

‘ĀKOHEKOHE RESPONSE TO FLOWER AVAILABILITY: SEASONAL ABUNDANCE, FORAGING, BREEDING, AND MOLT

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Abstract. We studied the relationship of flower availability to the seasonality of life history events of the ‘Ākohekohe (*Palmeria dolei*), a primarily nectarivorous and endangered Hawaiian honeycreeper from montane rain forests on Maui, Hawai‘i. For comparison, we also investigated temporal bird density and foraging behavior of three other competing Hawaiian honeycreepers: ‘Apapane (*Himatione sanguinea*), ‘I‘iwi (*Vestiaria coccinea*), and Hawai‘i ‘Amakihi (*Hemignathus virens*). All species except ‘amakihi fed primarily on nectar of ‘ōhi‘a-lehua (*Metrosideros polymorpha*), which produced flowers year-round but had an annual flowering peak in January. Flowers of several subcanopy shrubs and trees were important components of the diet for all nectarivores, and these were available seasonally depending upon the species. ‘Ākohekohe densities did not change temporally, suggesting a relatively stable population residing above 1,700 m. Monthly densities of ‘Apapane, ‘I‘iwi, and Hawai‘i ‘Amakihi were positively correlated with monthly ‘ōhi‘a-lehua flower abundance, and 50–80% of these populations departed temporarily from our high-elevation site in July. There was a positive correlation with the timing of ‘Ākohekohe breeding and high abundance of ‘ōhi‘a-lehua bloom. Molt followed breeding. From a conservation perspective, these results show that ‘Ākohekohe maintain a relatively stable population above the mid-elevation zone of disease transmission, particularly during the fall when ‘ōhi‘a-lehua bloom decreases and mosquitoes increase. ‘Ākohekohe remain on their territories partly by switching their foraging to subcanopy trees and shrubs, most of which require protection from feral pigs (*Sus scrofa*).

Key Words: ‘Ākohekohe; breeding; foraging; Hawaiian honeycreeper; *Metrosideros*; *Palmeria dolei*; phenology.

The seasonal rhythms of breeding, molt, and population movements in birds are often correlated with the temporal availability of primary food resources (Skutch 1950; Stiles 1975, 1980, 1985; Clutton-Brock 1991). Breeding is often timed to peak availability of food resources such that the young are adequately nourished and adults can satisfy the energetic demands for breeding (Stiles 1985, Ralph and Fancy 1994b). Birds breed and molt throughout the year in the tropics, but some are restricted to breeding and molting during certain times of the year based on a species' foraging niche (Skutch 1950; Stiles 1980, 1988; Poulin et al. 1992; Ralph and Fancy 1994b). Altitudinal bird migrations are also found to be in response to fluctuating food supplies and occur predominantly among nectarivores and frugivores (Wolf et al. 1976; Stiles 1985, 1988; Loiselle and Blake 1991). In general, these birds have limited food choices and must be highly mobile to locate new sources of flowers or fruits.

Nectarivorous Hawaiian honeycreepers (Fringillidae: Drepanidinae) respond to seasonal fluctuations of flower abundance (Baldwin 1953, van Riper 1984, Carothers 1986a; Ralph and Fancy 1994b, 1995). For example, at one site on the island of Hawai‘i, breeding and molting periods of ‘Apapane (*Himatione sanguinea*), ‘I‘iwi (*Vestiaria coccinea*), and Hawai‘i ‘Amakihi (*Hemignathus virens*) were associated with nec-

tar availability, but insectivorous species, which had a more constant food supply, had longer, less defined breeding and molting periods (Ralph and Fancy 1994b). ‘Apapane and ‘I‘iwi practice altitudinal movements on the island of Hawai‘i, dictated by the timing of bloom of certain nectar producing plants (Baldwin 1953, Ralph and Fancy 1995). The larger ‘Ākohekohe (*Palmeria dolei*), the focus of our study, also feeds primarily on nectar. The ‘Ākohekohe has undergone extirpation on the island of Moloka‘i, is currently endangered (USFWS 1998), and survives only in montane rain forest on the windward slope of east Maui. ‘Ākohekohe are closely associated with ‘ōhi‘a-lehua (hereafter ‘ōhi‘a, *Metrosideros polymorpha*), the dominant tree of Hawaiian rain forests. ‘Ākohekohe feed primarily on ‘ōhi‘a nectar and nest exclusively in ‘ōhi‘a canopies (Carothers 1986a,b; VanGelder 1996, VanGelder and Smith *this volume*).

Flowering ‘ōhi‘a trees can be found at all times of the year in different areas of forest as flowering progresses from high elevations in winter to lower elevations in spring and summer (Baldwin 1953, Bridges et al. 1981). However, at most sites honeycreepers do not permanently inhabit the lowest elevations, where higher incidence of contact with introduced avian diseases has apparently depleted the birds' populations (Scott et al. 1986, Ralph and Fancy 1995). Mosquitoes (*Culex quinquefasciatus*) can

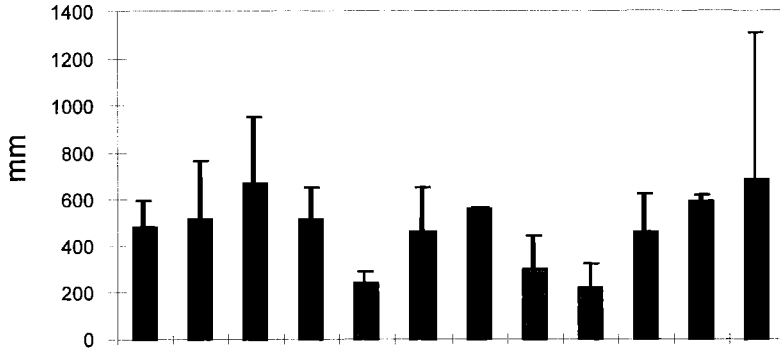


FIGURE 1. Mean monthly rainfall at 2,100 m elevation in the Hanawā Natural Area Reserve, Maui, Hawai‘i, for the period January 1995 through May 1997.

spread avian malaria (*Plasmodium relictum*) and poxvirus (*Poxvirus* spp.) and are most abundant at elevations below 1,500 m (van Riper et al. 1986). The prevalence of these diseases appears to restrict most native bird populations to high-elevation forests where mosquitoes are less abundant or absent (Warner 1968, Scott et al. 1986, van Riper et al. 1986, Atkinson et al. 1995). Seasonal migrations to lower elevations, where mosquitoes exist in greater abundance, would compromise native birds that have little or no tolerance to these alien diseases. Conservation of native habitats and bird species must therefore consider how seasonal availability of dominant food sources such as ‘ōhi‘a affect bird behavior and the timing of life history events.

