

## DREPANIDINE MOVEMENTS IN RELATION TO FOOD AVAILABILITY IN SUBALPINE WOODLAND ON MAUNA KEA, HAWAI'I

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**Abstract.** Flowers of the māmane tree (*Sophora chrysophylla*) are the primary nectar source for Hawaiian honeycreepers in subalpine woodland on Mauna Kea Volcano on the island of Hawai'i. Māmane seeds are the primary food resource of the endangered Palila (*Loxioides bailleui*), which is now restricted to subalpine woodland on Mauna Kea. The objectives of this study were to determine the patterns and relative scales of movements of the drepanidine community in relationship to food availability and tree density on leeward Mauna Kea. 'I'iwi (*Vestiaria coccinea*) and 'Apapane (*Himatione sanguinea*) densities were related to māmane flower abundance. Palila densities were related to māmane pod abundance. These species also had higher densities in māmane woodland than in naio-māmane woodland, unlike the more insectivorous Hawai'i 'Amakihi (*Hemignathus virens*) whose densities did not differ between woodland types. Palila and Hawai'i 'Amakihi do not make movements on the same scale as 'I'iwi and 'Apapane, whose densities changed by more than an order of magnitude. Ungulate eradication, grass reduction, fire management, and restored corridors of māmane woodland would benefit all drepanidines on Mauna Kea, particularly the Palila.

**Key Words:** 'Apapane; food resources; Hawai'i 'Amakihi; *Himatione sanguinea*; *Hemignathus virens*; 'I'iwi; *Loxioides bailleui*; Palila; subalpine woodland; *Vestiaria coccinea*.

Drepanidines (Hawaiian honeycreepers—Fringillidae: Drepanidinae) in dry subalpine woodland of Mauna Kea Volcano, on the island of Hawai'i (Fig. 1), may make movements in response to nectar and pod availability of the leguminous māmane tree (*Sophora chrysophylla* [Salisb.] Seem.). These movements may be limited by site tenacity (Fancy et al. 1993b), habitat fragmentation, or the use of alternate food resources. Movements of drepanidines have been described in Hawaiian wet forests (Baldwin 1953, MacMillen and Carpenter 1980; Ralph and Fancy 1994a, 1995), but there have been few comprehensive studies of drepanidine movements within subalpine woodland (van Riper 1978, 1980a,b, 1987; van Riper et al. 1978, Fancy et al. 1993b, Ralph and Fancy 1995).

'Apapane (*Himatione sanguinea*) and 'I'iwi (*Vestiaria coccinea*) are primarily nectarivorous and breed mostly in wet forests of the Hawaiian Islands, but they make seasonal and daily movements from wet forest to subalpine woodland and leeward dry woodlands, following availability of nectar (Ralph and Fancy 1995). Hawai'i 'Amakihi (*Hemignathus virens*) have a larger component of arthropods in their diet than other nectarivores (van Riper 1978) and may not need to make large-scale movements in response to availability of food resources (Baldwin 1953). Palila (*Loxioides bailleui*), an endangered drepanidine finch, is primarily a māmane seed and flower predator living exclusively in subalpine woodlands of Mauna Kea. Palila are highly de-

pendent on māmane woodlands for food and nesting sites (van Riper 1980a). Drepanidines may also take advantage of other superabundant and relatively aseasonal plant resources, such as the flowers or fruits of the naio tree (*Myoporum sandwicense* A. Gray) when māmane seeds and flowers are scarce.

Subalpine woodland habitat has been reduced and degraded by herbivorous feral mammals since the arrival of Europeans in Hawai'i (Warner 1960, Scowcroft and Giffin 1983). Māmane regeneration has recently improved after feral mammals were reduced beginning in 1981 (Hess et al. 1999). However, Palila have not recovered in much of their former range, despite improvement in habitat conditions around Mauna Kea. The 1980–1995 mean population of 3,390 Palila has been inhabiting a 139 km<sup>2</sup> area that is <5% of their historical distribution (Scott et al. 1984, 1986; Jacobi et al. 1996). This entire area is now susceptible to destruction by fire due to invasion by nonnative grasses, making Palila highly vulnerable to catastrophic habitat loss.

The objectives of this study were to determine the patterns and relative scales of movements of the drepanidine community in relationship to food resource availability and tree density on leeward Mauna Kea. The quality and extent of māmane habitat on Mauna Kea may be important for drepanidines as seasonal foraging grounds during periods of nectar scarcity in wet forests. Palila are probably more affected than other drepanidines by subtle changes in subalpine woodland habitat because of their special-

