced fewer fledglings than older males, but female age did not affect territory size or reproductive success. Recruitment age was younger where population density was lower.

Key words: age structure; *Chasiempis sandwichensis*; demography; ‘Elepaio; habitat disturbance; Hawaii; site fidelity; survival; territory size.

INTRODUCTION

Naturally and human-altered ecosystems often exist as a mosaic of different habitats that may vary in quality for a given species (Brown 1969, Wiens 1976, Cody 1985). Variation in habitat quality can strongly influence the distribution of species on a landscape scale, and may affect demographic parameters such as population density, survival, and reproduction (Lomnicki 1980, Pulliam and Danielson 1991). Conversely, demographic comparison of a particular species among habitats can reveal whether certain habitats are of lower quality (e.g., Andr n 1990, Hatchwell et al. 1996, Holmes et al. 1996, Purcell and Verner 1998). Populations in high-quality habitats may act as sources where reproduction exceeds mortality, while populations in suboptimal habitats may act as sinks that are not self-sustaining and must be maintained by immigration (Pulliam 1988).

Natural ecosystems in many regions have become increasingly disturbed by human activities such as clearing of land for development and agriculture, harvesting of plant and animal products, introduction of

alien species, and alteration of natural hydrology and climate. These activities often drastically alter resource abundance and habitat structure, and therefore can be expected to cause changes in the distribution and demography of species occupying those areas. In birds, for example, Robinson et al. (1995) found that forest fragmentation in North America has resulted in reduced nest success of several species of neotropical migratory birds, and that populations in the most fragmented areas were declining and likely acted as sinks. In contrast, Wesolowski (1983, 1987) found that abundance and reproductive success of wrens (*Troglodytes troglodytes*) and Great Tits (*Parus major*) were lower in a primeval forest than in second growth forest where populations were aided by nest boxes, demonstrating that human activities do not always have negative impacts on all native species.

In the Hawaiian Islands, destruction and alteration of native ecosystems has been extensive, beginning with colonization by Polynesians over 1500 years ago, and accelerating in the last 200 years with the advent of more advanced technologies (Kirch 1982, 1983, Cuddihy and Stone 1990). The Hawaiian Archipelago is well known for its high rate of endemism resulting from prolonged isolation (Carlquist 1970, Freed et al. 1987), and many Hawaiian species are vulnerable to habitat disturbance and the introduction of alien predators, competitors, and pathogens (Stone and Stone

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1989). The endemic Hawaiian avifauna is especially sensitive to habitat disturbance and alien predators (Scott et al. 2001), and many species have very poor immunity to alien diseases such as avian malaria (*Plasmodium relictum*) and avian poxvirus (*Poxvirus avium*) (Warner 1968, van Riper et al. 1986, Atkinson et al. 1995, Jarvi et al. 2001, Shehata et al. 2001). Despite the pervasive alteration of native habitats in Hawaii and the apparent vulnerability of many Hawaiian birds to disturbance, the demographic effects of habitat disturbance on wild populations of Hawaiian birds have rarely been quantified (see Sakai 1988). Such information is needed to determine whether native bird populations in disturbed habitats are self-sustaining, or if they have reduced survival or reproduction and act as sinks that must be supported by immigration or perpetually managed to ensure their survival.

In this study I investigated the demography of the Hawai'i 'Elepaio (*Chasiempis s. sandwichensis*), a forest-dwelling monarch flycatcher (Monarchidae) endemic to the island of Hawai'i (VanderWerf 1998), in three areas that differed either in degree of human habitat disturbance or in population density due to previous variations in local disease prevalence. My goal was to determine whether 'Elepaio populations in areas with disturbed forest or low population density were self-sustaining or if they acted as sinks. An epizootic of avian pox occurred at one of the sites in 1992 (VanderWerf 2001a), so instead of examining the direct effects of disease on demography, this study documented the demographic consequences of reduced population density and subsequent recovery. To allow demographic comparisons, at each site I measured survival, reproduction, age structure, territory size, and site fidelity of banded birds, and I calculated the rate of population growth. Many previous studies have examined demography of birds among habitats (e.g., van Balen 1973, Blondel et al. 1987, Holmes et al. 1996), and several have compared areas with varying degrees of human disturbance (e.g., Porneluzi et al. 1993, Robinson et al. 1995, Hatchwell et al. 1996, Purcell and Verner 1998). This study further examines the impacts of human habitat disturbance on bird populations, with the added dimension of increasing population density following demographic perturbation by disease.

METHODS

Study species

'Elepaio are well suited for demographic studies because they are non-migratory and territorial year-round, making it relatively easy to monitor individuals over several years. 'Elepaio are adaptable, prey on a variety of arthropods that they capture with diverse behaviors, and occur in a variety of forested habitats (Conant 1977, Scott et al. 1986, VanderWerf 1998, van Riper 1995), but areas disturbed by logging and cattle grazing may be lower-quality habitat for 'Elepaio because their

open structure constitutes a more difficult foraging environment (VanderWerf 1993, 1994). 'Elepaio populations can be seriously affected by avian poxvirus (VanderWerf 2001a), but the persistence of 'Elepaio at low elevations in some areas suggests that at least some individuals have greater immunity to alien diseases than most Hawaiian forest birds (VanderWerf et al. 1997, VanderWerf and Smith 2002).

Study sites

I conducted this study at Hakalau Forest National Wildlife Refuge (Hakalau), on the eastern slope of Mauna Kea volcano on the island of Hawai'i (Fig. 1). Hakalau protects >13 000 ha in one of the largest tracts of native forest remaining in Hawai'i, and the area supports the largest populations of several species of Hawaiian forest birds, including 'Elepaio (Scott et al. 1986). The dense montane rainforest at Hakalau has been variously altered by cattle grazing, timber harvesting, and other human uses during the last 100 years, resulting in a mosaic of forest habitats, ranging from largely intact forest with a dense understory, to highly disturbed open woodland with a groundcover of alien grasses.

I studied 'Elepaio in three sites at Hakalau that were selected so they differed in either degree of habitat disturbance or 'Elepaio population density, or both. One of the sites, middle Pua 'Akala, had relatively dense forest, while sites at upper Pua 'Akala and Maulua were more disturbed. The two Pua 'Akala sites were contiguous, but the Maulua site was 10 km to the north and 300 m lower in elevation (Fig. 1). Middle Pua 'Akala and upper Pua 'Akala had dense, stable 'Elepaio populations. At Maulua, the 'Elepaio population experienced an epizootic of avian poxvirus in 1992; population density was low at the start of the study in 1994, but had recovered to its presumed original level by 1996 (VanderWerf 2001a; see *Results: Territory size*). Plant species composition was similar at all three sites; 'ohi'a (*Metrosideros polymorpha*) and koa (*Acacia koa*) were the dominant tree species, and other fairly common trees included 'olapa (*Cheirodendron trigynum*), kolea (*Myrsine lessertiana*), kawa'u (*Ilex anomala*), and pilo (*Coprosma montana*). Common understory plants were 'ohelo (*Vaccinium calycinum*), 'akala (*Rubus hawaiiensis*), pukiawe (*Styphelia tameiameiae*), saplings of tree species, and occasional tree ferns (*Cibotium* sp. and *Saddleria* sp.). Ground cover consisted of native herbs, numerous species of ferns, particularly *Dryopteris* spp. and *Pteridium aquilinum*, and alien grasses, primarily Kikuyu grass (*Pennisetum clandestinum*), meadow ricegrass (*Erharta stipoides*), sweet vernalgrass (*Anthoxanthum odoratum*), and velvet grass (*Holcus lanatus*).

