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# DEMOGRAPHY AND MOVEMENTS OF APAPANE AND IIWI IN HAWAII[1]

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*Abstract.* Density, annual survival, philopatry, and movements of two species of Hawaiian honeycreepers, the Apapane (*Himatione sanguinea*) and the Iiwi (*Vestiaria coccinea*), were studied at four sites on the island of Hawaii. Highest densities of both species occurred during the breeding season and were highly correlated with flowering by *Metrosideros*. Annual survival probability (the complement of which includes permanent emigration) was 0.13 ± 0.07 for hatching-year (HY) Apapane, 0.72 ± 0.11 for adult Apapane, 0.09 ± 0.05 for HY Iiwi, and 0.55 ± 0.12 for adult Iiwi. Survival of adult Iiwi was the lowest of six species of native Hawaiian forest birds and may be related to their high susceptibility to avian disease. Small resident populations of both species remained on our study sites throughout the year, but 78% of 1,361 Apapane and 82% of 891 Iiwi were never captured or seen after their initial capture. Widespread movements of Apapane and Iiwi in response to the seasonal and patchy availability of *Metrosideros* nectar have important implications for disease transmission since Apapane are the primary carrier of avian malaria and avian pox in Hawaii, and Iiwi appear to be highly susceptible to mortality from malaria.

*Key words: Apapane; Iiwi;* Himatione sanguinea; Vestiaria coccinea; *demography; survival; movements; Hawaii.*

## INTRODUCTION

The Apapane (*Himatione sanguinea*) and Iiwi (*Vestiaria coccinea*) are locally abundant species of Hawaiian honeycreeper (Fringillidae: Drepanidinae) found in mesic and wet forests of the Hawaiian Islands. The Apapane is the most abundant honeycreeper, with more than 1,000,000 birds on the island of Hawaii (Scott et al. 1986). The Iiwi was once one of the most abundant and widely distributed honeycreepers (Perkins 1903). Now, it is rare or absent on Lanai, Molokai, and Oahu, and during the past 50 years has disappeared from several areas on other islands (Baldwin 1953; Scott et al. 1986; National Biological Service, unpubl. data). Neither species has undergone any important geographical differentiation, and for both the nominate race was previously found on all of the main Hawaiian islands (Berger 1981).

Both species are well known for their long, high flights over the forests in search of flowers of the ohia (*Metrosideros polymorpha*) tree, their primary food source (Perkins 1903, Baldwin 1953, Pimm and Pimm 1982). *Metrosideros* flowering does not appear to be regulated by environmental cues, and patches of ohia forest at peak flowering can be found at any time of year in different areas of the forest (Perkins 1903, Baldwin 1953, Bridges et al. 1981). Perkins (1903:407) noted that Apapane and Iiwi "pass over a wide area in search of the ohia flowers, as well as making regular migrations when the flowering season demands." Baldwin (1953) found that during the nesting season, Apapane and Iiwi had loosely-held nesting territories but sometimes left the nesting area altogether on daily foraging flights. Baldwin thought that this allowed "wide foraging by the breeding birds at relatively great distances from the nest." Eddinger (1970) found that Apapane and Iiwi on Kauai defended small territories around the nest and foraged near the territory during the breeding season. Baldwin (1953) found pronounced seasonal population shifts by both species that corresponded closely with flowering periods of ohia.

MacMillen and Carpenter (1980:31) observed evening flights of Apapane and Iiwi at Keauhou Ranch, Hawaii, and thought that both species made daily flights from foraging areas to a common roosting area near Kulani Cone. They noted that evening flights of Apapane and Iiwi during June–August "generally commenced between 16:00 and 17:00 and consisted of a nearly continuous stream of individuals and small groups

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passing overhead in the same direction for 2 hr." They thought that flights began during spring and ceased during fall and winter.

As part of a larger study of population dynamics and foraging ecology of Hawaiian forest birds, we studied Apapane and Iiwi on Hawaii to provide information on the demography and movements of these common but poorly known species. We report here on densities, philopatry, and survival of Apapane and Iiwi on Hawaii and their movements in relation to the seasonal availability of ohia nectar.

## STUDY AREAS AND METHODS

We studied demography and movements of Apapane and Iiwi on the island of Hawaii between November 1976 and January 1982 at four study areas: Keauhou Ranch (19°31'N, 155°20'W; 1,740 m elevation), Kilauea Forest (19°31'N, 155°19'W; 1,630 m), Hamakua (19°47'N, 155°20'W; 1,770 m), and Kau Forest (19°13'N, 155°39'W; 1,750 m). Vegetation of the study areas was described in Mueller-Dombois et al. (1981) and Ralph and Fancy (1994a).

We estimated the density of Apapane and Iiwi using the variable circular-plot method (Reynolds et al. 1980) during 8-min counts, as described in Ralph (1981) and Ralph and Fancy (1994b). We determined densities with the program VCP2 (Roeder et al. 1987; E. Garton, unpubl. data), and we compared densities among study sites and month by two-way ANOVA.

We captured birds in mist nets at the Keauhou Ranch ($n$ = 62,006 net hr, November 1976 to January 1982) and Kilauea Forest ($n$ = 16,958 net hr, April 1978 to November 1979) study areas, and processed birds as described by Ralph and Fancy (1994b). Sex was determined by presence of a brood patch or cloacal protuberance (Ralph et al. 1993). We identified juvenile birds on the basis of plumage characteristics (Fancy et al. 1993), skull ossification (Pyle et al. 1987), and behavior. In this paper, we define juveniles as hatching-year (HY, birds in their first calendar year of life) and second-year birds retaining juvenal feathers. All birds captured were marked with a unique combination of three colored plastic bands and a numbered aluminum band. We conducted monthly searches for color-marked birds at the Keauhou Ranch and Kilauea Forest study sites as described in Ralph and Fancy (1994a).

We estimated age-specific annual survival of Apapane and Iiwi at the Keauhou Ranch site from capture-recapture data and resightings of color-banded birds with model A2X of program JOLLYAGE (Pollock et al. 1990), which allows time-specific capture and survival probabilities and incorporates data from resightings. The complement of survival probability includes both mortality and permanent emigration. We selected a four-month sampling period each year from May through August, 1976–1981, based on goodness-of-fit tests from preliminary runs. Birds captured or resighted during the eight-month period from September through April were coded as resightings and used to calculate survival probabilities (Pollock et al. 1990). Survival probability for Apapane was calculated from 1,584 captures and resightings of 201 after-hatching-year (AHY) and 228 HY Apapane that were captured between May and August in at least one year. Survival probability for Iiwi was similarly calculated from 1,238 captures and resightings of 123 AHY and 212 HY Iiwi.

Movement patterns of Apapane and Iiwi were studied between February 1978 and August 1981 at the Keauhou Ranch and Kilauea Forest study sites, and at 11 sites along the Stainback Highway (Fig. 1) ranging in elevation from sea level to 1,400 m. The number of individuals of each species passing through a 90° cone centered above and with its apex at the observer, and each bird's direction of travel to the nearest 10°, was recorded by two individuals during each of 1,580 20-min sampling periods distributed throughout the study. Surveys were conducted between 06:00 and 19:00 hr; 990 of the surveys (63%) were completed before 09:00 hr or after 16:00 hr.