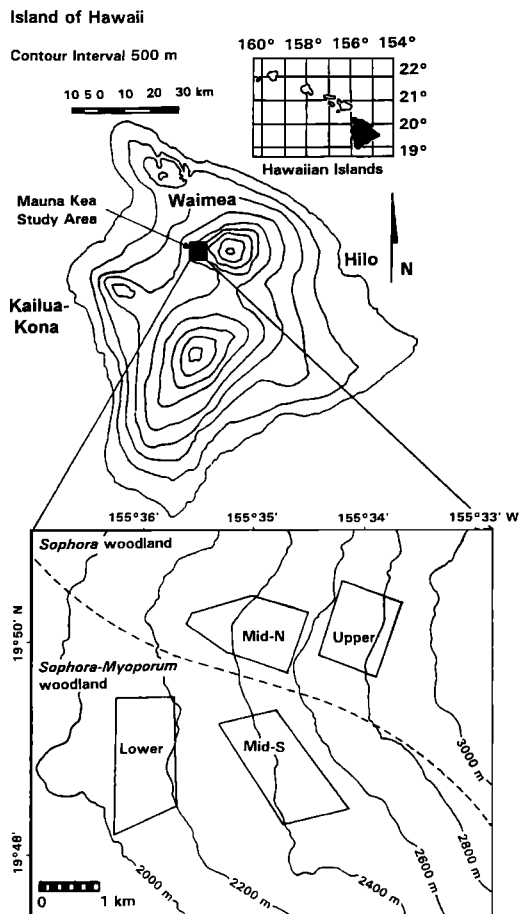


FIGURE 1. Map of Hawaiian Islands (upper inset), island of Hawai'i, study area (lower inset), and four study sites (Upper; Mid-N, mid-elevation-North; Mid-S, mid-elevation-South; Lower) with elevation contours on the west slope of Mauna Kea Volcano, Hawai'i.

ized diet and restricted range. If Palila do not exploit temporal-spatial patterns of food resource availability, then translocation may be necessary to reestablish populations or to expand their current range (Fancy et al. 1997). However, if Palila do make movements that correspond to gradients in food resources, then connecting isolated fragments of suitable habitat by improving corridors of marginal subalpine woodland may be more effective in expanding Palila range and population (Scott et al. 1984).

## METHODS

### STUDY AREA

Four study sites, each with five transects, were located on a gradient from 1,978 to 2,816 m in leeward, dry subalpine woodland in the Mauna Kea Forest Re-

serve, on the island of Hawai'i (19°50' N, 155°35' W; Fig. 1). The sites were designated, in order of descending elevation: upper, mid-elevation north, mid-elevation south, and lower. The upper- and mid-elevation north sites above 2,317 m were dominated by māmane with 5–30% canopy cover, whereas the mid-elevation south and lower sites below 2,437 m contained a high proportion of codominant naio with as much as 60% overall canopy cover. Overall canopy cover averaged 30% and canopy height was generally short (3–8 m). Vegetation structure and plant phenology were described by van Riper (1980b) and Hess et al. (1999). Climate was investigated by Juvik and Nullet (1993) and Juvik et al. (1993).

### TREE DENSITY

We sampled five transects from each of the four sites (Fig. 1) using the point-centered quarter method for estimating mature tree density (Mueller-Dombois and Ellenberg 1974). Transect length varied from 900 to 1,200 m. In each study area, we randomly selected 20 point-centers along two transects and ten point-centers along three transects. We selected the nearest mature tree within each quarter that had a crown size >2 m high and wide. We measured the distance from the center of the selected tree's crown to the sample point  $\pm 0.5$  m. All conspecific stems emerging from the ground within 1 m radius of the selected tree were considered to be from the same selected tree. We also measured elevation at each point-center.

### PHENOLOGY

We counted the number of expanded green pods (face of the seeds >3 mm) and the number of open flowers on the nearest māmane tree >2 m tall located at 150 m intervals along the same transects where we estimated mature tree density. We multiplied the mean number of pods and flowers for each transect by the estimate of tree density at each transect to estimate availability of flowers and pods per ha. We log transformed both independent variables and analyzed them with the General Linear Model (GLM) procedure (SAS Institute 1985) to test for differences among study sites and assessment periods. Although Palila eat the fruit of naio, availability of this resource was not included in the analysis because it constituted <10% of food items consumed, and it was superabundant during the entire study in the two study sites where naio was codominant (S. Hess and P. Banko, unpubl. data). Nectarivorous drepanidines also used naio flowers but to a lesser extent than māmane flowers.

### POINT COUNTS

We used variable circular-plot (VCP) counts (Reynolds et al. 1980) to estimate the densities of drepanidines on the four study sites. VCP counts were conducted six times at irregular intervals from July 1994 until August 1996 concurrently with phenological measurements. Observers received 2–3 months training in identification of local bird vocalizations and distance estimation (Kepler and Scott 1981). During 6-minute count periods between 05:45 A.M. and 11:00 A.M., we recorded the distance to every bird seen or heard (Scott et al. 1984). Counts were not conducted when wind speed exceeded 30 km/hr or during rain.

Cloud cover was recorded in 10% increments and wind speed was recorded on the Beaufort scale.

#### ANALYSIS

We calculated tree densities with Pollard's (1971) formula for an unbiased population density estimate. We log transformed mature māmane tree densities and analyzed these data by transect with the GLM procedure (SAS Institute 1985). We used Tukey's studentized multiple range test to determine which sites differed in māmane density and ANOVA contrasts to determine the significance of orthogonal comparisons. We averaged drepanidine densities by transect across the six bird counts, log transformed the data, and related them to the estimate of māmane density by transect with ANOVA ( $\alpha = 0.05$ ).

