THE INFLUENCE OF NECTAR RESOURCES ON NESTING SUCCESS AND MOVEMENT PATTERNS OF THE COMMON AMAKIHI (*HEMIGNATHUS VIRENS*)

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ABSTRACT.—The objectives of this study were to investigate the influence of nectar re-sources on: (1) territory establishment, (2) breeding success, and (3) postbreeding dispersal in *Hemignathus virens* on Mauna Kea, Hawaii. I observed color-banded individuals from 1971 to 1981 and manipulated food during the 1975 breeding season by placing supplementary nectar resources in an area where breeding had not occurred in the previous 4 yr.

The results of this study demonstrated that *H. virens* is intrinsically tied to the nectar resources available within its breeding territory and that a minimum of 2,000 µl/day (1,400 cal) of nectar must be present before territory establishment will occur. This finding was further supported by the fact that no breeding occurred in the experimental area during the 6 yr after removal of the supplementary nectar.

Breeding success of *Hemignathus virens* was influenced by different levels of nectar avail-ability. The most successful breeding occurred at nectar levels of 20,000–40,000 µl/day (14,000–28,000 cal). More than 35,000 µl/day (24,500 cal) of nectar within a territory generally in-hibited successful breeding, presumably because too much time was spent in the defense of the nectar sources. Birds with larger amounts of nectar within their territories had concom-itantly larger clutch sizes. Postbreeding dispersal, an annual phenomenon in the *H. virens* population on Mauna Kea, did not occur if adequate food supplies remained available during the nonbreeding period. *Received 30 November 1982, accepted 6 September 1983.*

AVIAN ecologists often speak of food-limited populations, but evidence of competition for a specific food supply during the breeding sea-son is meager (Stenger 1958, Walsberg 1977). There seem to be two reasons for this lack of evidence: (1) Mere observations on nesting success and food supply are likely to be equiv-ocal. A multitude of factors affect nesting suc-cess as well as one another, and this interde-pendence of factors often obfuscates results. Avian nectivores, however, provide an unusu-al case in which individuals are largely depen-dent upon only one easily measurable re-source. (2) It is difficult to change one, and only one, factor. Occasionally, it is possible to con-duct an experiment that demonstrates the re-lationship between a single ecological param-eter and an organism's behavior. During my study of the Common Amakihi (*Hemignathus vi-rens*) such a situation arose, which enabled me to examine the effect of nectar resources upon territory establishment, breeding success, and postbreeding dispersal.

I shall present results from two kinds of studies: (1) an experiment in which, by the ad-dition of nectar resources, birds were induced to nest in an area that had not been used for breeding in the previous 4 yr; and (2) obser-vations of nesting success and postbreeding dispersal as a function of the amount of nectar present within each territory.

METHODS

Study area and vegetation.—The study site was a 25-ha plot at 2,130 m elevation on the southwestern slope of Mauna Kea, Hawaii (Fig. 1). It was located in one of the last extensive dry forests in Hawaii, a high montane savanna dominated by two tree species, *So-phora chrysophylla* (Leguminosae) and *Myoporum sandwicense* (Myoporaceae).

Sophora is by far the most important nectar source for *H. virens* on Mauna Kea and will be the only one considered in this paper. The phenology of *Sophora* has been studied on Hawaii by Baldwin (1953), La-moureux et al. (1981), and van Riper (1975b, 1980). Most flowering is in November through June, but a few widely scattered trees flower in other months. Flowering on Mauna Kea was greater in 1974 than in either 1973 or 1975.

