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BREEDING CHARACTERISTICS OF THE ʻĀKOHEKOHE ON EAST MAUI

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Abstract. The breeding biology of the endangered ʻĀkohekohe (*Palmeria dolei*) was studied from 1992 to 1993 in the Waikamoi Reserve on east Maui. Nesting success was examined in relationship to habitat characteristics, inter- and intraspecific interactions, and other biotic and abiotic factors. Twenty-four nests were examined and all were constructed in ʻōhiʻa (*Metrosideros polymorpha*) trees between 1,655 and 1,836 m elevation. Nesting occurred during months of high rainfall, January through late June. Nesting success was higher in 1992, when weather was drier and ʻōhiʻa flowering was believed to be more profuse. The number of fledglings produced per successful nest was similar between years. The majority of nest failures occurred during the nestling stage. Chases directed at non-conspecifics were observed more frequently at nests that failed than at successful nests during 1993. ʻApapane (*Himatione sanguinea*) were the target of 46% of chases, while chasing of intraspecifics was rare and no chases involving nonnative species were observed. Whereas predation, especially by Short-eared Owl (*Asio flammeus sandwichensis*), and weather were implicated in some nest failures, further research will be required to determine their importance. Although ʻōhiʻa nectar was found to be the single most important food source, the variety of plants on which ʻĀkohekohe were found to forage stresses the importance of maintaining undisturbed forest understories and subcanopies. To reduce the extinction risk of ʻĀkohekohe populations, restoration of existing habitats is critical.

Key Words: ʻĀkohekohe; breeding biology; endangered birds; Hawaiʻi; Hawaiian honeycreeper; *Palmeria dolei.*

The Hawaiian honeycreepers (subfamily Drepanidinae), endemic to the Hawaiian Islands, represent perhaps the most celebrated example of an avian adaptive radiation in the world (Freed et al. 1987a, Tarr and Fleischer 1995). They also comprise a large proportion of one of the world's most critically endangered avifaunas. At least 14 species, known only from subfossils, went extinct after Polynesian settlement (circa 400 A.D.) but before European contact in 1778 (Olson and James 1982b, James and Olson 1991). Less than 75% of the historically known species remain today (Scott et al. 1986). Of these, the ʻĀkohekohe or Crested Honeycreeper (*Palmeria dolei*) is one of 13 drepanids listed as endangered (Scott et al. 1986, Pyle 1990). Once endemic to the islands of Maui and Molokaʻi, the ʻĀkohekohe is now found only in the eastern, high-elevation rain forests on Maui. Like most honeycreepers, numerous factors threaten the remaining population (Smith and Fancy 1998), including habitat loss and alteration by humans and alien species (Scott et al. 1986), competition with alien species (Mountainspring and Scott 1985), and disease (Warner 1968, van Riper et al. 1986, Atkinson et al. 1995).

Maintaining viable ʻĀkohekohe populations will depend on sound knowledge of their life-history characteristics and ecology. Much of the available information is anecdotal, consisting of observations made by naturalists over the last century (Perkins 1903). While recent research has provided information on population size, distribution (Scott et al. 1986), and competition (Mountainspring and Scott 1985, Carothers 1986a), information on the breeding biology is lacking.

Here we report observations of the first recorded nests of the ʻĀkohekohe. We describe and document its breeding biology, particularly those aspects that potentially will be useful in managing the remaining populations. These include: nest and nest-site selection, nesting success and timing of nesting in relation to biotic and abiotic factors, and other aspects of breeding that may be important in their conservation.

METHODS

STUDY AREA

Fieldwork was conducted for 10 months (10 March–27 June 1992, and 3 February–20 July 1993), in The Nature Conservancy's Waikamoi Reserve. This 2,100 ha reserve is located on the north slope of Haleakalā Volcano between 1,400 and 2,600 m elevation. The 25 ha study site is located between 1,640 and 1,880 m elevation in the western portion of the reserve and includes 3 km of foot trails (VanGelder 1996). Vegetation of the study area consists primarily of wet forest (Kitayama and Mueller-Dombois 1992) and ʻōhiʻa (*Metrosideros polymorpha*) comprises >25% of the canopy cover (Scott et al. 1986).