We analyzed VCP counts by adjusting detection distances by the significant effects of different observers, weather variables, and time of day with respect to a reference condition (Ramsey et al. 1987, Fancy 1997). The reference condition was: an experienced observer (P. Banko) common to all counts at 9:00 A.M. hours with no clouds or wind. We pooled observers having <26 detections of a species with the reference observer. Detection distances at each station were adjusted by only the significant regression coefficients of the model under the actual conditions when the station was sampled. We analyzed adjusted distances with the program DISTANCE (Laake et al. 1994) to calculate the effective area surveyed under reference conditions and bird density by transect. We calculated variation in the effective area surveyed with 5,000 bootstrap samples from a random normal distribution centered on the mean effective area using the computer program VCPADJ (Fancy 1997).

We used analysis of covariance (ANCOVA) to relate the log transformed densities of the four drepanidine species to māmane flowers/ha (each by transect), and the class covariates of assessment period and study site, in that order, with the GLM procedure (SAS Institute 1985). We also related Palila density to māmane pods/ha with the same design. We used ANCOVA because the bird counts were not conducted at standard intervals and because we had a combination of numerical and class variables to examine simultaneously. The model assumed equal slopes over the levels of the class variables. We used conservative alpha levels ( $\alpha = 0.01$ ) to control type I error due to autocorrelation from repeated sample points (Hatfield et al. 1996). We used ANOVA contrasts to determine the significance of orthogonal comparisons.

Additionally, we present māmane phenological data from both the upper and mid-elevation north study sites for April 1990–April 1994. During this period, we conducted monthly counts of pods and flowers using the same methodology described above. We multiplied the mean number of pods and flowers per transect by the 1996 estimate of tree density, and then averaged the five transects to obtain a monthly estimate of resource availability for each year. Data from the month of October 1993 are not represented. We also present mist net capture data standardized by effort for the four species of drepanidines from years 1989 to 1993. Four fixed mist net stations were operated in the vicinity of each of the four study sites. Ten

12 × 2 m nets were operated between 07:30 A.M. and 05:30 P.M. hours at each station. Effort was variable among years. Sampling was conducted each month in at least three different years, except for January for which there are only two years of data.

## RESULTS

### TREE DENSITY

Mature māmane tree densities differed significantly among study sites (ANOVA,  $df = 3$ ,  $P < 0.005$ ). The upper study site had a higher density of mature trees than the other three sites ( $df = 1$ ,  $P < 0.001$ ; Fig. 2). The māmane dominated upper and mid-elevation north sites had higher densities of māmane ( $df = 1$ ,  $P < 0.001$ ) than mixed naio-māmane woodland in the lower and mid-elevation south study sites. Differences in naio densities between māmane and mixed naio-māmane woodland sites ( $df = 1$ ,  $P < 0.001$ ) resulted from the rarity of naio in the upper and mid-elevation north sites and abundance of naio in the lower and mid-elevation south sites (Fig. 2).

### PHENOLOGY

Mean monthly māmane flower and pod availability varied throughout the year (Fig. 3). The lowest period of annual flower availability was July in both the upper and mid-elevation north study sites. Flower availability peaked in September–December in the upper site and October–December in the mid-elevation north site. A second, more variable period of flowering occurred in January–March at both sites. Pod availability was lowest in November in the upper site and September in the mid-elevation north site.

During the concurrent phenology and point count study period, māmane flower availability differed among study sites (ANCOVA,  $df = 3$ ,  $P < 0.001$ ; Fig. 4). The upper study site had higher flower availability than the other sites ( $df = 1$ ,  $P < 0.001$ ) and the two māmane woodland study sites had higher flower availability than the naio-māmane woodland sites ( $df = 1$ ,  $P < 0.001$ ). Flower availability also differed significantly among assessment periods ( $df = 5$ ,  $P < 0.001$ ; Fig. 5). Flower availability in September 1995 was higher ( $df = 1$ ,  $P < 0.001$ ), and in July 1994, it was lower ( $df = 1$ ,  $P < 0.001$ ) than other assessment periods. Overall flower availability was not related to pod availability ( $df = 1$ ,  $P > 0.37$ ).

Pod availability also differed among study sites ( $df = 3$ ,  $P < 0.001$ ; Fig. 4), being highest in the upper study site ( $df = 1$ ,  $P < 0.003$ ). The two māmane woodland study sites had higher pod availability than the naio-māmane study sites ( $df = 1$ ,  $P < 0.001$ ). Pod availability also