Sophora flowers occur in terminal clusters of about 14 ($\bar{x} = 13.78$, SE = 1.22). Each flower is approximate-
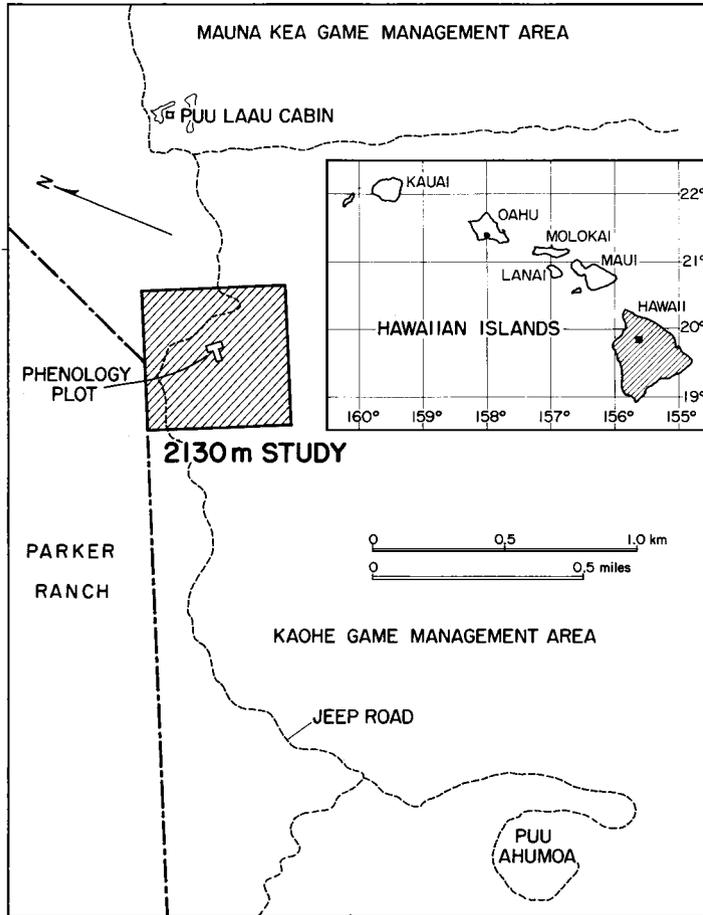
Fig. 1.   Map of the study site on the southwestern slope of Mauna Kea, Hawaii.

ly 25 mm long, with four elongated, curved yellow petals. Nectar is produced and stored at the base of the corolla. Individual flowers within a cluster open asynchronously, and approximately three ($\bar{x} = 2.77$, SE = 0.13, range = 0–8) produce nectar concurrently. Each flower produces nectar for 3–5 days after opening and may remain on the tree for up to 7 days after cessation of nectar production.

Nectar production was measured by bagging 19 clusters consisting of 244 flowers on 6 trees. Nectar was extracted with micropipettes at first light (0630), midday (130Q), and sunset (1830). This procedure was repeated for the entire nectar-producing period of each cluster (range 3–10 days). Nectar concentration was measured with an Itago hand-refractometer for 109 samples, and sugar concentrations averaged 19.21% (SE = 0.68, range = 5.8–53.7%). Nectar was produced in each cluster at an average rate of 2.63 μl/h (SE = 0.40, range = 1.70–3.36 μl) during the day. Very little nectar was produced over the night ($\bar{x} =$

2.25 μl/cluster, SE = 0.25). The average cluster, therefore, produced 33.81 μl of nectar over a 24-h period.

During 1975, flower abundance throughout 45 *H. virens* breeding territories was measured at weekly intervals over the nesting cycle (Table 1). Full flowering trees averaged 244 flower clusters (SE = 35.3, range = 123–460 clusters), while medium flowering trees averaged 54 flower clusters (SE = 194, range = 17–103 clusters). The amount of daily nectar (N_d) available to each breeding pair of *H. virens* was calculated using the formula:

$$N_d = (C_i)(F_i)(N_c)(T),$$

where C_i = the average number of flower clusters present at any one time in the territory over the nesting cycle, F_i = the average number of flowers/cluster, N_c = the average amount of nectar produced by a flower cluster each hour, and T = the time period throughout 24 h when nectar is produced. The av-
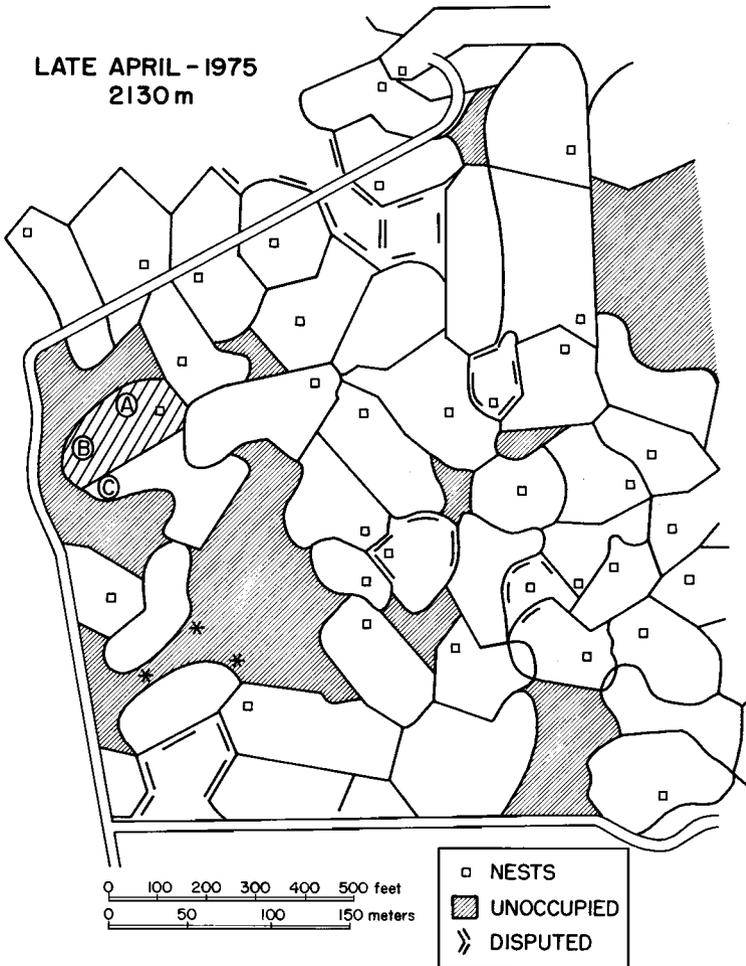
Fig. 2.   Map of *Hemignathus virens* breeding territories during April 1975 at 2,130-m elevation on Mauna Kea, Hawaii. Circled letters are the 3 supplemental feeding stations; asterisks are the 3 control feeding stations. The cross-hatched area is the experimentally initiated territory.

erage *H. virens* breeding territory contained 4.6 flowering trees (SE = 0.68, range = 1–9 trees).

The bird.—*Hemignathus virens* is a member of the endemic Hawaiian honeycreepers (Drepanidinae). A number of investigators have studied its breeding, ecology, and behavior (Baldwin 1953; Berger 1969; Kamil 1978; Kamil and van Riper 1981; van Riper 1975a, b, 1976, 1977, 1978; Kern and van Riper in prep.). It is the most abundant bird in the dry forest on Mauna Kea (van Riper et al. 1978). The diet consists principally of nectar and insects, although it will take various fruits. Territories are mutually exclusive and are reoccupied each year by the same individuals. Between breeding periods the territorial structure breaks down into a home-range system, and most birds undergo postbreeding dispersal, respond-

ing to temporal changes in flowering *Sophora*. A few pairs may remain on or near their breeding territory but occupy an area that encompasses 3–6 times as much space. These birds subsist chiefly upon insects, and conspecifics are permitted to forage within the home range.

From 1971 through 1981 I captured over 1,000 birds by mist net and banded them with aluminum Fish and Wildlife Service bands in combination with plastic color bands for subsequent individual identification in the field. I also closely monitored the population in terms of territory boundaries, movement patterns, and breeding success.

The experiment.—Immediately prior to the 1975 breeding season, within an area in which *H. virens* had not attempted to nest during the previous 4 yr,

TABLE 1. Potential *Sophora chrysophylla* nectar supplies and breeding information from *Hemignathus virens* territories during 1975, at 2,130 m elevation on Mauna Kea, Hawaii.