In this paper we examine the relationship between availability of flowers, particularly ‘ōhi‘a, with seasonality in bird abundance, foraging ecology, breeding, and molt in the ‘Ākohekohe. We compare seasonality in abundance and foraging of ‘Ākohekohe with the three other nectarivorous honeycreepers (‘Apapane, ‘I‘iwi, and Hawai‘i ‘Amakihi) on our study site. We also present data on seasonality of mosquito presence and discuss the possible influence of habitat quality and flower availability on bird movements and mortality from avian disease.

METHODS

STUDY AREA

Our study was conducted continuously from April 1994 to December 1997 between the east and west forks of Hanawā Stream at 1,550–2,125 m elevation on the windward slope of Haleakalā Volcano, east Maui, Hawai‘i (20° 44' N, 156° 8' W). The topography is rugged, steep, and dissected by many small ravines and wide valleys. The forest canopy, dominated by ‘ōhi‘a trees, is dense and continuous throughout most of the study site. The subcanopy is also dense with trees and shrubs including ‘ōlapa (*Cheirodendron tri-*

gynum), pilo (*Coprosma ochracea*), na‘ena‘e (*Dubautia plantaginea*, *D. reticulata*), kāwa‘u (*Ilex anomala*), ‘alani (*Melicope clusiifolia* mainly, also *M. spp.*), kōlea (*Myrsine lessertiana*), pūkiawe (*Styphelia tameiameia*), and ‘ōhelo (*Vaccinium calycinum*), with kanawao (*Broussasia arguta*), ‘ākala (*Rubus hawaiiensis*), ferns, grasses, sedges, and mosses dominating the understory, and epiphytes cloaking the branches (Jacobi 1989, Kitayama and Mueller-Dombois 1992; this study). Rare plants producing flowers sought by birds included lobelias (*Clermontia*, 4 spp.; *Cyanea*, 3 spp., and *Lobelia* spp.) and mint (*Stenogyne kamehamehae*).

The climate is dictated by the northeasterly trade winds; fog and mist occur almost daily, and rainfall is among the highest in the state. We set two standard 26-inch (66.3 cm) National Weather Service rain gauges at 1,700 m and 2,125 m elevation. Annual rainfall at these sites averaged 5,154 mm ± 1,192 SE and 5,114 mm ± 1,359 SE, respectively, for the period January 1995 through May 1997. Precipitation was not seasonal, although monthly and year-to-year fluctuations were high (Fig. 1). Average monthly temperatures ranged from 9 to 13° C, with slightly cooler temperatures and sharply decreased solar radiation in winter months for the same period (T. Giambelluca, unpubl. data, as further described in Berlin et al. 2000).

FLOWERING PHENOLOGY AND BIRD DENSITY

Data on flowering phenology of ten native plant species and bird counts were taken during the first or second week of every month from January 1995 through December 1997. We established four transects running downslope from 2,150 to 1,550 m elevation; each transect had ten stations at approximately 150-m intervals. Transects ran along parallel, nonadjacent ridges roughly 100 m apart. We used ridge trails due to the difficult terrain encountered off the ridges, but the geography was such that we could hear birds in adjacent valleys and on facing ridges.

At each station, we recorded flowering activity of the following native plants: ‘ākala, ‘alani, kanawao, kāwa‘u, kōlea, ‘ōhelo, ‘ōhi‘a, ‘ōlapa, pilo, and pūkiawe. The species selected were represented on the four transects across elevations and constituted the majority of

the woody flora at this site. We tagged individual plants ($N = 275$) that (1) were of minimum size to be expected to flower, (2) were the closest to the station without being on the trail to minimize bias in selecting plants, and (3) could be viewed clearly. With the aid of binoculars, we counted the number of flowers ('āk-ala) or inflorescences (hereafter referred to as "flowers" for kanawao, 'ōhi'a, and 'ōlapa), or estimated the percentage of live stems with flowers (all others). For the purposes of this paper, we report mean number of 'ōhi'a flowers per month during the three year study (i.e., the total number of flowers for all trees in a given month divided by the number of trees). For nine tree and shrub species other than 'ōhi'a, we calculated the monthly percentage of species with flowering peaks (i.e., the number of species for which flowering peaked in a given month divided by the total number of species). Detailed statistical analyses of phenology of all species is reported in Berlin et al. (2000).

Bird counts were conducted beginning one-half hour after sunrise and continuing usually no later than 12:00, weather permitting. Two nonadjacent transects were chosen per day to avoid recording the same birds from two observers. We believe this was achieved, as effective detection distances range from 32 m for Hawai'i 'Amakīhi to 46 m for 'Ākohekohe (Scott et al. 1986), a small fraction of the distance between our transects. All counts were conducted at designated stations and began from the highest elevation and continued downhill. In models testing variables influencing counts, we found no significant effect for time of day that might confound effects of elevation (unpubl. data). We estimated bird density following the variable circular-plot method (Reynolds et al. 1980, Fancy 1997). The estimated distance of a bird either seen or heard from each station was recorded during eight-minute counts. Weather conditions were recorded using the Beaufort scale for wind speed, and cloud cover was recorded to the nearest 10%. Rain was recorded on a scale of 0 to 4, with 0 = no rain, 1 = mist or fog, 2 = light drizzle, 3 = light rain, and 4 = heavy rain. Counts were postponed if sustained wind speeds exceeded 13 mph or rain was greater than 3.

Analyses of densities for each Hawaiian honeycreeper were performed using four-way nested analysis of variance (ANOVA; SAS Institute 1987) to investigate temporal and spatial variability in densities. Elevation was divided into three categories based on habitat changes within the site that appear to influence 'Ākohekohe distribution. Between 2,040 m and 2,130 m ($N = 8$ stations, mean elevation = 2,092 m), the habitat is a transition between shrubland found on the upper slopes beyond our study area and 'ōhi'a forest, which, in this zone, is shorter in stature than the forest at lower elevations. Within the mid-section of our site, from 1,750 m to 2,039 m ($N = 20$ stations, mean elevation = 1,897 m), the canopy of 'ōhi'a trees is taller and more continuous. At the lowest elevations of our study area, from 1,567 m to 1,749 m ($N = 12$ stations, mean elevation = 1,659 m), the 'ōhi'a canopy becomes more sparse. Thus, our four-way ANOVA model included the main effect variables of month, year, elevation category, and station, with stations nested within elevation categories, along with the various

two-way and three-way interaction terms of month, year, and elevation category.

