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DEMOGRAPHIC COMPARISONS BETWEEN HIGH AND LOW DENSITY POPULATIONS OF HAWAI'I 'ĀKEPA

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Abstract. A comparison of demographic traits between large and small populations is a promising tool for revealing proximate causes of rarity in the smaller population. In the Hakalau Forest National Wildlife Refuge on the island of Hawai'i, a "distributional anomaly" for the endangered Hawai'i 'Ākepa, *Loxops coccineus coccineus,* has persisted for at least 15 years in which population densities decrease by over an order of magnitude within 5 km of similar forest at similar elevations. I compared demographic and individual fitness characteristics of 'Ākepa within high and low density populations in relation to hypotheses of regulation. No important differences were detected in annual adult survival, reproductive success, age structure, mean fat level, mean weight, external indicators of disease, or sex ratios. This is evidence that, for the period of this study, populations were being regulated in a similar way. Most importantly, predation and disease do not appear to be affecting the low density site disproportionately, nor have stochastic effects played a role in misshaping population structure at that site. Since both populations have been relatively stable over the past 15 years, these results indicate that differences in environmental carrying capacity, possibly through nest-site availability, maintain current patterns of density.

Key Words: 'Ākepa; demographic comparison; distributional anomaly; *Loxops coccineus coccineus*; small population.

To conserve and manage many threatened populations in a natural setting, it is necessary to understand the factors that determine a population's average abundance and changes in numbers (Smith et al. 1991). As a general rule, population regulation is considered density dependent when birth rate decreases and/or mortality increases with increasing population size (Nicholson 1933, Murray 1994b). For birds, this type of population regulation is often associated with carrying capacity of the environment. Food limitation (Lack 1954, 1966; Klomp 1980, van Balen 1980, Dunning and Brown 1982, Martin 1987, Newton 1991) and nest-site limitation (Cavé 1968, van Balen et al. 1982, Bock et al. 1992, Dobkin et al. 1995) are the most important aspects of carrying capacity. Density dependent mechanisms of population regulation not closely related to carrying capacity include predation (Perrins and Geer 1980, Marcström et al. 1988, Potts and Aebischer 1991) and disease (Anderson and May 1978, Anderson 1979, Hudson 1986). In contrast, population regulation is considered density independent when frequent severe weather or other environmental disturbance is most important in limiting population size (Andrewartha and Birch 1954). For birds, severe weather has often been shown to periodically reduce population densities in otherwise density dependent populations (Kikkawa 1977, Valle and Coulter 1987, Smith et al. 1991).

The Hawai'i 'Ākepa, (*Loxops coccineus coccineus*) is a specialized, long-lived, honeycreeper that was once widespread in 'ōhi'a (*Metrosideros polymorpha*) and 'ōhi'a-koa (*Acacia koa*) forests throughout the island of Hawai'i (Perkins 1903). The bird now exists mainly in four widely separated populations (Scott et al. 1986). Habitat destruction, primarily from cattle ranching, and mosquito (*Culex quinquefasciatus* and *Aedes albopictus*) transmitted disease appear to be the two major factors responsible for the decline of this bird over much of its former range (van Riper et al. 1986, Lepson and Freed 1997). However, huge tracts of apparently suitable 'ōhi'a-koa forest exist at elevations above the upper range of disease carrying mosquitoes in which these birds are rare or absent. This scarcity of birds in what appears to be suitable habitat was first identified as a "distributional anomaly" by the 1986 Hawai'i Forest Bird Survey and has since been corroborated by annual surveys. In the 13,247 ha Hakalau Forest National Wildlife Refuge on the eastern slope of Mauna Kea, the Hawai'i 'Ākepa exists in populations that vary linearly in density by over three orders of magnitude in what qualitatively appears to be the same habitat (Scott et al. 1986). This distribution provides a natural experiment for comparing population structure and dynamics, and aspects of carrying capacity, between sites that appear to vary mainly in density of birds.