Territory number	Sophora nectar produced daily (μl)	Clutch size	Number fledged
5-75	32,001	3	0
12-75	21,938	0	...
16-75	32,001	2	1
17-75	21,938	(Eggs broken)	
18-75	54,924	3	0
19-75	26,554	2	1
21-75	32,001	3	3
22-75	23,755	0	...
23-75	18,308	2	2
24-75	20,124	2	0
25-75	28,370	3	0
26-75	18,308	0	...
27-75	49,478	3	0
28-75	9,078	2	2
29-75	1,816	2	2
31-75	13,693	3	2
32-75	28,370	3	2
34-75	27,386	0	...
35-75	5,447	2	0
36-75	21,938	2	1
37-75	28,370	3	0
38-75	3,631	0	...
39-75	20,124	2	0[a]
40-75	11,878	2	0
42-75[b]	0	2	2
43-75	18,308	3	1
44-75	38,412	0	...
45-75	11,878	2	1
48-75	5,447	3	0
50-75	11,878	0	...
51-75	23,755	2	2
52-75	3,631	2	0
53-75	3,631	2	0
54-75	16,492	2	0
55-75	10,062	0	...
56-75	20,124	0	...
57-75	26,554	0	...
58-75	10,062	0	...
59-75	10,062	0	...
60-75	11,878	2	0
65-75	13,693	3	0
66-75	8,246	0	...
70-75	20,124	2	2
71-75	20,124	(Not followed)	
75-75	10,062	2 (Fate unknown)	

[a] Nest predation; not included in calculations.
[b] Experimental feeder nest.

I established three supplementary food stations (Fig. 2). Each station was placed far enough from known territorial boundaries and from the other two stations (average 51.8 m) that birds had an adequate area in which to establish a territory. Each feeding station consisted of three 1,000-ml nectar feeders hung on bright yellow boards. The yellow simulated *Sophora* flower color and served to attract birds. A control, which consisted of the same number of boards and empty feeders, was established in another area (Fig. 2). The nectar feeders were filled with 20% sugar water, approximately the same sugar concentration as *Sophora* nectar. Feeders were filled on 10 January 1975, well before breeding commenced (the first active nest was found on 6 February), and were maintained daily into the period of postbreeding dispersal (10 June 1975). Observations were made during 24 sessions, each with a duration of not less than 1 h; using stopwatch, binoculars, and a tape recorder, I spent a total of 49 h observing bird use at each feeder from a blind.

RESULTS

Experimental improvement of a territory.—Territory establishment had not been observed in the experimental area for a period of 4 yr preceding 1975. Shortly after initiation of the supplemental "nectar" supplies, birds began to frequent the area. The majority were *H. virens*, but the introduced *Zosterops japonicus* also used feeders throughout the experimental period. Two 22-month-old *H. virens* males, WBk-X and OP-X, were first observed using the feeders on 21 January; WBk-X concentrated his efforts around Station A, while OP-X frequented the feeders at B. Neither bird had bred in the study area during 1974. Station C was incorporated into the adjacent territory of X-G, an established resident male. In addition to these birds, *H. virens* females X-PY and X-YY consistently used the feeders throughout early February.

By late February WBk-X and both females had disappeared; OP-X had taken over sole use of stations A and B. This male paired with WYY-X, a young bird whose complete life history was not known. The pair maintained a territory around these stations throughout the entire breeding season and successfully fledged two young. No birds nested at the control site. Birds were not observed nesting in this experimental area during the subsequent 6 yr following removal of the supplemental "nectar" supplies.

The added food resources had little or no effect upon other established *H. virens* pairs within the study site. Contiguous territorial boundaries, as they were delineated in the previous breeding season, did not change appreciably during 1975. Only the territory of male X-G was slightly enlarged to encompass feeding

Station C. At no time during the breeding season did I record other territory holders from within the study area at any of the feeders. The majority of birds (other than the resident pairs) recorded within the experimental area were yearling floaters (143 of 156 feeding observations).

