EVENING ROOSTING FLIGHTS OF THE HONEYCREEPERS *HIMATIONE SANGUINEA* AND *VESTIARIA COCCINEA* ON HAWAII

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ABSTRACT.—The Hawaiian honeycreepers *Himatione sanguinea* and *Vestiaria coccinea* regularly make evening flights in mixed flocks above *Metrosideros* forest canopy during the summer. These flights originate throughout the forest and converge on a common roosting area on the eastern flank of Mauna Loa, Hawaii. An estimated 42,000 birds (with *Himatione* far outnumbering *Vestiaria*) comprised the 1.5-h flight on the evening of 26 July 1974 between observation stations located at elevations of 1,350 and 1,850 m (linear distance of 7.6 km). The magnitudes of the evening flights are directly related to the quality of the forest (both structural and floral) from which the flights originate, with the nectar-producing tree *Metrosideros collina* being the primary determinant and food source. Although these flights are energetically costly, we believe they result in an overall overnight energy savings as a result of the thermal protection afforded by the mature forest comprising the common roosting area and escape from a lower elevation nightly fog belt. The formation of loose, mixed-species flocks during the evening roosting flights may provide greater awareness of and protection from aerial predation. The presence of rather widely separated foraging and roosting areas in *Himatione* and *Vestiaria* indicates the need for better understanding of their movements and spatial requirements, which are important factors to the continued survival of these presently common honeycreeper species. *Received 23 March 1979, accepted 17 September 1979.*

ALTHOUGH most common in flocking birds, the use of communal roosting areas by solitary feeding birds has been documented in many species and several orders (Ward and Zahavi 1973). During our investigations of the energetic and community relationships of certain honeycreepers (Drepanididae) and the forest tree *Metrosideros collina* (Myrtaceae) on the island of Hawaii (MacMillen 1974; Carpenter 1976, 1978; Carpenter and MacMillen 1976a, b, MS; MacMillen and Carpenter 1977), we regularly observed loosely knit mixed flocks of Apapane (*Himatione sanguinea*) and Iiwi (*Vestiaria coccinea*) flying unidirectionally on summer evenings. In addition, along the slopes between 1,350 and 1,850 m on the east flank of the volcano Mauna Loa, we observed that the lines of flight of these flocks converged on a common area when extrapolated. These observations suggested the presence of an unusual kind of flocking behavior and the likely use of a common roosting area by these otherwise solitary-foraging, nectar-feeding birds. In this paper we describe and interpret this behavior.

METHODS

All of the observations were made between 1972 and 1978 on the Keauhou Ranch, Kau District, Hawaii, particularly during the summer of 1974. Keauhou Ranch is located on the east flank of the volcano Mauna Loa; our study site extended along the Puu Oo Trail, between 1,350 and 1,850 m elevation (Fig. 1); the habitat consists of stands of mature ohia (*Metrosideros collina*)—koa (*Acacia koa*)—tree fern (*Cibotium glaucum*) montane forest alternating with logged areas of grassland subject to cattle grazing. Such habitat supported large populations of *Himatione* and *Vestiaria* during the day. The nectar of *Metrosideros* flowers served as their chief food source during the summer.

Our observations began in July 1972 when MacMillen first noticed evening flights, predominantly of *Himatione*, moving north above the forest canopy at 1,350 m on the Puu Oo Trail. We observed similar flights repeatedly during July and August 1973, but no counts were made. During the remainder of the