The aim of this study was to use a demographic comparison between high and low density populations (1) to examine the relative importance of various nonmutually exclusive hypotheses for regulation or limitation at each site, and (2) to determine if the mechanisms of regulation or limitation are different between sites. An examination of the way demographic characteristics such as survival rate, reproductive

TABLE 1. PREDICTIONS OF FOUR HYPOTHESES FOR MAINTENANCE OF DIFFERENT POPULATION DENSITIES BETWEEN PUA 'ĀKALA AND PEDRO

	Predictions[a]						
Hypotheses	Adult survival rate	Reproductive success	Age-structure	Fat	Weight	Disease	Sex ratio
Food limitation	S	S	S	S	S	S*	S*
Nest-site limitation	S*	S	S*	S*	S*	S*	S*
Predation	L	L	D	S*	S*	S*	D
Disease	L	L	D	L	L	H	S*

[a] (L) lower at Pedro; (H) higher at Pedro; (D) different; (S) similar; (S*) no particular difference is logically specified by hypothesis.

success, age structure, fat levels, weight, disease, and sex ratios are similar or different between sites should point to the cause of rarity of the smaller population. The nonterritorial nature of the 'Ākepa makes it an appropriate species for this comparison because the demographic effects of resource limitation (environmental carrying capacity) can be distinguished from the mediating effects of territorial behavior. Approximately 10 years of demographic information from the high density site indicate that the 'Ākepa is a species whose life-history characteristics have been shaped by carrying capacity of the environment. These birds are extremely long lived (>11 yr), have high annual adult survival (0.81) for a 10–12 g passerine, have small clutch sizes (mean = 2), and are highly specialized cavity nesters (Lepson and Freed 1995). In addition, population size in this area has not undergone large fluctuations in density during the past 10–15 years (J. Jeffrey, pers. comm.).

An assumption of this study is that the high density site (Pua 'Ākala) represents a healthy and relatively stable 'Ākepa population. Under the food limitation and nest-site limitation hypotheses, birds at the low density site (Pedro) are being regulated in a similar way to those at the high density area, but carrying capacity is lower. A prediction of these hypotheses is that demographic and fitness characters will be similar between sites (Table 1). Since similar limiting factors should affect population structure in similar ways, this would be evidence that the smaller population is a merely a "scaled down" version of the larger and not under a disproportionate external threat. For example, predation and outbreaks of disease have been shown to decrease annual adult survival (Perrins and Geer 1980). Similar annual adult survival between sites would indicate that predation or levels of lethal disease are not greater at Pedro. Alternately, under the predation and disease hypotheses, carrying capacity is similar at each site, but birds at the low density site are being regulated below carrying capacity by predation or disease (Table 1). For example, lower annual adult survival at Pedro would point to greater levels of predation or disease there. Of course, differences in one demographic parameter must be examined in relation to differences in others. For example, food limitation could also be responsible for lower annual adult survival at one site but not if fat levels and mean weights are similar.

METHODS

This study was conducted from January 1994 through December 1996 at two sites separated by approximately 5 km of contiguous old growth (>200 yr) forest within Hakalau Forest National Wildlife Refuge (Fig. 1). The elevation of the high density site (Pua 'Ākala) ranges from 1,850 to 1,900 m and the low density site (Pedro) ranges from 1,750 to 1,800 m. Mean annual rainfall was 225 cm during the study period. The canopy at both sites is from 15 to 30 m in height and is comprised almost exclusively of 'ōhi'a and koa. Over a century of use as a cattle ranch has resulted in a degraded understory dominated by introduced grasses, but native ferns, shrubs, and small trees (primarily *Cheirodendron trigynum* and *Myrsine lessertiana*) are patchily abundant at both sites.

Beginning in January 1994, a system of canopy-level mist nets was established to capture 'Ākepa. At Pua 'Ākala, I added 6 mist nets to 15 erected by earlier researchers. At Pedro, I established 20 new nets at similar heights and orientation to foliage as those at Pua 'Ākala. All individuals captured were extensively measured, examined for external disease, molt, and breeding condition, and given a unique combination of one aluminum U.S. Fish and Wildlife Service band and three plastic color-bands for individual identification in the field. Adult males and females of this sexually dichromatic bird were identified by plumage and presence of a cloacal protuberance or brood patch during the breeding season. Fledgling and hatch-year birds (<9 mo) were identified by plumage and behavior. Second-and third-year males were distinguished by intermediate plumage characteristics following criteria reported by Lepson and Freed (1995). Age class of females could not be accurately determined in the field.