To compare bird densities with 'ōhi'a flowers, we calculated the mean number of 'ōhi'a flowers at each station for each month and year and included this variable as a continuous covariate in the four-way model above. This five-way analysis of covariance (ANCOVA) was then used to test for the significance of 'ōhi'a flower abundance on bird densities, at the scale of the station level.

We ran some simpler analyses at a much broader scale, the scale of the entire study area, rather than at the scale of each station. We calculated the mean densities for each species and for 'ōhi'a flowers for each month, averaged over the entire time period, and calculated the Pearson's correlation coefficient ($N = 12$ per species) between mean densities and mean 'ōhi'a flowers for each species. We also ran some simple ANCOVAs in which we calculated the means by both month and elevation category ($N = 36$ per species), and tested for association of bird densities and mean 'ōhi'a flowers along with elevation categories and the interaction of elevation and 'ōhi'a flowers. This is similar to the correlation coefficients, except that it tests for whether elevation category is important in the association between mean bird densities and mean 'ōhi'a flower abundance. Finally, one last ANCOVA ($N = 108$ per species) added year along with all the interactions to learn whether year effects were important in the associations among mean bird density, mean flower abundance, and elevation for each species.

FORAGING

Foraging behavior was recorded for the four nectarivorous honeycreepers between December 1994 and June 1997. All observations were taken between 07:00 and 18:30 during various weather conditions. Foraging observations were not taken sequentially and were treated as independent events. Upon detecting a bird, the observer waited ten seconds, then recorded the first foraging maneuver by the bird. For each observation, we recorded the bird's age class, foraging maneuver (e.g., probing, plucking), plant species, substrate type (e.g., flower, twig, leaf), food type, estimated foraging height, and estimated canopy height. Age of the bird was classified as immature or adult and was determined at the time of observation based on plumage characteristics (Simon et al. 1998). Sex was determined for 37 adult and 25 immature 'Ākohekohe based on other behavioral data or morphometric analyses of color-banded individuals (Simon et al. 1998). We used a two-way ANOVA to analyze sex and age categories of 'Ākohekohe in comparing monthly foraging heights, and chi-square contingency tables to compare monthly categorical data on plant species used, stratum occupied (canopy, subcanopy, understory), and food type.

SEASONALITY OF BREEDING AND MOLT

We examined breeding biology and molt of 'Ākohekohe between December 1994 and June 1997. Throughout the study, we searched the study area for nests, repeatedly covering all trails over a 3–4 day period. We located nests between November and May by observing nest building, nest defense, or courtship, by

following adults going to and from the nest, and by occasional chance discovery. Most nests were observed with a spotting scope at 2–3 day intervals from a blind to determine nesting status. Mean incubation and mean nestling periods were calculated for nests for which laying, hatching, and fledging could be closely approximated; these means were used to back-date the start of incubation and the presence of hatched chicks for nests found later in their cycle. The proportion of juveniles in the sample of birds observed foraging was also used as an index of breeding activity.

Feather molt was recorded from birds captured in multilevel mist nets primarily from May to October (Simon et al. 1998). Birds were netted either near banding stations or selectively as they visited blooming shrubs. The presence of either flight or body molt was calculated for second-year and older adults combined. We used Pearson’s correlation to analyze the timing of breeding and molting with ‘ōhi’a flowering.

DISEASE

Culex quinquefasciatus, the only mosquito found routinely at elevations above 1,200 m (Goff and van Riper 1980), serves as the main vector for avian malaria and avian pox (van Riper et al. 1986) and is easily attracted to artificial breeding sites (Reiter 1987). The presence of mosquitoes along the elevational gradient was determined monthly at 24 oviposition pans set along the same transects used for plant phenology and bird counts. We placed one plastic pan in a flat area on the forest floor at every other station and one at the lower most station on each transect. Rabbit food and soil were put into each pan and combined with rainwater to create an organic mixture suitable for mosquito larvae. Any evidence of mosquito eggs, larvae, pupae, or adults in the pans was recorded. The liquid contents of the pans were drained after inspection to remove mosquitoes. Rainfall refilled the pans each month, except in a few monthly checks (<5%) during dry periods. Food and soil were replenished periodically as needed.

Evidence for avian pox was also checked upon examination of all birds captured in mist nets. We recorded the presence or absence of poxlike lesions, such as missing toes and open or closed sores.

RESULTS

FLOWERING PHENOLOGY AND BIRD DENSITY

‘Ōhi’a flowers were present year-round with an annual peak evident in January; flowering increased gradually such that flowers were relatively abundant for 4–5 months (Fig. 2a). In summer months, ‘ōhi’a flowering had virtually ceased at high elevations but continued at elevations below 1,750 m. Understory trees and shrubs flowered at various times of the year; peaks occurred predominantly from April to June (Fig. 2b). Of the species most visited by nectarivorous birds, ‘ākala and ‘ōhelo flowered in spring months, and kanawao flowered between August and October.

‘Ākohekohe densities averaged 2.89 birds/ha ± 0.07 SE throughout the study site for all years.

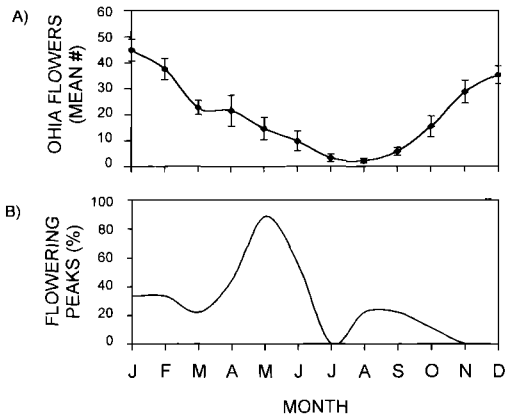


FIGURE 2. Monthly flower abundance for the period January 1995 through December 1997. A. Monthly mean number of ‘ōhi’a flowers per marked tree over three years with standard error bars (N = 92 trees). B. Monthly percentage of understory plant species with flowering peaks (N = 183 plants of 9 species).

Significant differences were found among months ($F_{11,1295} = 4.38, P < 0.001$), years ($F_{2,1295} = 16.74, P < 0.001$), and elevation categories ($F_{2,37} = 64.98, P < 0.001$), and also many of the higher-order interactions of these variables ($P < 0.05$). No strong pattern existed among consecutive months (Fig. 3a), but the highest densities occurred in 1996 (mean = 3.34 birds/ha) while 1995 and 1997 were very similar (mean = 2.72 and 2.61 birds/ha respectively). Elevation was such a significant factor because nearly the entire population (93%) resided above 1,700 m elevation. The highest average density occurred in the mid-elevation category, with a mean of 4.08 birds/ha (Fig. 3b). The high-elevation area had a mean of 2.69 birds/ha, and the low-elevation area had the lowest average at 1.04 birds/ha (Fig. 3b). When the ANCOVA was performed by adding the ‘ōhi’a flower variable to the four-way ANOVA, there was no significant effect of ‘ōhi’a flowers on ‘Ākohekohe densities ($F_{1,1292} = 0.17, P = 0.678$), at least at the scale of stations over which we measured these variables.