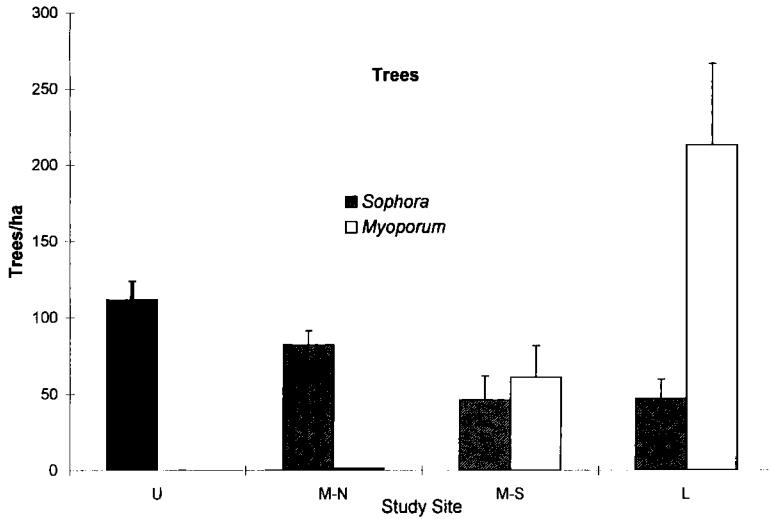


FIGURE 2. Density of *Sophora chrysophylla* and *Myoporum sandwicense* >2 m tall (trees ha<sup>-1</sup> ± SE) at 4 study sites (U = Upper, M-N = Mid-elevation-North, M-S = Mid-elevation-South, L = Lower) on the west slope of Mauna Kea Volcano, Hawai'i.

differed among assessment periods (df = 5,  $P < 0.001$ ; Fig. 5). Pod availability in July 1994 was higher (df = 1,  $P < 0.001$ ), and in September 1995, was lower (df = 1,  $P < 0.001$ ) than other assessment periods. Overall pod availability was not related to flower availability (df = 1,  $P > 0.36$ ).

#### VCP COUNTS

In addition to observers, time of day affected VCP detection distances for both Palila and Hawai'i Amakihi (df = 1,  $P < 0.001$ ). Detection distances decreased with time of day. Weather variables did not significantly affect detection distances of Palila, 'I'iwi, or 'Apapane (df = 1,  $P > 0.05$ ); however, detection distances increased with cloud cover for Hawai'i Amakihi (df = 1,  $P < 0.001$ ). We adjusted detection distances for only the significant effects of the models (Fancy 1997).

#### DREPANIDINE ABUNDANCE IN RELATION TO FOOD AND HABITAT

The majority of known-age 'Apapane (84%) and 'I'iwi (74%) were captured in the postbreeding months of September–November (Fig. 6), corresponding to peak flowering in the upper elevation study site (Fig. 3). In contrast, resident Palila and Hawai'i 'Amakihi were captured in all months of the year, with annual low capture rates during the postbreeding months of July–August for Hawai'i 'Amakihi and July–September for Palila.

Palila density, determined by point counts,

was not as strongly related to flower availability (ANCOVA, df = 1,  $P > 0.06$ ) as it was related to pod availability (df = 1,  $P < 0.001$ ), assessment period (df = 5,  $P < 0.003$ ; Fig. 5), and study site (df = 3,  $P < 0.001$ ; Fig. 4). Although Palila density was not related to māmane density (df = 1,  $P > 0.80$ ), it was higher in the two māmane dominated sites than the naio-māmane sites (df = 1,  $P < 0.001$ ).

'Apapane density was related to flower availability (df = 1,  $P < 0.001$ ; Fig. 5), assessment period (df = 5,  $P < 0.001$ ), study site (df = 3,  $P < 0.001$ ; Fig. 4), and māmane density (df = 1,  $P < 0.04$ ). 'Apapane in the māmane dominated sites approached significantly higher densities than in the naio-māmane sites (df = 1,  $P < 0.013$ ).

'I'iwi density was related to flower availability (df = 1,  $P < 0.009$ ), assessment period (df = 5,  $P < 0.003$ ; Fig. 5), and study site (df = 3,  $P < 0.001$ ; Fig. 4), but it was not related to māmane density (df = 1,  $P > 0.67$ ). However, 'I'iwi density was higher in the māmane dominated sites than the naio-māmane sites (df = 1,  $P < 0.001$ ). 'I'iwi were not detected in the lower elevation study site.

Hawai'i 'Amakihi density was not related to flower availability (df = 1,  $P > 0.19$ ), but it was related to assessment period (df = 5,  $P < 0.002$ ; Fig. 5) and study site (df = 3,  $P < 0.001$ ). Hawai'i 'Amakihi density was not related to māmane density (df = 1,  $P > 0.089$ ) nor was it different between the two māmane dominated