Relative 'Ākepa density at each site was estimated using mist-net capture rates (number of individuals captured per net hour) and yearly fixed-plot censuses. These censuses were conducted each January–March

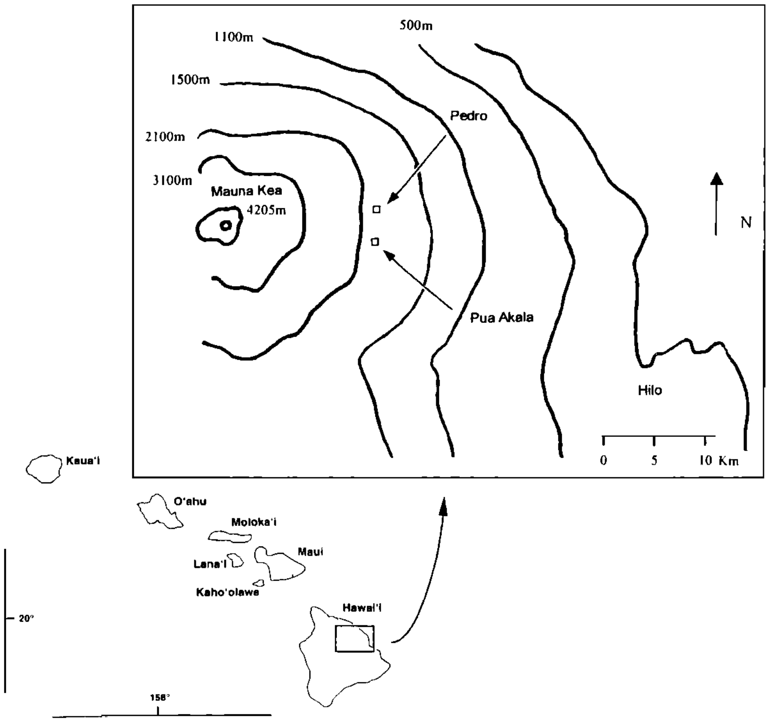

FIGURE 1. Map of the main Hawaiian Islands with inset showing location of study areas.

within 25-m radius stations set at 100-m intervals along established transects. All adult 'Ākepa seen or heard within 5 min at each station were recorded.

Annual adult survival rate is an important demographic parameter with respect to the food limitation, predation, and disease hypotheses (Table 1). Annual adult survival at both sites was estimated by weighted enumeration (total number of individuals captured or resighted relative to the total number available for detection). 'Ākepa are year-round residents at the study site and have relatively small home ranges (female mean = 3.07 ha, male mean = 4.49 ha; Ralph and Fancy 1994a). Because recapture and resighting probabilities are high for this bird, enumeration estimates of survival are similar to those for the SURVIV (White and Garott 1990) and JOLLY (Brownie et al. 1986) programs (Lepson and Freed 1995).

Annual reproductive success has importance to all four hypotheses being examined here (Table 1). It was estimated as the proportion of hatch-year birds to adults within mixed-species, postbreeding flocks. These flocks usually form soon after 'Ākepa fledge each June and are joined by most individuals, regardless of breeding success (P. Hart, pers. obs.). Flocks were followed from the ground and color-banded individuals were identified with Leica 10 × 42 binoculars. All hatch-year birds within a given area were easily counted because of their conspicuous and highly vocal begging behavior that lasts approximately two months. My estimate of reproductive success therefore is for individuals within two months of fledging. Most subadult and adult 'Ākepa (mean = 8.6, SE = 1.1) in an average flock (mean = 35, SE = 2.1) were identified within the first one and one-half hours of observation. In contrast, nest-site observation did not yield sufficient information about reproductive success at the population level. Because this technique is so time-consuming, I was never able to adequately monitor more than 12 nests per season.

Age structure is important with respect to the food limitation, predation, and disease hypotheses (Table 1). Age structure may reveal information about present limiting factors or past disturbance within the population. For example, significantly more sub-adult males at Pedro could indicate higher adult mortality there within the past one to three years. Age-structure estimates for males were based on mist-net capture data at both sites and were calculated simply as the proportion of captured subadult and adult males.

For this study, fat level and weight are considered comparative measures of individual fitness. An analysis of the way fat and weight vary between sites may be important with respect to the food limitation and disease hypotheses (Table 1). These measurements were also obtained from mist-net captured birds. Subcutaneous fat deposits within the furcula were categorized from zero to three with zero as no fat visible. Bird weight was measured to the nearest 0.1 g using a 30-g Avinet scale.