Among the other nectarivorous species, ‘Apapane densities were the highest, with an average of 14.42 birds/ha ± 0.29 SE (Fig. 3a). ‘Iiwi densities were 3.59 birds/ha ± 0.09 SE over the study area and lowest of the nonendangered species, while Hawai‘i ‘Amakihi had a mean of 11.82 birds/ha ± 0.23 SE. As for the ‘Ākohekohe, months and years were very significant ($P < 0.001$) for ‘Apapane, ‘Iiwi, and Hawai‘i ‘Amakihi in the four-way ANOVA. Concerning months, highest mean densities occurred in January for ‘Apapane and Hawai‘i ‘Amakihi, and in October for ‘Iiwi, although January had the

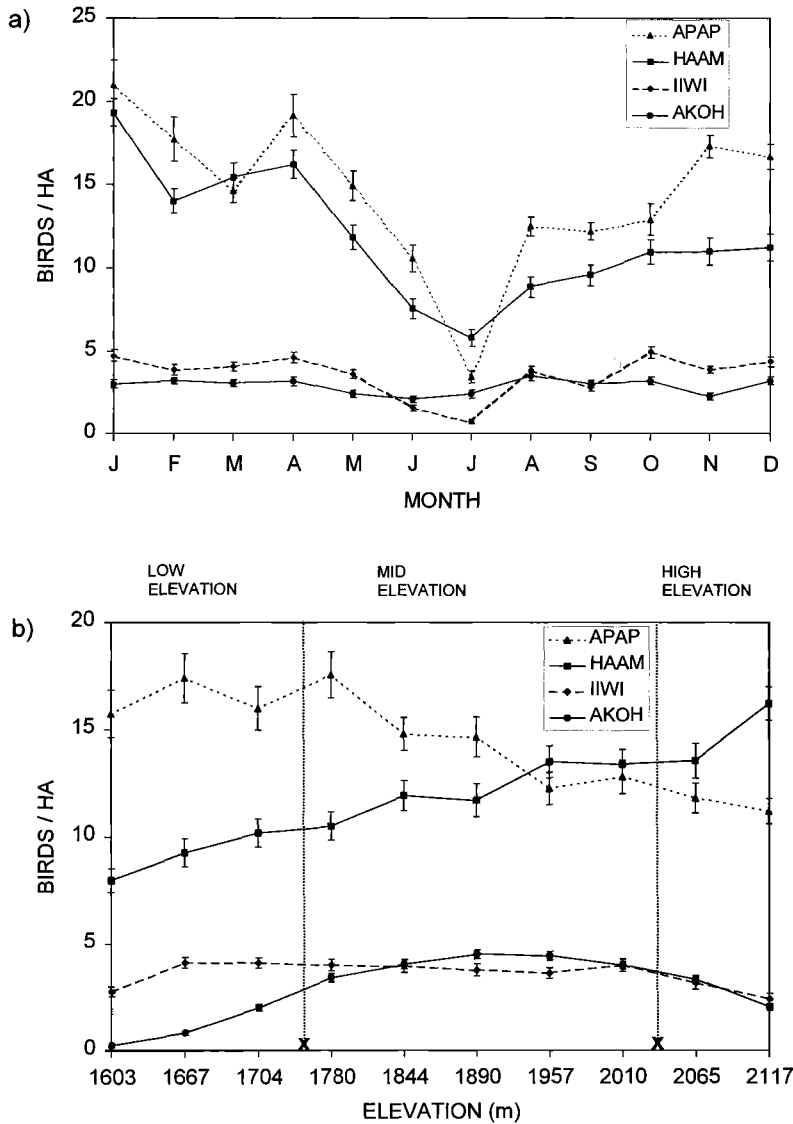


FIGURE 3. Mean bird density (birds/ha) and standard error bars for four nectarivorous Hawaiian honeycreepers (A) by month, and (B) by mean elevation.

second highest mean for that species. Lowest densities occurred in July for all three species (Fig. 3a). The highest densities occurred in 1997 for 'Apapane and in 1996 for Hawai'i 'Amakihi and 'I'iwi. Elevation category was also very significant in explaining variability in densities for all three species ('Apapane, $F_{2,37} = 10.25$, $P < 0.001$; 'I'iwi, $F_{2,37} = 6.61$, $P = 0.004$; Hawai'i 'Amakihi, $F_{2,37} = 25.83$, $P < 0.001$). Like the 'Akohekohe, the 'I'iwi had the highest mean density in the mid-elevation area, while the highest mean density occurred in the low-elevation area for the 'Apapane and in the high-

elevation area for the Hawai'i 'Amakihi (Fig. 3b). However, as in the 'Akohekohe analysis, the 'ohi'a flower variable was not significant in explaining any of the variability in bird densities for these species in these ANCOVAs ('Apapane, $F_{1,1292} = 0.01$, $P = 0.935$; 'I'iwi, $F_{1,1292} = 0.03$, $P = 0.854$; Hawai'i 'Amakihi, $F_{1,1292} = 1.44$, $P = 0.230$), at least at the scale of the station level.

However, using the 12 monthly averages over the entire time period for the number of 'ohi'a flowers and densities of each species, and performing Pearson's correlation, the correlation coefficients were positive and significant for

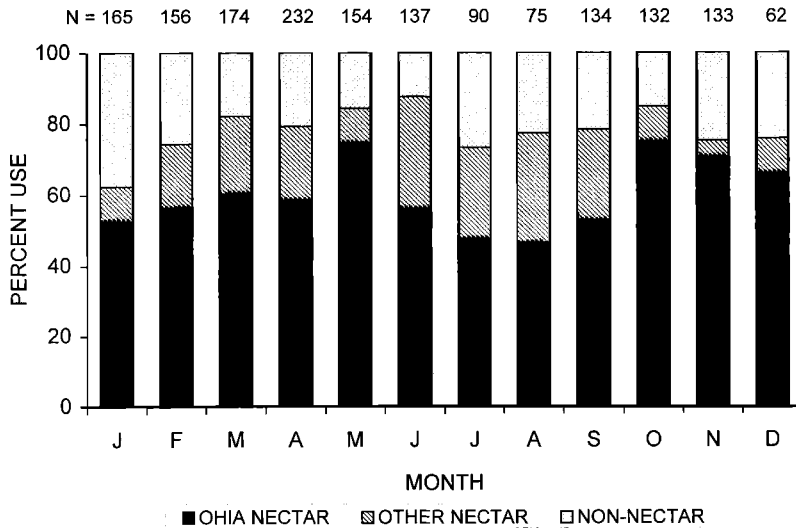


FIGURE 4. Percentage of monthly observations for 'Ākohekohe foraging, by food type: 'ōhi'a flowers, other flowers (subcanopy trees and shrubs listed in Methods), and substrates other than flowers. Sample sizes appear above graph.