Precipitation on Haleakalā's north slope is largely determined by prevailing trade winds and temperature inversions (Lyons 1979). The temperature inversion occurs between approximately 1,900 and 2,000 m elevation (Kitayama and Mueller-Dombois 1992) and limits the up-slope movement of clouds. Below the inversion adiabatic cooling produces up to 7,000 mm of annual rainfall (Giambelluca et al. 1986), making the windward slopes of Haleakalā one of the wettest places on earth. The greatest rainfall generally occurs from October to April, when trade winds are less frequent and storm related rainfall is more common (Giambelluca et al. 1986); however, seasonality in wet areas is less pronounced than in dry areas. The annual rainfall regime of wet windward areas usually consists of three seasonal peaks. At west Honomanū (elevation 915 m) on Haleakalā's windward slope, peaks in rainfall occur during December, March–April, and August (400 to 650 mm), with lows during June, October, and January (300 to 400 mm; Giambelluca et al. 1986). Rainfall during both years was considerably below the annual average and coincided with an El Niño period. Annual rainfall during 1992 and 1993 was 892 mm and 1,094 mm, (34% and 25% below average), respectively (U.S. Department of Commerce 1993).

NEST CHARACTERISTICS

Nest searches were conducted throughout the study and, while not quantified in 1992, exceeded 380 person-hours in 1993 (VanGelder 1996). To identify factors important in nesting success, seven nest-placement variables were recorded, including species of nest tree, nest and nest tree height, direction of the nest from the trunk, percentage of foliage cover above the nest, nest location in the canopy, and orientation of twigs supporting the nest (see VanGelder 1996). In addition, broad habitat characteristics at nest sites were estimated by sampling a 16-m radius circular plot centered on the nest tree. The percentage canopy and subcanopy cover were estimated at 1, 8, and 16 meters in each cardinal direction by holding a 0.5 m diameter metal ring overhead at arm's length. Trees >12 m were considered canopy, 4.5–12 m subcanopy, and <4.5 m understory. Estimates for each plot were averaged to obtain mean percentage of cover for the canopy and subcanopy. Percentage of cover of seven native understory plants on which ʻĀkohekohe are known to forage (e.g., *Myrsine* sp., *Melicope* sp., *Vaccinium reticulatum, Rubus hawaiiensis, Styphelia tameiameiae, Broussaisia arguta, Cheirodendron trigynum*) were estimated within 1-m radius subplots located at 8 m and 16 m in each of the four cardinal directions from the trunk of the nest tree. In addition, the number of canopy trees (not including the nest tree) within the nest plot, their condition (live or dead) and the diameter at breast height (dbh) of each tree in the plot were measured to obtain a mean plot dbh. Nest tree dbh and distance from the trunk of the nest tree to the nearest canopy tree within the plot were also measured. Elevation of the nest tree was recorded at the trunk using an altimeter, and slope was measured from the trunk of the nest tree to a point at least 16 m downslope using a clinometer.

To identify important factors in nest-site selection, we compared variables from known nest trees with those from 18 randomly chosen trees (VanGelder 1996). Sites were generated such that an equal number of random sites were located at low (<1,730 m), middle (1,731–1,790 m) and high (1,790–1,850 m) elevations to control for elevational differences.

BEHAVIOR, ABUNDANCE, AND ʻŌHIʻA FLOWERING

ʻĀkohekohe nests were observed daily or every other day, for one to four hours between 0530 and 1900. Observations were conducted using binoculars or a 10 × spotting scope from a concealed location at least 20 m from the nest. Because nests were located in the crowns of trees and observers could not see into the nest, various nest stages were approximated from the behavior of adults (VanGelder 1996). These behaviors included building (carrying nesting material), incubation (sitting on nest for extended periods), brooding (actively feeding, removing fecal sacs, etc.), and fledging (see VanGelder 1996 for details). The period that a nest was active was determined by backdating from the day of fledging or, if the nest did not fledge young, from the estimated hatch date. ʻĀkohekohe chase behavior was recorded two to three times a week at selected nests for a total of 19 and 104 hours during 1992 and 1993, respectively. For each chase we recorded number, species, and age of individuals chased. A chase was defined as an adult rapidly flying toward an individual(s) of any species in an aggressive manner and occurring within 30 m of the nest. Foraging behavior was quantified during 1993 by recording all foraging observed and included recording plant species, substrate (e.g., leaf or flower), and location (e.g., canopy, subcanopy, understory). Only foraging observations at least three minutes apart were used in analysis to minimize autocorrelation of behavior on the same bird.