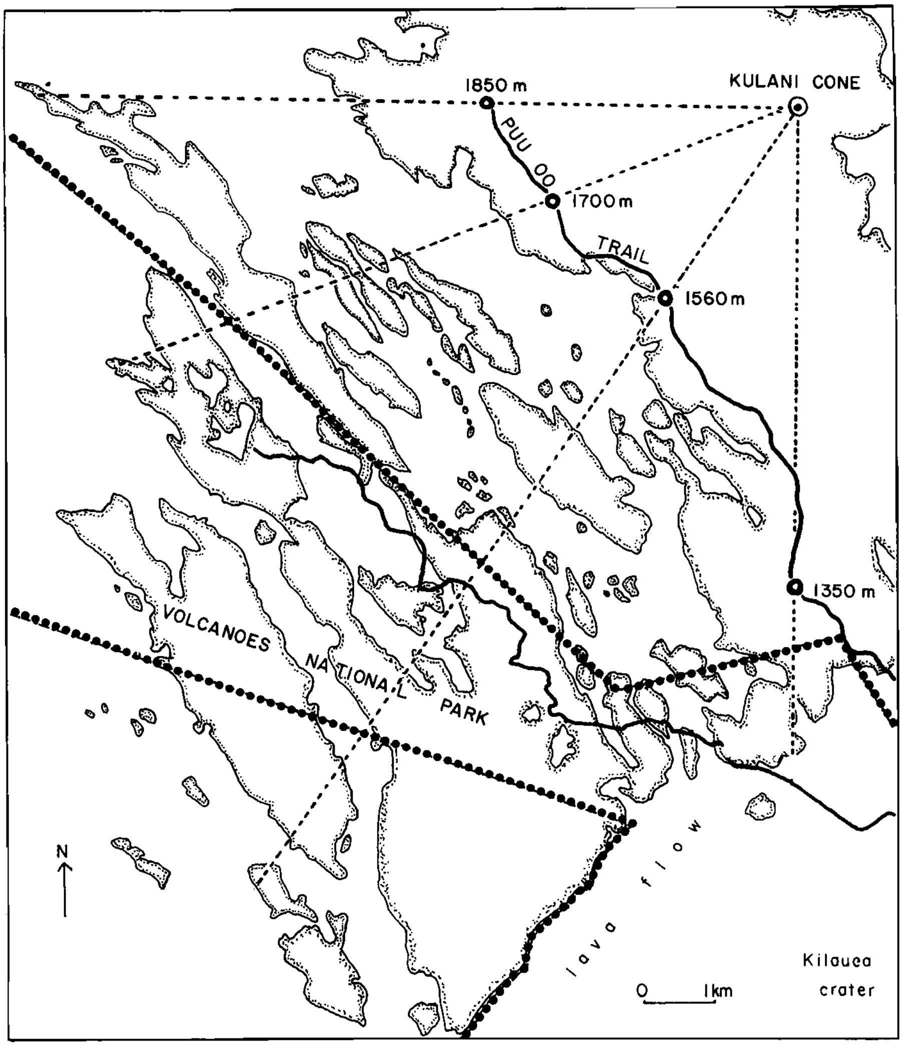

Fig. 1. A map showing the relationships between the observation stations (at 1,350 m, 1,560 m, 1,700 m, 1,850 m) along the Puu Oo Trail, Volcanoes National Park and the common roosting area near the base of Kulani Cone. The dashed lines represent extrapolations along the axes of unidirectional, above-canopy evening flights at each station. The dotted line is the boundary of Volcanoes National Park. The enclosed stippled irregular shapes represent those habitat islands suitable for foraging by *Himatione* and *Vestiaria* (after Mueller-Dombois and Fosberg 1974, Conant 1975). The dashed lines extend only to the last accessible habitat islands available in the area.

study, we quantified flights by identifying and counting the number of birds flying toward the north, south, east, or west for 15 min during each daylight hour. Although we could not always distinguish between *Himatione* and *Vestiaria* (both similar-sized red birds), we could readily distinguish between the red birds and other avian species. We distinguished within- and above-canopy flights and for the latter included only birds flying within 100 m of the observer. Here we concentrate on evening movements; a more thorough treatment of daytime flights commencing at first light appears in Carpenter and MacMillen (MS). To triangulate the destination of the above-canopy flights, observers at four elevations along a 7.6-km segment of Puu Oo Trail (Fig. 1) simultaneously counted birds for continuous 15-min periods from the beginning of the roosting flights until their cessation, assigning exact compass directions to their