three of the four species ('Ākohekohe, $r = 0.22$, $P = 0.484$; 'Apapane, $r = 0.81$, $P = 0.001$; 'I'iwi, $r = 0.58$, $P = 0.047$; Hawai'i 'Amakihi, $r = 0.86$, $P < 0.001$; $N = 12$ for each species). This implies that, at the scale of the entire study area, these species tended to move into the area when 'ōhi'a flowers were most abundant (in the winter), but this relationship does not hold up at the scale of individual stations (at least the way we measured 'ōhi'a flowers at each station by counting the same 2–3 trees per visit). When we ran the ANCOVA on these means, adding in elevation category, year, and the interactions, year effects were significant in three of the four species ($P < 0.005$ for all but 'I'iwi, for which $P > 0.05$, $N = 108$ per species), but the conclusions for mean bird densities versus mean 'ōhi'a flower abundance and elevation categories were similar, so we prefer to present the simpler models without year effects (see below).

These simpler ANCOVA models tested for an association between mean bird densities, mean 'ōhi'a flower abundance, elevation, and the interaction of elevation and 'ōhi'a flowers. For 'Apapane and 'I'iwi densities, 'ōhi'a flowers were significant ('Apapane, $F_{1,30} = 28.05$, $P < 0.001$; 'I'iwi, $F_{1,30} = 12.09$, $P = 0.002$; $N = 36$ per species), but elevation category and the interaction were not significant ($P > 0.05$), implying that over the scale of the entire study area, these birds are moving into the different elevation bands at the time when the 'ōhi'a flowers are most abundant there. (Recall that elevation was very significant in the five-way ANCOVA

for these species.) Hawai'i 'Amakihi densities also had a significant association with mean 'ōhi'a flowers ($F_{1,30} = 25.16$, $P < 0.001$), but there was a significant elevation effect, too ($F_{2,30} = 5.92$, $P = 0.007$), implying that something more complicated was happening. For the 'Ākohekohe, however, we found no association between mean densities and 'ōhi'a flower abundance even at the scale of the entire study area ($F_{1,30} = 1.54$, $P = 0.225$), but as in the four-way and five-way analyses, there was a very significant elevation effect ($F_{2,30} = 35.01$, $P < 0.001$). This suggests that, despite small fluctuations among months and years, 'Ākohekohe density was not associated with 'ōhi'a flower abundance as it was for the other three species. However, statistical power may be a problem, considering that the 'Ākohekohe had the lowest densities of the four species.

FORAGING

Foraging maneuvers of 'Ākohekohe ($N = 1,544$) were classified as probing (63%) into a flower or the base of a leaf cluster, gleaning (23%) primarily for invertebrates from the surface of leaves or bark, and biting (12%). Other maneuvers such as drilling, tapping, or hawking were less common and collectively composed $< 1\%$ of all foraging observations.

'Ōhi'a nectar was the primary food for 'Ākohekohe and constituted 50–75% of the monthly foraging observations throughout the year (Fig. 4). Nectar of many subcanopy trees and shrubs, particularly 'ākala, kanawao, and 'ōhelo, was

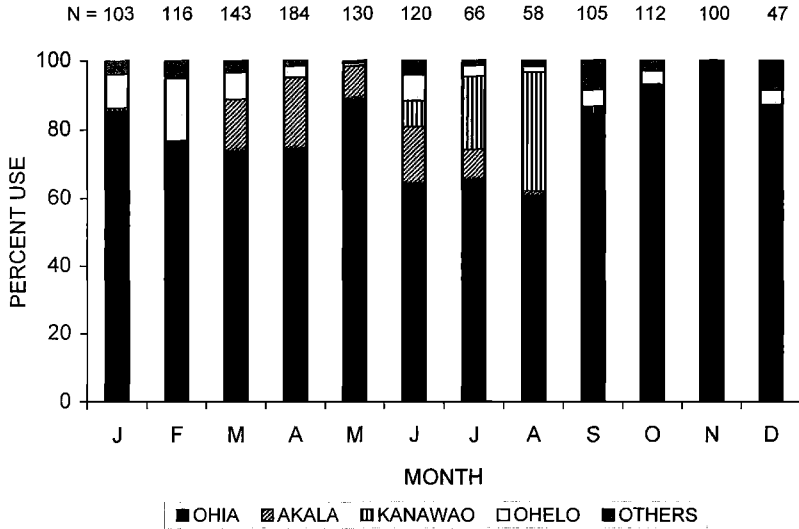


FIGURE 5. Percentage of monthly observations for 'Ākohekohe foraging on flowers. Sample sizes appear above graph.

also important in the diet (Fig. 5). Use of 'ākala and kanawao was seasonal and constituted up to 20–35% of 'Ākohekohe monthly foraging observations when 'ōhi'a bloom declined. 'Ākala was utilized most between March and July, and kanawao mainly between July and September. 'Ōhelo flowers were most numerous in winter and spring, but were used by 'Ākohekohe year-round. Other nectar sources included 'alani, kōlea, 'ōlapa, and pūkiawe, but these composed <10% of the monthly foraging observations (Fig. 5). 'Ākohekohe foraged in the canopy during 64% of all observations ($N = 1,956$) at a mean height of $9.5 \text{ m} \pm 0.90 \text{ SE}$. There were no significant differences between adults and juveniles or between males and females in monthly

comparisons of foraging height, location in the forest strata, food type, or plant species used.

'Ākohekohe use of nonnectar foods (entirely invertebrates) did not change among months (Fig. 4). 'Ākohekohe foraged for invertebrates primarily on 'ōhi'a (35–75% of observations per month) and secondarily on 'ōhelo and 'alani (Table 1). 'Ākala and kanawao, which were important sources of nectar for 'Ākohekohe, were infrequent sources of nonnectar foods.

