FORAGING FOR INSECTS BY A TROPICAL HUMMINGBIRD

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Evolutionary-ecological studies of tropical plants and animals have illustrated that certain tropical organisms respond to differences between wet and dry seasons. Certain species of trees show distinct flowering and fruiting patterns in relation to the dry season in various regions of Costa Rica (Janzen 1967). It has been hypothesized that wetter habitats could be expected to contain a greater proportion of those predators specialized for feeding upon small insects than would drier habitats (Janzen and Schoener 1968). This reasoning stems primarily from the observation that there is a distinct paucity of small insects associated with drier habitats, because of problems of desiccation associated with small body size (Janzen and Schoener 1968). Similar arguments can be made for changes in local distributions and abundances of these predators between wet and dry seasons. Despite these interesting ideas, studies on seasonal patterns of interactions between insectivorous vertebrates and their prey have not appeared in the literature. Such experimental studies are needed as a vehicle for increasing our understanding of tropical communities and the impact of season upon their temporal and spatial persistence.

This paper discusses foraging for insects in one Costa Rican species, the Long-tailed Hermit Hummingbird, *Phaethornis superciliosus* (hereafter referred to as *Phaethornis*). This species ranges from southern México to Bolivia and Brazil, inhabiting thinned forests and woodland borders (Slud 1964). Certain aspects of the biology of this species and the Little Hermit (*P. longuemareus*) have been studied in Costa Rica (Skutch 1951, 1964), while other species of *Phaethornis* have been similarly studied elsewhere (Skutch 1950; Snow and Snow 1964). However, there are no published accounts of long-term, systematic studies on foraging for any members of this large genus. While it has been suggested that most species of hummingbirds spend relatively little time foraging for insects (at least from data available on the Anna Hummingbird; see Pearson 1954), Slud (1964) alludes briefly to active insect foraging by *Phaethornis,* and Wagner (1946) contends that insects are a major food source for many species of hummingbirds. However, quantitative data on such foraging for any species are lacking.

The data discussed here are from two sources: monthly observations on the foraging of several marked individuals gleaning for prey on understory plants in primary-growth wet tropical forest, and from detailed observations on a single individual feeding on insects trapped in webs of a large orb-spinning spider, *Nephila clavipes,* situated in a well-lighted (exposed) area at a forest edge.

MATERIALS AND METHODS

STUDY AREA AND CLIMATE

These studies were conducted at Finca La Selva (hereafter referred to as La Selva), a research field station of The Organization for Tropical Studies located near the village of Puerto Viejo (10° 26′ N; 89 m elevation), Heredia Province, Costa Rica, from early November 1968 through late August 1969. This locality is situated in the wet evergreen forest that extends almost continuously down the Caribbean coast of Central America from about Veracruz, México. Although such a region usually experiences very little dry season, during 1969 the dry season was unusually severe, lasting two months longer than usual and with about 2.5 months of almost no rainfall (fig. 2A). Rainfall data were obtained daily from a standard rain gauge maintained at the field station and situated in an open, cleared area. Temperatures (fig. 2A) were usually recorded on three to seven days per week, although no data were recorded for some weeks.

PROCEDURES

Observations were made on *Phaethornis* as a "leaf-gleaning" predator and as a "web-gleaning" predator. In this paper, foraging is defined as probing among leaves or webs for prey; it includes the actual motion of picking up prey in the bill as well as searching for prey; the term "insectivorous" includes predation upon spiders and other terrestrial arthropods in addition to insects.

Frequent observations made in October 1968 in a 40 × 25 m rectangular area of primary-growth wet tropical forest bounded on three sides by heavily-used foot paths (and more forest) and on the fourth side by an open, sunny, swamp, confirmed that *Phaethornis* in this area forages for prey among understory plants (mainly palms). No observations were made in other parts of the forest. The entire study