Relative number of adults and juveniles were estimated from surveys in 1993. Approximately 3 km of trails were walked biweekly from 11 March to 20 July by one of two trained observers at a rate of approximately 0.54 km/hr. When an ʻĀkohekohe was sighted, it was observed for 5 min and its behavior was recorded, as well as the time, age (juvenile or adult), location, and weather (VanGelder 1996). After 5 min an observer would then walk approximately 90 m before searching for another individual.

ʻŌhiʻa flower abundance was estimated twice during February and once a month thereafter during 1993. Estimates of flower abundance were made at 80 fixed locations, 30 m apart. The canopy in flower was visually estimated from a randomly chosen quarter of a 30-m diameter circular plot centered on a fixed location on the trail. After the subplot was selected, it was used for all subsequent sampling. Flowering was categorized visually as 1 = trace (<1%), 2 = low (1–5%), 3 = medium (6–25%), and 4 = high (26–50%).

RESULTS

NESTING SUCCESS

Nesting occurred during months of high rainfall, from January through late June, with peak nesting earlier in 1993 (March) than in 1992 (May; Fig. 1). Twenty-four nests were found during the study, 11 in 1992 and 13 in 1993 (Table 1). From these nests a total of 20 chicks successfully fledged. Nesting success was twice as high in 1992 when weather was drier and ʻōhiʻa flowering was believed to be more profuse (VanGelder 1996) than in 1993 (Table 1). The number of fledglings produced per successful nest, however, was similar between years.

Of the nine nest failures, the majority oc-

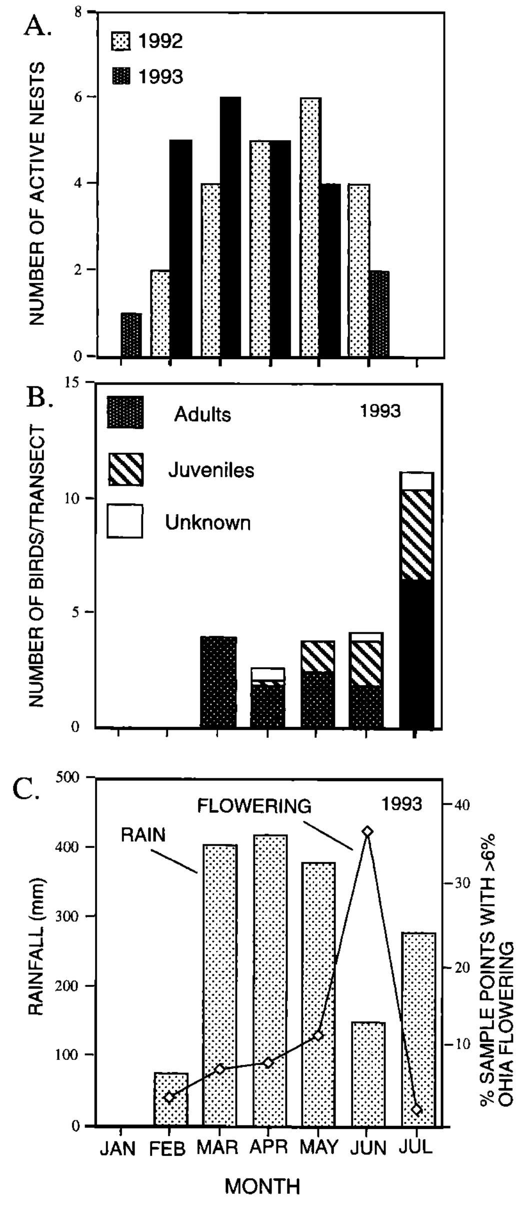

FIGURE 1. Seasonal trends in: (A) monthly nesting activity of 'Ākohekohe during 1992 and 1993. Active nests are those in incubation or nestling stage. (B) Relative abundance of 'Ākohekohe as determined by transects, and (C) rainfall and 'ōhi'a flowering. No rainfall data were collected during January, and no abundance data were collected for January or February (see VanGelder 1996).