'Apapane and 'I'iwi had foraging preferences for nectar similar to 'Ākohekohe, but Hawai'i 'Amakihi foraged more generally upon five species: 'ōhi'a, 'ākala, kanawao, 'ōhelo, and pūkiawe (Table 2). Visits to 'ōhi'a flowers composed only 26% of the total observations for Hawai'i

TABLE 1. PERCENT OF OBSERVATIONS OF 'ĀKOHEKOHE FORAGING ON SUBSTRATES OTHER THAN FLOWERS^a

Plant species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
'Ōhi'a (<i>Metrosideros polymorpha</i>)	42	35	39	69	75	59	63	71	48	65	48	73
'Ōhelo (<i>Vaccinium calycinum</i>)	27	38	35	13	4	6	21	0	10	5	3	7
'Alani (<i>Melicope</i> spp.)	8	13	10	0	4	6	4	29	17	5	15	13
Kōlea (<i>Myrsine lessertiana</i>)	5	5	10	10	4	12	0	0	10	0	0	0
'Ōlapa (<i>Cheirodendron trigynum</i>)	8	8	3	4	0	0	0	0	7	10	15	0
Pūkiawe (<i>Styphelia tameiameia</i>)	0	3	0	0	0	12	4	0	3	5	0	0
'Ākala (<i>Rubus hawaiiensis</i>)	0	0	0	0	8	6	8	0	0	0	0	0
Kanawao (<i>Broussasia arguta</i>)	3	0	0	2	0	0	0	0	0	5	9	0
Kāwa'u (<i>Ilex anomala</i>)	3	0	0	0	0	0	0	0	3	0	6	7
Pilo (<i>Coprosma ochracea</i>)	3	0	0	2	4	0	0	0	0	5	3	0
Nā'ena'e (<i>Dubautia</i> spp.)	0	0	3	0	0	0	0	0	0	0	0	0

^a By plant species and month from December 1994 through June 1997 ($N = 360$ observations).

TABLE 2. PERCENT OF OBSERVATIONS OF FOUR HAWAIIAN HONEYCREEPERS FORAGING ON FLOWERS

Plant species	‘Ākohekohe	‘Iwi	‘Apapane	Hawai‘i ‘Amakihi
‘Ōhi‘a	77	57	69	26
‘Ākala	8	22	9	25
Kanawao	6	4	12	15
‘Ōhelo	6	9	4	16
Pūkiawe	<0.5	0	4	11
‘Alani	2	0	1	5
‘Ōlapa	<0.5	2	1	0
Pilo	0	1	0	2
Lobelia	<0.5	3	0	0
<i>Stenogyne</i>	<0.5	2	0	0
Kōlea	<0.5	0	0	1
Kāwa‘u	<0.5	1	0	0
Sample size	1284	116	94	132

TABLE 3. PERCENT OF OBSERVATIONS OF FOUR HAWAIIAN HONEYCREEPERS FORAGING ON SUBSTRATES OTHER THAN FLOWERS, MAINLY FOR INVERTEBRATES

Plant species	‘Ākohekohe	‘Iwi	‘Apapane	Hawai‘i ‘Amakihi
‘Ōhi‘a	54	33	64	25
‘Ōhelo	17	40	16	19
Pilo	2	7	4	17
‘Ōlapa	6	13	0	6
Kōlea	5	7	8	2
‘Alani	9	0	8	4
‘Ākala	1	0	0	11
Pūkiawe	2	0	0	10
Kanawao	2	0	0	5
Kāwa‘u	2	0	0	1
Na‘ena‘e	<0.5	0	0	0
Sample size	360	15	25	100

‘Amakihi but 57–77% for the other three honeycreepers. ‘Ākala, kanawao, and ‘ōhelo were a substantial portion of all honeycreeper nectar diets. For nonnectar foraging, a wide variety of understory and canopy species were utilized, but ‘ōhi‘a and ‘ōhelo were visited the most by all honeycreepers (Table 3).

SEASONALITY OF BREEDING AND MOLT

‘Ākohekohe bred during the coldest, wettest time of the year, with the shortest day length, and when ‘ōhi‘a flowers were most abundant (Fig. 6). The breeding season lasted seven months with peak nesting between January and April. The number of nests active per month was

positively correlated with mean monthly abundance of ‘ōhi‘a flowers (Pearson’s $r = 0.66$, $P = 0.01$). The first nests were initiated in November, while ‘ōhi‘a bloom was increasing. Nesting peaked in March, two months after peak ‘ōhi‘a bloom in January, and continued through May. The percentage of active nests declined with declining ‘ōhi‘a bloom.

Juvenile ‘Ākohekohe were observed mainly between March and October (Fig. 7). The highest proportion of observations of juveniles occurred in May, two months after peak nesting when many understory plants were in flower. Observations on juveniles declined temporarily in July, coincident with the lowest densities of

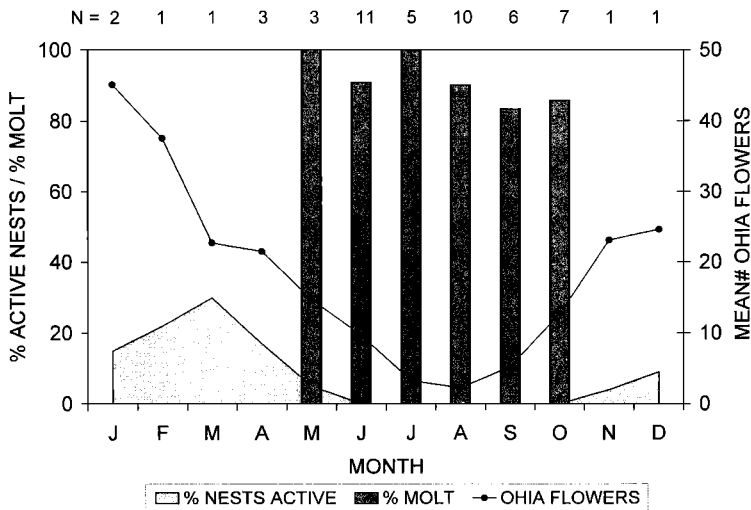


FIGURE 6. Timing by month of ‘ōhi‘a bloom, ‘Ākohekohe breeding, and ‘Ākohekohe molt. Line graph: mean number of ‘ōhi‘a flowers (N = 92 trees and 3,312 observations). Area graph: breeding activity measured by percentage of nests active/mo (N = 49 nests). Bar graph: molting period measured by percentage of birds ≥ second year in either flight or body molt (N = 38). Monthly sample sizes for molt appear above graph.