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 The Condor 73:36–45, 1971

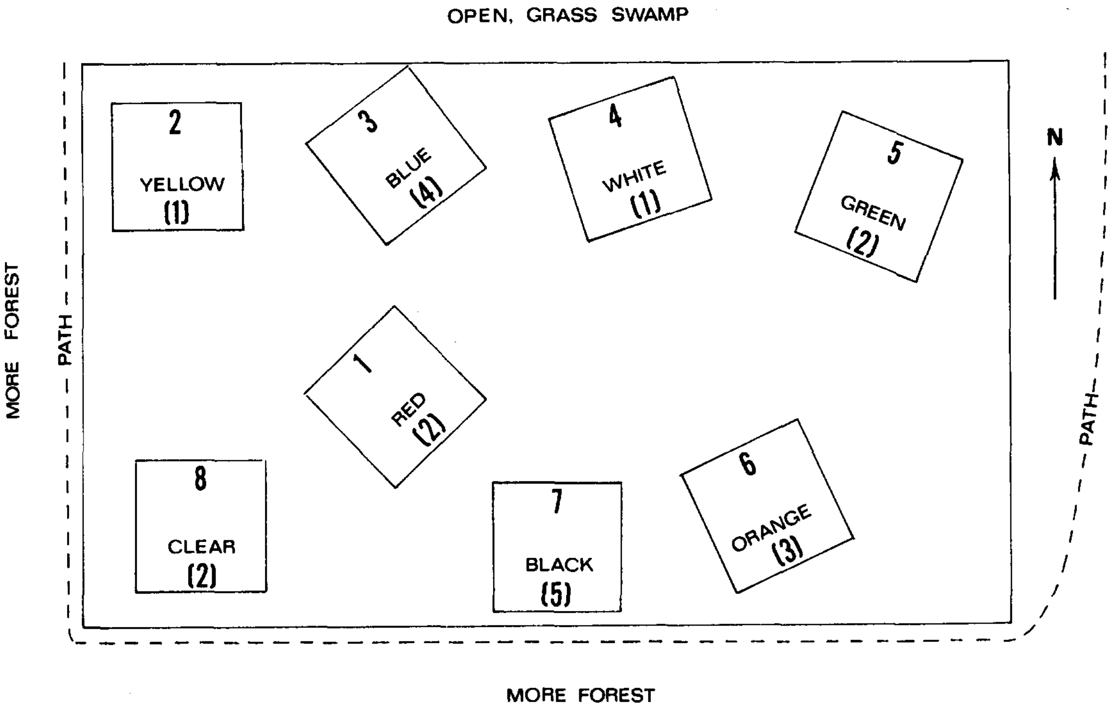

FIGURE 1. The study area in well-shaded tropical forest understory at Finca La Selva. The approximate positions within this area of eight foraging sites visited by foraging *Phaethornis* are indicated diagrammatically by squares. In each square the top figure is the number assigned to the foraging site; the color is that used to mark the individuals captured at that site; and the numbers of birds marked appears in parentheses (total = 20).

area (fig. 1) sloped gently down to the swamp side and was probably well drained of excess water during the wet season. It contained 39 large canopy trees scattered over the terrain and the understory palms frequently visited by foraging *Phaethornis* were *Welfia georgii* and *Geonoma binervia,* which together comprised close to 90 per cent of all plants 5–13 ft tall in this area. I located and staked out eight "tree clumps" that were visited regularly by *Phaethornis.* Figure 1 shows that these "foraging sites," each about 20 ft square (range, 16–21 ft square), were scattered over the study area, with adjacent sites usually no closer than 15 ft. Some individual birds at each site were netted and color-marked with thin strips of plastic ribbon tied to one leg and then released at the place of capture. All individuals from a given site had the same color code, but a different color code was used for each site. In cases where there was more than one individual at a site, it was not possible to distinguish between individuals at those sites. Each of these foraging sites was assigned a number (1–8) and from 5 November 1968 through 7 June 1969 each was usually observed on one or two days per month. The numbers of individuals initially marked and their color codes are given in figure 1. For each month's observations, the actual sequence of studying marked birds at each site was determined by use of a table of random numbers. Observations were usually made from 06:15 to 11:00 and from 14:00 to 17:00 CST.

From 9 May through 27 May at foraging sites 3 and 5, a simple experiment was carried out to assess the relation between the amount of foliage (leaves) scanned for prey and the length of time spent foraging by *Phaethornis.* After measuring approximate surface areas of several leaves on all palms used for foraging at each of the two sites (18 and 10 small trees, respectively), the distal one-third of every leaf was snipped off perpendicular to the midrib (i.e., across the leaf). On the following two days, the usual records were kept on occurrence of *Phaethornis* at these "treated" palms. On the third day the middle one-third of the same leaves were snipped away, leaving only one-third of the original amount of foliage available to search by *Phaethornis.* For the next two days the same data were recorded as before. Then the remaining foliage was removed and records on bird activity kept for two more days. Finally the stems were removed to within 2–3 ft of the ground (essentially eliminating the trees) and the occurrences of marked *Phaethornis* were noted during the next 10 days. While these observations were being made, observations for each phase of the above experimental manipulations were also made at the 6 remaining "control" foraging sites to eliminate effects other than those resulting from the experiment.