At each site I mist-netted and color-banded 'Elepaio, sometimes using playbacks of recorded 'Elepaio vocalizations to lure a bird into a net. I monitored survival, reproduction, age structure, territory size, dis-

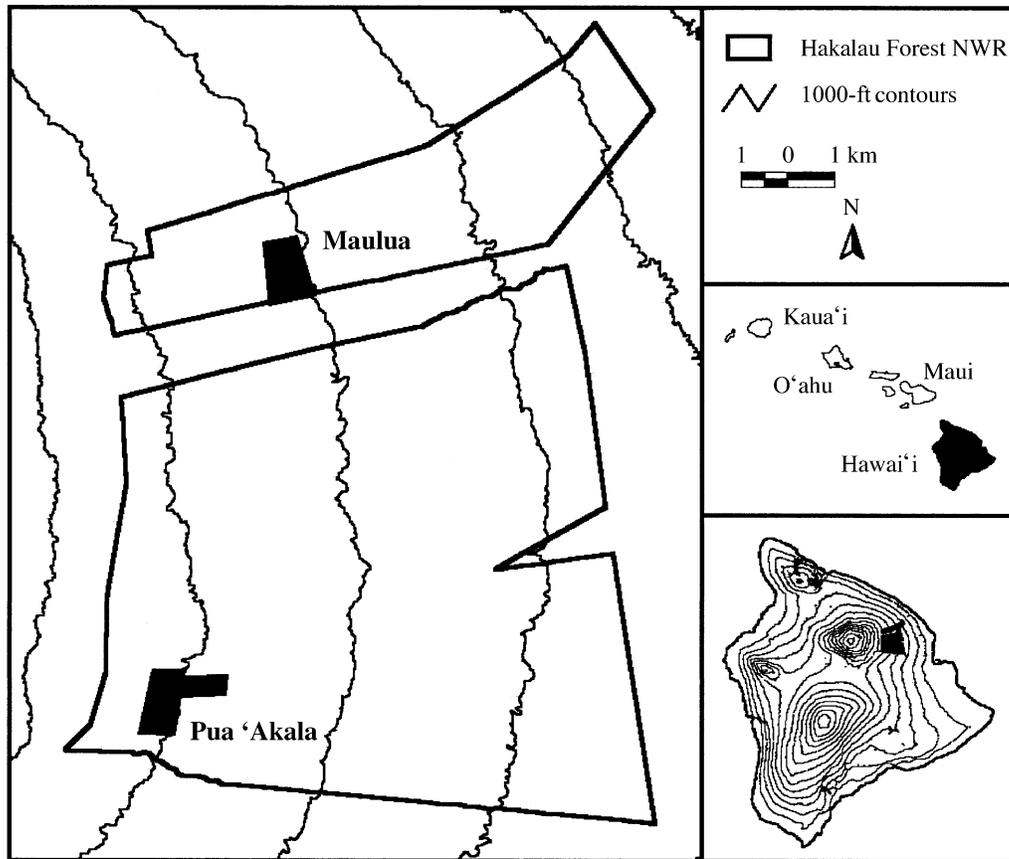


FIG. 1. Location of the three study sites (shown in black) at Hakalau Forest National Wildlife Refuge (NWR), Hawaii, USA. The two Pua 'Akala sites are contiguous: The rectangle on the left is upper Pua 'Akala, and the rectangle on the right is middle Pua 'Akala. Note that contour lines are in feet (1000 ft = 304.8 m).

persal, site fidelity, and mate fidelity from 1994 to 1997, with additional data on survival and site fidelity from 1991 and 1998. All analyses were conducted with Minitab (1995).

Habitat structure

I measured habitat structure at each site using a method based on that by James and Shugart (1970), as modified by Noon (1981). A grid system with numbered poles at 100 m intervals was used to systematically select points that served as centers of 15 m radius circular quadrats. Within each quadrat, the numbers of trees and shrubs were counted, the diameter of all trees >5 cm in diameter was measured 1.5 m above ground, and maximum canopy height was measured with a clinometer. Percent canopy cover and percent ground cover type (native, alien grass, or bare rock or soil) were estimated from 20 points at 3-m intervals along north-south and east-west diameters of each quadrat. Variation in habitat structure among sites was examined with a one-way ANOVA for each variable. If the overall *F* test was significant, I made pairwise comparisons among sites with Tukey's *a posteriori* correction.

To facilitate examination of the relationship between habitat structure and territory size, a single measure of habitat structure was created with a Principal Components Analysis (PCA) of tree density, shrub density, percent canopy cover, and percent native ground cover within each territory. The number of quadrats per 'Elepaio territory averaged 1.6 ($n = 77$). For each variable, higher numbers represented more dense structure and less disturbance, making the value of the principal components easier to interpret.

Territory size

'Elepaio have a distinctive display that is used to establish and confirm territory boundaries, in which two males fly side by side in a long, pendulous arc along the territory boundary (VanderWerf 1998). Territory boundaries were identified by locations of these display flights, and in some cases with playbacks of recorded songs (Falls 1981). In cases where pairs had no immediate neighbors in certain directions, the farthest point where they were observed in that direction was used as the edge of the territory. Territories proved to be non-overlapping, and territory size was measured

by the minimum convex polygon method (White and Garrott 1990), as calculated by WILDTRAK (Todd 1992). If the minimum convex polygon encompassed areas that were not used by 'Elepaio, such as large meadows without trees, then the area of the unused feature was excluded (White and Garrott 1990:153).

I examined variation in territory size using an Analysis of Variance, with site, year, male age, female age, and all two-way interactions as factors. Three-way interactions could not be evaluated because there were too few degrees of freedom. First-year and second-year age classes were combined into "subadult" for analysis due to small sample sizes at some sites. The relationship between territory size and habitat structure was investigated with linear regression, using territory size in 1996 as the dependent variable and the first principal component of habitat structure as the independent variable.

Age structure

'Elepaio have a two-year delay in plumage maturation in both sexes, resulting in three age classes that can be recognized by plumage: first-year subadults, second-year subadults, and adults (three or more years old; VanderWerf 2001b). I measured age structure of the breeding population at each site by the proportion of territory-holders in each age class. I measured recruitment age of each sex by the ages of birds that filled vacant territories. Most birds filling vacancies probably were floaters acquiring a territory for the first time (recruits), but observations of banded birds showed that a few vacancies were filled by older birds switching territories. Variation in age structure of each sex among sites and years was examined with chi-square analysis. Variation in recruitment age among sites was examined by chi-square analysis, with data for both sexes and from all years combined due to small sample sizes.