External indications (sores, lesions, or missing appendages) of past or active avian pox (*Poxvirus avium*) were noted through thorough examination of feet, legs, and mandibular regions of all captured birds. Blood samples (mean volume = 50 μl) were taken from the

TABLE 2. ʻĀKEPA POPULATION DENSITY ESTIMATES

Method	Pua ʻĀkala	Pedro	Ratio P.A./Pedro
Fixed-plot census[a]	1.46/station	0.45/station	3.24
Mist-net[b]	0.0386 captures/net hour	0.0133 captures/net hour	2.9

[a] Fixed plot censuses were conducted at 70 stations per study site.
[b] Mist-netting was conducted for a total of 854 net hours at Pua ʻĀkala (P.A.) and 2554 net hours at Pedro.

brachial vein of each captured bird to detect the presence of avian malaria (*Plasmodium relictum*).

Sex ratio estimates were based on capture data at both sites and were calculated as the proportion of males and females captured during the three-year study period.

RESULTS

POPULATION DENSITY ESTIMATES

Both censusing and mist-netting demonstrated that there were approximately three times more ʻĀkepa at Pua ʻĀkala than at Pedro in the years 1995 and 1996 (Table 2). A similar difference in population size between these two areas was reported by Scott et al. (1986), based on surveys conducted from 1976 to 1983. At that time, ʻĀkepa density ranged from 400 to 800 birds/km^2 at Pua ʻĀkala and from 100 to 200 birds/km^2 at Pedro. My fixed-plot census information extrapolates to 743 birds/km^2 at Pua ʻĀkala and 229 birds/km^2 at Pedro. These data indicate that the general difference in population size between sites has persisted for at least 15 years.

DEMOGRAPHIC CHARACTERISTICS

Annual adult survival was slightly higher at Pedro than at Pua ʻĀkala between 1995 and 1996. Forty-three individually marked adults were known to exist in 1995 at Pua ʻĀkala and 26 (60%) were resighted the following year in 326 search hours. At Pedro, 21 birds were known in 1995 and 17 (81%) were resighted in 1996 in 299 search hours. This estimate for an-

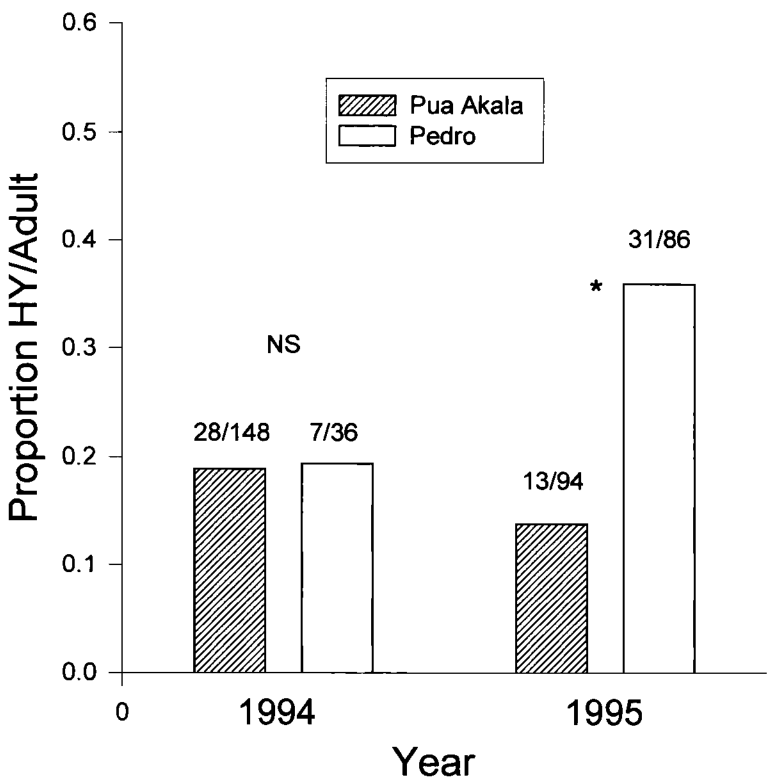

FIGURE 2. Reproductive success for 1994 and 1995 of Pua ʻĀkala and Pedro populations of ʻĀkepa. Sample sizes are shown above and an asterisk indicates significant difference at $P < 0.05$.