About 30 m from one side of the study area and situated in a well-kept, cleared, open, sunny area, there is a two-story, wooden-frame field station building that, at least during 1968 and 1969, harbored prodigious numbers of the orb-spinning spider, *Nephila clavipes,* on the outsides of all four walls. Part of this spider population (the webs on one of the walls) was visited regularly by a *Phaethornis* from early November 1968 through early June 1969. This was always the same individual, recognizable by a

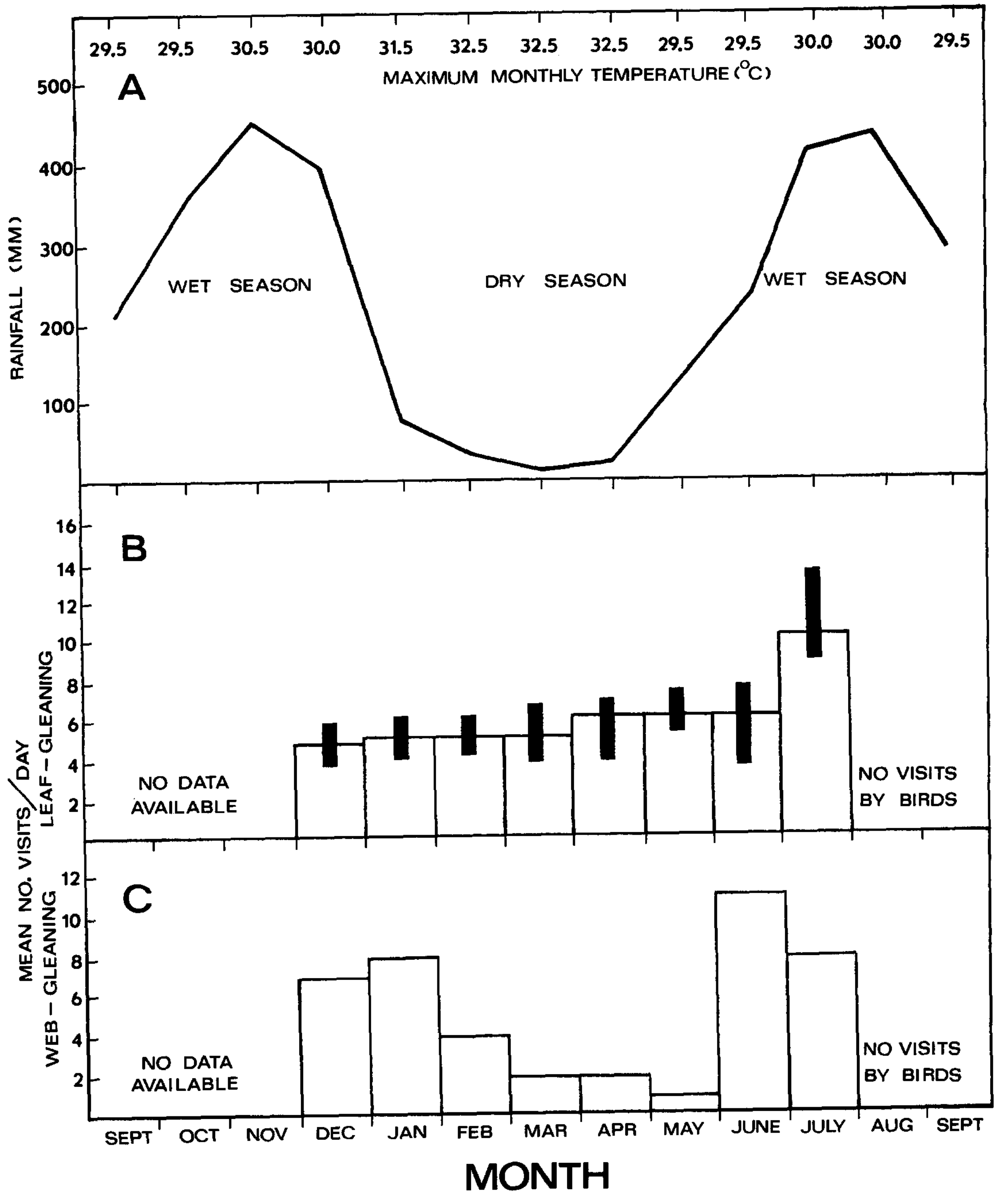

FIGURE 2. A. Monthly (and seasonal) trends in rainfall and maximum temperatures during parts of 1968 and 1969 at Finca La Selva (near Puerto Viejo, Heredia Province, Costa Rica). B. Mean number of daily leaf-gleaning visits by single color-marked individuals of *Phaethornis* at foraging sites 2 and 4 located in well-shaded wet tropical forest understory. (Ranges are indicated by the vertical black bars.) C. Mean number of daily visits made by a single individual of *Phaethornis* foraging for insects trapped in spider webs located in an open, sunny, cleared area.

sizable portion of its tail missing throughout the entire study period. When I was at La Selva, daily records were kept on the numbers of days per month that this individual visited *Nephila* webs and plucked off trapped insects. The amount of time spent at the webs was also recorded for this bird. Careful counts of insects trapped in the webs were made on several mornings (no later than 06:30) each month. Similar counts were made on the same days after 16:45, the time at which *Phaethornis* usually ceased to visit the webs. In early June the webbing of *Nephila* had been torn down completely, and further observations were made for only a short time thereafter.