We compared distributions of flight directions of Apapane and Iiwi between two seasons: Peak bloom (April–June), when ohia nectar at our study sites was most available (Ralph and Fancy 1994a), and Minimum bloom (October–December). Ohia bloom was quantified by monthly counts of ohia flowers at each site as described by Ralph and Fancy (1994a). For each season, we assigned each survey to one of four time periods: 06:00–09:00 hr, 09:01–13:00 hr, 13:01–17:00 hr, or 17:01–19:00 hr. For each season and time period, we grouped flight directions into eight 45° intervals and tested for randomness of flight directions with a Chi-square test (Zar 1984:441) by comparing the number of birds within each interval to the expected number.

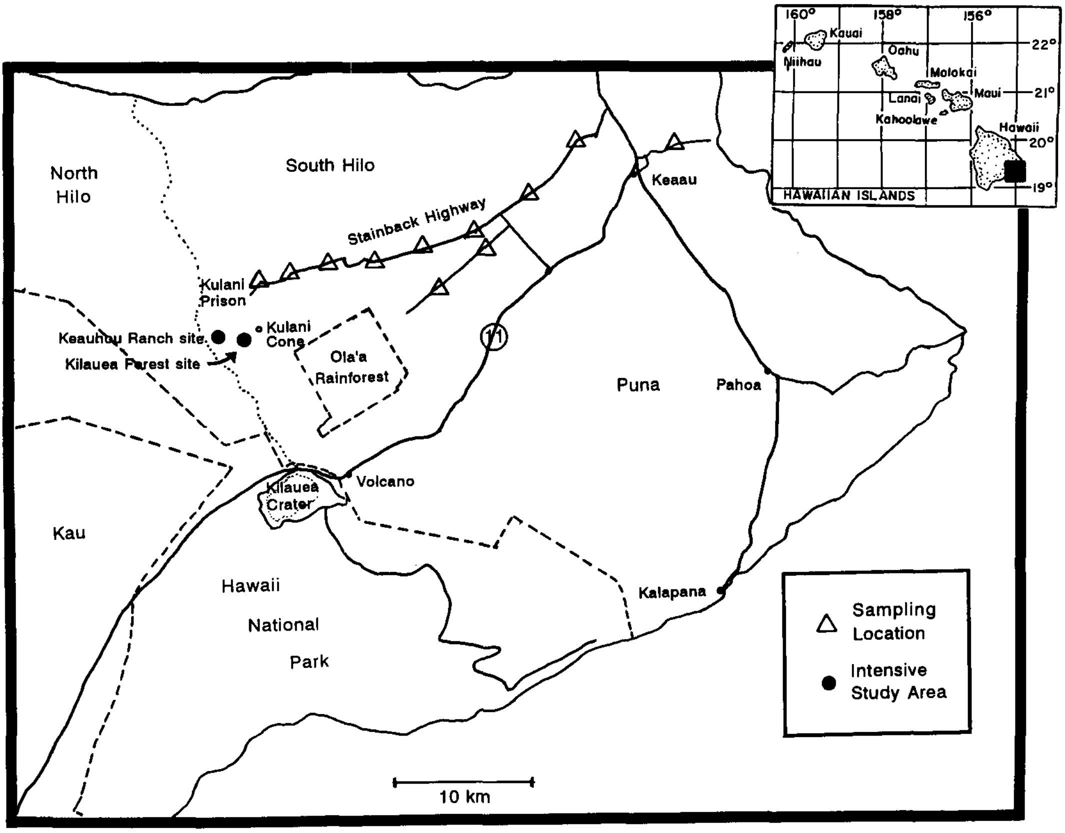

FIGURE 1. Location of the Keauhou Ranch and Kilauea Forest study areas, and 11 sites along the Stainback Highway where movements of Apapane and Iiwi were studied.

## RESULTS

### DENSITY

Apapane density estimates differed greatly among months ($F_{11,59}$ = 3.48, $P$ = 0.001) and study sites ($F_{3,59}$ = 5.31, $P$ = 0.003, Tables 1, 2). Highest densities of Apapane were usually recorded during March–June each year, coinciding with the start of the breeding season and fledging of young (Ralph and Fancy 1994a). Monthly densities were correlated with availability of ohia flowers at both Keauhou Ranch ($r$ = 0.26, $n$ = 55, $P$ = 0.05) and Kilauea Forest ($r$ = 0.47, $n$ = 20, $P$ = 0.04). Mean monthly density ± SE (birds/ha) of Apapane was 12.74 ± 0.77 at Keauhou Ranch, 13.68 ± 1.63 at Kilauea Forest, 15.63 ± 4.04 at Kau Forest, and 7.15 ± 2.10 at Hamakua. Mean monthly densities at the Hamakua study area were lower (Tukey's test, $P$ < 0.05) than those at Kilauea Forest and Kau Forest. We examined the overall trend in Apapane densities at Keauhou Ranch over the five years of study and found that density declined at a monthly rate of 0.175 ± 0.04 SE Apapane/ha between July 1977 and January 1982 (regression, $n$ = 55, $P$ = 0.0001).

Iiwi densities also varied among months ($F_{11,60}$ = 7.82, $P$ = 0.0001) and study sties ($F_{3,60}$ = 9.94, $P$ = 0.0001, Tables 1, 2). Iiwi densities usually peaked during March–June each year (Tables 1, 2), and were highly correlated with ohia flowering at Keauhou Ranch ($r$ = 0.50, $n$ = 55, $P$ = 0.0001) and Kilauea Forest ($r$ = 0.68, $n$ = 21, $P$ = 0.0007). Mean monthly density ± SE (birds/ha) of Iiwi was 3.71 ± 0.37 at Keauhou Ranch, 2.25 ± 0.33 at Kilauea Forest, 5.86 ± 1.40 at Kau Forest, and 6.80 ± 2.89 at Hamakua. Mean monthly densities at the Hamakua study area were higher (Tukey's test, $P$ < 0.05) than those at Keauhou Ranch and Kilauea Forest, and densities at Kau Forest were higher than those at Kilauea Forest.