Survival, site fidelity, and mate fidelity

Each year I regularly visited every territory in each study site to determine which banded birds were still present, and I searched 300–1000 m in all directions from each study site for banded birds that might have dispersed. I thus knew from direct observation the status of every territorial bird on the study sites each year. I calculated annual survival of territory-holders by enumeration, or the proportion of banded birds that survived to the next breeding season. Site fidelity was calculated as the proportion of banded birds remaining on the same territory between years. Mate fidelity was calculated as the proportion of banded pairs remaining together between breeding attempts, based only on cases where both birds were banded and were known to have survived. Breeding dispersal distance was measured as the distance between the geometric centers of territories.

Enumeration can be expected to provide an accurate estimate of survival in this case, and more formal survival estimation procedures based on mark–recapture methods would not provide an advantage because the probability of resighting a bird was very high (Lepson and Freed 1995; see *Results: Survival, site fidelity, and mate fidelity*). In two instances, a bird reappeared after a one-year absence, but both birds were replaced in their former territories by new birds, indicating they were not missed, but rather left the study area and subsequently returned. It is possible that a few additional birds emigrated and did not return, but the number of emigrants must have been small. Undetected emigration would cause a slight underestimate of survival and a slight overestimate of site fidelity.

Reproduction

I regularly visited the territory of each pair throughout the nesting season to monitor their reproductive status. 'Elepaio exhibit characteristic vocalizations and behaviors when they are nesting that make it relatively easy to determine whether a bird is nesting and to locate nests. During incubation male and female 'Elepaio switch nest attendance approximately every 12 min, and each parent feeds nestlings and recent fledglings approximately every 4 min (VanderWerf 1998). If an 'Elepaio was observed for at least 20 min and did not visit a nest or feed fledglings it was not considered to be nesting. Nest success was calculated as the proportion of nests that fledged at least one chick, based only on nests in which eggs were laid. Nests were counted as abandoned if incubation was never observed. Pairs were counted as successful only if they were observed with fledglings. All pairs holding territories were included in calculations of number of fledglings, even those that did not attempt to nest, because they were still part of the potential breeding population. 'Elepaio fledglings are easy to locate by their persistent begging calls, are fed by their parents for over a month after leaving the nest, and remain with their parents on the natal territory for up to nine months until the subsequent breeding season (VanderWerf 1998). I may have missed some nests that failed before hatching, but it is very unlikely that I overlooked any fledglings that survived more than a few days after leaving the nest. Because the reproductive status of each pair was known, it was not necessary to use the Mayfield method to estimate nest success.

The primary measure used to compare reproduction among sites was number of fledglings per pair. Because age structure of the breeding population differed among sites (see *Results: Age structure*), and reproductive success often varies with age (Saether 1990), I also examined the effect of parental age on reproduction. Variation in number of fledglings was examined with Poisson regression, because number of fledglings per pair closely fit a Poisson distribution, using number of fledglings per pair as the dependent variable, and site,

TABLE 1. Comparison of habitat density and amount of vegetation (means \pm 1 SE) per 'Elepaio territory at three study sites in Hakalau Forest National Wildlife Refuge, Hawaii, USA.

Habitat variable	Middle Pua 'Akala (<i>n</i> = 16)	Upper Pua 'Akala (<i>n</i> = 34)	Maulua (<i>n</i> = 27)
Trees/ha	490 \pm 38*	252 \pm 31	203 \pm 22
Trees/territory in 1996	461 \pm 36	396 \pm 49	384 \pm 41
Shrubs/ha	1736 \pm 240*	666 \pm 92	563 \pm 62
Shrubs/territory in 1996	1631 \pm 226	1046 \pm 144	1064 \pm 116
Canopy height (m)	22.1 \pm 0.6	20.9 \pm 0.7	19.8 \pm 0.7
Canopy cover (%)	77 \pm 2.6*	51 \pm 3.7	53 \pm 5.5
Native ground cover (%)	59 \pm 6.3*	27 \pm 3.0	31 \pm 3.6

Note: Asterisks (*) indicate values significantly different ($P < 0.05$) from those at other sites (ANOVAs with Tukey's correction for multiple comparisons).

year, male age, female age, and their two-way interactions as independent variables. However, due to lack of variation in reproductive success of subadult age classes at some sites in some years, it was necessary to do two separate Poisson regressions, one with male age, female age, and their interaction as factors, and another with site, year, and their interaction as factors, using only adults. Although distribution of number of fledglings violated the assumption of normality, I then used a General Linear Model (GLM) to corroborate results of the Poisson regression using the full data set with birds of all ages, and to examine interactions between pairs of variables that could not be included together in the Poisson regression. Nest success among sites was compared with chi-square analysis. Timing of nesting was measured by the number of nests initiated each month, and variation in timing of nesting among years and sites was compared with chi-square analyses. Due to small sample sizes it was necessary to combine data for March and April and for June and July.

Population growth

To determine whether the population at each site was self sustaining, I calculated the rate of population growth, or lambda (λ), using the formula

$$\lambda = P_A + P_J B$$

where P_A is annual adult survival, P_J is juvenile survival, and B is the mean number of fledglings produced per pair per year (Pulliam 1988). Values of lambda $>$ 1 indicate population increase, those $<$ 1 indicate decline, and a value not different from 1 indicates no change. All parameter estimates used in the formula were based on data collected during this study. Adult survival was averaged for males and females, and fledglings per pair was averaged over birds of all ages at each site. Annual variation in population growth at each site was measured by calculating the value of lambda separately each year, then calculating the mean and variance over all years.

RESULTS

Habitat structure

The vegetation was more dense and less disturbed at middle Pua 'Akala than at upper Pua 'Akala or Mau-

lua; middle Pua 'Akala had higher tree density, higher shrub density, greater canopy cover, and more native groundcover than the other two sites (Table 1). Upper Pua 'Akala and Maulua were similar in habitat structure, and did not differ in any habitat variable. Canopy height did not differ among any of the sites. Most (77%) of the variation in habitat structure was explained by the first principal component, which was characterized by high tree density, high shrub density, extensive canopy cover, and a high proportion of native groundcover (PC loadings -0.51 , -0.50 , -0.47 , and -0.52 , respectively).