TABLE 1. Foraging by marked *Phaethornis* for insects and spiders in well-shaded wet tropical forest understory.

		$\bar{x}$ min/visit,[b] and $\bar{x}$ no. visits/individual per day (in parentheses)[c]							
		Foraging site							
Months	No. days observation[a]	1	2	3	4	5	6	7	8
Nov.	16	11	12 (4)	10	9 (4)	14	18	13	10
Dec.	8	14	12 (4)	10	11 (4)	14	18	19	10
Jan.	16	14	18 (7)	13	11 (3)	15	16	19	14
Feb.	14	12	16 (5)	14	14 (4)	15	20	23	14
March	14	10	14 (5)	14	14 (7)	21	20	23	16
April	16	16	14 (6)	13	12 (7)	16	16	24	16
May	12	14	14 (7)	16	10 (5)	20	20	18	15
June	16	7	9 (14)	10	6 (11)	7	8	10	9
July	10		(0)		(0)				

[a] These are the total number of days on which observations were made; usually each site was observed 1–2 days per month.
[b] These values probably include periods of perching among understory trees.
[c] Numbers of visits were calculable for foraging sites 2 and 4 since only a single bird was marked at each of these sites.

RESULTS

Figure 2 shows that, in terms of average number of daily visits, leaf-gleaning for insects and other arthropods in forest understory is unaffected by the dry season, but that in open sunny conditions, web-gleaning for insects is reduced during the dry season. The data in table 1 indicate further that the amount of time spent leaf-gleaning during visits by *Phaethornis* in forest understory is unaffected by the dry season at La Selva. The increase in number of visits and associated decrease in time spent per visit (table 1) seen for the first week of June (and actually including the last four days in May) can be attributed to a concurrently observed large increase in numbers of small flying insects (mostly Diptera) on palm leaves during the transition between wet and dry seasons. Based on some records kept for insect densities prior to this time, it appeared that there was about a twofold increase in numbers at this time. An increase in abundance of prey for a predator that possesses a "routine" time schedule of foraging (table 1) implies that less time is required to obtain the necessary amounts of food stuffs (i.e., less time spent per visit at a food source) but that it still may take advantage of this temporary preponderance by feeding at more frequent intervals (i.e., an increased number of visits per unit time).

Color-marked individuals always appeared at the same foraging sites over a period of several months (table 2). There was very little overlap between various foraging sites for marked individuals even though sites were generally close to one another. For the entire study period, percentage of overlap of marked individuals among foraging sites was always low (table 2).

TABLE 2. Evidence of low overlap of foraging sites for insectivorous individuals of *Phaethornis* in well-shaded wet tropical forest understory at Finca La Selva, during parts of 1968–1969.

			Length of observation periods[c] $\bar{x}$ min ± SE		% occurrence of marked birds							
Site	No. days observation[a]	No. observation periods[b]	AM	PM	Yellow	Blue	White	Green	Clear	Red	Black	Orange
1	18	36	250 ± 9.6	180 ± 5.5	2	1	1	4	–	92	–	–
2	14	24	302 ±10.0	180 ± 6.0	95	–	2	2	–	1	–	–
3	16	32	278 ±14.0	175 ± 6.5	1	90	2	2	–	2	2	1
4	16	36	300 ± 5.8	178 ±10.0	5	–	90	–	–	2	2	1
5	12	22	300 ± 4.0	180 ± 7.0	3	–	–	87	–	6	–	4
6	12	26	293 ± 7.0	180 ± 5.5	–	–	3	–	2	–	–	95
7	18	34	300 ± 6.0	178 ± 6.0	–	–	–	–	–	–	100	–
8	16	30	296 ± 5.0	180 ± 4.5	–	–	6	–	90	4	–	–

[a] Foraging sites were observed either one or two times per month, but this varied from month to month. Therefore, the greatest number of visits at a given site could be 18 days (for entire study period) and no site was visited only once each month (nine days). Observations were made only on days when marked birds were present.
[b] On a day of observation at a given site, there were usually (but not always) two separate periods of observation (AM and PM).
[c] These values give the average amount of time spent by the observer at a given foraging site; usually five hr were spent in the AM and 3 hr in the PM. In calculating SE, *n* was usually taken as the value given in the "no. days observation" column, since on most days, sites were visited twice.