TABLE 1. Density (birds/ha) of Apapane and Iiwi at the Keauhou Ranch and Kilauea Forest study areas, island of Hawaii, 1977–1982.

| | | Keauhou Ranch | | | | | Kilauea Forest | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Number of stations | Apapane | | Iiwi | | Number of stations | Apapane | | Iiwi | |
| Month | Year | | Mean | SE | Mean | SE | | Mean | SE | Mean | SE |
| Jul | 77 | 25 | 17.14 | 6.83 | 6.63 | 4.03 | | | | | |
| Aug | 77 | 25 | 26.54 | 8.05 | 4.63 | 3.16 | | | | | |
| Sep | 77 | 25 | 28.08 | 8.61 | 4.77 | 2.36 | | | | | |
| Oct | 77 | 25 | 8.99 | 3.04 | 11.33 | 4.74 | | | | | |
| Nov | 77 | 25 | 18.32 | 5.46 | 4.82 | 2.07 | | | | | |
| Dec | 77 | 25 | 23.84 | 8.68 | 6.24 | 2.65 | | | | | |
| Jan | 78 | 25 | 18.96 | 5.68 | 2.78 | 1.14 | | | | | |
| Feb | 78 | 25 | 20.59 | 6.47 | 5.68 | 2.05 | | | | | |
| Mar | 78 | 50 | 13.12 | 3.24 | 4.24 | 1.12 | | | | | |
| Apr | 78 | 50 | 28.06 | 8.54 | 6.54 | 1.80 | 50 | 16.82 | 3.12 | 7.00 | 1.96 |
| May | 78 | 75 | 19.88 | 4.57 | 4.11 | 1.00 | 49 | 10.27 | 1.82 | 3.54 | 0.99 |
| Jun | 78 | 75 | 7.56 | 1.37 | 3.60 | 0.83 | 50 | 24.21 | 5.81 | 4.93 | 1.79 |
| Jul | 78 | 62 | 7.32 | 2.51 | 4.11 | 1.34 | 75 | 3.40 | 1.06 | 1.79 | 0.47 |
| Aug | 78 | 75 | 7.09 | 1.43 | 2.66 | 0.77 | 75 | 5.70 | 1.02 | 2.19 | 0.61 |
| Sep | 78 | 76 | 7.59 | 1.33 | 2.33 | 0.58 | 75 | 8.55 | 1.86 | 2.67 | 0.72 |
| Oct | 78 | 62 | 6.08 | 1.32 | 2.19 | 0.64 | 75 | 13.85 | 2.41 | 1.46 | 0.44 |
| Nov | 78 | 75 | 10.39 | 1.96 | 2.16 | 0.62 | 75 | 18.39 | 3.42 | 1.56 | 0.54 |
| Dec | 78 | 25 | 11.87 | 4.81 | 1.79 | 1.09 | 44 | 9.85 | 2.10 | 1.73 | 0.73 |
| Jan | 79 | 75 | 10.27 | 1.75 | 2.10 | 0.54 | 27 | 20.98 | 7.86 | 0.47 | 0.35 |
| Feb | 79 | 75 | 9.56 | 1.84 | 1.30 | 0.31 | 74 | 32.14 | 6.16 | 1.46 | 0.70 |
| Mar | 79 | 81 | 14.88 | 2.55 | 2.60 | 0.76 | 50 | 20.99 | 4.02 | 2.04 | 1.45 |
| Apr | 79 | 100 | 24.44 | 4.31 | 4.70 | 1.09 | 87 | 33.35 | 5.82 | 2.49 | 0.97 |
| May | 79 | 75 | 10.84 | 1.81 | 2.59 | 0.66 | 75 | 22.83 | 4.43 | 1.75 | 0.62 |
| Jun | 79 | 101 | 14.76 | 2.34 | 5.56 | 1.29 | 75 | 13.22 | 2.58 | 2.06 | 0.83 |
| Jul | 79 | 75 | 12.09 | 2.90 | 2.83 | 0.94 | 75 | 4.84 | 1.05 | 0.68 | 0.30 |
| Aug | 79 | 72 | 12.11 | 3.36 | 3.72 | 1.14 | 75 | 8.51 | 2.05 | 1.88 | 0.58 |
| Sep | 79 | 79 | 5.23 | 1.07 | 0.62 | 0.35 | 75 | 10.99 | 2.11 | 1.04 | 0.48 |
| Oct | 79 | 76 | 8.26 | 1.52 | 0.72 | 0.30 | 75 | 8.76 | 2.02 | 0.16 | 0.11 |
| Nov | 79 | 87 | 9.49 | 2.51 | 0.98 | 0.34 | 75 | 17.11 | 2.98 | 1.10 | 0.41 |
| Dec | 79 | 87 | 14.16 | 2.40 | 2.42 | 0.62 | | | | | |
| Jan | 80 | 96 | 12.44 | 2.03 | 2.93 | 0.84 | | | | | |
| Feb | 80 | 88 | 19.73 | 4.14 | 5.30 | 1.60 | 162 | 11.87 | 3.43 | 5.07 | 1.05 |
| Mar | 80 | 76 | 12.11 | 2.83 | 4.40 | 1.12 | | | | | |
| Apr | 80 | 87 | 14.12 | 2.66 | 9.23 | 2.19 | | | | | |
| May | 80 | 125 | 17.46 | 2.51 | 15.97 | 3.81 | 138 | 11.46 | 3.37 | 5.98 | 1.45 |
| Jun | 80 | 75 | 15.04 | 2.88 | 8.89 | 2.46 | | | | | |
| Jul | 80 | 73 | 9.75 | 3.53 | 4.52 | 1.62 | | | | | |
| Aug | 80 | 100 | 8.44 | 1.49 | 5.20 | 1.73 | 150 | 1.74 | 0.47 | 0.30 | 0.14 |
| Sep | 80 | 124 | 8.08 | 1.59 | 1.47 | 0.47 | | | | | |
| Oct | 80 | 25 | 10.39 | 4.90 | 0.45 | 0.30 | 76 | 7.04 | 1.43 | 2.64 | 1.32 |
| Nov | 80 | 63 | 9.16 | 2.02 | 3.60 | 1.50 | 50 | | | 1.88 | 0.93 |
| Dec | 80 | 49 | 10.86 | 2.38 | 2.01 | 0.72 | | | | | |
| Jan | 81 | 88 | 9.27 | 1.93 | 2.78 | 0.90 | 63 | 15.03 | 2.64 | 0.94 | 0.37 |
| Feb | 81 | 75 | 13.75 | 2.96 | 2.11 | 0.56 | 87 | 3.88 | 1.40 | 2.01 | 0.58 |
| Mar | 81 | 100 | 8.67 | 1.12 | 1.94 | 0.50 | | | | | |
| Apr | 81 | 50 | 8.82 | 1.58 | 3.05 | 1.46 | | | | | |
| May | 81 | 75 | 7.84 | 1.10 | 3.24 | 0.99 | | | | | |
| Jun | 81 | 75 | 8.16 | 1.28 | 1.43 | 0.54 | | | | | |
| Jul | 81 | 75 | 11.13 | 1.94 | 2.96 | 1.00 | | | | | |
| Aug | 81 | 75 | 10.85 | 2.28 | 2.01 | 0.67 | | | | | |
| Sep | 81 | 75 | 9.09 | 1.48 | 0.95 | 0.39 | | | | | |
| Oct | 81 | 75 | 6.95 | 1.43 | 1.40 | 0.46 | | | | | |
| Nov | 81 | 75 | 12.80 | 2.18 | 3.16 | 1.02 | | | | | |
| Dec | 81 | 75 | 9.45 | 1.76 | 2.53 | 0.90 | | | | | |
| Jan | 82 | 61 | 8.80 | 1.57 | 1.70 | 0.52 | | | | | |