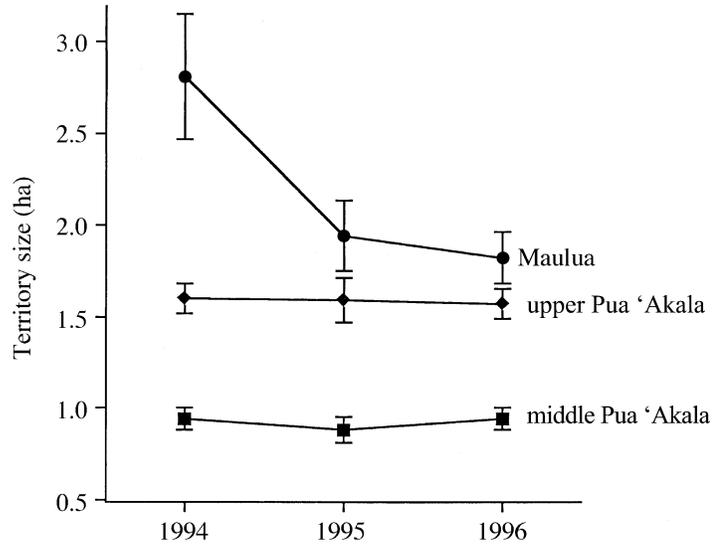
Territory size

Territory size differed among sites ($F_{2,19} = 14.03$, $P < 0.001$) and between male age classes ($F_{1,19} = 5.61$, $P = 0.02$), but did not differ among years ($F_{2,19} = 0.24$, $P = 0.78$) or between female age classes ($F_{1,19} = 0.04$, $P = 0.84$), and there was an interaction between site and year ($F_{4,19} = 8.14$, $P < 0.001$). Territories were smallest at middle Pua 'Akala (0.92 ± 0.04 ha, all years combined), where the forest was most dense, intermediate in size at upper Pua 'Akala (1.59 ± 0.05 ha), and largest at Maulua (2.16 ± 0.14 ha), where the forest was less dense and population density was low due to a previous epizootic of pox (Fig. 2). Territory size was strongly related to the first principal component of habitat structure (Fig. 3; $R^2 = 43\%$, $F_{1,45} = 34.15$, $P < 0.001$). Smaller territories were associated with higher tree density, higher shrub density, greater canopy cover, and more native ground cover, and these conditions were more frequent at middle Pua 'Akala.

Territory size did not differ among years at either middle Pua 'Akala or upper Pua 'Akala, but at Maulua territory size declined over time (Fig. 2; Tukey's a posteriori test), accounting for the interaction between site and year. Territories were larger at Maulua than at upper Pua 'Akala in 1994, but by 1996, territory size no longer differed between these two sites (Tukey's a posteriori test).

Territories of pairs with a subadult male were smaller (1.45 ± 0.20 ha; mean \pm 1 SE) than territories of pairs with an adult male (1.61 ± 0.07 ha) at all three sites (Fig. 4), indicating male age was an important deter-

FIG. 2. ‘Elepaio territory sizes at three sites in Hakalau Forest National Wildlife Refuge, Hawaii, from 1994 to 1996. Middle Pua ‘Akala had dense forest and high ‘Elepaio density, upper Pua ‘Akala had disturbed forest and moderate ‘Elepaio density, and Maulua had disturbed forest with increasing ‘Elepaio density after an epizootic of poxvirus in 1992.



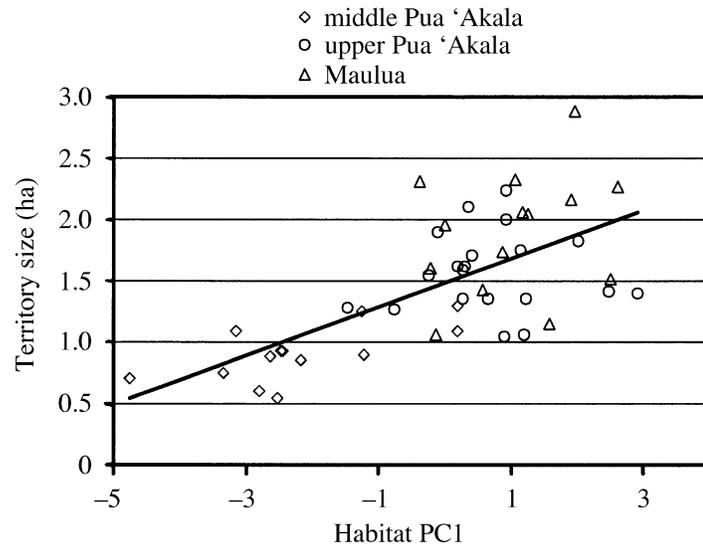
minant of territory size. Territory size was not related to female age at either Pua ‘Akala site. At Maulua territory size appeared to be related to territory size, but female age was confounded with male age at Maulua because most subadult females were paired with subadult males. At middle Pua ‘Akala and upper Pua ‘Akala there were more mixed-age pairs, and those two sites better indicate the real pattern.

The boundaries and size of a given territory generally were similar between years, but changes often occurred when a territory changed ownership, especially if the new owner was a subadult male that was unable to control the entire area occupied by the previous adult male. Territories of subadults usually were small at first, often occurring on the forest edge or filling the interstices between adult territories, and increased in size in subsequent years.

Age structure

Age structure of male territory-holders differed among sites ($\chi^2 = 16.8$, $df = 4$, $P = 0.002$, $n = 188$), with the lowest proportion of territories occupied by subadult males at middle Pua ‘Akala, the least disturbed site with dense forest, and the highest proportion of territories occupied by subadult males at Maulua, where the habitat was more disturbed and population density was lowest (Fig. 5). The pattern was similar for female territory-holders, but the difference among sites was not quite significant ($\chi^2 = 8.50$, $df = 4$, $P = 0.08$, $n = 186$). Fewer subadult males held territories than did subadult females (Fig. 5), and the difference was most evident at middle Pua ‘Akala ($\chi^2 = 10.44$, $df = 1$, $P < 0.001$), intermediate at upper Pua ‘Akala ($\chi^2 = 2.52$, $df = 1$, $P = 0.11$), and smallest at Maulua ($\chi^2 = 0.74$, $df = 1$, $P = 0.39$).

FIG. 3. Regression of ‘Elepaio territory sizes in 1996 on the first principal component (PC1) of habitat structure at Hakalau Forest National Wildlife Refuge, Hawai‘i, with best-fit least-squares line ($R^2 = 0.43$). PC1 was associated with higher tree density, shrub density, canopy cover, and native ground cover.



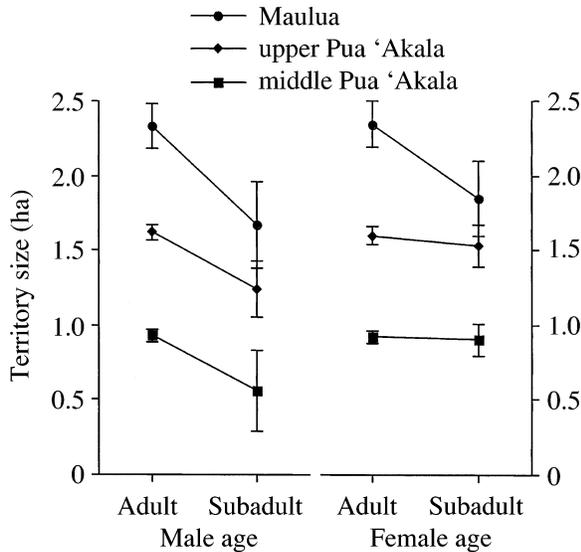


FIG. 4. 'Elepaio territory size by male age and female age at three sites in Hakalau Forest National Wildlife Refuge, Hawaii, 1994–1996 combined.

Age structure of territory-holders at middle Pua 'Akala and upper Pua 'Akala was relatively stable over time and did not differ among years for either males or females ($\chi^2 = 3.64\text{--}6.04$, $df = 6$, $P = 0.40\text{--}0.51$, $n = 58\text{--}95$). At Maulua, however, age structure of territory-holders differed among years for both males and females ($\chi^2 = 17.97$, 18.19 , $df = 6$, $P = 0.007$, 0.006 , $n = 93$, 92 , respectively). In 1994, many subadults of both sexes held territories at Maulua, but the proportion of subadults declined each year, and in 1996 and 1997 age structure at Maulua was similar to that at upper Pua 'Akala (Fig. 6).