The influence of Sophora *nectar abundance upon breeding success.*—The mean daily nectar available within a territory influenced breeding success, including the maintenance of a territory, clutch size, and the number of young produced. Each *H. virens* territory that I recorded in 1975 had *Sophora* flowering within its confines except the one with supplemental food supplies (Table 1). The minimum daily nectar requirement necessary for the maintenance of a breeding territory appears to be 2,000 µl (1,400 cal). Except for territory 29, however, it appears that in order to raise young successfully, a pair requires at least 9,000 µl (6,300 cal) of daily nectar. In most of the territories there was 10,000–30,000 µl (7,000–21,000 cal) of *Sophora* nectar produced daily, but production in those territories that were most successful in fledging young ranged from 20,000 to 40,000 µl (14,000–28,000 cal; Fig. 3). It appears that birds are unable to defend more nectar than this and still successfully fledge young. Indeed, when nests were divided into categories of success, the only pairs with a disproportionate difference in the amount of daily nectar produced within their territorial boundaries were those that did not successfully fledge any young (ANOVA, df = 39, $F = 4.51$, $P < 0.01$; Fig. 4).

An example of a "resource overload" situation in *H. virens* is the nesting history of male X-OR and female WP-X in 1974 and 1975. In the 1974 breeding season, this pair built nest #132-74 in an area of their territory in which five closely spaced *Sophora* trees subsequently came into heavy flower. At the height of this flowering, there was over 37,000 µl of nectar being produced each day just in the immediate vicinity of the nest. This pair of birds spent an inordinate amount of time chasing intruders. Throughout egg laying and early incubation periods, the birds averaged 10.2 chases/h (SE = 1.81), as compared to the mean chasing rate of 1.99 chases/h (SE = 0.22) of the Mauna Kea *H. virens* population during the breeding season (van Riper 1978). Their clutch of two eggs was not incubated, presumably because of the distraction caused by intruders. In 1975, however,
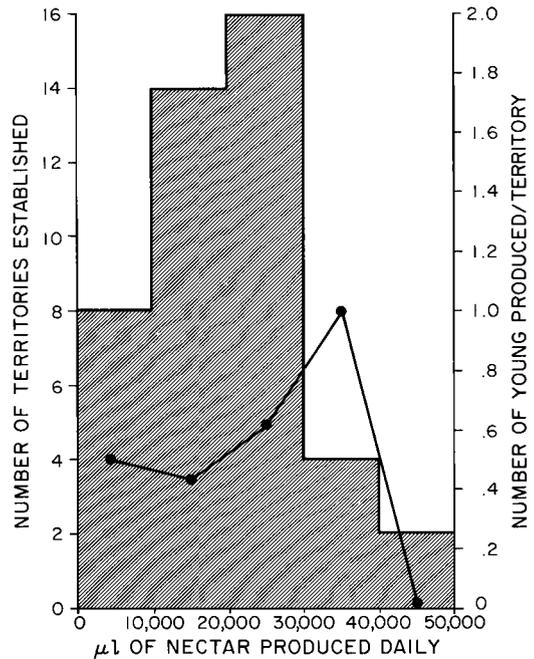

Fig. 3. The shaded bar graph depicts the relationship between the number of *Hemignathus virens* territories established and the amount of *Sophora chrysophylla* nectar contained within each territory (*n* = 45). The solid line is the average number of young produced within territories in relation to the amount of *Sophora chrysophylla* nectar within those territories (*n* = 41).

this pair built nest #36-75 in the same territory, but this year an average of only 22,000 µl/day (15,400 cal) of *Sophora* nectar was available throughout the entire territory (Table 1). The pair again had a clutch of two eggs, but this time successfully fledged one young.

The yearly mean clutch size of *H. virens* has been shown to be influenced by *Sophora* nectar production (van Riper 1978). The results of this experiment support my earlier findings, in that clutch size varied in relation to the nectar available to each pair. Birds in territories with more than 30,000 µl/day (21,000 cal) of nectar produced larger clutches (Fig. 5).