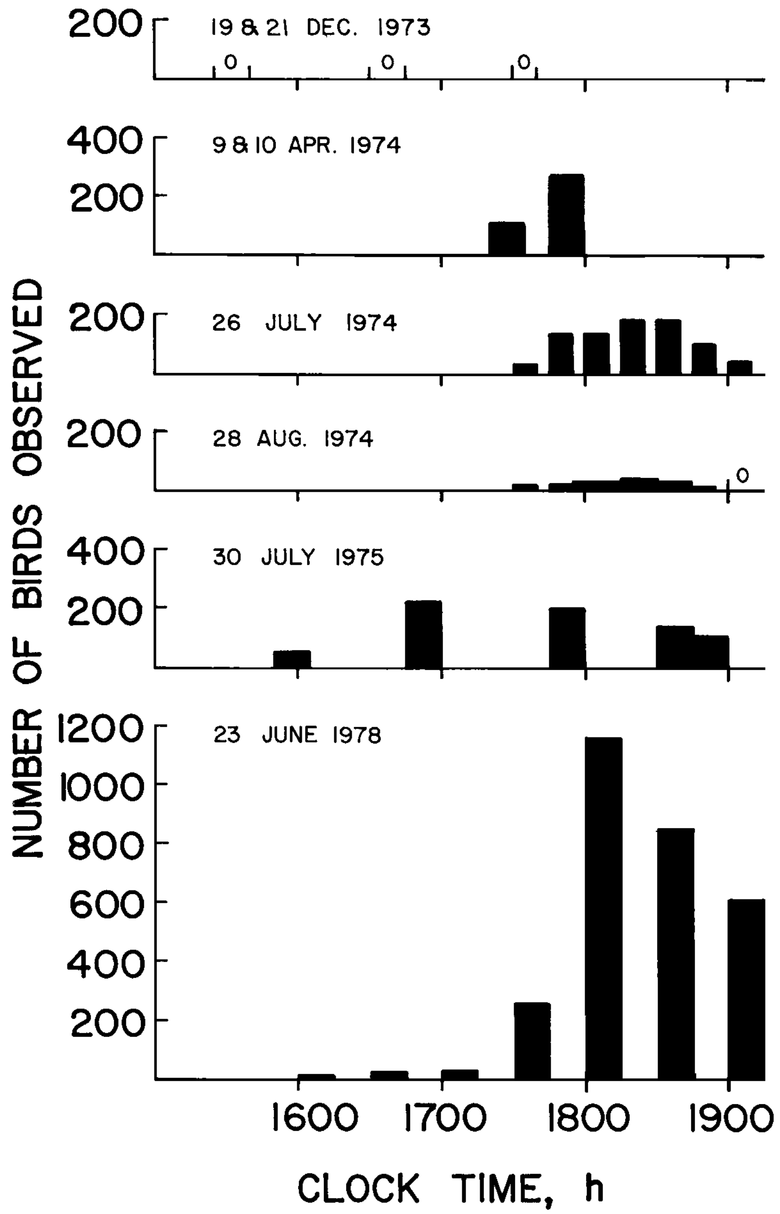

Fig. 2. The timing and magnitude of above-canopy evening flights of *Himatione sanguinea* and *Vestiaria coccinea* toward a common roosting area. These data are all from a single observation station at 1,350 m on the Puu Oo Trail. Zeroes indicate those periods when counts were made but no above-canopy flights were observed; except for April 1974 all counts were continued until flights ceased.

flights. This technique also permitted an estimate of the total number of birds involved in the flight over Puu Oo Trail.

The number of birds counted during the 15-min intervals was plotted against time at each elevation to give the total number of birds crossing a 200-m strip along the relatively straight trail between 1730 and 1910 (see Fig. 1). We then plotted these estimates at each station and interpolated the number of birds similarly passing over each consecutive 200-m corridor between stations to provide a combined

TABLE 1. Directional movements of flight of red honeycreepers (*Himatione sanguinea* and *Vestiaria coccinea*) and other birds below and above the forest canopy on the Keauhou Ranch, elevation 1,350 m, on 30 and 31 July 1975.