TABLE 1. SUMMARY OF 'ĀKOHEKOHE NEST PRODUCTIVITY IN WAIKAMOI RESERVE, MAUI, FOR 1992 AND 1993 (NUMBERS IN PARENTHESES ARE PERCENTAGES)

	Year		
	1992	1993	Total
Nests	11	13	24
Successful nests[a]	8 (73)	4 (31)	12 (50)
Failed nests[a]	2 (18)	7 (54)	9 (38)
Abandoned	1	1	1
Unknown	1	1	2
Nesting success[b]	0.80	0.36	0.57
Fledging success[c]	1.30	0.64	0.95
Fledglings/successful nest	1.63	1.75	1.67

[a] Number of successful versus failed nests approached significance between years (Fisher's Exact test, P = 0.056).

[b] Proportion of nests that produced young out of total number of nests of known outcome.

[c] Number of fledglings produced out of the total number of nests of known outcome.

curred during the nestling stage. Three occurred when chicks were 5 to 8 days old, three at 12 to 14 days old, and one at 18 days old. At three of the failed nests, Short-eared Owl (*Asio flammeus sandwichensis*) were seen in the nest vicinity either on the day of failure, or within 48 hours prior, and owls were observed flying within 10 m of the nest at two of these nests. Owls were observed on the study area on 32 (21%) of 151 days during 1993, often flying low over the canopy. Although we never found remains of nestlings, we did find remains of an adult 'Ākohekohe on the ground near a stump where an owl had been sighted.

Three failures (two during the nestling stage, one during incubation) were associated with periods of high winds and rain. In one case we observed a nest slowly disintegrating over several days until only a small corner remained. One of two chicks disappeared during this period, while the other remained perched on a remnant piece of nest and eventually fledged. One nest failed after 16–18 days of incubation. The protracted incubation period suggests that this failure could have resulted from embryo death or infertility.

Renesting occurred on two occasions, each at different localities. In 1992, a pair fledged two young from one nest, and within 48 hours after the last chick fledged, a second nest was discovered in a tree approximately 8 m away from the first nest tree. The fledglings from the first nest were observed begging from the adults as the adults built the second nest. In 1993, a single pair apparently nested three times and could have been responsible for half of all fledged young produced for the year. For this pair, the first nest failed after at least 16 days of incubation, and within two days adults built a second nest in a tree approximately 17 m from the first nest tree. Twelve days after two young fledged from the second nest, adults built a third nest

TABLE 2. ʻĀKOHEKOHE NEST PLACEMENT CHARACTERISTICS IN WAIKAMOI PRESERVE, MAUI (DATA FROM 1992 AND 1993 ARE COMBINED)

Characteristic		N	χ^2	P
Location in forest	Canopy	23		
	Subcanopy	1	20.17	0.001
Location within canopy (of nest tree)	Top 20%	14		
	Mid 40%	8		
	Bottom 40%	1	11.14	0.004
Estimated foliage cover over nest cup	0–33%	0		
	34–66%	1		
	67–99%	21	38.45	0.001
Orientation of twigs supporting nest	Vertical	13		
	Horizontal	10	0.39	0.532
Canopy quadrant in which nest is located	NE	9		
	NW	8		
	SE	6		
	SW	0	8.55	0.036

within 6 m and in the same tree as the first nest. Fledglings were seen begging from an adult during building and could be observed near the nest tree through fledging of the third nest. Adults often chased these juveniles from the nest tree and adjacent areas. Other evidence of renesting is more circumstantial but suggests that renesting was widespread. Evidence includes the discovery of new nests in the immediate area of recently fledged or failed nests (N = 2), observations of recently fledged or juvenile birds approaching active nests (N = 2), and repeated observations of pairs of juvenile birds observed in the immediate area of an active nest (N = 3).