That eight foraging sites persisted for a small population of *Phaethornis* over several months time is not meant to imply that there were no other such sites being used for insect foraging in the general vicinity. There was very little difference between the trees comprising these particular foraging sites and trees in other parts of the surrounding forest understory. As with trees in the foraging sites, insects and other arthropods were seen crawling on the leaves and stems of trees located throughout the study area. In general, insects were less numerous than were various species of small spiders and the bulk of insects represented by Diptera, Hymenoptera, Homoptera, and Coleoptera. Samples of understory insects taken with a standard sweep net from July 1969 through March 1970 in a section of forest at La Selva similar to the one used as a study area in the present report indicated that these groups of insects were the most abundant forms after spiders. In the present study, attempts were made to actually count arthropod densities on palms visited by *Phaethornis*; densities ranged from 3 to 27 individuals per leaf, with the average number (68 counts) being 15. Unfortunately it was not possible to count numbers and types of different prey consumed by foraging individuals, as their movements were fast and sudden and the birds were not always visible among the leaves while flying and perching.

Foraging in the understory was done among palm leaves of the following size ranges (surface areas and stem lengths): *Welfia georgii*, 1632–58080 cm^2 with stems 240–660 cm long and with the majority of leaves (85 per cent) being over 30,000 cm^2 ($n = 147$); *Geonoma binervia*, 1865–2160 cm^2 with stems 43–65 cm long and the majority of leaves (75 per cent) being over 2000 cm^2 ($n = 150$). *Welfia georgii* possesses pinnately-compound leaves, and those leaves usually gleaned over for insects by *Phaethornis* had from 32–48 pinnae per leaf; *Geonoma binervia* has a simple leaf that is often broken up into a few large sections. As *Welfia* was less abundant than *Geonoma* in the study area, *Welfia* palms were visited to a lesser extent by *Phaethornis*, although both species of palms supported the same types of arthropods in about the same numbers on an individual tree basis.

Loss of foliage leads to a sharp decline in the abundance of prey, despite the presence of nearby trees supporting many insects and spiders. When 66 per cent of the available foliage was removed from foraging sites, *Phaethornis* ceased to spend the usual amount of time searching for prey; when all foliage was removed, the effect was even greater (table 3). When stems were also removed, the birds disappeared from these trees and apparently foraged elsewhere. At this time, these marked individuals did not appear at other foraging sites already used by other marked birds.

TABLE 3. Relation between decreasing amounts of palm foliage and the foraging activity of marked *Phaethornis*.

No. days since experimental manipulation	Visits/hr		Min./visit	
	Site 3	Site 5	Site 3	Site 5
⅓ total leaf surface area removed				
1	6	4	11	14
2	6	4	11	14
⅔ total leaf surface area removed				
1	3	2	16	20
2	3	2	16	20
Entire leaf surface area removed				
1	2	2	4	5
2	2	2	3	5
Stems removed				
1	2	2	2	2
3	1	2	2	2
5	1	0	2	0
7	0	0	0	0
10	0	0	0	0

Observations on a single *Phaethornis* as a web-gleaning predator in an open sunny habitat offer interesting comparisons with leaf-gleaning predation in forest understory by this species. This individual visited only the webs on the side of the building nearest the forest edge, and was never seen to visit at the extensive webbings located on the other three sides, despite the abundance of both spiders and trapped insects there. The particular side of the building visited by this *Phaethornis* was 12 m from the forest edge (and parallel to it), and during the study period it harbored from 11–62 spiders (of various sizes and ages); the associated webbing covered 26,600–84,400 cm^2 of wall space at various times. The data pertinent to web-gleaning are summarized in table 4. It is apparent that the dry season affected the foraging activity of this *Phaethornis*. During the dry season (January–April), this individual visited webs only half as many times, both on a monthly (about 12 days fewer per month) and daily basis (three visits per day fewer), and spent less time foraging per visit (about 4 min less). However, during this time it took

TABLE 4. Foraging of a single *Phaethornis* at webs of the spider, *Nephila clavipes*, at Finca La Selva in 1968–1969.

Month	No. days observation	No. days bird seen	No. visits/day[a] $\bar{x} \pm$ SE	min/visit $\bar{x} \pm$ SE	Insects in webs[b] $\bar{x} \pm$ SE	Insects removed $\bar{x} \pm$ SE	%
Nov.	22	22	7 ± 1.0	6 ± 0.8	170 ±28.5	48 ± 9.0	28
Dec.	13	13	8 ± 0.8	6 ± 1.0	184 ±18.8	40 ± 7.5	22
Jan.	12	12	4 ± 0.5	2 ± 0.4	66 ±12.5	30 ±12.5	46
Feb.	8	8	2 ± 0.0	2 ± 1.0	73 ±16.5	42 ± 8.0	58
March	14	9	2 ± 0.5	3 ± 0.5	48 ±10.5	24 ± 5.5	53
April	12	8	1 ± 0.0	2 ± 0.8	40 ± 8.5	28 ± 7.0	69
May	18	18	11 ± 2.5	10 ± 1.2	265 ±38.5	97 ±11.6	37
June	14	14	8 ± 2.0	9 ± 1.0	198 ±26.5	89 ± 7.0	45

[a] Observations were usually made during these hours: 05:00–06:00, 11:00–14:00, 17:00–18:00.
[b] These values are computed from early morning counts of trapped insects of the size classes 1–5 mm body length.

a large percentage of the small insects trapped in the webs. Unfortunately it was not possible to determine how many and what kinds of insects were eaten per visit; only the gross estimate of how many insects "disappeared" from the webs between early morning and late afternoon (disappearance was assumed equivalent to being eaten, in this case) could be determined.