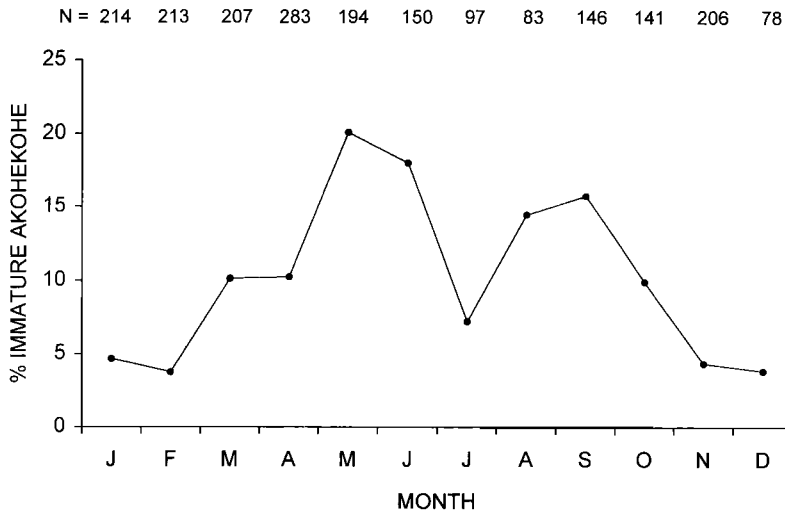


FIGURE 7. Monthly proportion of juvenile 'Ākohekohe seen during foraging observations. Sample sizes appear above graph.

'Apapane, 'I'iwi, and Hawai'i 'Amakihi, as well as the lowest flower availability (see Figs. 2, 3a).

'Ākohekohe molt began abruptly in May as nesting activity declined and was recorded at high frequencies through October (Fig. 6). In no case did individual birds exhibit breeding and molting conditions simultaneously, but there was slight breeding-molt overlap in May and June for the population overall. The percentage of birds in molt per month with years pooled was negatively correlated with mean monthly 'ōhi'a flowering (Pearson's $r = -0.82$, $P < 0.001$).

DISEASE

Mosquitoes were collected from oviposition pans only in the months of September, October, and November. During these three months, 16.5% of the pans ($N = 24/\text{mo}$) had mosquitoes. Larvae were found only below 1,650 m, with the exception of one pan at 2,100 m elevation in November 1997.

The prevalence of birds captured with physical signs of avian pox was low: 'Apapane 3.4% ($N = 147$), 'I'iwi 3.2% ($N = 62$), Maui Creeper (*Paroreomyza montana*) 1.0% ($N = 96$), and Hawai'i 'Amakihi 5.6% ($N = 268$) were caught with open or closed lesions on the legs, or missing toes. The most severe case was an 'Apapane that was missing its upper mandible in addition to having other lesions. Because bacterial infections from other causes can create similar lesions, we cannot be sure of the real prevalence of avian pox in this sample. No endangered or introduced bird species were found with poxlike lesions.

DISCUSSION

TEMPORAL AND SPATIAL ABUNDANCE OF 'ŌHI'A BLOOM AND HAWAIIAN HONEYCREEPERS

'Ākohekohe densities did not vary greatly by month nor correlate with abundance of 'ōhi'a flowers, suggesting that this species is relatively sedentary and that recruitment and loss rates are roughly equivalent. 'Ākohekohe are heavily dependent upon 'ōhi'a as a nectar source, but our data indicate that this species is able to maintain its population at high elevation during periods of depleted 'ōhi'a flowering. 'Ākohekohe are highly aggressive and displace 'Apapane, 'I'iwi, and Hawai'i 'Amakihi from foraging sites (Mountainspring and Scott 1985; Carothers 1986a,b; VanGelder 1996, VanGelder and Smith *this volume*). This dominance may enable 'Ākohekohe, especially adults, to remain at high elevation, whereas most juvenile 'Ākohekohe and individuals of other species are forced to depart. For example, during periods of depleted 'ōhi'a flowers, 'Ākohekohe actively defended patches of blooming 'ākala and kanawao (K. Berlin et al., pers. obs.). In contrast, monthly densities of 'Apapane, 'I'iwi, and Hawai'i 'Amakihi were temporally associated with 'ōhi'a bloom. Densities of all three species were lowest in July concurrent with the lowest availability of 'ōhi'a and understory flowers (see Figs. 2, 3a). These data suggest that a substantial proportion of nectar-feeding birds depart from high elevations and are consistent with the hypothesis that the birds follow 'ōhi'a flowering as it progresses downhill below the study area. The presence of juvenile 'Ākohekohe also declined temporarily in July,

and may indicate that juveniles, subordinate to adults (Carothers 1986a,b), must also disperse (Scott et al. 1986). On the island of Hawai‘i, ‘Apapane and ‘I‘iwi make daily long-distance foraging and roosting flights and seasonal altitudinal movements in response to fluctuating ‘ōhi‘a flowering (Baldwin 1953, MacMillen and Carpenter 1980, Ralph and Fancy 1995). Daily foraging and roosting flights do not occur on Maui to the extent found on Hawai‘i (Mountainspring and Scott 1985; Pacific Island Ecosystems Research Center, PIERC, unpubl. data), but the positive correlation of ‘ōhi‘a flowering with densities of all nonendangered nectarivorous birds supports the hypothesis of seasonal altitudinal movements on Maui.

FORAGING

‘Ōhi‘a nectar was the food source most frequently exploited by ‘Ākohekohe (Fig. 4). Even in summer months when ‘ōhi‘a flowers were scarce, use of ‘ōhi‘a decreased only slightly. ‘Ākala and kanawao flowered most heavily during spring and summer, respectively, coincident with the period of declining or low ‘ōhi‘a bloom. Alternate food sources such as ‘ākala and kanawao were used frequently in summer months, although their use remained secondary to ‘ōhi‘a. In two other studies, ‘alani and kōlea were the main alternate sources of nectar for ‘Ākohekohe during spring and fall months (VanGelder 1996, VanGelder and Smith *this volume*; H. Baker and P. Baker, unpubl. data). Native lobelias (Campanulaceae) have also been noted as a nectar source for many Hawaiian birds (Spieth 1966, Lammers and Freeman 1986). Lobelias in our study area bloomed from summer through fall (PIERC, unpubl. data), producing nectar for honeycreepers when the high-elevation ‘ōhi‘a bloom declined. Because a variety of flowering understory plants supplement the diets of ‘Ākohekohe and other honeycreepers, habitats must therefore contain a diversity of these plants to maintain populations of nectarivorous birds.

Our study did not show any age- or sex-related differences in ‘Ākohekohe foraging preferences. However, J. Carothers (*this volume*) recorded that immature ‘Ākohekohe fed less frequently on ‘ōhi‘a nectar than did adult ‘Ākohekohe, and more often on arthropods. He attributed this difference to the nutritional need of immatures for a high-protein diet during the early postfledging stage of development. We cannot say whether the difference between our results and Carothers’ can be explained by differences in methodology or the habitats studied.