TABLE 2. Density (birds/ha) of Apapane and Iiwi at the Hamakua and Kau Forest study areas, island of Hawaii, 1979–1980.

| | | Hamakua study area | | | | | Kau Forest study area | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Number of stations | Apapane | | Iiwi | | Number of stations | Apapane | | Iiwi | |
| Month | Year | | Mean | SE | Mean | SE | | Mean | SE | Mean | SE |
| Feb | 79 | 45 | 10.47 | 2.80 | 9.41 | 2.66 | | | | | |
| Mar | 79 | | | | | | 45 | 31.58 | 7.53 | 13.29 | 3.19 |
| May | 79 | 30 | 14.96 | 4.02 | 24.38 | 9.42 | | | | | |
| Jun | 79 | | | | | | 45 | 13.13 | 3.24 | 5.65 | 1.81 |
| Aug | 79 | 45 | 2.26 | 0.95 | 0.28 | 0.12 | | | | | |
| Sep | 79 | | | | | | 45 | 8.49 | 2.60 | 3.59 | 0.89 |
| Dec | 79 | 40 | 4.63 | 1.12 | 2.01 | 0.50 | | | | | |
| Jan | 80 | | | | | | 45 | 14.75 | 3.75 | 4.89 | 1.10 |
| Mar | 80 | 15 | 11.21 | 6.41 | 17.14 | 6.15 | | | | | |
| Apr | 80 | 15 | 0.30 | 0.12 | 0.31 | 0.09 | 30 | 15.78 | 3.25 | 10.56 | 3.71 |
| Jun | 80 | 38 | 1.15 | 0.46 | 0.66 | 0.24 | | | | | |
| Jul | 80 | | | | | | 40 | 2.57 | 1.73 | 2.33 | 1.24 |
| Aug | 80 | 45 | 2.56 | 0.99 | 1.07 | 0.47 | | | | | |
| Oct | 80 | | | | | | 45 | 5.17 | 1.62 | 2.67 | 1.24 |
| Dec | 80 | 38 | 16.81 | 4.01 | 5.96 | 1.82 | 40 | 33.60 | 6.22 | 3.90 | 1.44 |

Monthly densities of Iiwi at Keauhou Ranch declined at a monthly rate of 0.048 ± 0.02 SE Iiwi/ha between July 1977 and January 1982 (regression, $n = 55$, $P = 0.038$).

## CAPTURE RATES AND PREVALENCE OF AVIAN POX

Highest capture rates occurred during the breeding season (Ralph and Fancy 1994a) in March–May for Apapane and April–May for Iiwi (Fig. 2). Monthly capture rates at Keauhou Ranch for all years combined were highly correlated with monthly densities for both Apapane ($r = 0.547$, $n = 55$, $P = 0.0001$) and Iiwi ($r = 0.517$, $n = 55$, $P = 0.0001$). At Kilauea Forest, monthly capture rates were correlated with densities for Iiwi ($r = 0.517$, $n = 20$, $P = 0.020$), but not for Apapane ($r = 0.071$, $n = 20$, $P = 0.77$).

We did not take blood samples of birds we captured to test for prevalence of avian malaria, but we did inspect the bills and legs of all birds that we captured for crusty, scabby swellings characteristic of avian pox. Of the 1,361 Apapane we captured, five had missing digits, five others (all captured in November and December) had pox-like lesions on their feet, one had a pox-like lesion on its lower mandible, and another was missing its lower mandible. Two of the 891 Iiwi that we captured were missing digits.

## SURVIVAL PROBABILITY

Mean survival probability of juvenile Apapane (0.13 ± 0.07) was lower ($\chi^2 = 60.7$, df = 3, $P < 0.001$) than that of adults (0.72 ± 0.11). Iiwi juveniles also had lower survival (0.09 ± 0.05) than did adults (0.55 ± 0.12); $\chi^2 = 52.2$, df = 3, $P < 0.001$). The probability of resighting an individual in a given year, if that individual was alive and in the study area, was 0.07 ± 0.02 for Apapane and 0.22 ± 0.06 for Iiwi.

## SITE FIDELITY

Of the 1,361 Apapane that we captured, 78% were never captured or resighted again. However, some individuals appeared to be resident breeders on our study sites. For example, we observed 22 Apapane in at least five different months during the study. The number of months between captures or resightings exceeded four years for 16 Apapane, three years for an additional 23 Apapane, and two years for another 47 Apapane. With the exception of one female with an active brood patch, all of the Apapane that were captured at least four years apart were males that were in breeding condition at least once.

Iiwi had higher fidelity to the study site than did Apapane. Of the 891 Iiwi captured, 82% were never seen or captured again, but one Iiwi was captured or resighted in 29 different months, another was observed in 22 months, and three others were each observed in more than 10 months. The number of months between captures or resightings exceeded five years for three Iiwi, and three years for an additional nine Iiwi. All of the Iiwi that remained on the grid for at least four