Recruitment age also differed among sites (Fig. 7; $\chi^2 = 9.77$, $df = 4$, $P = 0.045$), with the fewest subadult recruits at middle Pua 'Akala, the site with dense forest, and the most subadult recruits at Maulua, where the forest was more disturbed and population density was lowest. The difference was more extreme in the first three years of the study; in 1994, most recruits at Maulua were first-year subadults, and in 1995 and 1996, all recruits at Maulua were second-year subadults. At middle Pua 'Akala almost half the recruits were adults (at least three years old).

Survival, site fidelity, and mate fidelity

There was no difference among sites in survival of territorial males ($\chi^2 = 1.10$, $df = 2$, $P = 0.58$) or territorial females ($\chi^2 = 2.58$, $df = 2$, $P = 0.28$). Annual survival of territorial males (0.86 ± 0.04 [mean \pm 1 SE], range 0.72–0.98, $n = 6$ years) was higher than survival of territorial females (0.79 ± 0.05 , range 0.54–0.90, $n = 6$ years; $\chi^2 = 4.21$, $df = 1$, $P = 0.04$) at all sites combined. These estimates were based on a mean of 63.0 ± 8.2 birds per year. Juvenile survival was 0.33 from 1991 to 1998 ($n = 33$). The probability of resighting a bird that was still alive was 0.994 ($n = 312$ bird-years); only twice did I resight a bird in a subsequent year that I had assumed to be dead. Both birds were replaced on their former territories, indicating they left the study area and then returned.

Site fidelity was very high in both males (0.98, $n = 179$ bird-years) and females (0.93, $n = 99$), and there was no difference among sites in site fidelity of males and females combined ($\chi^2 = 2.02$, $df = 2$, $P = 0.36$). Most birds remained on the same territory for the duration of the study or until their presumed death. The few cases of breeding dispersal occurred between

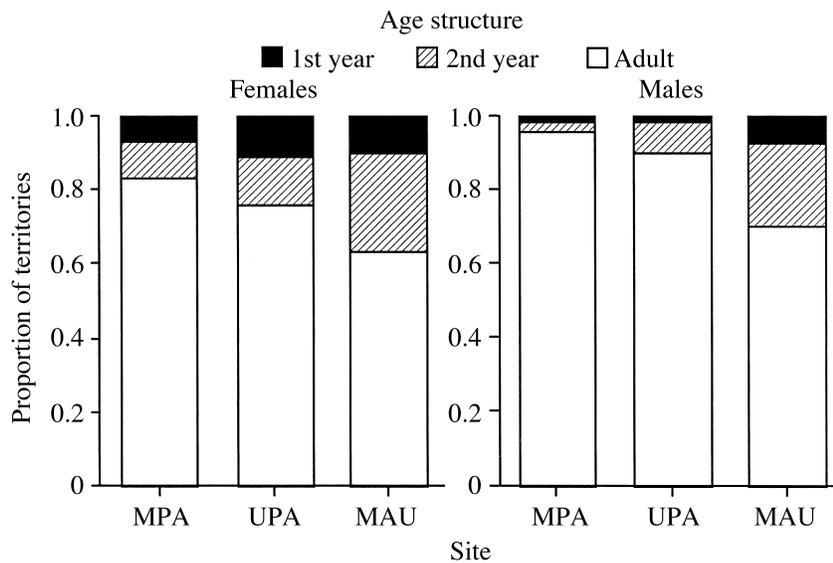


FIG. 5. Age structure of territorial male and female 'Elepaio at three sites in Hakalau Forest National Wildlife Refuge, Hawaii, 1994–1997 combined. Abbreviations are: MPA = middle Pua 'Akala; UPA = upper Pua 'Akala; MAU = Maulua.

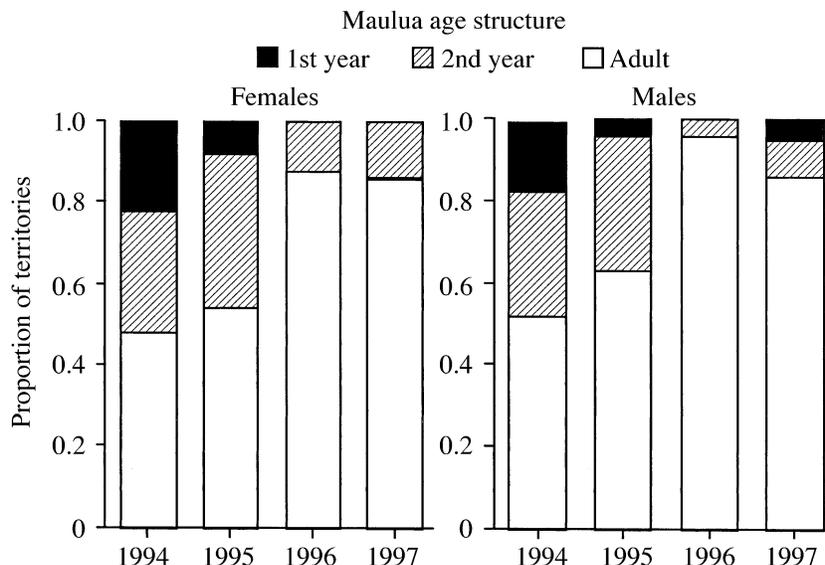


FIG. 6. Age structure of territorial ‘Elepaio at Maulua from 1994 to 1997. Population density increased over this period as the population recovered from an epizootic of poxvirus in 1992.

years; there were no instances of within-season breeding dispersal in 15 known reneating attempts. Breeding dispersal distances were short and did not differ between males (238 ± 39 m, range 146–334 m, $n = 4$) and females (170 ± 31 m, range 106–334 m, $n = 7$; Mann-Whitney test, $P = 0.11$). Cases of breeding dispersal involved two pairs switching territories together, one pair splitting up and moving to different territories, three females leaving territories that had been taken over by a young male after the original male died, one female leaving an adult male, and one male switching territories and mates after attempting polyterritorial polygyny for one year.

Reproduction

Of 244 pairs at all sites in all years combined, 7% fledged two young, 41% fledged one young, 30% laid eggs but failed to fledge any young, 7% built a nest but did not lay eggs, and 15% did not attempt to nest. The mean number of clutches per pair, including only pairs that laid eggs, was 1.09 (range 1–2). No pairs reneated if the first nest was successful.

The mean number of fledglings per pair per year was 0.56 ± 0.06 (range 0–2) at all sites combined from 1994 to 1997. Poisson regression of number of fledglings showed significant effects of site ($\chi^2 = 10.97$, $df = 2$, $P = 0.004$) and year ($\chi^2 = 16.17$, $df = 3$, $P = 0.001$), and a weak interaction between site and year ($\chi^2 = 11.25$, $df = 6$, $P = 0.081$). Number of fledglings per pair was similar among years at Maulua, but at both Pua ‘Akala sites the numbers of fledglings per pair varied among years (Fig. 8). In 1995 and 1997, success was lower at both Pua ‘Akala sites than at Maulua. There was no difference in number of fledglings between middle Pua ‘Akala and upper Pua ‘Akala in any year.