Time (h)	Kinds of birds	Number of honeycreepers flying toward compass direction							
		Below canopy				Above canopy			
		North	South	East	West	North	South	East	West
0630–1100	Red	14	21	11	5	107	116	13	15
	Other	17	8	1	0	2	0	0	0
1100–1530	Red	5	4	4	2	18	7	4	3
	Other	4	4	2	1	0	1	0	0
1530–2000	Red	4	4	6	1	710	8	1	3
	Other	4	1	9	2	2	0	0	0
Total	Red	23	29	21	8	835	131	18	21
	Other	25	13	12	3	4	1	0	0

estimate of the total number of *Himatione* and *Vestiaria* (red birds) flying over the canopy toward the roosting area along the entire 7.6-km transect for each of the two evenings.

In order to assess the quality of the forest from which evening flights originated, we constructed a composite overlay map for the southeast slope of Mauna Loa, which superimposed vegetation types on a USGS topographic map (from Mueller-Dombois and Fosberg 1974). From each observation station along the Puu Oo Trail we drew a line along the main direction of over-canopy flights (dashed lines in Fig. 1). These lines intercept those stands of *Metrosideros* forest considered by Conant (1975) to represent major foraging areas for these species. Conant's (1975) preferred habitats were directly translatable into Mueller-Dombois and Fosberg's (1974) vegetation types. Based upon the combined densities of *Himatione* and *Vestiaria* in their preferred foraging habitats (Conant 1975), we assigned vegetation types to three habitat quality categories with quality values (0.53, 0.35, 0.12) equivalent to the proportions of red birds observed foraging in each of the three habitat categories. These three habitat categories accounted for 96% of the red birds observed by Conant (1975) in all of the vegetation types. We calculated a Vegetation Quality Index for the line of flight over each counting station by assigning the appropriate quality value to each segment of vegetation type intercepted by the line of flight toward a given station, multiplying that value by the linear distance (m) intercepted, and summing all of the products along the line running from each station. The lines end to the west and south where our map indicated appropriate habitat stops. The relationship between the Vegetation Quality Index for each station and the estimated number of red birds comprising the unidirectional, over-canopy, roosting flight at that station was then determined graphically and by least squares regression analysis (see Fig. 4). The vegetation type designations (after Mueller-Dombois and Fosberg 1974) of the three habitat categories (after Conant 1975) and their corresponding quality values are given in the Appendix.

RESULTS

The evening flights of honeycreepers in June, July, and August generally commenced between 1600 and 1700 and consisted of a nearly continuous stream of individuals and small groups passing overhead in the same direction for 2 h. The groups that formed did not necessarily represent birds from a single foraging area, as birds foraging in one area frequently joined individuals or flocks passing overhead. *Himatione* frequently flew in erratic flight paths, calling and fluttering their wings audibly. Usually one or more individuals foraging in nearby trees would join such displaying birds, adding to the flock as it progressed toward the roosting area. Sometimes a low-flying bird or group of birds dropped into the upper branches of a tree and perched or foraged for a few seconds or minutes before continuing on. Once very late when it was nearly dark and most of the flights had passed over, we saw a lone, seemingly agitated *Himatione* swooping and fluttering in the air and calling repeatedly; no other bird joined it after several seconds, and it ceased calling