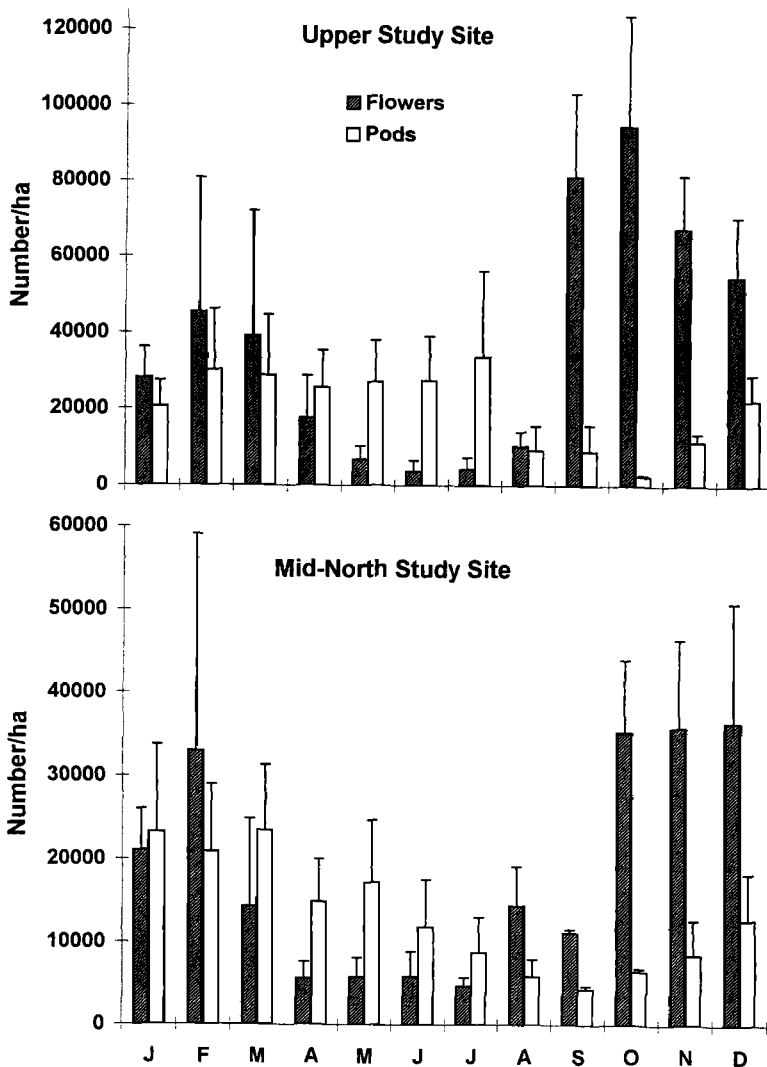


FIGURE 3. Mean monthly *Sophora chrysophylla* flower and pod availability and annual variation (number  $\text{ha}^{-1} \pm \text{SE}$ ) at two study sites on the west slope of Mauna Kea Volcano, Hawai'i from April 1990 to April 1994.

sites and the naio-māmane sites ( $df = 1, P > 0.26$ ).

Hawai'i 'Amakihi exhibited the least variable change in density of the four drepanidine species over time (Figs. 4, 5), with only 34% coefficient of variation. Palila exhibited only slightly greater change in density than Hawai'i Amakihi, with  $CV = 89\%$ . 'Apapane exhibited the largest change in density,  $CV = 198\%$ . 'I'iwi also had high relative change in density,  $CV = 188\%$ .

#### DISCUSSION

Lower densities of mature māmane in mixed naio-māmane woodland sites relative to māmane woodland sites are probably a result of browsing

by introduced feral ungulates (Warner 1960, Scowcroft 1983, Scowcroft and Giffin 1983, Scowcroft and Sakai 1983, Juvik and Juvik 1984, Mountainspring et al. 1987), because māmane sapling density was at least as high in mixed naio-māmane woodland as in māmane woodland (Hess et al. 1999). Feral sheep and mouflon sheep prefer māmane foliage over other plant species (Giffin 1976, 1982). Therefore, browsing may have selectively reduced māmane in the mixed-species woodland sites, resulting in a shift towards naio dominance (van Riper 1980b, Hess et al. 1999). Other comparable sub-alpine woodland sites with high ungulate browsing pressure, such as Kīpuka 'Alalā on Mauna