The influence of Sophora *nectar upon postbreeding dispersal.*—By May 1975, the majority of *H. virens* had left the 2,130-m study area in a postbreeding dispersal. This movement pattern is an annual occurrence and coincides with the cessation of *Sophora* flowering (van Riper 1978).
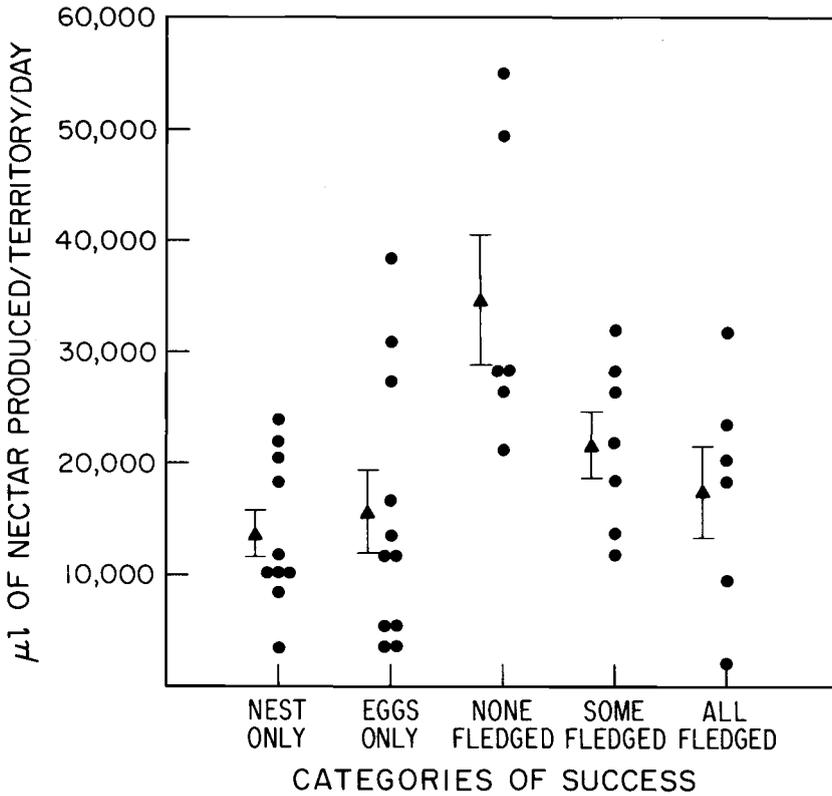
Fig. 4. Success categories of *Hemignathus virens* nests in relationship to the amount of daily *Sophora chrysophylla* nectar within that territory. Triangles are the mean nectar production for each group, and lines are standard errors.

For example, during the peak breeding period (April), over 10% of the *Sophora* branches throughout the 2,130-m study area bore flowers, while in May less than 2% were in flower (van Riper 1980). The birds apparently move around Mauna Kea in search of nectar.

The experimental area was the only portion of the 2,130-m study area in which I recorded *H. virens* in any numbers after the postbreeding exodus. The pair associated with the experimental feeders, along with their young, remained until June, when the feeders were removed. After the fledging of their young (22 April), defense of the feeders waned, until by mid-May there was little territorial aggression observed. During this latter period I recorded for the first time instances of resident *H. virens* breeders from other areas of the 2,130-m study area, as well as a large number of recently fledged young, using the feeders. During this

time birds would line up on the yellow boards waiting to feed.

Although the feeders were an artificial situation that resulted in a more intense use of an area than might normally occur, the feeder experiment indicates what happens when food resources become available to *H. virens* in the nonbreeding season. In another area of the 2,130-m study site during 1973–1974, I recorded a banded pair within their territory for 15 consecutive months. Within the original breeding territory, two *Myoporum sandwicense* trees were heavily fluxing sap, and this resource, together with the insects it attracted, was apparently enough food so that the birds and their young could remain in the area throughout the entire nonbreeding period. Paton (1980) has recently described this same phenomenon occurring in a number of honeyeaters (Meliphagidae) in Australia. The postbreeding dispersal

of this pair of *H. virens* was obviously sup-
pressed by the presence of a copious food sup-
ply, as was that of the pair associated with the
experimental feeders.