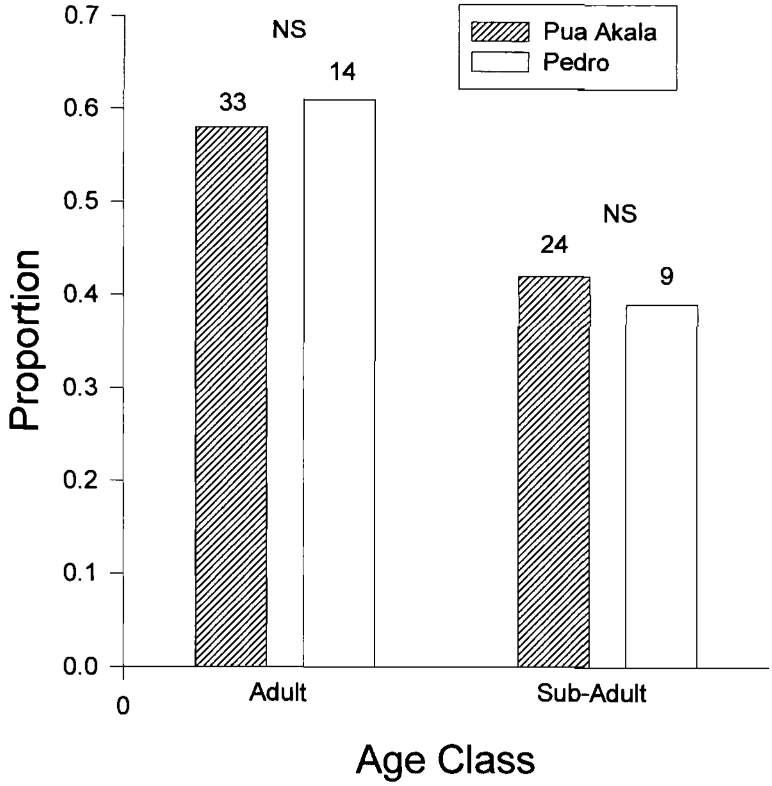

FIGURE 3. Proportional representation by age class of male ‘Ākepa at Pua ‘Ākala and Pedro from 1994 to 1996. Sample sizes are shown above. NS indicates no significant difference (P > 0.05).

nual adult survival at Pedro is identical to estimates provided by Lepson and Freed (1995) based on five years of data at Pua ‘Ākala using similar techniques. Subsequent searches (320 hours) at Pua ‘Ākala in winter and summer of 1997 detected only two additional ‘Ākepa known in 1995 and not seen in 1996. My estimate for adult survival at Pua ‘Ākala is low compared to past years and appears to reflect an unusually bad year for adults there. No additional ‘Ākepa were detected at Pedro in 1997 (150 search hours).

There was no difference in reproductive success between sites in 1994 (χ^2 = 0.005, P = 0.94), but reproductive success was higher at Pedro in 1995 (χ^2 = 12.00, P = 0.001; Fig. 2). For 1996, reproductive success at Pua ‘Ākala increased to 0.64 fledglings per adult, the highest value for either site during the study, but there was insufficient information collected from Pedro to make an appropriate comparison. There was no difference in age structure between sites for males for 1994 through 1996 (χ^2 = 0.06, P = 0.80; Fig. 3), suggesting that the balance between adult mortality and recruitment of young males was similar.

The condition of birds was similar between sites. There was little difference in mean fat level for 1995 (two-sample t = −1.68, P = 0.10), but Pedro birds were significantly fatter in 1996 at the low fat levels characteristic of all honeycreepers captured during this study (t = 3.32, P = 0.002; Fig. 4). In addition, there was no difference in mean weight between sites for the years 1995 (t = −1.49, P = 0.14) and 1996 (t = 1.35, P = 0.19; Fig. 5). There was also little external evidence of disease for the years 1994–1996 at either site. At Pua ‘Ākala (N = 112), an otherwise healthy adult male was missing a toe, a likely sign of past poxvirus. At Pedro (N = 42) there was no external evidence of present or past disease. A laboratory analysis of blood samples for presence of malaria during this study period has not yet been completed, but prior laboratory tests (N = 47) revealed no instances of infection at Pua ‘Ākala (Feldman et al. 1995).