Number of fledglings was affected more strongly by male age ($\chi^2 = 2.79$, $df = 1$, $P = 0.095$), than by female age ($\chi^2 = 0.0083$, $df = 1$, $P = 0.93$). Pairs composed of two subadults fledged the fewest young of any age-class combination at all three sites, and pairs in which only the male was subadult did as poorly or nearly so (Fig. 9). Pairs in which only the female was subadult produced more fledglings than pairs with two subadults or pairs with a subadult male, illustrating the greater importance of male age. At Maulua, pairs in which only the female was subadult were the most successful. Moreover, success of all combinations in-

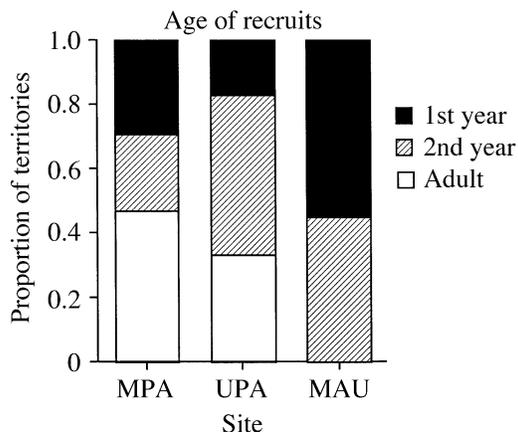


FIG. 7. Ages of ‘Elepaio recruits (birds filling vacant territories) at three sites in Hakalau Forest National Wildlife Refuge, Hawaii, 1994–1996 combined. Abbreviations are: MPA = middle Pua ‘Akala; UPA = upper Pua ‘Akala; MAU = Maulua.

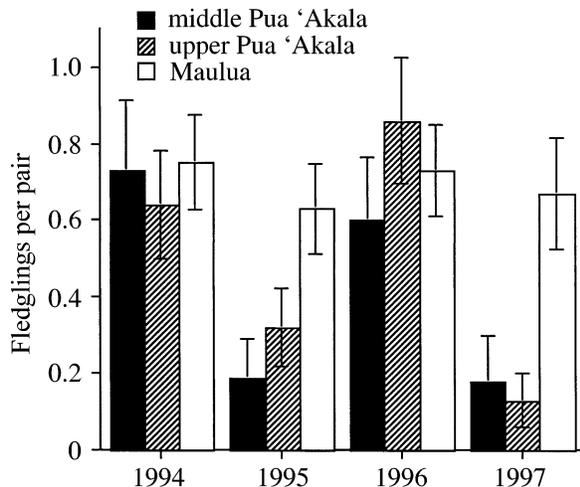


FIG. 8. Reproductions of 'Elepaio at three sites in Hakalau Forest National Wildlife Refuge, Hawaii, from 1994 to 1997.

volving subadults increased from middle Pua 'Akala to upper Pua 'Akala and Maulua. Pairs with two subadults always failed at middle Pua 'Akala and upper Pua 'Akala, but at Maulua they sometimes were successful. Results of the GLM simultaneously using site, year, male age, female age, and all interactions agreed with results of the Poisson regression, but indicated a stronger effect of male age ($F_{1,216} = 4.36, P = 0.038$).

Nest success was 65% in all years combined, and did not differ among sites ($\chi^2 = 2.96, df = 2, P = 0.23$; 75%, $n = 28$ at middle Pua 'Akala; 58%, $n = 59$ at upper Pua 'Akala; and 69%, $n = 36$ at Maulua). Nest success did not differ between pairs with at least one subadult (52%, $n = 23$) and pairs with two adults (65%, $n = 85$; $\chi^2 = 1.21, df = 1, P = 0.27$), but the proportion of pairs that attempted to nest was lower in pairs with at least one subadult (69%, $n = 54$) than in pairs with two adults (92%, $n = 120$; $\chi^2 = 15.22, df = 1, P < 0.001$), and pairs with at least one subadult were less likely to lay eggs once the nest was built (61% vs. 86%; $\chi^2 = 13.34, df = 1, P < 0.001$). There was no difference in timing of nesting among sites ($\chi^2 = 9.20, df = 6, P = 0.16$), but timing of nesting did vary among years ($\chi^2 = 29.17, df = 6, P < 0.001$), with nests initiated earlier in 1996 and later in 1991 (Fig. 10).

Population growth

The population growth rate, or lambda (λ), did not differ from 1.0 at middle Pua 'Akala (0.96 ± 0.03 ; mean ± 1 SE) or upper Pua 'Akala (1.02 ± 0.04) during 1994–1997, indicating 'Elepaio populations at those sites were stable. At Maulua, lambda was 1.12 ± 0.04 over the same period, indicating population growth. These population growth rates are consistent with the observed stable territory sizes at middle Pua 'Akala and upper Pua 'Akala and decreasing territory size at Maulua. Moreover, the sites with more habitat distur-

bance, upper Pua 'Akala and Maulua, did not have lower population growth rates than the less disturbed site, middle Pua 'Akala.

DISCUSSION

Is disturbed habitat lower quality?

The disturbed, open canopy forest at upper Pua 'Akala and Maulua contained larger 'Elepaio territories, supported less dense 'Elepaio populations, had a higher proportion of subadult birds in the breeding population, and thus can be considered lower-quality habitat for 'Elepaio. In addition, the open structure of the disturbed forest presented a more challenging foraging environment for 'Elepaio by requiring more frequent use of difficult foraging behaviors and greater expense of time and energy on foraging (VanderWerf 1994). However, 'Elepaio populations in the more disturbed sites did not have lower survival or reproduction, and there was no net dispersal away from or into disturbed sites. 'Elepaio populations in disturbed forest were not declining and did not act as sinks that were maintained by immigration; the disturbed forest simply had a lower carrying capacity.

Effects of habitat disturbance and population density

The primary effect of habitat disturbance on the demography of 'Elepaio was an increase in territory size and thus a decrease in population density. Territory size was closely related to habitat structure, with larger territories at two sites where the forest was more disturbed by cattle grazing and logging than at a site with less disturbance and dense forest. If the mean territory size at each site is multiplied by the mean numbers of trees

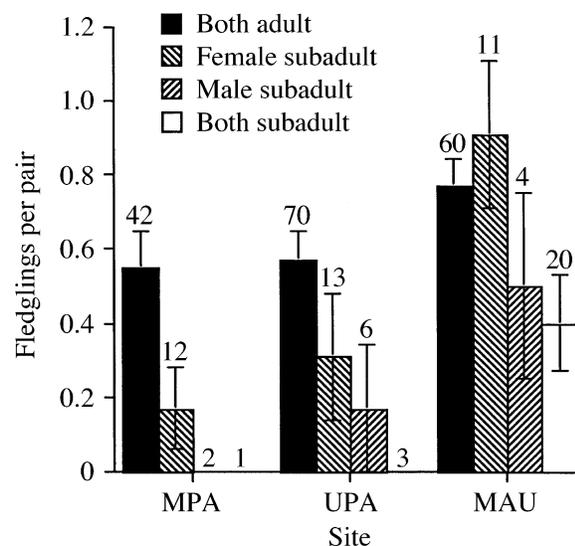


FIG. 9. Reproduction of 'Elepaio at three study sites in Hakalau Forest National Wildlife Refuge, Hawaii, by male-female age combination. Numbers above each column are sample sizes. Population density was highest at middle Pua 'Akala, and lowest at Maulua.