DISCUSSION

The results of this study demonstrate that the
H. virens population on Mauna Kea is influ-
enced by *Sophora* nectar resources in several re-
spects: (1) territory establishment will not oc-
cur unless a minimum amount of nectar is
available within an area; (2) breeding effort is
most successful in territories that contain nec-
tar within an optimum range, balanced be-
tween the minimum amount necessary to pro-
duce the largest possible clutch size and an
upper limit determined by what can be eco-
nomically defended; and, (3) postbreeding
movement, an annual phenomenon in the pop-
ulation, need not occur if adequate food sup-
plies are made available in the nonbreeding
season.

Territory establishment.—Hemignathus virens on
Mauna Kea defend strict territorial boundaries.
Brown (1969) believed that only where the
density of food resources exceeded a certain
level did it become economical in terms of time
and energy to defend a territory. On Mauna
Kea this level appears to be about 2,000 µl (1,400
cal) of daily *Sophora* nectar, because only after
nectar resources rose above this threshold was
a territory established. The daily nectar avail-
able to breeding *H. virens* is considerably less
than has been reported for other nectarivorous
species. Gill and Wolf (1975) found that Gold-
en-winged Sunbirds (*Nectarinia reichenowi*) de-
fended a feeding territory only when there was
from 5,500 to 13,375 µl (3,850–9,712 cal) of nec-
tar available per day. A similar situation exists
with *Selasphorus rufus* in eastern Arizona (Ko-
dric-Brown and Brown 1978). Carpenter and
MacMillen (1976) reported nectar quantities
from six feeding territories of nonbreeding
Vestiaria coccinea (Drepanidinae), and all were
greater than what I recorded for *H. virens*
breeding territories. Perhaps, as Hainsworth
(1977) showed in *Colibri coruscans*, nectar for *H.
virens* on Mauna Kea is important as a primary
food source because of its stationary predict-
able nature rather than the proximate ability of
the birds to exploit nectar more efficiently than
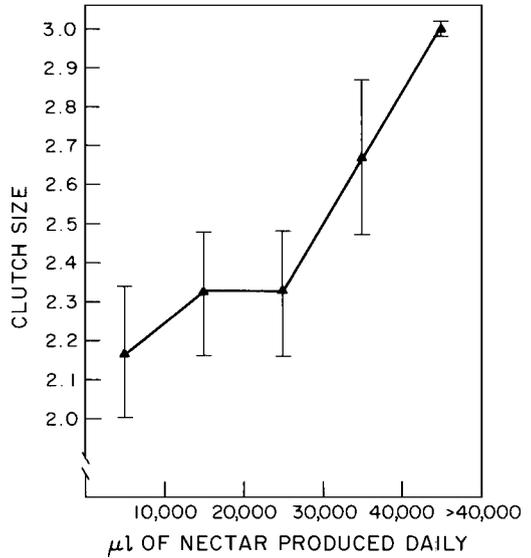insects. It must also be remembered that insects

Fig. 5. The relationship between *Hemignathus vi-
rens* clutch size and the amount of daily nectar avail-
able within a territory (*n* = 26). Triangles are the
means; lines are the standard errors.

form an important component of *H. virens*' diet,
particularly when they are raising young
(Baldwin 1953, van Riper 1978). Nevertheless,
a certain quantity of nectar appears to be a pre-
requisite within an area for successful breed-
ing.

Breeding success.—Hemignathus virens pairs in
territories with very low and very high quan-
tities of nectar were often not successful in
fledging young. Defense of a greater food
source would seem to require a disproportion-
ate amount of time and energy. The experi-
mental nectar feeders provided an unlimited
amount of daily "nectar," but, as they were sit-
uated on the opposite side of the territory from
the nest, they were easily defended. Therefore,
the amount of nectar being defended appears
in most cases not to be the upper limiting fac-
tor of successful breeding, but rather the ability
of the bird to defend the nectar sources.