For 1994–1996, there was no difference in

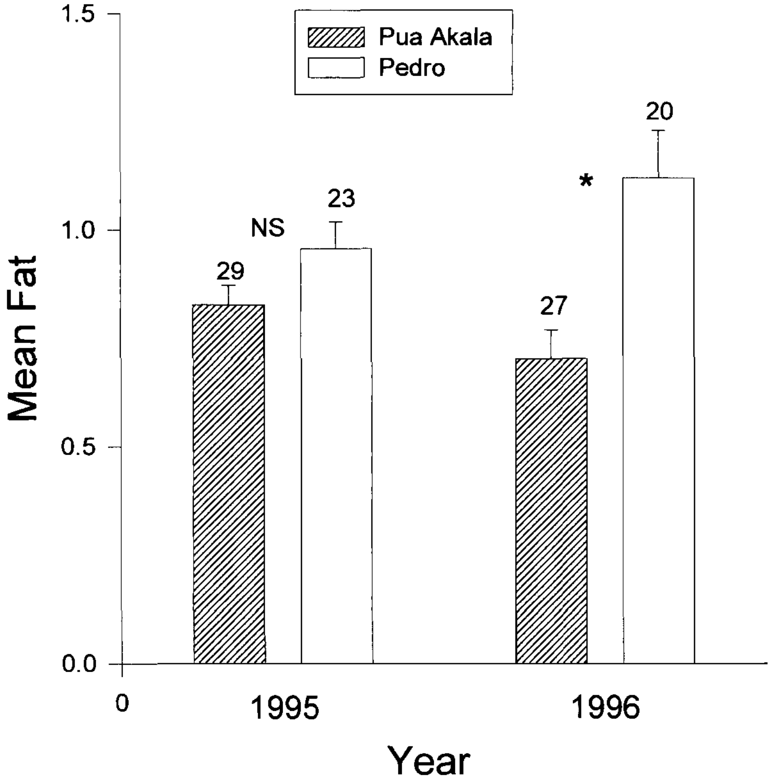

FIGURE 4. Mean fat level of 'Ākepa sampled at Pua 'Ākala and Pedro during 1995 and 1996. Error bars indicate SE, sample sizes are shown above, and an asterisk indicates a significant difference at $P < 0.05$.

sex ratio of Hawai'i 'Ākepa between sites ($\chi^2 = 0.027$, $P = 0.87$; Fig. 6). The 1.13 male to 1 female sex ratio I found for Hawai'i 'Ākepa at Pua 'Ākala agrees well with the 1.14 male to 1 female ratio reported by Lepson and Freed (1995) for Hawai'i 'Ākepa at Pua 'Ākala between the years 1988 and 1993.

DISCUSSION

This study has shown that Hawai'i 'Ākepa populations persist in two locations that differ in density by a ratio of 3:1. In addition, most demographic parameters of the two populations are similar. Elsewhere I will present a demographic model reflecting the stability of the two populations at different densities. Here, I will discuss these findings in relation to four hypotheses that have been proposed to account for regulation or limitation of bird populations. The relatively close proximity and similar elevations of the two sites logically rules out the idea of disproportionately severe weather.

PREDATION AND DISEASE

Given sufficient resources and favorable conditions, 'Ākepa populations theoretically have the capacity to double each year, or at least to recover relatively quickly after bad years. The mean clutch size for 'Ākepa at Pua 'Ākala (N = 5) is two and second-year birds of both sexes are physiologically capable of reproduction (Lepson and Freed 1995). The sympatric 'Elepaio (*Chasiempis sandwicensis*) also has a mean clutch size of two, and E. VanderWerf (pers. comm.) found population densities of this bird to increase 58% within one year following a year of disease-related high mortality. In addition, most replacement was by known second-year birds from within the population. The fact that the densities of 'Ākepa have not significantly increased in 15 years at Pedro constitutes initial evidence that either the carrying capacity is different there or that cycles of disease or predation act with more frequency there.

Introduced predators, especially rats (*Rattus rattus*, *R. norvegicus*, and *R. exulans*) are thought to be responsible for the reduction and possible extinction of numerous native Hawaiian birds (Atkinson 1977, Berger 1981). Introduced avian disease, especially malaria and poxvirus, have played perhaps the largest role in shaping