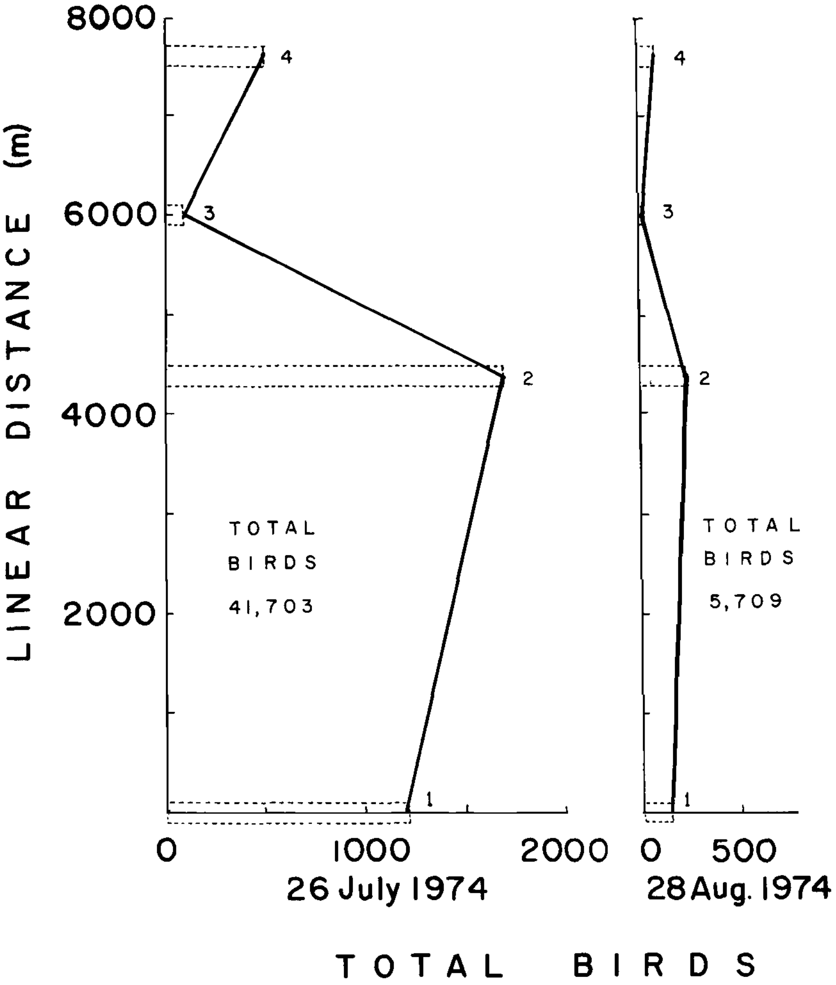

Fig. 3. The magnitudes of simultaneously counted, above-canopy evening flights of *Himatione sanguinea* and *Vestiaria coccinea* at four observation stations along the Puu Oo Trail on 26 July and 28 August 1974. The dashed bars represent the 200-m corridors and the total number of birds at each station, and the numbers 1–4 represent the stations at elevations of 1,350 m, 1,560 m, 1,700 m, and 1,850 m, respectively. The ordinate represents the cumulative linear distance along the Puu Oo Trail between successive stations from 1 to 4.

and flew directly toward the roosting area. On another occasion we saw one other very late bird flying straight toward the roosting area. Thus, this display behavior typically resulted in temporary but conspicuous aggregations of birds. Although certainly *Vestiaria* and perhaps *Himatione* are solitary feeders (Carpenter and MacMillen MS), the constitution of the evening above-canopy flights varied from single birds or groups of 3–5 individuals to, occasionally, aggregations of 20 or more. These groups consisted largely of *Himatione* but often contained single *Vestiaria* in addition. Although we have observed groups of exclusively *Himatione,* we have never observed groups of the rarer *Vestiaria*; the latter most frequently accompanied small groups of *Himatione* and less frequently flew individually. Although these