The range of most successful breeding oc-
curred in territories in which the daily *Sophora*
nectar production was between 20,000 and
40,000 µl (14,000–28,000 cal). This was the range
of maximum fitness, determined on the one
hand by clutch size (pressure to produce the
largest clutch and therefore most potential

young) and on the other by the ability of the pair to defend as large an area as possible and still be able to raise young (pressure to occupy a territory that was easily defensible). Less than half (20 of 44 pairs) of the population defended an optimal nectar supply. The *H. virens* breeding on Mauna Kea have contiguous territories (Fig. 2), and it may be that the large number of suboptimal territories are a result of differential social dominance forcing certain individuals to contract their territories below the otherwise optimal size, as suggested by Hixon (1980).

There is some evidence to suggest that elsewhere food may not be as critical to *H. virens* as it is on Mauna Kea. Eddinger (1970) found that on Kauai, *H. virens* territories consisted of a small circle around the nest, usually extending to a radius of 5.5 m. Baldwin (1953) worked with this species on Mauna Loa, Hawaii and reported that territories were loosely held and often shifted within limits. Perhaps *H. virens* uses different territorial strategies in different habitats, as does *Phainopepla nitens* (Walsberg 1977).

Postbreeding movement.—Movement patterns have been linked to changes in food availability for a number of nectarivorous species (Skead 1967; Gill and Wolf 1975; Carpenter 1976, 1978; Carpenter and MacMillen 1976). Stiles (1973) felt that as a group, nectar feeders are the most nomadic of small land birds. Movement patterns in the nectarivorous guild of the Drepanidinae have been linked with changes in flowering on Hawaii (Baldwin 1953, MacMillen and Carpenter 1980). I have also found that the end of seasonal *Sophora* flowering on Mauna Kea occurs concurrently with *H. virens* postbreeding dispersal, at which time the birds move around the mountain seeking patches of flowering trees (van Riper 1978). In fact, a reasonable generalization based upon these varied accounts is probably that avian species whose life habits include reliance upon a nectar source demonstrate movement patterns in one form or another in at least some period of their annual cycle.

As has been demonstrated in this study, however, these movements can be overridden if food supplies remain available at a fixed location. Stiles (1973) found that in California many of the recently introduced nectar producing plants have curtailed movement patterns in the Anna's Hummingbird (*Calypte*

anna). Kodric-Brown and Brown (1978) were able to keep migrant Rufous Hummingbirds (*Selasphorus rufus*) on territories with the addition of an artificial nectar supply. Pimm (pers. comm.) has demonstrated in southeastern Arizona that with a constantly available food supply, three species of hummingbirds will forego seasonal movements. It thus appears that nectar levels control seasonal movement patterns in many nectarivorous species, and this is particularly true of *H. virens* on Mauna Kea.

CONCLUSIONS

The results of this study demonstrate that the *Hemignathus virens* population on Mauna Kea is intrinsically tied to its food supplies. It is also evident that a lack of food, in this case *Sophora* nectar, was probably the limiting factor that, in the 4 yr previous to and the 6 yr following the experiment, had prevented this species from breeding within the experimental area. Further credence is lent to this argument by the facts that the artifically stimulated territory was the only one of 45 that totally lacked *Sophora* flowering throughout the 1975 breeding season and that the pair associated with the supplemental food was able to fledge two young successfully in a year of lower than normal fledgling productivity. Nectar resources also influenced breeding success in that the birds responded to different levels of this food supply. The lowest level (approximately 2,000 μl/day; 1,400 cal) appears to be essential for territory establishment but in most cases is not adequate for successful breeding. The next threshold is reached at approximately 10,000 μl/day (7,000 cal), which seems to be the minimum amount necessary for feeding young. The maximum nectar level is reached abruptly at 35,000 μl/day (14,500 cal), after which it appears that successful breeding cannot usually take place, presumably because a disproportionate amount of time has to be spent in defense. Finally, postbreeding dispersal was found to be influenced by the amount of food resources available within a region.

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