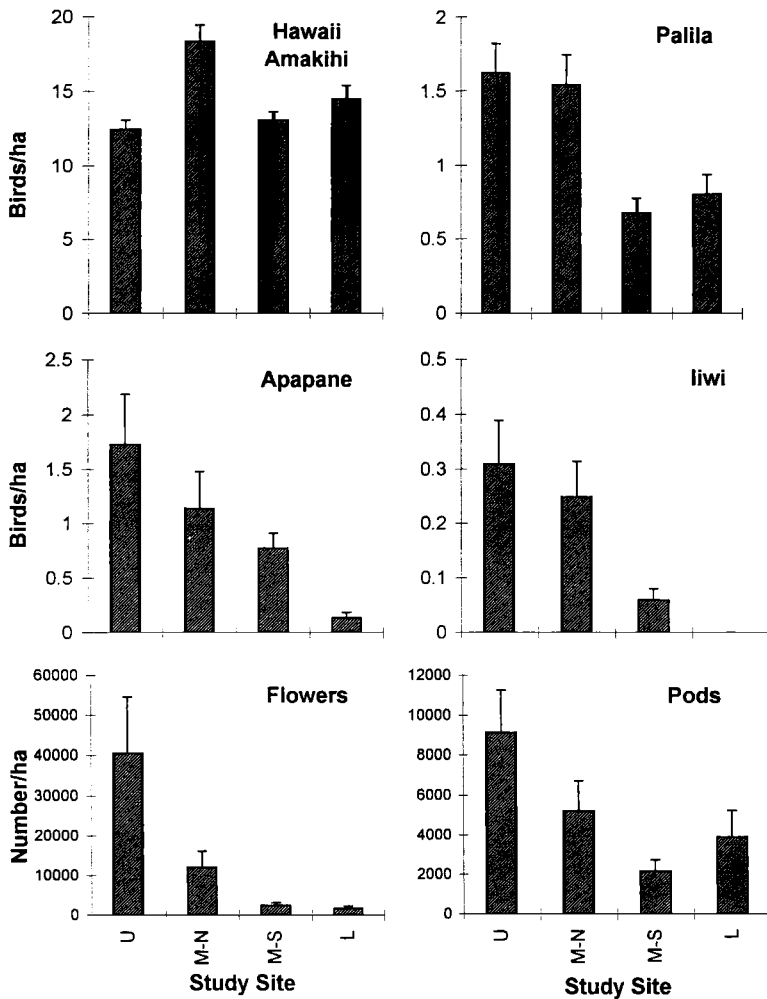


FIGURE 4. Mean densities of four species of drepanidines and availability of *Sophora chrysophylla* flowers and pods (number ha<sup>-1</sup>  $\pm$  SE) at four study sites (U = Upper, M-N = Mid-elevation-North, M-S = Mid-elevation-South, L = Lower) on the west slope of Mauna Kea Volcano, Hawai'i.

Loa, also exhibit extremely high naio regeneration concurrent with extremely low māmane regeneration (P. Banko, unpubl. data). If ungulate browsing is controlled, the plant community will probably shift towards increased māmane density in the future.

Tree density was a strong determinant of food resource availability. The highest māmane flower and pod availability occurred in the upper elevation site, where māmane density was highest. Annual development of flowers and pods occurs first at higher elevations (van Riper 1980b; P. Banko, unpubl. data). Rainfall, another primary determinant of flower and pod production, was approximately 25% greater in 1994 and 50% less in 1995 than the long-term average (J. Ju-

vik, unpubl. data). Pod availability in 1994 and 1995 was relatively low, but flower availability was normal (P. Banko, unpubl. data). In 1994, rainfall was normal during the flowering period but declined sharply afterwards, which may have resulted in limited pod development. Pod availability in 1995 was less than the other years due to below normal rainfall for the entire year. The year of highest pod availability was 1996, which also coincided with the greatest number of nest attempts by Palila (P. Banko, unpubl. data).

Palila densities were greater at sites dominated by māmane and peaked during the breeding season when pod availability was greatest. The importance of pods in relation to movement and

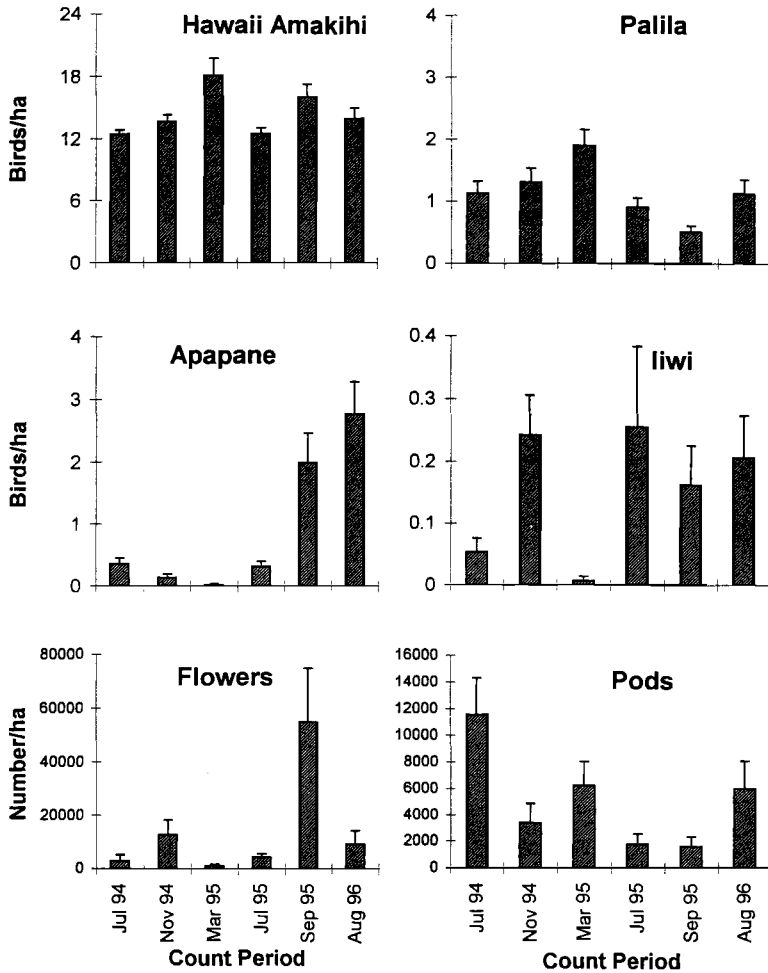


FIGURE 5. Mean densities of four species of drepanidines, and availability of *Sophora chrysophylla* flowers and pods (number  $\text{ha}^{-1} \pm \text{SE}$ ) during six count periods (July 1994, Nov. 1994, March 1995, July 1995, Sept. 1995, and August 1996) on the west slope of Mauna Kea Volcano, Hawai'i.