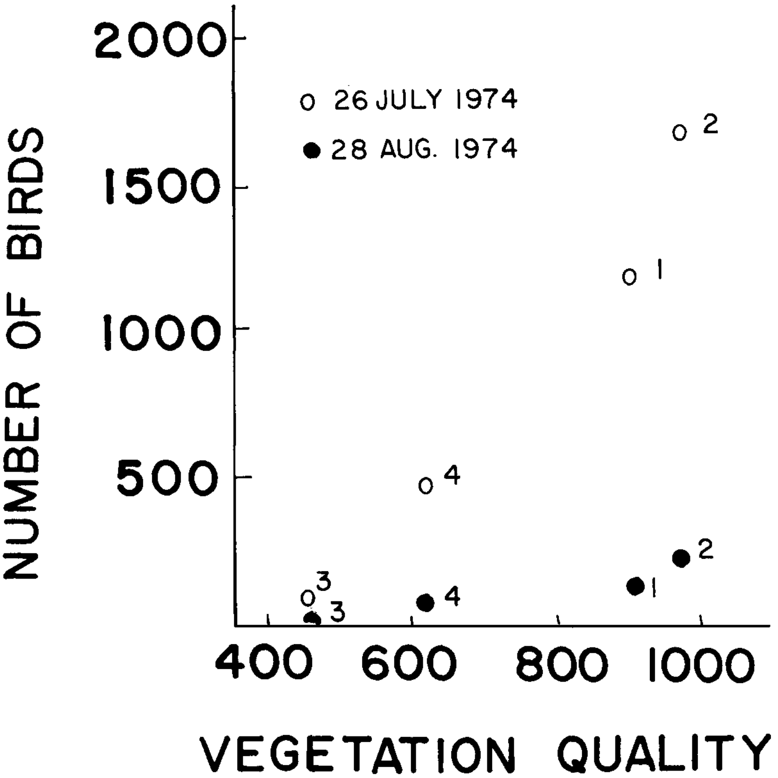

Fig. 4. The relationship between the numbers of *Himatione* and *Vestiaria* comprising an evening above-canopy flight at each station and the Vegetation Quality Index of the forested areas traversed by the line of flight toward that station. The numbers 1–4 are as in Fig. 3. For both dates there is a significant correlation (26 July, $r = 0.984$, $P < 0.05$; 28 August, $r = 0.941$, $P < 0.05$). The relationship for 26 July is described by the least squares regression equation, $Y = 2.913X - 1{,}297.37$, and that for 28 August by $Y = 0.352X - 140.73$ (Y is the number of birds, and X is the Vegetation Quality Index).

groups did not fly in formation, the birds were obviously flying together and formed loosely knit flocks.

At the 1,350-m observation station on the Keauhou Ranch, evening above-canopy flights of *Himatione* and *Vestiaria* occurred predictably during the summer months, with virtually all birds flying in a northerly direction. These flights involved only *Himatione* and *Vestiaria,* and summer flights of these magnitudes were confined nearly exclusively to those above the canopy during the evening hours (Table 1). Distinguishing between *Himatione* and *Vestiaria* was difficult in distant individuals, so we do not have accurate counts of their proportions, other than the qualitative estimate that many more *Himatione* than *Vestiaria* were involved. We presume that their proportions are similar to the 8:1 ratio reported for *Himatione*:*Vestiaria* by Conant (1975) for habitats similar to those near the observation stations. While we have inadequate observations of above-canopy flights in some seasons, our studies in December 1973 recorded no flights, while flights did occur on 9 and 10 April 1974 and on each June, July, and August evening during which observations were made between 1972 and 1978 (Fig. 2). Large flights occurred on 26 July 1974, but the number of birds observed diminished considerably by 28 August 1974 (Fig. 2).

Table 2. Magnitudes of above-canopy flights of honeycreepers at the 1,350-m observation station on Mauna Loa and percentages or estimates of *Metrosideros* trees flowering in different seasons and years.

		Extent of flowering		
Month	Year	Mean percentage[a]	Estimate	Total birds
December	1973	—	Very light	0
July	1974	38	Moderate	1,201
August	1974	27	Light	140
July	1975	77	Heavy	2,025
June	1978	—	Very heavy	5,587

[a] From Carpenter and MacMillen (MS).

These data suggest that the flights commence during spring, continue through summer, and then likely cease during fall and winter. Although the flights were generally confined to the period between 1600 and dark, their timing and magnitudes varied from month to month and year to year (Fig. 2).

Temporal and spatial variation in magnitude of flight is shown in our simultaneous observations of flights at four stations along an elevational gradient on the Puu Oo Trail (Fig. 3). Far more birds were involved in the flight of 26 July 1974 than that of 28 August 1974. The four observation stations differed consistently between periods in rank order of birds observed from them, and there was no correlation between elevation and number of birds comprising the evening above-canopy flight at a station (Fig. 3).