Chases directed at non-conspecifics were observed more frequently at nests that failed than at successful nests during 1993. For the 11 nests monitored, 0.96 chases/hr were recorded at failed nests, whereas the chase rate at successful nests was only 0.06 chases/hr ($\chi^2 = 25.62$, $P < 0.001$). This suggests that chases may have been a factor leading to nest failure; however, determining the relative importance of chases on nesting is complicated by the fact that in 1992 when nesting success was higher, we observed a much greater rate of chasing (3.0 chases/hr). All nests monitored for chases in 1992 were successful, so comparisons with failed nests for this year were not possible.

ʻĀkohekohe chases for both years (N = 123) were directed at four native species, ʻApapane (*Himatione sanguinea*), ʻIʻiwi (*Vestiaria coccinea*), Hawaiʻi ʻAmakihi (*Hemignathus virens*), and Maui Creeper (*Paroreomyza montana*), although the species could not be determined in 49% of the chases. ʻApapane was the target of 46% of chases, the highest proportion, while chasing of intraspecifics was recorded rarely. We observed no chases involving nonnative species.

NEST-SITE SELECTION

All nests were constructed in ʻōhiʻa trees between 1,655–1,836 m elevation. The distance to the nearest nest ranged from zero (in the case of renesting) to 263 m. However, the majority of nests (83%) were constructed within 80 m of the nearest nest, producing a clustered distribution. All but one nest were located in the canopies of large ʻōhiʻa trees in the top 20% of the canopy and had dense foliage above the nest (Table 2). The one exception was located in a small ʻōhiʻa on the edge of a dieback area where few trees were taller than 12 m. Mean nest height was 15.33 m (N = 13, SE = 0.55).

Random sites and nest sites were significantly different for 4 of the 15 habitat variables (Table 3). Canopy cover, percentage of *Myrsine* sp., percentage of living trees, and tree density were all significantly higher at nest sites than at random sites. The relative importance of any single variable is difficult to determine because all variables except percentage of *Myrsine* sp., were positively correlated ($r_s < 0.6$, $P < 0.001$), and sample size was insufficient for multivariate analyses. Nevertheless, results suggest that ʻĀkohekohe selected nest trees with greater canopy cover in denser stands of live trees where the percentage of ground cover of *Myrsine* sp. was high.

Subcanopy cover, slope, and elevation were significantly lower at successful nests than failed nests (Table 4). This suggests that birds that chose to nest in areas with sparser subcanopies, on sites with less slope, and at slightly lower elevations were more successful. However, as was the case for nest-site selection, all variables are significantly correlated ($r_s < 0.5$, $P < 0.01$). No differences were found between successful

TABLE 3. SIGNIFICANT HABITAT VARIABLES (MEAN ± SE) COMPARING RANDOM SITES (N = 10) WITH NEST SITES (N = 16) OF ʻĀKOHEKOHE

Variable	Nest Site	Random Site	U[a]	P
Percentage canopy cover	28.16 ± 2.01	21.21 ± 2.24	117	0.051
Percentage *Myrsine* sp. cover	2.64 ± 0.49	0.73 ± 0.38	133	0.005
Percentage living trees	9.50 ± 1.04	5.80 ± 1.01	124	0.021
Number canopy trees	10.56 ± 0.97	6.00 ± 1.01	133	0.005

[a] U = Mann-Whitney U statistic.

and unsuccessful nests with respect to their location within the canopy of the nest tree (Fischer's exact test, N = 20, P > 0.10), or orientation of twigs supporting the nest (Fisher's exact test, N = 20, P > 0.1).

NESTING PERIODS

Nest building

Building activity was recorded at seven nests. Although birds were not individually marked, it appeared that one adult of each pair did the majority of the building, and the second adult was often present and commonly called near the nest. Material was collected from up to 50 m from the nest (VanGelder 1996). Nests were cup shaped and constructed of twigs, lichens, and mosses. Two nests collected after fledging in 1992 measured 104 mm and 65 mm in depth, and 153 and 180 mm in diameter, respectively. The deeper nest consisted of two distinct layers, suggesting a second nest had been built on top of an existing nest. Both nests were deposited in the Bernice P. Bishop Museum (Catalogue No. BPBM 1992.223).

