



BEHAVIORAL, ECOLOGICAL AND MORPHOLOGICAL
CORRELATES OF FORAGING FOR ARTHROPODS BY THE
HUMMINGBIRDS OF A TROPICAL WET FOREST¹

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Abstract. This paper seeks to clarify the ecological and evolutionary impacts of foraging for arthropods vs. nectar in hummingbirds, using data on morphology, sites, and tactics of arthropod foraging, and prey taken by 11 species of hummingbirds of La Selva, a Costa Rican lowland wet forest, as well as information on time budgets of male and female hummingbirds from two other sites. Hermit hummingbirds have long, curved bills and are nearly exclusively understory hover-gleaners that take mostly spiders. Most glean from webs but *Threnetes ruckeri* differs in foraging behavior and takes mostly jumping spiders. Non-hermits have shorter, straighter bills and employ a greater range of foraging tactics and sites, taking a wider variety of prey. In most species flycatching is frequent and flies and wasps are the predominant prey items, but some also take many spiders and ants; in particular, *Heliothryx barroti* is predominantly a hover-gleaner of the canopy and takes more spiders than flies. In *Thalurania colombica*, males and females differ in sites and tactics of arthropod foraging during the breeding season but not at other times. Breeding female hummingbirds spend much more time foraging for arthropods than do males in the same times and places, although flower visitation still constitutes the majority of foraging time.

Among La Selva hummingbirds, bill curvature is strongly correlated with the proportion of gleaning vs. hawking, and with the proportion of prey taken from the substrate (spiders, ants) as opposed to volant prey (flies, wasps). Broad wings (low aspect ratio) and high wing disk loading are correlated with hovering, gleaning, and the proportion of spiders and ants in the diet; narrow wings and high wing disk loading, with flycatching. Except for the three species that engage in the most flycatching, females have broader wings than males and in virtually all species, females have higher wing disk loading. However, no parameter of wing morphology shows a clear relationship to strategies of nectar exploitation, probably reflecting the facultative nature of the latter.

Hermits and nonhermits differ strongly in their preferred foraging levels in the vegetation, both for nectar and for arthropods, with the former using the understory almost exclusively, the latter using the canopy to a much greater extent, in both forest and second growth. Nevertheless, the two groups do not differ in the proportion of foraging attempts for nectar vs. arthropods, nor in the distribution of foraging through the day, in either habitat. In nearly all species, bills of females are longer than those of males, and this could increase their ability to forage for arthropods at least as much as for nectar.

Much of the controversy regarding frequency and energetic importance of arthropod foraging vs. flower visitation reflects the biases inherent in observing each type of foraging or in interpreting data from stomach contents or emetic samples, or from failure to consider the specific tactics of foraging for arthropods. Reports that hummingbirds can exist for extended periods or breed without access to nectar or alternative sugar sources require confirmation, as does a report that availability of arthropods rather than nectar determines hummingbird breeding seasonality in dry areas. The major impact of arthropods in hummingbirds' diets appears to be at the daily, rather than seasonal, level. Data on arthropod prey do not support the notion that hummingbirds visit flowers for insects rather than nectar, and there is no evidence to suggest that their bills are specialized for extracting insects from

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flowers. Rather, it appears that the bills of hummingbirds are adapted to extracting nectar from particular types of flowers, and that these bill specializations in turn constrain the tactics of arthropod foraging—in particular, the long, curved bills of the hermits might preclude effective flycatching. Selection on wing morphology from flower visitation might well be mostly indirect, via constraints on arthropod foraging tactics imposed by bill morphology, rather than directly through nectar foraging strategies. There is no basis for considering hermits to be more insectivorous than nonhermits; they represent a separate radiation within the Trochilidae, in a different habitat and in association with a different group of flowers, than do several major radiations of the nonhermits.

Key words: Ecomorphology; foraging behavior; insectivory; nectarivory; hummingbirds; Phaethorninae; Trochilinae; time budgets.

INTRODUCTION

Of all avian food resources, nectar is perhaps the most easily quantified and subjected to experimental manipulation. Nearly all of the many studies of the ecology and behavior of hummingbirds over the last 20 years have thus revolved around bird-flower (or bird-feeder) interactions. Flower nectar is deficient, however, in proteins, lipids, and other essential nutrients (Baker and Baker 1982). Hummingbirds therefore consume many small arthropods daily (Remsen et al. 1986). Aviculturists have long known that these birds survive poorly in captivity without frequent access to arthropod prey, protein-vitamin supplements, or both (Lasiewski 1962; Scheithauer 1966; see also Brice 1992, Brice and Grau 1991). Given the importance of small arthropods in the daily maintenance of hummingbirds, the ecological and evolutionary implications of arthropod foraging have received surprisingly little study.