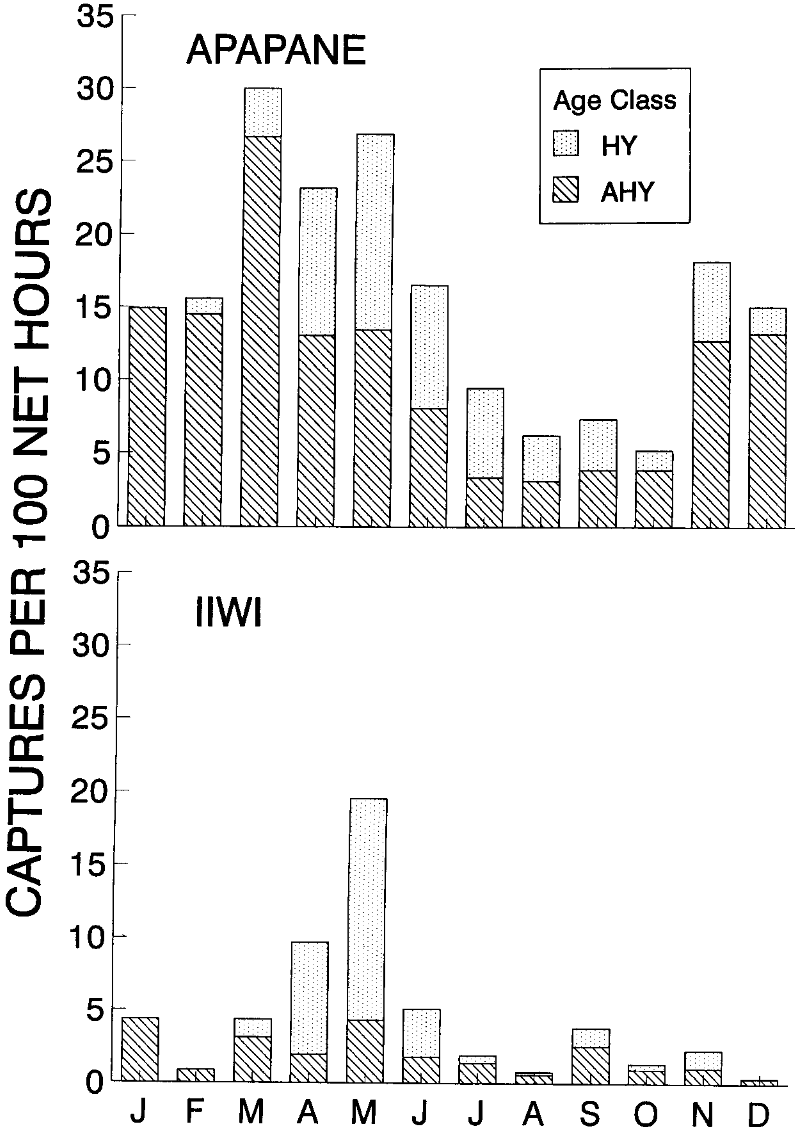

FIGURE 2. Monthly capture rates of HY and AHY Apapane and Iiwi at Keauhou Ranch, Hawaii, 1976–1981.

years were adult males that were in breeding condition at least once.

MOVEMENT PATTERNS

We recorded highest rates of Apapane and Iiwi passing through our sampling locations during the first two hours and last two hours of the day (Fig. 3). The number of Apapane recorded per hour was approximately 30 times higher than the number of Iiwi per hour. Highest passage rates for both species occurred between 18:00–19:00 hr, when we recorded 200 Apapane/hr and four Iiwi/hr (Fig. 3). The number of birds flying as a group ranged from 1–38 for Apapane and 1–7 for Iiwi, but 85% of the 17,535 Apapane and 94% of the 791 Iiwi that we recorded were flying alone or with only one other bird.

With the exception of one survey on the morning of 21 March 1979, when 155 Apapane were observed during 140 minutes of surveying at our

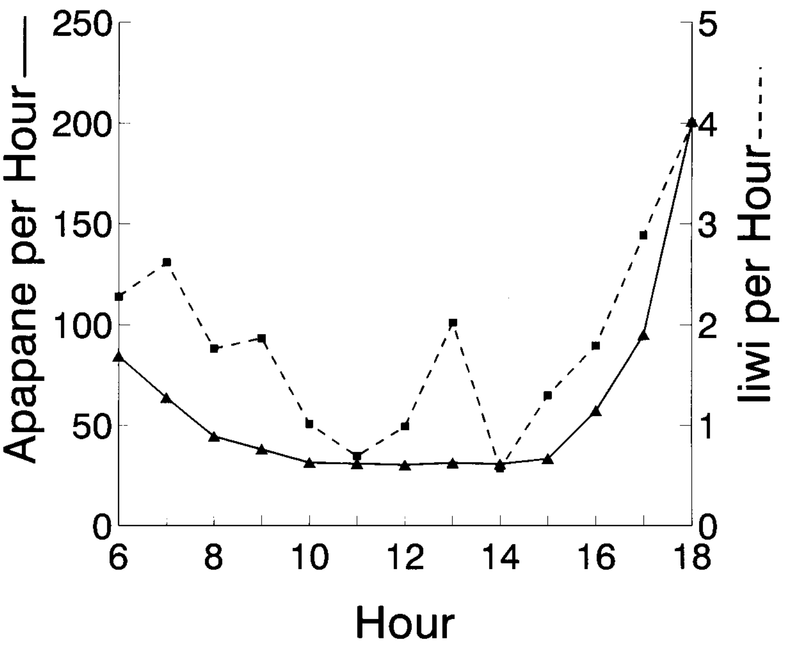

FIGURE 3. Rates (birds/hr) of Apapane and Iiwi recorded each hour at sampling locations along the Stainback Highway and at the Keauhou Ranch and Kilauea Forest study areas, Hawaii, 1978–1981.

600 m elevation site, we observed few Apapane or Iiwi below 1,000 m elevation (Fig. 4). Highest passage rates were recorded at 1,600 m elevation for Apapane and 1,200 m elevation for Iiwi.

Mean monthly passage rates for Apapane, for all 13 sampling locations combined, peaked in June and were lowest in August (Fig. 5). Monthly passage rates for Iiwi were relatively constant at 1–3/hr. Passage rates of Apapane at our Keauhou Ranch study area were correlated with ohia availability ($r = 0.37$, $n = 37$, $P = 0.02$), but we found no correlation between ohia flowering and passage rates of Apapane at Kilauea Forest or of Iiwi at either study site (Fig. 6). At Keauhou Ranch, the mean direction of movement for Apapane was similar between October–December (mean = 316°, Table 3), when ohia flowers were scarce at the study site, and April–June (mean = 329°), when ohia nectar was most available. At Kilauea Forest, the mean direction of movement for Apapane was towards the east (mean = 81°) during October–December but towards the north (mean = 2°) during April–June (Table 3). We found no significant flight direction for Iiwi at either site during October–December. During peak bloom, Iiwi generally moved in the same direction as Apapane (Table 3).

Directions of movement by Apapane were nonrandom (Chi-square test, $P < 0.05$) for all but three of the combinations of study site, season, and time period, but we found no consistent pattern of movement directions (Fig. 7). At Keauhou Ranch and Kilauea Forest, we recorded higher numbers of Apapane during peak bloom than during minimum bloom, and the modal flight direction during peak bloom was towards the NNW at both sites (Fig. 7). We recorded the fewest flights during the 09:01–13:00 hr time interval at both the Keauhou Ranch and Kilauea Forest sites. The high frequency of Apapane recorded at Kilauea Forest after 17:00 during peak bloom resulted primarily from a single 20-min survey on 20 June 1979 during which we recorded 550 Apapane flying due north. We never observed a "nearly continuous stream of individuals and small groups passing overhead in the same direction for 2 hr" as reported by MacMillen and Carpenter (1980).