breeding of Palila has been well documented (van Riper et al. 1978, van Riper 1980a, Scott et al. 1984, Fancy et al. 1993b, Lindsey et al. 1995a). Palila probably dispersed from higher elevation sites after the breeding season because of declining pod availability. During January–March 1995, a period of extremely low pod availability in the lower elevation site, Palila were present and were observed eating naio fruit, indicating that they had switched to alternate food resources (S. Hess, unpubl. data). Palila densities fluctuated least in the mixed naio-māmane woodland, although Palila densities in these areas were never as great as in māmane dominated sites.

van Riper (1987) found that Hawai'i 'Amakihi nested in higher density in predominantly māmane habitat; however, we did not find Ha-

wai'i 'Amakihi in greater density in māmane woodland than in mixed naio-māmane woodland, unlike the other drepanidines. This pattern may be related to the higher proportion of naio flowers and arthropods in the diet of Hawai'i 'Amakihi (Baldwin 1953, van Riper 1978), and, for the other species, preference for māmane food resources, as well as reduced predator densities in māmane woodland (Amarasekare 1993, 1994). At the lower elevation study site, only one 'Iiwi was captured during four years of mist netting operations and none were detected during the three years of point counts. Although 'Iiwi are very susceptible to introduced avian malaria, it is unlikely that mosquito-vectored disease is responsible for the rarity of this species (van Riper et al. 1986, Atkinson et al. 1995). There is no larval mosquito habitat pres-

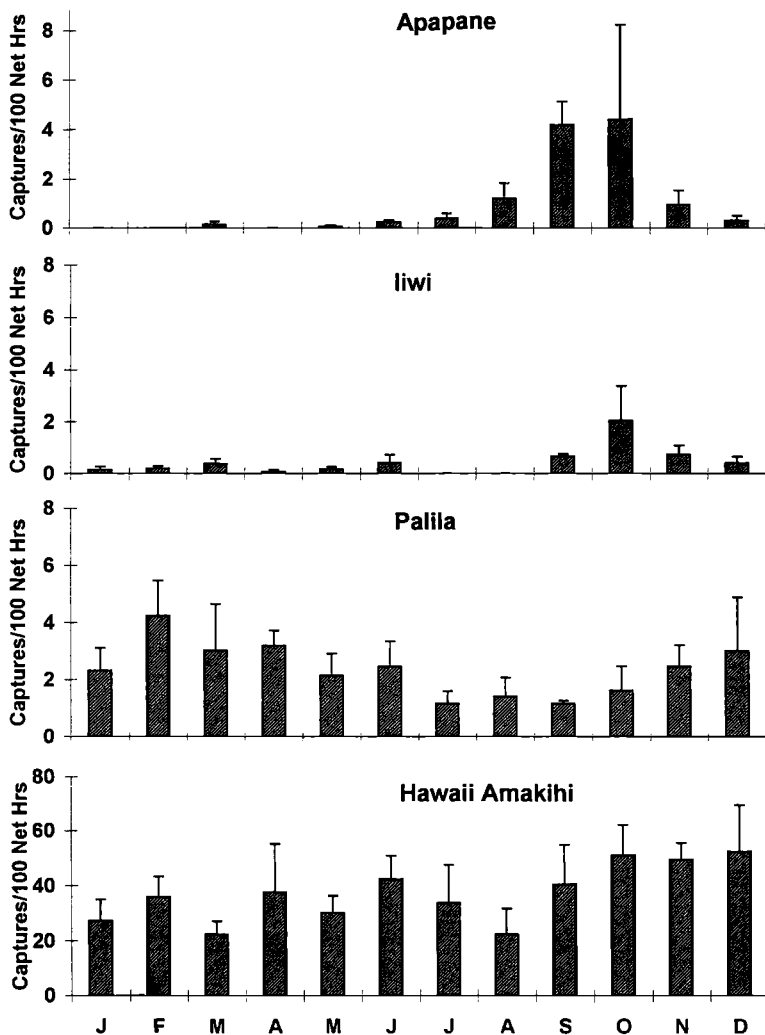


FIGURE 6. Mean monthly capture rates and annual variation (captures/100 net hours  $\pm$  SE) of four species of drepanidines on the west slope of Mauna Kea Volcano, Hawai'i from 1989 to 1993.

ent at this site and thermal constraints would inhibit parasite development within vectors dispersing from lower elevations (D. LaPointe, unpubl. data). The rarity of 'I'iwi was most likely due to other habitat features such as food resources or predators. If māmane density continues to increase in the mixed naio-māmane woodland, drepanidine densities may also increase, although predators may ultimately limit bird densities (Amarasekare 1993, 1994).

Banding data and point count data show similar patterns and scales of movement for each of the four drepanidine species. Hawai'i 'Amakihi exhibited the least change in overall mean densities during the study. Palila exhibited only slightly greater change in densities than Hawai'i

'Amakihi, indicating small-scale movements, and generally high site tenacity (Fancy *et al.* 1993b), or scarcity of māmane pods in accessible adjacent areas during the study. 'Apapane exhibited the largest proportional change in mean density of any drepanidine, consistent with their movements between windward to leeward slopes. 'Apapane are known to have the greatest change in densities among drepanidines (Baldwin 1953, Scott *et al.* 1986, van Riper 1987; Ralph and Fancy 1994a, 1995). A small population of breeding 'I'iwi (T. Pratt, unpubl. data) resides in the study areas, but there was also high change in 'I'iwi densities, which was second to 'Apapane, thus indicating large-scale movements.