Substantial numbers of small insects were usually found in the webs during early morning counts, although fewer were found during the dry season. Invariably most of the trapped insects (Diptera, Ephemeroptera, Hymenoptera, and Lepidoptera predominating) were already dead at the time of counting, indicating that *Phaethornis* will feed on dead insects. And while some of these insects were undoubtedly trapped during the day, by far the majority of them were trapped by the spiders during the night through attraction to electric lights turned on in the building for several hours. This is also indicated by the typically high numbers of 3–5 species of Ephemeroptera (mayflies) seen trapped in webs, since these insects are primarily nocturnal in habit. La France (1968) found that most species gather at lights in Canada between 21:00 and 22:00 (a maximum of 28 per cent of all insect species captured on a given night) during most of the year. Young (in prep.) found insect density and diversity at lights at La Selva to be highest between 20:00 and 22:00 over a 10-month period.

In some habitats exposed to a prolonged period of dryness, it has been observed that there is a distinct paucity of small insects (Janzen and Schoener 1968). In a secondary growth vegetation habitat at La Selva there was no noticeable decline in numbers for all size classes of adult insects during the dry season (Janzen and Young, in prep.). Thus, in a locality such as La Selva, different habitats may show different responses to the effect of prolonged dryness in terms of changes in numbers of individuals of various species. The decline in numbers of small insects trapped in webs during the dry season resulted in a larger percentage of these prey being eaten by *Phaethornis* at this time (table 4). Furthermore, there were no small (young) individuals of *Nephila* present on the webs during the dry season as these size classes were most abundant during November, December, early January, and again in late May. The possibility that the paucity of small insects trapped in webs during the dry season was due to large numbers of them being eaten by small spiders can be ruled out. Probably young spiders do feed primarily upon small insects (that is, those smaller than sizes eaten by adult or large spiders) and this could account for disappearance of prey if the small spiders are present and numerous. Numbers of spiders varied with season in this *Nephila* population. A detailed account of the population dynamics of this spider will be presented elsewhere (Young, in prep.) and it suffices only to mention here that this "population" persisted during both wet and dry seasons with the largest adult numbers (218 individuals) appearing in late December 1968 (end of the wet season). At the height of the dry season at La Selva (mid-March during 1969), this population contained only 36 individuals; this drastic reduction in numbers was most likely due to massive starvation. In general, very few insects (of all size classes) were seen trapped in the webs during the dry months, and many large (adult) spiders dropped from their webs and died on the ground within a few days. Large individuals of *Nephila* (46 mm long and larger) attack and devour only those trapped insects larger than 15 mm in body length; presumably smaller insects fail to produce tremors in the webs large enough to attract the spiders.

When the webs were removed in June (and many of the disturbed spiders relocated at other places on the building), this single *Phaethornis* continued to visit the same side of the building where it had been foraging, but failed to appear after the third day, nor did it appear at the other three sides of the building where *Nephila* webs were still intact and containing trapped insects. Other individual *Phaethornis* were not seen visiting these webs. This observation is strikingly similar to the observed relatively small overlap among individuals from different foraging sites in the forest understory. Potential major food sources (other arthropod-laden understory trees versus other insect-laden webs of *Nephila*) located very close to the selected feeding sites were ignored when the exploited food source was removed.

While observations on web-gleaning were in progress, I noticed, beginning in mid-April, that this single *Phaethornis* had begun to tear away strands of the coarse, yellow silk from the same webbing from which it was removing insects. Intermittently, while taking insects, small sections of the silk were plucked off and carried into the nearby forest understory, always in the same direction, on different visits to the webs. Subsequent searching at the forest edge area revealed that a partially-built nest of this individual was situated about 13 m from the foraging area (*Nephila* webs) in well-shaded forest understory. At the date of its discovery, this nest consisted only of a small accumulation of various materials suspended along (and flat against) the underside and near the tip of a large, low-hanging palm (*Welfia georgii*) frond. Further observation showed that at least 24 days (excluding initial days not accounted for) were needed for completion of nest construction. During this period no eggs were seen in the nest. At completion, the nest was a cone-shaped structure hanging against the ventral surface of the palm frond and composed primarily of dried-leaf fragments and earth. The nest was completed by the onset of the first wet season rains (late May); no eggs were seen in the nest at this time or during June.