## DISCUSSION

Seasonal changes in population densities of Apapane and Iiwi are more pronounced than those of any other native Hawaiian forest bird (Baldwin 1953; Scott et al. 1986; van Riper 1987,

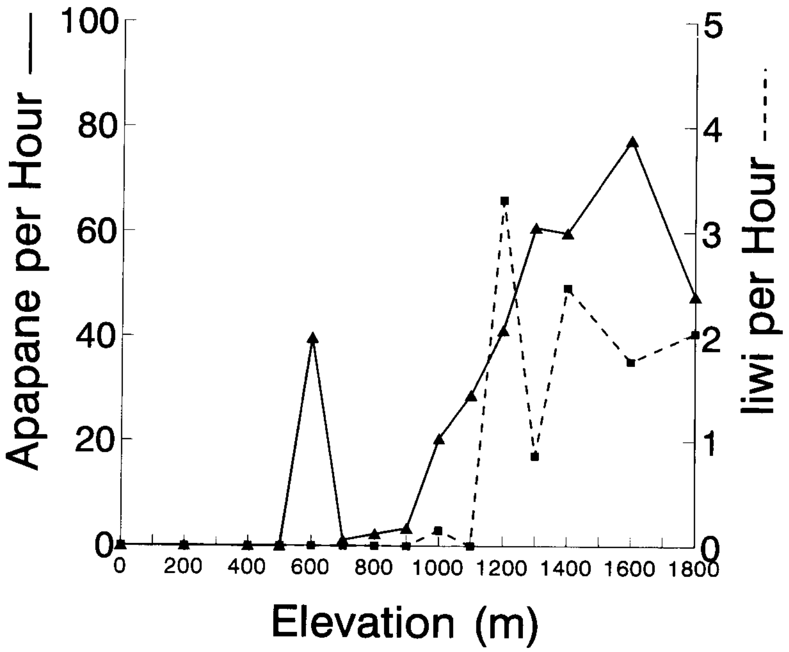

FIGURE 4. Rates (birds/hr) of Apapane and Iiwi recorded at different elevations on the island of Hawaii, 1978–1981.

1995; Ralph and Fancy 1994b, 1994c; National Biological Service, unpubl. data). In all four of our study areas, densities of both species were usually highest each year during March–June. By July or August, densities were often at or near lowest levels for the year. Seasonal population shifts were correlated with availability of ohia flowers for both species, and differences in density between years was explained by annual differences in ohia nectar availability in our study areas.

The reduction that we found in densities of Apapane and Iiwi during summer has been observed elsewhere. Baldwin (1953) found a summer reduction in numbers of Apapane and Iiwi at most plots in Hawaii National Park, but noted an increase in density in one plot at 1,230 m that he thought reflected "an upward movement from the lowlands in summer in correlation with the advance of flowering periods of *Metrosideros*." Surveys conducted by the National Biological Service (NBS, unpubl. data) in 1994 near our

TABLE 3. Number of individuals (*n*) recorded and mean direction of travel of Apapane and Iiwi during months when ohia nectar was scarce (Minimum bloom, October–December) and abundant (Peak bloom, April–June). The distribution of flight directions was non-random ($P < 0.001$) for all categories except Iiwi during minimum bloom at Kilauea Forest.

| Species | Study area | Ohia bloom | *n* | Mean direction |
|---|---|---|---|---|
| Apapane | Keauhou Ranch | Minimum | 1,800 | 316° |
| | | Peak | 2,241 | 329° |
| | Kilauea Forest | Minimum | 1,841 | 81° |
| | | Peak | 3,027 | 2° |
| Iiwi | Keauhou Ranch | Minimum | 89 | 23° |
| | | Peak | 90 | 332° |
| | Kilauea Forest | Minimum | 76 | |
| | | Peak | 289 | 34° |

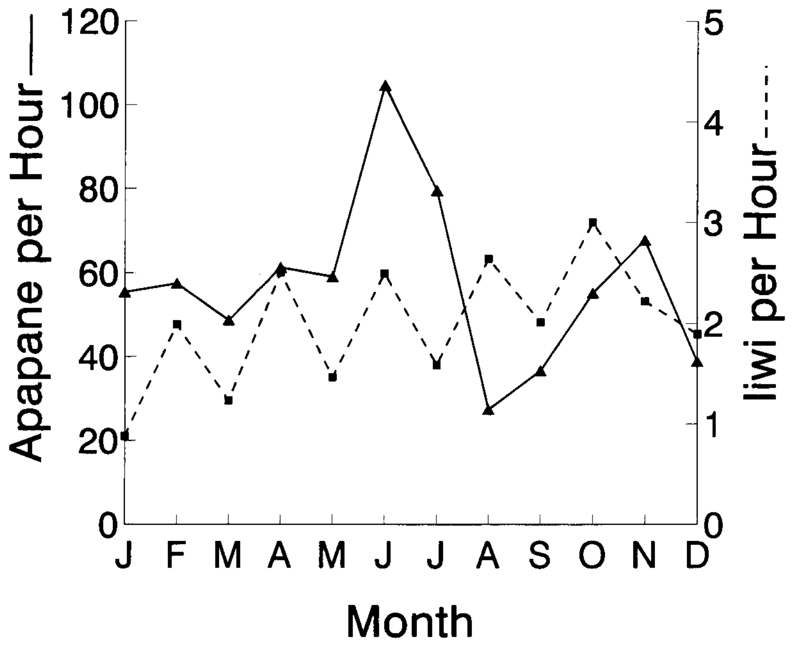

FIGURE 5. Mean monthly rates (birds/hr) of Apapane and Iiwi recorded at 13 locations on the island of Hawaii, 1978–1981.

Keauhou Ranch and Kilauea Forest study areas found a mean density ± 90% CI (birds/ha) of Apapane of 24.00 ± 7.86 in February and 7.27 ± 1.81 in June. Mean density of Iiwi similarly showed a reduction from 6.24 ± 1.52 in February to 1.47 ± 0.35 in June. Other surveys by NBS (unpubl. data) at Nauhi Camp near our Hamakua study area showed a decrease in the density ± 90% CI (birds/ha) of Apapane from 4.55 ± 2.14 in February 1994 to 0.76 ± 0.47 in August 1994, and in the density of Iiwi from 19.82 ± 4.90 in February to 12.31 ± 3.31 in August.

Because of the magnitude of these seasonal population shifts, and annual differences caused by changes in ohia availability, comparisons of Apapane and Iiwi densities between years and even identification of long-term trends are problematic. For example, we found a significant downward trend in densities of Apapane and Iiwi at Keauhou Ranch and Kilauea Forest during 1977–1982, and we compared our density estimates to those obtained at Keauhou Ranch and Kilauea Forest Reserve in 1994 to determine if the downward trend continued after our study. The estimated density of Apapane in February 1994 for an area that included our Keauhou Ranch study site (NBS, unpubl. data) was 24.00 birds/ha. The 1994 density estimate for Apapane was higher than densities we estimated during February during 1978–1981 (range = 9.56–20.59 birds/ha), suggesting that densities increased during the past 15 years. However, the estimated density of Apapane in June 1994 was 7.27 birds/ha, compared to our June estimates that ranged from 7.56 to 15.04 Apapane/ha during 1978–1981. If surveys were conducted only in June each year, one might infer that Apapane densities had declined over the 15-year period. These results indicate the need to conduct series of monthly or bimonthly surveys and to collect concurrent data on the extent of ohia availability in an area before meaningful inferences can be made from density estimates for these two species.