‘Apapane and ‘I‘iwi had similar foraging preferences to ‘Ākohekohe, confirming prior ob-

servations of interspecific competition among these species (Mountainspring and Scott 1985; Carothers 1986a,b). ‘Ākohekohe dominate ‘Apapane, ‘I‘iwi, and Hawai‘i ‘Amakihi and often defend food sources from these species (Carothers 1986a,b). Hawai‘i ‘Amakihi foraged more generally and did not show a strong preference for any particular plant species or food type. Baldwin (1953) also found that Hawai‘i ‘Amakihi forage more generally, and Carothers (1986a) noted that Hawai‘i ‘Amakihi did not forage extensively in ‘ōhi‘a canopies and were not involved in as many interspecific interactions as were ‘Ākohekohe, ‘Apapane, or ‘I‘iwi. Hawai‘i ‘Amakihi are at the bottom of the nectarivorous hierarchy, and ‘Ākohekohe, ‘Apapane, and ‘I‘iwi probably prevent them from utilizing higher-quality nectar sources (Pimm and Pimm 1982; Carothers 1986a,b).

SEASONALITY OF BREEDING AND MOLT

‘Ākohekohe initiated nesting during the coolest, wettest time of the year when the photoperiod was decreasing and ‘ōhi‘a bloom was increasing. Decreasing daylight and heavy rainfall are considered to be an unfavorable time for plants to flower and for birds to breed, and in most humid tropical forests these events occur during the dry period (Foster 1974, Frankie et al. 1974, Stiles 1978). However, hummingbirds in Costa Rica breed during the coolest, wettest time of the year when the greatest numbers of ornithophilous flowers are in bloom at high elevations (Wolf et al. 1976, Stiles 1985).

‘Ākohekohe nesting was positively correlated with ‘ōhi‘a bloom, although peak nesting lagged two months behind peak bloom. ‘Ōhi‘a flowering has been associated with the timing of breeding of nectarivorous birds on the island of Hawai‘i, but the timing and sequence of these peaks is variable (Baldwin 1953, Ralph and Fancy 1994b). Along the western periphery of native forest on eastern Maui and at a slightly lower elevation, ‘ōhi‘a bloom peaked two months after peak ‘Ākohekohe nesting (VanGelder 1996, VanGelder and Smith *this volume*). We question whether peak bloom at this site corresponded instead with the flowering of glabrous ‘ōhi‘a, which are more common at mid-elevations than the pubescent varieties predominating at our site (Berlin et al. 2000). On the island of Hawai‘i, breeding of ‘Apapane and ‘I‘iwi coincided with ‘ōhi‘a bloom (Ralph and Fancy 1994b).

As with most Hawaiian honeycreepers (Ralph and Fancy 1994b), molt in ‘Ākohekohe followed breeding (Simon et al. 1998). Molt did not coincide with flowering ‘ōhi‘a, but instead was initiated while many understory plants were flow-

ering. Flowering of these understory species in spring and summer months may provide adequate resources during the energetically costly molting period and allow populations to maintain an extended breeding season as 'ōhi'a sources diminish.

IMPLICATIONS FOR CONSERVATION

'Ōhi'a is the single most important element in the habitat of the 'Ākohekohe and other nectarivorous Hawaiian honeycreepers at Hanawī. It is the main structural component of the forest community (Jacobi 1989) and provides the principal source of food (Carothers 1986a, VanGelder and Smith *this volume*) and nest sites (VanGelder and Smith *this volume*; PIERC, unpubl. data; this paper) for these birds. In this paper, we have also demonstrated that for the 'Ākohekohe, 'ōhi'a bloom probably influences timing of breeding and molt. The health and extent of 'ōhi'a populations is therefore of concern for the survival of Hawaiian honeycreepers. The phenomenon of 'ōhi'a dieback—when a stand of 'ōhi'a dies simultaneously and is replaced by a new cohort of 'ōhi'a—has been much studied (Mueller-Dombois 1980, Jacobi et al. 1988) and dictates the need for large reserves to sustain extensive forests of 'ōhi'a in a landscape of patchy dieback and cyclical succession. Reserve design must also take into account the variation with elevation in phenology of 'ōhi'a bloom (Berlin et al. 2000). An elevational gradient within a reserve increases the seasonal availability of 'ōhi'a flowers, particularly for 'Apapane and 'I'iwi which travel greater distances between patches of bloom.

When 'ōhi'a bloom declines in the summer, nectarivorous birds switch to other sources of nectar and many emigrate, perhaps because they are denied access to limited resources by 'Ākohekohe or are even driven out by 'Ākohekohe. The switch to foraging on understory plants underscores their importance in two respects, first as an alternate source of food, and second as a means of lessening emigration. Prior to the introduction of avian malaria, avian pox, and disease-transmitting mosquitoes, birds could emigrate from higher elevations with few risks and follow the summer 'ōhi'a bloom downslope (as proposed in van Riper et al. 1982). At present, such movements pose great risks of exposure to avian diseases so prevalent below 1,500 m. Indeed on the island of Hawai'i, epizootics happen during fall (van Riper et al. 1986; C. Atkinson, pers. comm.). On Hawai'i and at our Maui site, this problem is exacerbated by the upslope movement of mosquitoes during the fall (van

Riper et al. 1986; D. LaPointe, pers. comm.). A further consideration is that some populations of 'Apapane and Hawai'i 'Amakihi have greater resistance to avian malaria (Jarvi et al. *this volume*), and the movement of infected individuals to higher elevations may facilitate the transmission of diseases. We never captured any 'Ākohekohe with physical signs of disease. However, Feldman et al. (1995) detected avian malaria through blood sampling of one bird above 2,000 m elevation. The low prevalence of disease detected in 'Ākohekohe coupled with the species' confinement to elevations above 1,300 m (Scott et al. 1986) may indicate high susceptibility and mortality of infected 'Ākohekohe.

The best action to increase 'Ākohekohe populations at elevations above the lethal mosquito zone is to restore the vegetation of the birds' habitat to its former complexity and diversity. Forest understory across the east Maui watershed has been damaged to varying degrees by feral pigs (*Sus scrofa*), which in places have removed the understory and caused severe erosion. Enclosures where pigs have been removed have substantially recovered an understory of tree seedlings, 'ākala, kanawao, lobelias, and ferns. Eight rare lobelia species found at Hanawī presently grow epiphytically or clinging to cliff faces where they survived beyond the reach of pigs. In protected habitats, some of these lobelias are now growing on the forest floor, a positive sign for habitat recovery. Recovery of understory plants increases the year-round nectar supply for 'Ākohekohe and other honeycreepers. We emphasize that removal of pigs and restoration of the forest understory will provide food for birds that otherwise, during the summer and fall, may be forced to emigrate, never to return.

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