The lines of flight (Fig. 1) were oriented in such a way that they fanned out laterally toward their origins and converged medially toward their destinations. All lines converged on a very dense stand of mature *Acacia—Metrosideros—Cibotium* montane rain forest (after Conant 1975) in the Kilauea Forest Reserve near the base of Puu Kulani, a prominent cinder cone. We have not been able to investigate this area but presume that birds congregate there at night in very high densities. Although we refer to this as a common roosting area, its dimensions and roosting densities remain to be described. The number of birds comprising the evening flights at each station is positively related to the Vegetation Quality Indices of the forest intercepted by the lines of flight toward that station for both 26 July and 28 August 1974 (Fig. 4). Furthermore, at the 1,350-m observation station, where evening flights were toward the north and upslope, the magnitudes of evening flights corresponded directly with the magnitudes of *Metrosideros* flowering observed in the forest stands from which these flights originated (Table 2).

Discussion

The apparent presence of a common roosting area from which birds emerge in the morning to forage in the areas of richest flowering by day and to which they return by above-canopy flights in the evening suggests that the magnitude of the evening flights at any one place should be directly proportional to the quality (in terms of resource richness) of the diurnal foraging areas from which the flights originated. Our data in fact show a very close positive relationship between quality of the foraging area and magnitude of evening flight toward the common roosting area (Fig. 4, Table 2). Thus, we believe that the above-canopy evening flights we have observed repeatedly during summers on the Keauhou Ranch reflect the quality (both structural and floral) of the forests from which these flights emerge; as such, the system may involve thousands of birds whose absolute numbers appear to be determined by the distribution and abundance of flowering (Figs. 3 and 4). Such a view is consistent with recent refuging and central place theory (Hamilton and Watt 1970), and this system is similar in many ways to the refuging system commonly observed in starlings and several species of blackbirds on the American mainland (Hamilton and Gilbert 1969). For management purposes, a specific knowledge of *Metrosideros* forest structure and phenology in these foraging areas could perhaps be used to predict with some accuracy the numbers of honeycreepers likely to emerge from forest stands at the end of a day. Conversely, the numbers of birds emerging can be used to assess the quality of the forest serving as the source.

On the Keauhou Ranch and adjacent Volcanoes National Park, these flights from diurnal foraging areas result in convergence upon a common roosting area, which is generally upslope and several (3–6) km distant. Not only do nonterritorial *Himatione* and *Vestiaria* abandon their foraging areas for the roosting area, but even territorial *Vestiaria* abandon their territories each evening (pers. obs. 1974). The energetic expense of the flight to the roosting area (3.3% of 24-h energy budget in territorial *Vestiaria,* 4.6% in nonterritorial *Vestiaria,* and 8.1% in *Himatione*; from Carpenter and MacMillen 1976b and MS) is not great, but the combined benefits of the roosting area must be considerable to compensate for the increased exposure to aerial predators during above-canopy flights and for the possibility of displacement of territories in *Vestiaria* during the initial stages of territorial establishment. In our estimation the most likely benefit provided by the common roosting area is one of thermal protection. Although the common roosting area is higher in elevation (ca. 1,580 m) than much of the foraging area, it is above the level of heavy fog that occurs almost nightly on the lower slopes during the summer months. While the forest canopy at lower elevations might protect a bird from wetting by rain, the continuous exposure to fog and to fog drip likely would result in wetting of the feathers. Lustick and Yee (1974) have shown in the Redwing Blackbird (*Agelaius phoeniceus*) that wetting of the feathers increased the standard metabolic rate fivefold, and that normal thermoregulation could not be maintained by wet birds at ambient temperatures below 15°C. The average monthly temperature minima (representing nocturnal temperatures) at an elevation (1,280 m) within the foraging area of *Himatione* and *Vestiaria,* and within the nightly fog zone, was 11.3°C for June, July and August 1974 (Bridges and Carey 1975). We do not believe that it is energetically economical for honeycreepers to withstand many nights of such exposure, particularly during periods of sparse bloom and reduced nectar availability, especially if they have a viable alternative. Our observations indicate that they do have an alternative in a common roosting area and that they avail themselves of it. Roosting at higher elevations provides the additional advantage of reducing encounter with night-flying *Culex* mosquitoes, carriers of avian malaria that are most numerous at lower elevations (Warner 1968). The mature *Acacia—Metrosideros—Cibotium* montane rain forest that covers the roosting area is extremely dense, with a canopy approaching 30 m in height. Such a forest should provide considerable insulation from the clear night sky, as well as considerable re-radiation within the forest canopy. Although this is a region of high annual rainfall (ca. 1,750 mm/yr; Bridges and Carey 1973), the least (ca. 44 mm) occurs during the summer observation months of June, July, and August; of this, 80% is confined to the daylight hours (Bridges and Carey 1975). Thus, the roosting area is a dense forest affording thermal insulation and shelter from rain. Energetic savings in thermoregulation likely readily compensate for the modest energetic expense of flying there and for any increase in cost of territorial re-establishment for *Vestiaria.*