Population shifts are more pronounced during the summer months, probably because of postbreeding dispersal of birds throughout the forest (Baldwin 1953) and because ohia flowering is more patchy during the summer months (Bridges et al. 1981). MacMillen and Carpenter (1980) recorded highest numbers of evening foraging flights at Keauhou Ranch during July and August. In Hawaii National Park, Baldwin (1953) noted that the duration of flowering by *Metrosi-*

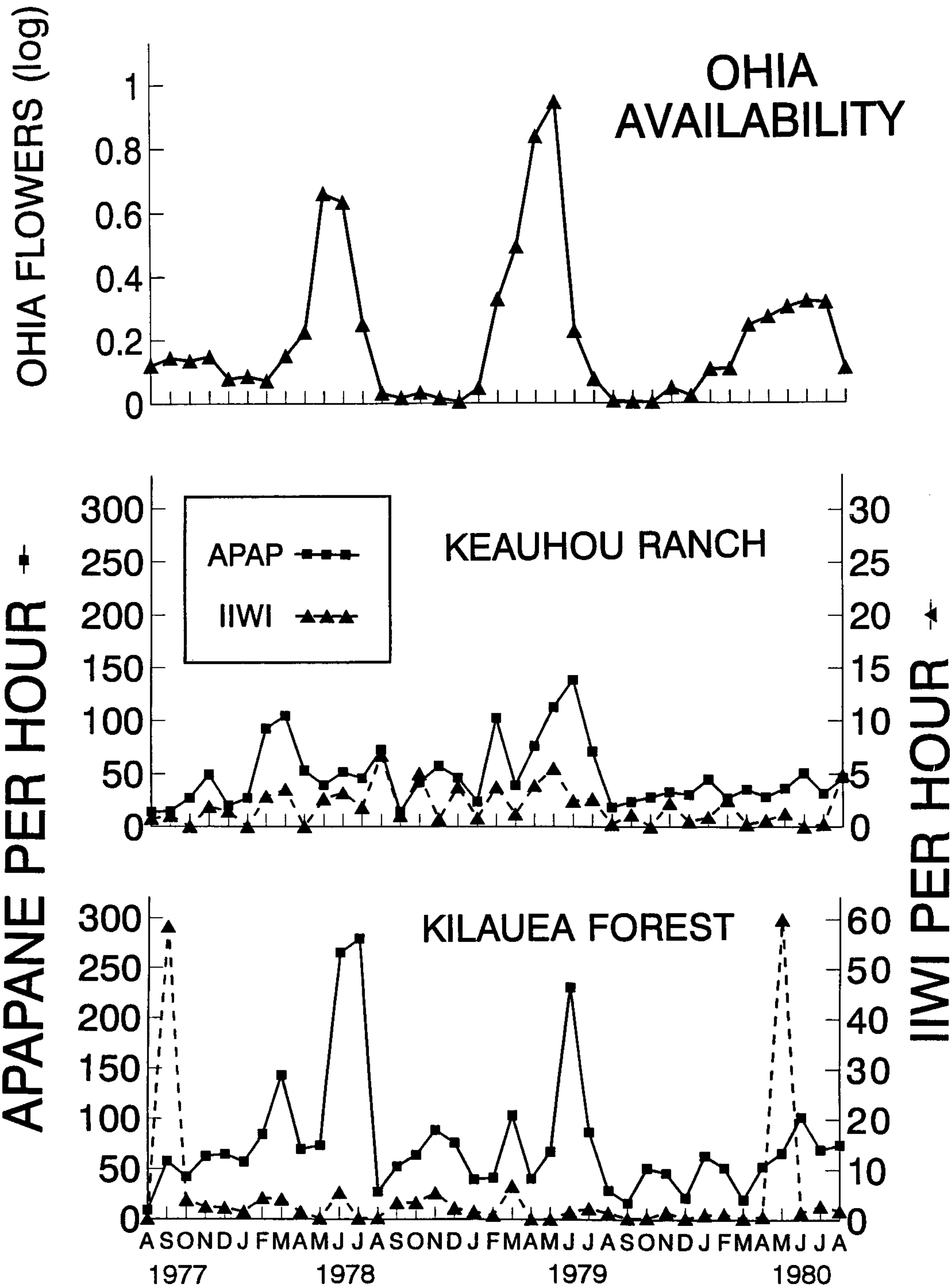

FIGURE 6. Comparison of rates (birds/hr) of Apapane and Iiwi recorded at the Keauhou Ranch and Kilauea Forest study areas each month to the availability of ohia flowers at Keauhou Ranch.