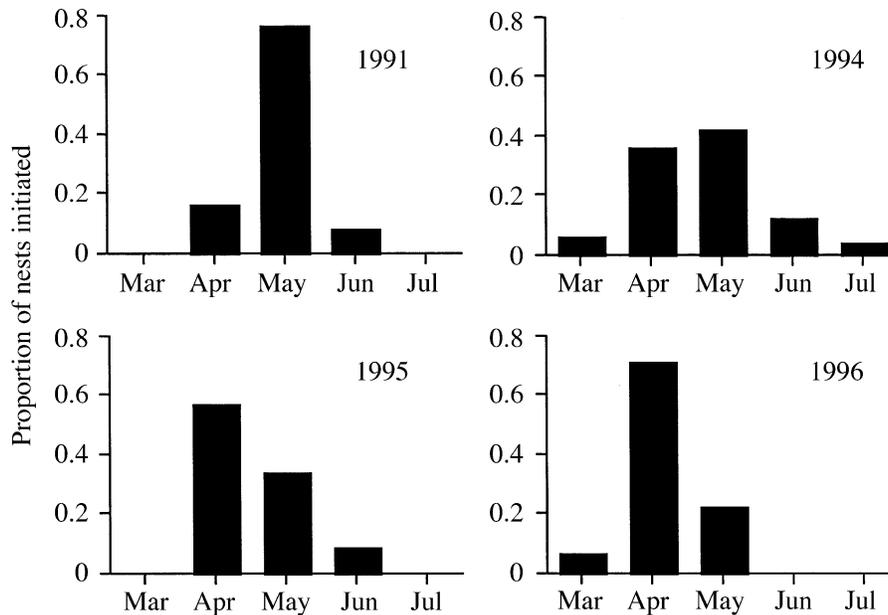


FIG. 10. Annual variation in timing of 'Elepaio nesting at Hakalau Forest National Wildlife Refuge, Hawaii, all sites combined.

and shrubs per hectare, the numbers of trees and shrubs per territory are remarkably similar among sites (Table 1). In other studies, 'Elepaio territory size averaged 1.08 ha on the west slope of Mauna Kea, Hawai'i (range 0.65–1.46 ha; van Riper 1995), 0.57 ha in Hawai'i Volcanoes National Park, Hawai'i (range 0.31–1.12 ha; Sarr et al. 1997), and 2.0 ha on O'ahu (range 1.2–2.9 ha; Conant 1977). Quantification of prey density or biomass per vegetative unit at Hakalau and these other sites should allow calculation of minimum resource requirements per 'Elepaio pair in each area. Similarly, Langen and Vehrencamp (1998) found a roughly equal number of *Acacia* trees per capita in group territories of White-throated Magpie Jays (*Calocitta formosa*), and Galeotti (1994) found that territory size in Tawny Owls (*Strix aluco*) varied in relation to habitat structure, and that prey biomass per territory was similar in urban and rural habitats.

Territory size is thought to vary in relation to environmental variables so as to maximize individual fitness, with optimum size occurring when benefits of territoriality maximally exceed costs (Klomp 1972, Davies 1980, Patterson 1980, Schoener 1983, Newton 1994). The primary benefit of territoriality is exclusive access to resources, usually food, while the primary cost is time and energy expended in defensive behavior, resulting in inverse relationships between territory size and resource availability (Gill and Wolf 1975, Davies and Lundberg 1984, Sherman and Eason 1998) and between territory size and intensity of competition (Myers et al. 1979, McCleery and Perrins 1985, Dunk and Cooper 1994). Resource abundance and territory size often are closely related to habitat structure (Wiens

1973, Morse 1976, Temeles 1987, Renken and Wiggers 1989), and it has been suggested that birds select habitat and regulate territory size by structural habitat features rather than actual food abundance because habitat structure varies less over time and is a better indicator of potential food abundance (Smith and Shugart 1987). In species with contiguous territories and boundaries that do not vary seasonally, territory size may be based on the area required to provide sufficient food during periods of scarcity (MacLean and Seastedt 1979, Sherman and Eason 1998). In 'Elepaio, annual variation in reproductive success is associated with variation in abundance of arthropod prey (J. S. Fretz, P. J. Hart, E. A. VanderWerf, and L. A. Freed, *unpublished manuscript*). The more open forest at upper Pua 'Akala and Maulua likely supported fewer 'Elepaio than the dense forest at middle Pua 'Akala because arthropod density per unit area was lower, requiring 'Elepaio to defend larger territories to obtain sufficient food.

The changes in territory size over time at Maulua indicate that territory size in 'Elepaio also is related to population density. Territories at Maulua were largest in 1994, when population density was low following an epizootic of poxvirus (VanderWerf 2001a), and decreased in size as young birds recruited into the breeding population and density increased. By 1996, territory size at Maulua and numbers of trees and shrubs per territory were similar to values at upper Pua 'Akala (Table 1), and perhaps similar to what they had been before the epizootic.

A more subtle, but demographically important effect of both habitat disturbance and reduced population density was a downward shift in recruitment age and con-

sequent age structure of the breeding population. Recruitment age was younger in disturbed forest at upper Pua 'Akala and younger still in disturbed habitat at Maulua where population density had been further reduced by disease. Several subadults at upper Pua 'Akala and Maulua first established territories at the forest fringe, where it may have been easier to defend a territory because there were neighbors on only one side. As birds aged and rose in social status their territories increased in size, and the boundaries expanded away from the forest edge. In subsequent years, additional young birds occasionally established new territories in the same way, gradually pushing older birds farther into the forest.

The dense forest at middle Pua 'Akala is more similar to the habitat conditions that prevailed in Hawaii prior to the arrival of humans (Kirch 1982, Cuddihy and Stone 1990) and in which 'Elepaio evolved. The modal age at which 'Elepaio recruited in that habitat was three years. Perhaps not coincidentally, that is the same age at which 'Elepaio first acquire adult plumage (VanderWerf 2001b). Subadult plumages in 'Elepaio appear to function as honest signals of subordinate status (VanderWerf and Freed 2003) that evolved to match the frequency of breeding opportunities. If habitat alteration and reduced population density due to disease continue to allow recruitment at a younger age, obviating the need for signals of subordination in young birds, it is conceivable that the rate of plumage maturation may increase until another equilibrium is reached, and that the rate of plumage maturation may vary among isolated populations in areas with differing population densities.