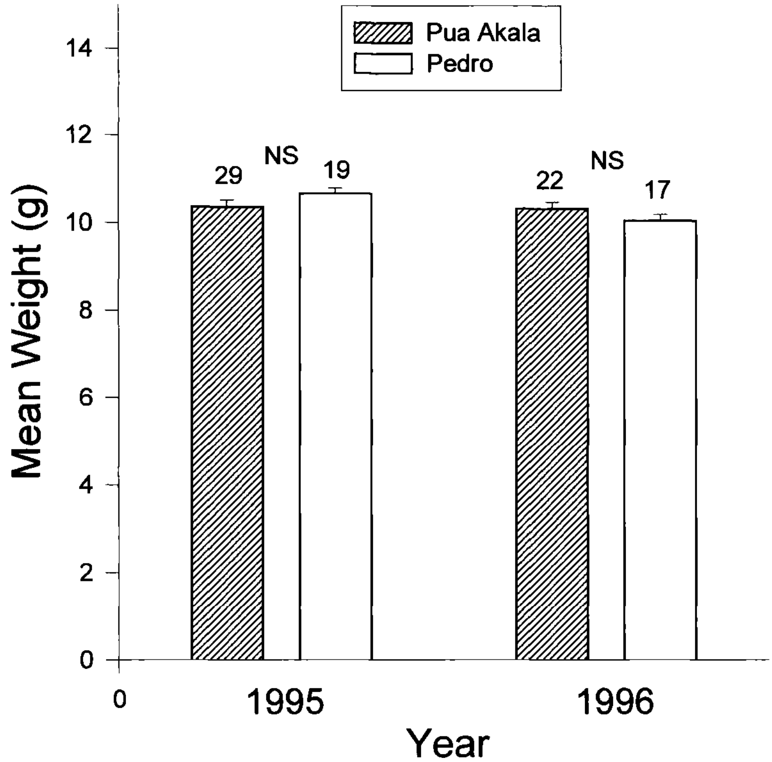

FIGURE 5. Mean weight of 'Ākepa at Pua 'Ākala and Pedro during 1995 and 1996. Error bars indicate SE, sample sizes are shown above. NS indicates no significant difference (P > 0.05).

the present distributions of native Hawaiian forest birds (Warner 1968, van Riper et al. 1986, Jarvi et al. *this volume*). It is not unreasonable to assume then that predation and/or disease are largely responsible for the anomalous distribution of 'Ākepa within Hakalau Forest NWR. Indeed, data from the Biological Resources Division of the U.S. Geological Survey show the refuge to contain some of the highest rat densities ever reported for a natural area (S. Fancy, pers. comm.). While rats have been shown to be efficient nest predators, the extent to which they prey on adult forest passerines in Hawaii is still unclear. Under the predation hypothesis, higher levels of rat predation at Pedro are responsible for lower 'Ākepa density there. This would be reflected through lower annual adult survival, reproductive success, and possibly a different population age structure. If levels of disease were greater at Pedro, annual adult survival, reproductive success, age structure, fat levels, and weight might all be lower. With a few exceptions, the demographic data presented here show great similarity between the high and low density populations and thus fail to support the predation or disease hypotheses.

Annual adult survival and reproductive success at Pedro were similar to or higher than at Pua 'Ākala. The 81% adult survival rate I found for Pedro is identical to mean annual survival at Pua 'Ākala (Lepson and Freed 1995). Reproductive success was similar in 1994 and greater at Pedro in 1995, but not outside of the known range for Pua 'Ākala (1996 reproductive success at Pua 'Ākala = 0.64). The high adult survival rate and similarities in reproductive success and age structure at Pedro reduce the importance of rat predation to the maintenance of different population densities. The similarities in adult survival, reproductive success, age structure, fat, weight, and the near complete absence of external indications of disease indicate that within the past three years, disease has not affected the low density site disproportionately.

Food and Nest-site Limitation

The apparently persistent difference in population size coupled with the similarity in demographic characteristics supports the hypothesis that the two populations are being regulated in a similar, density dependent way. The most likely way to have relatively long-term stability in