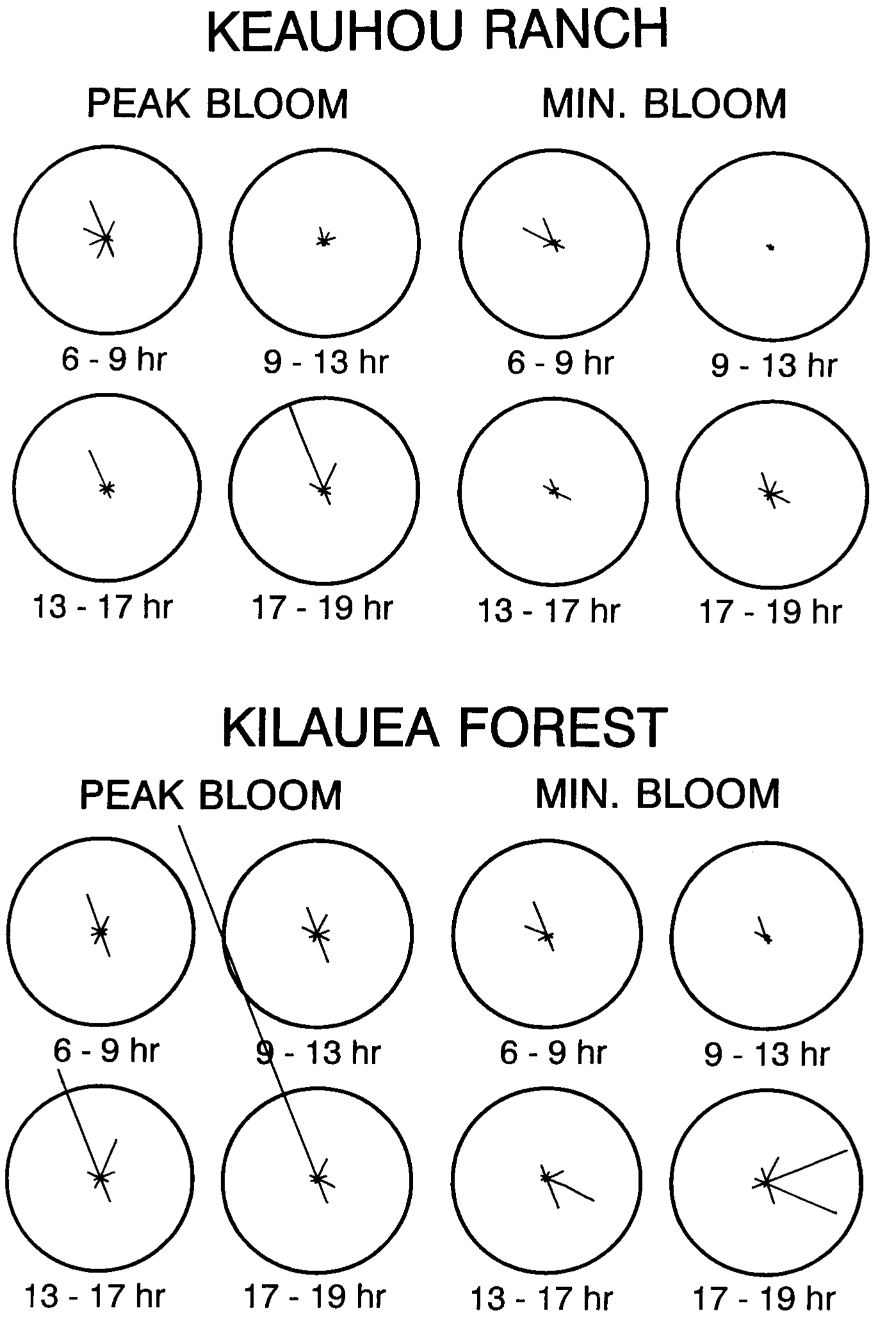

FIGURE 7. Frequency of disappearance (flight) directions of Apapane at Keauhou Ranch and Kilauea Forest, grouped into 45° intervals. The length of each line depicts the number of birds observed flying towards that direction per hour of survey; the radius of the circle equals 50 birds. Peak bloom occurred during April–June; Minimum bloom occurred during October–December.

*deros* increased with elevation, but some of his plots between 1,100–1,200 m did not come into peak flowering until July or November. He also recorded an annual influx of Apapane and Iiwi into these lower-elevation plots during late summer that corresponded with heavy flowering of ohia. Bridges et al. (1981:403) reported summer flowering peaks for *Metrosideros* at mesic forest sites at 1,200–1,300 m elevation, whereas cooler season flowering peaks occurred at sites between 1,500 and 2,130 m elevation.

During September–November, when mamame (*Sophora chrysophylla*) flowering is at its peak, large numbers of Apapane and Iiwi forage in dry, high-elevation forests on Mauna Loa and Mauna Kea. For example, 173 of the 210 (82%) known-age Apapane that were captured in mamane forests on Mauna Kea (National Biological Service, unpubl. data) were captured between September and November, and 51% of these were HY birds. Similarly, 187 of the 253 (74%) Iiwi were captured during September–November, and 53% of these were HY birds. On the eastern slope of Mauna Kea, when mamane is in flower, Apapane and Iiwi make daily foraging flights from lower elevation ohia-koa forests into the mamane forests (Scott et al. 1986; T. Pratt, unpubl. data; S. Fancy, pers. observ.).

We found that small, resident populations of both species remained at our study sites throughout the year. Perkins (1903), Baldwin (1953), and van Riper et al. (1986) also noted resident populations of Apapane and Iiwi in their study areas, with large scale movements of birds into and out of the area, depending on the extent of ohia flowering. Our results are consistent with the hypothesis that a small group of Apapane and Iiwi remain on the study area throughout the year, but make frequent flights, perhaps several per day, away from the study area to forage. We hypothesize that all adult Apapane and Iiwi return to some patch of forest where they are resident, but that these species make foraging flights of 10 km or more and may temporarily take up residence in another patch of forest where nectar is locally abundant.

MacMillen and Carpenter (1980) thought that flight lines of birds they observed on Keauhou Ranch converged at a site in the Kilauea Forest Reserve near the base of Kulani Cone, and they hypothesized that tens of thousands of Apapane and Iiwi shared a common roosting area near our Kilauea Forest study area. We found that densities of Apapane and Iiwi at Kilauea Forest were at their lowest levels in July and August, when MacMillen and Carpenter (1980) made their observations, and it is unlikely that a large concentration of Apapane and Iiwi occurred elsewhere in the Kilauea Forest during the summer months. We have observed that when Apapane and Iiwi return from foraging flights, such as when birds on the eastern slope of Mauna Kea return to ohia-koa forests from higher-elevation mamane forests, the birds spread out through the forest rather than concentrating in roosting groups.

MacMillen and Carpenter (1980) hypothesized that Apapane and Iiwi roost in mid-elevation forests (ca. 1,600–1,800 m) to escape a nightly fog belt and to obtain an energetic savings in thermoregulation costs. They also added that birds roosting at these elevations would reduce encounters with night-flying mosquitos that are more common at lower elevations, and that carry avian malaria and avian pox. On the eastern slope of Mauna Kea during the autumn months, we have observed that Apapane and Iiwi fly downslope from high-elevation (>2,100 m) mamane forests where they feed during the day to roost in the warmer ohia-koa forests above the nightly fog belt. These observations support MacMillen and Carpenter's (1980) hypothesis that thermal protection provided by dense ohia-koa forests has adaptive value for Apapane and Iiwi, and they also support our hypothesis that Apapane and Iiwi return to areas where they are resident after making long-distance foraging flights.

Movements of Apapane and Iiwi have important implications for transmission of avian malaria and avian pox, which have had a major impact on the numbers and distribution of native birds (Warner 1968; van Riper et al. 1986; Atkinson et al., in press). The species of mosquitos in Hawaii that transmit avian malaria and avian pox are relatively cold-intolerant, and most of the remaining strongholds for native birds are in mid- (ca. 1,500–1,800 m) to high-elevation (>1,800 m) forests where mosquitos are less abundant. Van Riper et al. (1986) thought that avian malaria and the distribution of mosquitos restrict native birds to higher-elevation forests and that avian disease is a cause of daily altitudinal migrations. However, based on the considerable evidence that daily flights occur in response to changing resource availability, it is likely that daily altitudinal migrations occurred before the introduction of mosquitos to Hawaii in the early 1800s.

Apapane appear to be an important transmitter of disease in Hawaii, since a relatively high proportion of Apapane carry the *Plasmodium* organism and pox virus (van Riper et al. 1986; C. Atkinson, unpubl. data) and the birds are highly mobile. In late summer when mosquito populations are at peak levels (van Riper et al. 1986; D. LaPointe, unpubl. data), Apapane and Iiwi fly to lower elevation ohia blooms (Baldwin 1953, Bridges et al. 1981) where they come into increased contact with mosquitos. The birds, many infected with malaria and pox, then return upslope where mosquitos are fewer, but still abundant enough to continue the disease cycle (van Riper et al. 1986; Fancy et al., unpubl. manuscript; C. Atkinson, unpubl. data). Iiwi are highly susceptible to avian malaria: van Riper et al. (1986) found them to be the most susceptible of the native birds they challenged with malaria, and Atkinson et al. (in press) found that nine of ten Iiwi died from malaria after a single bite by an infected mosquito. The annual survival probability of Iiwi (this study) is the lowest of the six native Hawaiian forest birds that have been studied (Ralph and Fancy 1994b, 1994c; Lindsey et al. 1995), and may be related to their high susceptibility to malaria. Although avian malaria and pox are only partly responsible for the decline of many species of native Hawaiian birds, the difficulty in controlling these diseases, and the possibility of a cold-hardy vector such as a temperate species of mosquito being introduced, makes them a major threat to the future of Hawaii's unique avifauna.

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