In order to evaluate the relative amounts of various nest components, a small section (about 8 cm^2) was cut (with small scissors) from one side of the nest. Assuming that the composition is relatively uniform throughout its construction, an analysis (by volume) of the removed sample indicated that the nest contained 42 per cent dried and decayed leaf fragments, 40 per cent moist earth, 9 per cent dried grasses, and 9 per cent *Nephila* silk. When the nest section was removed, the bird did not abandon the nest. While the repair was being completed (2.5 weeks), the rate of removal of silk from the webs increased from an earlier average of 6 times per week to 20 times per week. These observations on silk removal were made over several days per week, usually during the hours of 05:15–6:00, 11:00–14:00, and 17:00–18:00.

DISCUSSION

SEASONAL PATTERNS OF HUMMINGBIRD ACTIVITY

The dry season of tropical regions is considered to be a time when environmental stress upon various organisms is heavy. Webb et al. (1967) point out that in tropical rain forests the understory is usually well protected against major climatic effects by the canopy. The protection probably extends to specific parts of the flora and fauna of the understory so that season may not noticeably alter the diversity and/or abundance of these elements. At the same time, similar parts of the canopy may be drastically affected. In the present study, despite an unusually severe dry season, the feeding activity of an insectivorous vertebrate predator in the forest understory was not changed. This was primarily due to a lack of seasonal response by the understory fauna used for food by this predator. Furthermore, from the data in table 4, it can be speculated that *Phaethornis* individuals that normally forage in open, exposed areas may move into different foraging areas (well-shaded forest understory) in order to subsist during a dry season. On the other hand, individuals that forage continuously in forest understory would not have to undertake such movements. Individuals probably shift foraging locations when major food sources become scarce or in response to new food sources becoming abundant and accessable at other places in the local habitat.

On a diurnal basis, it is clear that throughout much of the year *Phaethornis* forages for insects during both afternoon and morning hours. Observations made at irregular intervals (e.g., varying numbers of days per month, but at least six days per month) over 20 consecutive months at La Selva indicate that individuals of *Phaethornis* are active from about 06:00 until 17:30. More data are needed on the activity of this species as a nectar-feeder in order to assess how *Phaethornis* budgets its foraging time between feeding on insects and feeding on nectar. Studies now in progress at La Selva by F. G. Stiles and L. L. Wolf will provide such information. At certain times over a 12-month period, *Phaethornis* may devote the bulk of its foraging effort to searching for insects, while at other times, the habit may be primarily nectarivorous. Ecological studies of the partitioning by organisms of their diurnal (and seasonal) time budgets, and of the parceling of energy intake among different life processes are badly needed. Of interest here is the possibility that *Phaethornis* populations at La Selva may undergo seasonal shifts in the major component of their diet. One explanation for the disappearance of *Phaethornis* from the forest understory study area at the end of the dry season is that with the beginning of the new wet season, this species becomes predominantly nectarivorous in its habit. During June, July, and August, many species of *Heliconia* (there are probably close to 10 species here) are in bloom at La Selva and are visited frequently by several species of hummingbirds, including *Phaethornis* (Larry L. Wolf pers. comm.). This is not true during the dry season (at least for 1969) at La Selva. Further studies at La Selva on the ecology of *Phaethornis* may show that this species alternates between a predominantly insectivorous diet during severe dry seasons and a predominantly nectarivorous diet during the major part of the wet season. Such a shift in diet would be a function of several properties of the local habitat. The phenomenon would be dependent to a great extent upon the local temporal patterns of flowering of preferred nectaries (including *Heliconia*) and the spatial distribution of these flowers over the terrain. However, such effects as these are only relevant if indeed data can be gathered over several successive years at La Selva since the length of the dry season, and more importantly, its inclusive dates are highly variable from year to year. The present study was conducted during an exceptionally dry year at La Selva and perhaps some effects were artifacts of the exceptional dryness. The dry season at La Selva during 1970 has been very wet and characterized by a pattern of weeks of steady persistent rainfall intermittent with weeks (no more than 10 days at one time as of 12 April 1970) of no rainfall.

For nine months, beginning with July 1969, the marked individuals did not appear at the forest study area. This was a sudden event. Nearby leks of marked *Phaethornis* being studied by F. G. Stiles and L. L. Wolf apparently did not contain these individuals (assuming that the birds I studied retained their color-markings). Since June 1969, I have seen only four of the birds I studied. Three were seen on 14 September 1969: one green-marked bird was seen in forest understory about 1000 m to the east of the study area (east edge of La Selva property) and two black-marked birds were seen about 1200 m NW of the study area, in forest understory. Another black-marked bird (perhaps the same individual) was spotted on 2 April 1970 about 700 m NE of the study area. From these observations, it is my impression that at least portions of certain *Phaethornis* populations at La Selva are extremely mobile over great distances at various times. *Phaethornis* populations appear to be of low density and perhaps this is related to the manner of dispersion of individuals over the forest area. Stimuli for dispersion and general movements of individuals in the forest could be related to availability of food; it may be that such behavior is brought about at times when major shifts in diet are made.