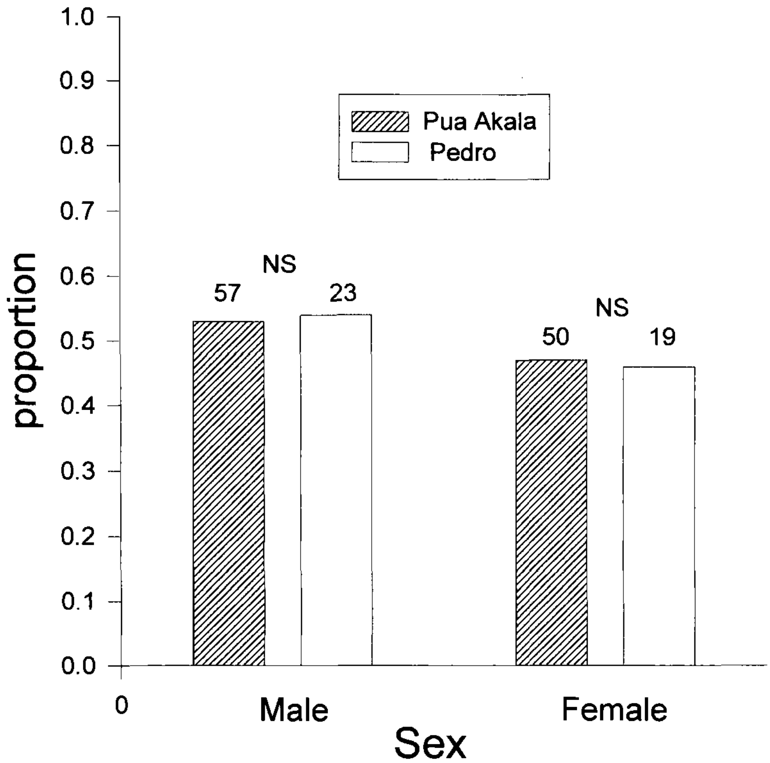

FIGURE 6. Proportion of male and female 'Ākepa captures at Pua 'Ākala and Pedro from 1994 to 1996. Sample sizes are shown above. NS indicates no significant difference ($P > 0.05$).

population size and similar demographic characteristics between years is if the carrying capacity, in terms of food or nest-site availability, is different between sites. Based on available information, it appears that the Pedro population is a "scaled down" version of the one at Pua 'Ākala. This idea seems counterintuitive because there is little apparent qualitative difference in habitat between sites.

It is possible that the sites vary in subtle but ecologically important ways. For example, differences in tree age, architecture, or canopy cover might affect abundance of arthropods, the primary source of food for 'Ākepa. However, the food hypothesis was not supported by weight or fat levels. Nest-site availability may also differ between sites. 'Ākepa are the only Hawaiian honeycreeper known to nest in natural cavities obligately (Freed et al. 1987b). Numerous studies have shown that nest sites are often in short supply for hole-nesting birds (Von Haartman 1956, Perrins 1979, Gustafsson 1988). All known 'Ākepa nests (N = 98) have been located in cavities or holes in large, old growth 'ōhi'a or koa trees (minimum 60 cm dbh; Lepson and Freed 1995). Furthermore, growth form (single versus multiple trunks) is an important determinant of nest-site availability in 'ōhi'a trees; appropriate cavities almost exclusively form in single-trunk trees (Freed *this volume*). Since soil type, soil age, or degree of previous human disturbance may vary between sites, it is possible that the abundance of large koa, and large single-trunk 'ōhi'a varies also. Under the nest-site limitation hypothesis, 'Ākepa density at each site is determined by the availability of nest cavities. A prediction of this hypothesis is that density of 'Ākepa varies in direct proportion to availability of large trees with cavities. Preliminary data support this prediction. Based on intensive habitat sampling in more than 60 15-m radius quadrats at each site, there are three times more large 'ōhia trees (>60 cm dbh) at Pua 'Ākala than at Pedro (P. Hart and L. Freed, unpubl. data). A relevant way to evaluate nest-site limitation would be to determine the proportion of "floaters" at each site or the response to artificial cavities. The nonterritorial nature of the 'Ākepa makes it difficult to identify floaters. There has been limited response at each site to artificial cavities. This is inconsistent with other cavity nesting birds studied elsewhere. Von

Haartman (1971) and Copeyon et al. (1991) found that experimental increases in nest cavities may dramatically increase population size of temperate, hole-nesting species. However, artificial cavities set up for passerines in neotropical forests have also been sparingly used (J. Terborgh, pers. comm.).

How viable is the Pedro population? Theoretical predictions (MacArthur and Wilson 1967b) and empirical evidence (Terborgh and Winter 1980, Belovsky 1987, Pimm et al. 1988) show that the dynamics of small populations are often different from those of larger populations, mainly because smaller populations are more vulnerable to stochastic environmental and demographic perturbations (Shaffer 1981, Gilpin and Soulé 1986). If population level characteristics such as sex ratios are greatly different between sites, this could indicate that the population has fallen to the critical level at which stochastic events have begun to misshape population structure. Small population size itself would be implicated in the maintenance of low densities, even if the original factor responsible for the decline (e.g., disease) is no longer operating. That there is no difference in sex ratios between sites indicates that the Pedro population is not so small that stochastic processes have begun to misshape population structure. It would be of interest to examine how sex ratios and other demographic characteristics might vary in an even smaller, more isolated population of 'Ākepa.

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