Laying and incubation

Date for egg laying and incubation could only be estimated from behavior patterns exhibited by birds at nests. Irregular nest visits occurred one to two days prior to onset of incubation. This period of irregular visitation was assumed to be the laying period. The incubation period was recorded at seven nests and varied from 14–16 days, but the period could only be estimated because of the difficulty in determining when egg laying had ceased and incubation had begun. Incubation bouts typically lasted 20 to 30 minutes, separated by absences of 1–10 minutes. It appeared as though one bird, possibly the female, did almost all of the incubating. During this period, what was presumed to be the male fed the female both on and off the nest.

Nestling period

The complete nestling period was observed at six nests and lasted 20 to 27 days (Fig. 1). Young were first visible at approximately 6–8 days of age. At this time they were partially covered with white or gray down. One 14-day-old nestling collected off the ground in 1993 had feathers half emerged from their shafts (VanGelder 1996). Plumage at fledging was slate gray with brown nape feathers. During the first week after hatching, adults were occasionally observed removing what appeared to be fecal sacs from the nest. By 6–8 days of age, chicks ejected feces over the side of the nest. Both adults fed chicks by regurgitation. During the last week of the nestling stage, chicks sometimes exhibited behavior characteristic of foraging and were seen probing ʻōhiʻa flowers and foliage near the nest with their bills.

Fledging and postfledging

The earliest and latest fledging dates recorded over the two years were 3 March 1993 and 27 June 1992. Fledging was a gradual process. Chicks initially ventured a few centimeters from the nest, then gradually increased the time and distance. A nestling was described as fledged

TABLE 4. SIGNIFICANT HABITAT VARIABLES (MEAN ± SE) COMPARING SUCCESSFUL NESTS (N = 9) WITH UNSUCCESSFUL NESTS (N = 9) OF ʻĀKOHEKOHE

Variable	Successful	Unsuccessful	U[a]	P
Percent subcanopy cover	14.41 ± 1.15	20.48 ± 2.09	14	0.034
Slope	11.94 ± 1.54	17.20 ± 1.28	14	0.019
Elevation	1710.44 ± 9.19	1748.65 ± 14.29	15	0.024

[a] U = Mann-Whitney U statistic.

when it moved more than 3 m from the nest. Postfledging activity was noted at three nests. During the first few days, fledglings perched or explored via climbing or fluttering in the canopy, remaining within approximately 40 m of the nest, and often perching under dense leaf clusters usually within a few meters, and sometimes a few centimeters, from a sibling. During this period, fledglings were fed regularly by the parents. Five to six days after fledging, young were observed aggressively pursuing adults and begging (VanGelder 1996). By 14 days after fledging, young foraged on their own but still uttered persistent begging calls while pursuing and begging from adults. Throughout this period, the adults occasionally fed the young birds but also frequently chased them for short distances. The oldest fledgling observed being fed by an adult was at least 33 days old. Two young were observed in the nest area for up to 32 days, and one young up to 41 days after it fledged.

IMPORTANCE OF ʻŌHIʻA

Percent ʻōhiʻa flowering varied significantly through the 1993 season ($\chi^2 = 87.937$, df = 12, $P < 0.001$), showing a steady increase between February and May, a high peak in June, and marked decrease in July (Fig. 1). The abundance of juveniles and adults peaked in July, which was after nesting had ceased and one month after peak ʻōhiʻa flowering (Fig. 1). Juvenile and adult abundance in July was, respectively, two and three times higher than in June.

Although ʻĀkohekohe were observed foraging on 13 plant species (VanGelder 1996), the majority (75%) of the 1,222 observations were on ʻōhiʻa, either taking nectar from flowers or feeding on invertebrates from leaves in the canopy. Across all species 63% of foraging events were on nectar from flowers and 46% foraged on invertebrates on leaves. Among all food sources, ʻōhiʻa was the most important for both adults and juveniles in all months ($\chi^2 = 52.170$, df = 5, $P < 0.001$ and $\chi^2 = 21.755$, df = 2, $P < 0.001$, respectively). In addition to ʻōhiʻa, other foods were seasonally important for adults. For example, during February, 78% of feeding observations were on kōlea (*Myrsine* sp.), and in March 91% were on either kōlea or ʻalani (*Pelea* sp.). In addition, ʻākala (*Rubus* sp.) flowers appear to be important sources of nectar in June (VanGelder 1996). Thus, these plants, in addition to ʻōhiʻa, represent important foods or substrates for foraging during the breeding season.