While mixed-species flocks occur quite commonly during foraging (see for example Morse 1970), such flocks are rare when individuals are not foraging, particularly in birds that feed solitarily. Thus, the formation of loosely knit flocks by *Himatione* and *Vestiaria* during the evening above-canopy flights to the common roosting area is unusual. Hamilton (1971), Vine (1971), and Pulliam (1973) have all provided models arguing that flocking behavior serves as a predator detection and avoidance mechanism; each deals with a different form of flocking, but collectively their predictions would seem to apply to flocking in general. Further, Murton (1968) states that in Wood Pigeons (*Columba palumbus*) the flock habit appears to be an important antipredator device, increasing the awareness of potential danger above that achievable by a single individual. These ideas are consistent with our view that, even though the exaggerated wing fluttering and showing of the white rump and undertail coverts by *Himatione* during flock formation increases the probability of detection by predators (*Asio flammeus* and/or *Buteo solitarius,* both diurnal raptors), flocking itself should also decrease the individual risk of predation below that of a nonflocking individual. The less common *Vestiaria* similarly benefit by joining flocks of *Himatione.* An observation by MacMillen on 29 December 1972 of a *Bueto solitarius* attempting to remove a *Himatione* from a mist net documents that this raptor will prey on honeycreepers.

This study demonstrates that each summer evening thousands of *Himatione* and *Vestiaria* move over the forest canopy from diurnal foraging areas to a nocturnal roosting area. Our observations are confined to a limited area on the east flank of Mauna Loa, but they indicate that many, if not most, of the birds involved in the evening flights have spent much of the day foraging in Volcanoes National Park, and that the nocturnal roost is an area of mature rain forest in the Kilauea Forest Reserve near the base of Kulani Cone (Fig. 1). The occurrence of these movement patterns is so predictable from year to year (Fig. 2) that the patterns must be integral parts of the adaptive repertoire of the two red species of honeycreepers. We believe, therefore, that undue disturbance to either the foraging areas or roosting area would result in disruption of the birds' movement patterns and would likely result in widespread decimation of *Himatione* and *Vestiaria* populations. We have recently learned (J. M. Scott pers. comm.) that similar above-canopy evening flights characterize populations of *Himatione* and *Vestiaria* around the entire flank of Mauna Loa, with the possible exception of Kona District. Thus, for successful wildlife management, biologists must identify and delineate these patterns of movement, the characteristics of the foraging areas, and the roosting areas of these honeycreepers in order to determine policies and priorities with regard to species preservation, both of birds and of the trees they pollinate (Carpenter 1976).

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APPENDIX. Habitat categories (Conant 1975) and corresponding vegetation type designations (Mueller-Dombois and Fosberg 1974) and quality values.

Habitat category	Vegetation type designation	Quality value (calculated from Conant 1975)
VI Closed *Metrosideros*—*Cibotium* montane rain forest	cM(C), cM, cM(ns)	0.53
92 Logged *Acacia*—*Metrosideros*—*Cibotium* montane rain forest	mx-AcSaM, AcSaM(ad), MAc(ns), ms-MAc	0.35
IV *Acacia*—*Metrosideros*—*Sapindus* savanna and closed mesic kipuka forest	mx-ns(AcSOM)	0.12