A higher proportion of subadult birds in lower-quality habitat and/or sparse populations also has been reported in magpies (*Pica pica*; Baeyens 1981), European Blackbirds (*Turdus merula*; Hatchwell et al. 1996), American Redstarts (*Setophaga ruticilla*; Hunt 1996), and Black-throated Blue Warblers (*Dendroica caerulescens*; Graves 1997). Holmes et al. (1996) found that first-year male Black-throated Blue Warblers were more common in less preferred habitat, and that first-year males returned at a lower rate in the poorer habitat, and they suggested this was due to dispersal to higher-quality habitat the following year. Similarly, Foppen and Reijnen (1994) found a higher proportion of young Willow Warblers (*Phylloscopus trochilus*) in lower-quality disturbed habitat near a highway, and that there was net breeding dispersal away from the highway. In migratory species like these warblers there often is considerable breeding dispersal within and between years, allowing birds of different ages and competitive abilities to "reshuffle" between breeding attempts, but this opportunity does not exist for 'Elepaio because they are nonmigratory and very sedentary. Most 'Elepaio spent their entire lives in the same territory in which they recruited, and enhancement of territory quality occurred primarily through gradual shifts in territory

boundaries and increases in territory size rather than by territory switching or dispersal to better habitat. Greenberg and Gradwohl (1986, 1997) found that territory sizes and boundaries were very similar among years in a population of Checker-throated Antwrens (*Myrmotherula fulviventris*) in Panama, even when territories changed ownership, and they suggested that boundaries were intrinsic and not dependent on the ability of the owner. Sizes and boundaries of 'Elepaio territories also were similar among years, but often did change as a result of territorial disputes and changes in ownership, indicating the ability and status of the owner were important.

Habitat disturbance did not affect survival, reproduction, or site fidelity in this study, but differences in several reproductive measures have been reported between habitats in a variety of bird species. Holmes et al. (1996) found that Black-throated Blue Warblers produced more fledglings in areas with a dense shrub layer than in areas with a sparse shrub layer because more pairs raised two broods per year, but they did not lay larger clutches, have higher nest success, or nest earlier. In contrast, Hatchwell et al. (1996) found that European Blackbirds in higher-quality woodland habitat did not produce more fledglings, lay larger clutches, nest earlier, or have higher nest success than blackbirds in farmland, but they did lay larger eggs. Lemel (1989) found that reproductive output of Great Tits did not differ between deciduous and coniferous forest, but Andr n (1990) found that European Jays (*Garrulus glandarius*) had higher breeding success in dense forest with older trees, and Lundberg et al. (1981) found that Pied Flycatchers (*Ficedula hypoleuca*) in deciduous forest laid eggs earlier and had higher breeding success than those in coniferous forest.

Age-specific demographic patterns

Young birds may produce fewer offspring than older birds because they are less skillful at foraging, less efficient at nesting, or have reduced access to resources or mates, and therefore they may provide less food to nestlings, breed later in the season, and produce smaller or fewer eggs (Saether 1990, Forslund and Part 1995, Martin 1995, Blums et al. 1997, Weggler 2001). Subadult 'Elepaio of both sexes do have lower foraging proficiency than adults (VanderWerf 1994), but the lower reproductive success of subadult 'Elepaio appeared to be caused by a constraint on access to food imposed by their low social status and inability to defend a territory. Reproductive success of subadult 'Elepaio was higher at upper Pua 'Akala than at middle Pua 'Akala, and higher still at Maulua, where population density was lowest and subadult males were able to defend larger territories. Territories of subadult males at Maulua in 1994 were as large as those of adult males each year at upper Pua 'Akala, where the habitat was similar, and their reproductive success was similar as well. When subadults had the opportunity to defend

territories as large as those of adults, their reproduction was not limited by lower foraging proficiency or lack of previous breeding experience. Desrochers and Magrath (1993) found that young European Blackbird females had lower success than older females because they nested later in the season and laid fewer eggs, and Desrochers (1992) found that providing supplemental food removed these differences, and suggested that food limitation caused by lower foraging proficiency could be the primary cause of lower reproductive success in many birds. If the lower reproductive success of subadult 'Elepaio was caused by a foraging constraint, one would expect female age to affect reproductive success also, but this was not the case.

Reproductive success of 'Elepaio was more closely related to male age than female age, likely because territory size was dependent on male age, but not on female age. Older, dominant males had larger territories and produced more fledglings, but female age did not affect territory size or number of fledglings. Male 'Elepaio are more active in territory defense than females (E. A. VanderWerf, *unpublished data*), so the status of the male plays a larger role in determining territory size. Female 'Elepaio are aggressive toward each other and chase other females from the territory, but territories of subadult females were not smaller, suggesting that females actually defend exclusive access to resources controlled by the male and his exclusive parental care, rather than the resources themselves. Similar results were obtained by Perrins and McCleery (1985) for Great Tits, in which older males produced more fledglings and recruits than young males, and female age affected clutch size and laying date, but did not affect number of fledglings or recruits. Arcese (1987) found that middle-aged Song Sparrows (*Melospiza melodia*) were more able to defend their territory than the youngest and oldest territory-holders.

CONCLUSIONS

Moderate habitat disturbance that resulted in a more open forest structure led to a reduction in carrying capacity of 'Elepaio, but did not reduce viability of 'Elepaio populations. The degree of habitat disturbance in the study sites at Hakalau was not that severe; some trees were removed and the understory was largely destroyed by cattle grazing, but the reduction in tree density and canopy cover were moderate. More extreme disturbance, in the form of clear-cutting, was found by Sakai (1988) to cause drastic declines in abundance of Hawaiian birds. 'Elepaio may be less affected by moderate habitat disturbance than many Hawaiian birds because they are versatile and adaptable, foraging in many plant species and on many substrates, using diverse foraging behaviors (VanderWerf 1993, 1994), and nesting in a variety of native and introduced plants (Conant 1977, VanderWerf et al. 1997, VanderWerf 1998, VanderWerf and Smith 2002).

The slightly lower survival of female 'Elepaio than male 'Elepaio at Hakalau may have been due at least partly to nest predation by rats, but the high rate of nest success at Hakalau in the absence of rat control indicates nest predation by rats is not a major threat to 'Elepaio at Hakalau. In contrast, on O'ahu rats are a serious threat to 'Elepaio, and low nest success (33%) and low female survival (50%) are major causes of decline. With rat control, these values increased significantly (to 58% and 83%, respectively; VanderWerf and Smith 2002), and were similar to values at Hakalau without rat control (65%, 79%). Rats are abundant at Hakalau (Nelson et al. 2002) and on O'ahu (VanderWerf and Smith 2002), but predation by rats on 'Elepaio nests may be more frequent on O'ahu due to differences in the species of trees used for nesting. On O'ahu, 'Elepaio usually nest in alien tree species, particularly strawberry guava (*Psidium cattleianum*), mango (*Mangifera indica*), kukui or candlenut (*Aleurites moluccana*), and christmasberry (*Schinus terebinthifolius*), all of which produce fruits or nuts that may attract rats into the forest canopy, where they encounter 'Elepaio nests (VanderWerf and Smith 2002). In contrast, 'Elepaio at Hakalau nest almost exclusively in 'ohi'a (VanderWerf 1998), which produces very small seeds contained in non-fleshy capsules that are less attractive to rats.

The 'Elepaio population at Maulua increased in density relatively quickly following an epizootic of avian poxvirus and was able to recover in this case. However, the long-term viability of this population and of other populations that exist in areas where epizootics of disease occur also depends on the frequency of epizootics, and this frequency is poorly known. If epizootics occur too frequently, 'Elepaio populations may not have sufficient time to recover between disease episodes (VanderWerf 2001a). Projected increases in global temperatures may cause the distribution of disease-carrying mosquitoes and the frequency of disease epizootics to increase, thereby potentially altering the population viability of 'Elepaio and other Hawaiian forest birds (Benning et al. 2002).

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