DISCUSSION

In many respects the breeding characteristics we recorded for ʻĀkohekohe are similar to those described for other Hawaiian honeycreepers (Baldwin 1953, Eddinger 1970, van Riper 1980a, Pletschet and Kelly 1990, Morin 1992a, Ralph and Fancy 1994b, Lepson and Freed 1995). There is a protracted breeding season in which the fledging period broadly overlaps with peak ʻōhiʻa flowering, a pattern similar to that reported for the ʻIʻiwi and ʻApapane (Baldwin 1953, Eddinger 1970, Ralph and Fancy 1994b). Although we can not directly compare nesting success with other studies of honeycreepers because we could not determine clutch size or hatching success, the level of nesting success we estimated is within the range of that for other drepanids (Eddinger 1970, van Riper et al. 1982, van Riper 1987, Pletschet and Kelly 1990, Morin 1992a).

Use of nonnectar food sources during the nesting cycle, especially between February and May, likely reflected the need for protein during egg production and nestling growth (Ricklefs 1974, Walsberg 1983). Our results support historical observations by Perkins (1903), who pointed out the importance of species other than ʻōhiʻa for foraging during certain times of year. Although we found ʻōhiʻa to be the single most important food source, the variety of plants on which ʻĀkohekohe forage stresses the importance of maintaining undisturbed forest understories and subcanopies.

A number of authors have suggested that honeycreepers move in search of flowering ʻōhiʻa trees and track ʻōhiʻa flowering over the season (Baldwin 1953, MacMillen and Carpenter 1980). Carpenter (1976b) found a two week lag between the onset of high ʻōhiʻa flowering and the influx of ʻApapane, but found no such lag for ʻIʻiwis. Our data for 1993 strongly suggest such a lag between peak flowering and ʻĀkohekohe abundance. Since this period also coincides with fledging and the end of nesting, it is unclear whether the dramatic increase in ʻĀkohekohe numbers could have been due in part to greater visibility of resident adults and recently fledged offspring. It seems somewhat doubtful, however, that these factors could completely explain the threefold increase in adults from June to July. Other evidence for the movement of ʻĀkohekohe into the study area is supported by the occurrence in July of individuals with vocalizations typical of the populations in Hanawī, on the far side of Haleakalā crater (VanGelder 1996). These data are also consistent with assertions by others suggesting ʻĀkohekohe may show seasonal movements (Conant 1981).

Despite small sample sizes, breeding success of ʻĀkohekohe approached being significantly different between years. Although we have no quantitative information on ʻōhiʻa flowering in

1992, flowering was apparently greater in 1992 (E. VanGelder, pers. obs.) and might explain the higher breeding success that year. Nectar availability has been shown to be a limiting factor influencing honeycreeper breeding success (van Riper 1984, 1987) and has been shown to be a limiting resource for larger nectarivores (Carpenter and MacMillen 1980, Pimm and Pimm 1982). Assessing the importance of 'ōhi'a flowering is difficult, however, because flowering is patchy and nectar quality and quantity are unpredictable (Carpenter 1976b). Further research over multiple years of differing resource levels will be needed to fully evaluate the relationship between 'ōhi'a flowering and reproductive success in the 'Ākohekohe.

In addition, weather, especially rain and associated high winds, may influence nesting success in given years. For the Hawaiian nectarivores, resources and weather are closely coupled (Carpenter 1976b, Carpenter and MacMillen 1976). First, storms have been implicated in breeding failures (Baldwin 1953, Eddinger 1970, Morin 1992a). Rain imposes thermal stress on adults and nestlings, and wind dislodges nests from trees and young from nests, as we found in 1993. Second, the typically cold, wet environment of Hawaiian high-altitude forests results in high energy requirements, and rain causes low nectar production rates and dilutes nectar in 'ōhi'a (Carpenter 1976b). Thus, rainy periods place higher energetic and foraging demands on individuals, especially adults feeding nestlings. It is interesting that although rainfall was greater in 1993 than in 1992, it was still 25% below normal. This begs the question of what breeding success is like in a year receiving average rainfall. Other research on the breeding biology of the 'Ākohekohe by the Biological Resources Division of the U.S. Geological Survey may shed light on this important question.