INTERACTIONS OF HUMMINGBIRDS AT FLOWERS

There are 15–20 species of hummingbirds at La Selva and severe competition may exist between some or all of these species at various times throughout the year and at different flowers. The degree or intensity of such competition is in part a function of the numbers of preferred plant species in bloom at a given time, their relative densities, their spatial distributions, and the overall pattern of synchrony of flowering among them. The diurnal pattern of nectar availability at different flowers must also be important for interactions among various hummingbirds. Hummingbird species that occupy low positions in social hierarchies involving several species may find themselves continually crowded out of obtaining sufficient levels of nectar. For such species a feasible alternate strategy would be to evolve a different mode of feeding (i.e., become insectivorous) that would allow such a weak competitor to shift to a different food source (insects) at those times when nectar is in very limited supply. The development of an insectivorous habit in hummingbirds could have been facilitated (in evolutionary time) by an increasing persistent amount of interspecific competition among various species in a social hierarchy taking place at preferred flowers. It thus may have become easier for *Phaethornis*, perhaps a weak competitor in the social hierarchy of hummingbirds that regularly visit *Heliconia* flowers, to search for another food source. To study competitive interactions of this sort, data are needed on the status of various species in social hierarchies and on the extent to which each of these species is insectivorous in its diet. Related to this is the fact that little is known about the degree of specialization in feeding for different species of hummingbirds visiting the same flowers; data of this sort (in terms of distribution of activity in time and space at various food sources) could provide a measurement of niche breadth for these species. Measurement of niche breadth has received much recent theoretical analysis (Hairston et al. 1960; Levins 1968a, b) and information on closely associated groups of species (e.g., leaf litter invertebrates, social hierarchies of hummingbirds) may provide suitable materials for experimental vertification of such ideas.

Recently, it has been hypothesized that high specialization in species can evolve only with respect to the highly predictable features of the environment (Slobodkin and Sanders 1970). The data given in tables 1 and 2 suggest that *Phaethornis* can forage in a very predictable manner over long periods of time; the same individuals tend to return on different days to the same areas in the forest for foraging. Such findings are of interest since it is held that narrow specializations of species can act as a diversity-producing mechanism since specific patterns of behavior can promote the spatial and temporal separation of populations (Slobodkin and Sanders 1970). Such effects would be characteristic of tropical environments since fluctuations of the physical features are usually in regular and predictive patterns with short periodicities. It would be interesting to examine such an hypothesis of "environmental predictability" by studying the temporal-spatial relationships of several species of hummingbirds in a habitat such as La Selva and estimating the relative degrees of behavioral specialization and the population sizes of each species.

SUMMARY

Observations were made from November 1968 through June 1969 in Costa Rica on the foraging for insects and spiders by *Phaethornis superciliosus* in well-shaded wet tropical forest understory and also at spider webs in a nearby open, cleared site. At the understory study area, several birds were captured and color-marked according to their points of capture. Each of eight foraging sites was visited by the same marked birds over successive months; interchange of marked birds between different sites was usually very low. These birds were leaf-gleaning for insects on understory trees and the frequency of visitations did not change for part of the wet season studied, and for the entire dry season. In the clearing the single individual studied fed on insects trapped in webs of a common orb-spinning spider, *Nephila clavipes*. During the dry season, which was unusually long and dry in 1969, the number of visits to these webs made by this bird dropped off considerably, presumably in response to the observed paucity of small insects trapped in the webs during this period. When the dry season ended, the marked birds in the understory study area no longer appeared. This observation is discussed in relation to the possible existence of a seasonal alternation between an insectivorous and nectarivorous diet by *Phaethornis*. An hypothesis on the relation between interactions of hummingbird species at flowers and the development of an insectivorous habit is also discussed.

ACKNOWLEDGMENTS

I am very grateful to Larry Wolf for numerous discussions on hummingbirds which clarified several of my thoughts about the data obtained in this study. Early drafts of the manuscript profited greatly from being read by Douglas Futuyma, Franklin H. Barnwell, F. Gary Stiles, and Larry Wolf. This study was carried out while I was a post-doctoral associate from The University of Chicago in the Comparative Ecosystem Study (Section VIII, Daniel H. Janzen, principal investigator, N.S.F. Grant 7805) of the Organization for Tropical Studies in Costa Rica.

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Accepted for publication 1 June 1970.