Baldwin (1953:354) observed that Hawai'i 'Amakihi, 'Apapane, and 'I'iwi near the summit of Kilauea Volcano and slopes of Mauna Loa Volcano, "...occur quite consistently throughout the year where they occur at all." Contrasting with Baldwin's findings, in subalpine woodlands of Mauna Kea, 'Apapane are not resident but make annual movements to and from other areas. We found a small number of 'I'iwi are resident in subalpine woodland throughout the year, while a greater number make annual movements to and from other areas. Hawai'i 'Amakihi have a large resident population with the least fluctuation in annual densities. Baldwin (1953) also stated that postbreeding dispersal results in widely and thinly distributed drepanidine populations in late summer months. This period corresponds to the highest annual densities of 'Apapane and 'I'iwi in subalpine woodland. Palila, with a protracted breeding season (van Riper 1980a, Pletschet and Kelly 1990), may also have a postbreeding dispersal that extends later into winter months than other drepanidines. Family groups of Palila with radio transmitters moved from upper and mid-elevation nesting areas to lower elevation areas after young had fledged in 1995 (L. Miller, unpubl. data); however, this did not occur in 1994 when family groups stayed close to their nesting territories. The 1995 postbreeding dispersal corresponded simultaneously with the lowest measured Palila densities and pod availability during this study. Although decreased vocalization rates could also be consistent with the calculated low density, Palila were also much more difficult to capture during this period, indicating that they had dispersed from the study area (L. Miller, unpubl. data).

Palila, as seed and flower predators, reduce their most important food resource and the most important food resources of other nectarivorous drepanidines when they eat flowers and flower buds. Although Palila eat more flowers and flower buds than seeds, they spend a greater proportion of time eating seeds and presumably consume more seed mass and receive more nutrition from seeds than from flowers (van Riper 1980a; S. Hess, unpubl. data). Other drepanidines, such as Hawai'i Amakihi, 'Apapane, and 'I'iwi, may provide an essential service through pollination of flowers that ultimately develop into pods. The loss of pollinating birds in subalpine woodland could result in reduced pod crops and may be detrimental to both Palila and māmane woodland. Continuous, high-quality subalpine woodland habitat must be available near Mauna Kea for wetland forest drepanidines in search of seasonal nectar sources.

Palila make short-range movements within the

west slope of Mauna Kea to follow māmane pod availability, but they do not exhibit the dramatic change in densities that 'Apapane or 'I'iwi do. 'Apapane and 'I'iwi may make movements of many kilometers to follow nectar resource availability among different forest types. Peak annual abundance of 'Apapane and 'I'iwi appears to be related to the peak availability of māmane flowers in subalpine woodland and the period of lowest annual *Metrosideros* flower availability in wet forests (Ralph and Fancy 1995). Subalpine woodland is an important foraging ground for a high proportion of young birds that may move from wet forests during periods of nectar scarcity. Fifty-one percent of 'Apapane and 53% of 'I'iwi captured on the west slope of Mauna Kea were hatching-year (HY) birds (G. Lindsey, unpubl. data), whereas the proportion of HY Palila ranged only from 3.1% to 22.6% (Lindsey et al. 1995a). High-elevation subalpine woodland may also serve as an important refuge for Hawaiian birds susceptible to avian poxvirus or avian malaria (*Plasmodium relictum*) epizootics that may occur in late summer months (see Jarvi et al. *this volume*). Birds that make movements to higher elevation risk less chance of becoming infected by these pathogens than those that move to lower elevations. Subalpine woodland may serve to maintain higher population levels of these species during periods of nectar scarcity in wetland forests by conferring higher survivorship through seasonally abundant food resources and reduced disease transmission. However, seasonally migrating birds may also bring avian pox to subalpine woodlands.

If corridors of quality māmane habitat eventually connect relatively distant isolated tracts of larger māmane woodland, such as the north and south slopes of Mauna Kea, Palila and other drepanidines may be able to disperse longer distances, make seasonal use of other areas, and breed where there are sufficient food resources. Nearby habitat accessible to Palila should be protected from ungulates, replanted with māmane, and allowed to recover sufficiently for Palila to exploit shifts in pod availability (Scott et al. 1984, 1986; Fancy et al. 1993b, Fancy 1997). Palila are at high risk of extinction as long as they continue to breed in the single largest habitable tract of māmane woodland on Mauna Kea, where the probability of habitat destruction by fire is extreme. Ungulate eradication, predator reduction, grass reduction, fire management, and restoration of māmane woodland would benefit all drepanidines on Mauna Kea (Scott et al. 1986, USFWS 1986). These efforts may also be less expensive, more effective, and longer lasting than intensive single-species recovery ef-

forts, such as translocation of Palila (Fancy *et al.* 1997).

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