While we found no evidence of interference competition between 'Ākohekohe and nonnative species, we did find such evidence with the 'Apapane. 'Ākohekohe chased 'Apapane at significantly higher rates at nests that subsequently failed than they did at successful nests, suggesting possible negative fitness consequences associated with chasing. Our observations are consistent with those of other researchers who recorded interference competition between 'Ākohekohe and 'Apapane (Perkins 1903, Carothers 1986a). However, determining whether 'Apapane populations have negative effects on overall breeding success of 'Ākohekohe will require further work. Nests observed in 1992 were successful, although chase rates were three times those of failed nests in 1993. However, the nests we chose to observe for chasing behavior in 1992 were all successful, not allowing a comparison of chase rates at failed and successful nests for the year. It is possible that the variability in chase behavior and its consequences depend on resource availability (Carpenter and MacMillen 1976), and future work will be required to determine this. Nevertheless, it is intriguing that the 'Apapane, the native species that is most resistant to avian malaria, is responsible for the highest levels of interference competition (C. Atkinson, pers. comm.). This raises the question of whether 'Apapane populations are greater than they were historically, and, if so, whether they are having negative impacts on other native species.

Many variables such as proximity to food resources, concealment from predators, protection from weather, and predator and competitor detection may play important roles in nest-site selection and nesting success (Calder 1973, van Riper 1984; Martin 1987, 1988; van Riper et al. 1993, With 1994). Our results show nonrandom nest placement with respect to several habitat variables. Pairs nest in denser stands of living trees where the canopy cover is higher. This preference could provide either greater shelter for nests, concealment from predators, or both. Successful nests had more open subcanopies, were on less extreme slopes, and occurred at slightly lower elevations than unsuccessful nests. However, what other factors may correlate with these variables is unclear. It could be that these variables are simply correlated with important microhabitat variables we did not measure. van Riper et al. (1993) found that 'Amakihi on the southwest slope of Mauna Kea nested predominantly on the southwest side of tree canopies. They reasoned that this was due to microhabitat influences on ambient temperature and associated advantages in thermoregulation. In contrast, we found 'Ākohekohe nested predominantly in the northern sector of tree canopies (never in the southwest quarter) on the north facing slope of Haleakalā and, thus, directly exposed to the northeast trade winds and accompanying precipitation.

We found only circumstantial evidence that predation may affect breeding success. While predation is the primary cause of nest failure for many bird species (Skutch 1985, Martin 1993), the possible impact of predation is difficult to assess in this study. We found circumstantial evidence that Short-eared Owls may have taken some nestlings, but the overall affect of this predation on breeding success is unclear. Although we found no evidence that alien mammals were preying upon 'Ākohekohe nests, the probability of detecting such predation in this study was very low.

CONSERVATION PRIORITIES

To reduce the extinction risk of ʻĀkohekohe populations, restoration of existing habitats is critical. In particular, our results suggest that maintaining undisturbed understory and subcanopies in addition to healthy stands of ʻōhiʻa is important, since they represent important foraging areas for ʻĀkohekohe. Although disease is a concern for many regions (Scott et al. 1986, Atkinson et al. 1995, Jarvi et al. *this volume,* Shehata et al. *this volume*), translocations of ʻĀkohekohe to other previously occupied regions, once they are restored, should also be considered.

Additional research also needs to be carried out to evaluate the impact of predation on ʻĀkohekohe populations and the importance of resource tracking. It should not be assumed that changes in abundance will be gradual. Rapid declines frequently occur in populations subject to stochastic events (Temple 1985, 1986). The year to year variation in breeding success found in this study and reported in other honeycreepers (Eddinger 1970, van Riper 1987, Morin 1992a) suggests yearly monitoring of populations may be essential.

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