Numerous studies have quantified the feeding niches of hummingbirds with respect to flower visitation, but characterization of these birds' arthropod foraging niches has been at best incomplete. Tactics and sites of arthropod foraging have been described in varying detail by Bene (1946), Wagner (1946), Snow and Snow (1972), Chávez-Ramírez and Dowd (1992), and Chávez-Ramírez and Tam (1993), but without data on the arthropods actually taken by the birds. Conversely, several studies identified arthropods in the stomach contents of hummingbirds (e.g., Lucas 1893, Clark 1903, Cottam and Knappen 1939, Poulin et al. 1994c), but without corresponding data on foraging. Relations between the bill and flight morphology of hummingbirds and patterns of flower visitation and community organization have also received considerable study (e.g., Feinsinger and Chaplin 1975, Feinsinger and Colwell

1978, Wolf et al. 1976, Snow and Snow 1980, Brown and Bowers 1985, Stiles 1985), but the possible impacts of arthropod foraging tactics and prey choice as selective factors on hummingbird morphology have been largely ignored.

Certain other aspects of the animal portion of hummingbirds' diets remain controversial. Small arthropods have been discounted as critical or limiting resources by most authors (e.g., Feinsinger 1976, Wolf et al. 1976, Stiles 1985), but arthropod availability was estimated crudely or not at all. Detailed measurements were attempted by Poulin et al. (1992), who suggested that at least in dry areas, the availability of arthropods might be more important than flower abundance in determining the timing of breeding in hummingbirds. Most authors (e.g., Wolf and Hainsworth 1971, Wolf et al. 1975) have considered the contribution of arthropods to hummingbirds' energy budgets to be insignificant, and foraging for arthropods contributed only a minor portion of the total time and energy devoted to foraging in a number of studies (review in Pyke 1980). Nevertheless, Hainsworth (1977) and Gass and Montgomerie (1981) suggested that flycatching might sometimes be as energetically profitable as flower visitation, and there are at least two reports of wild hummingbirds going for extended periods without flowers (Kuban and Neill 1980, Montgomerie and Redsell 1980).

In this paper, I attempt a balanced evaluation of the role of arthropods in the ecology and evolution of hummingbirds. I first describe sites and tactics of foraging for arthropods and the prey taken, by the hummingbirds of a relatively well studied tropical hummingbird community. I then consider sexual differences in time budgets, particularly with respect to arthropod foraging, using data from other sites in California and Costa Rica. Finally, I examine the relations between these variables and the bill and wing morphology

of male and female La Selva hummingbirds, using more detailed measurements than those employed previously.

STUDY AREAS

Most of the data reported here were gathered at Finca La Selva, a biological station of the Organization for Tropical Studies located 4 km S of Puerto Viejo in the Sarapiquí lowlands of the Caribbean slope of Costa Rica. The climate, vegetation, and avifauna of La Selva were recently summarized in McDade et al. (1994); the hummingbird-flower community has been studied by Stiles (1975, 1978, 1980, 1992) and Stiles and Wolf (1979). Most specimens for stomach and crop analysis were obtained at Hacienda La Trinidad, 1.5 km NE of La Selva, at a similar elevation (Stiles 1980); and at Finca El Plástico, about 6 km S of La Selva and at about 550 m elevation (Rosselli 1994). Data on hummingbird time budgets were obtained at Cerro de la Muerte, San José-Cartago Provinces, Costa Rica, and in the Santa Monica Mountains, Los Angeles County, California; these areas and their hummingbirds and flowers are described in detail in Wolf et al. (1976) and Stiles (1973), respectively.

METHODS

During regular census walks at La Selva during 1971 and 1972, and occasionally through 1989, I attempted to determine the activities of all hummingbirds heard or seen. I noted all instances of foraging, both at flowers and for arthropods, to determine the relative frequencies of the two types of foraging. Arthropod foraging was classified as gleaning when the prey was plucked from the substrate (e.g., vegetation, spider web) and as hawking when the prey was snatched from the air. Foraging bouts were further characterized as hovering if several prey capture attempts were made during continuous hovering flight, or as sallying if the bird left its perch, made one (rarely up to three) attempts, then returned to a perch (see Fig. 1). For each foraging bout, I also noted the species of hummingbird, time of day, habitat (forest, young or old second growth, edge), and stratum (understory, mid-level, canopy, aerial).

I conducted extensive mist-netting of hummingbirds at La Selva between 1971 and 1975, and intermittently through 1989; and many of the same species were captured in intensive mist-

netting at Finca El Plástico in 1987–1988. Particularly from 1983 on, detailed measurements (with dial calipers, to the nearest 0.1 mm) were taken of exposed and total culmen, wing chord, and tail length; mass was measured to the nearest 0.1 g with 10-g and 50-g Pesola spring balances that were recalibrated annually. Bill curvature was determined by taking the arc:chord ratio of the exposed culmen of freshly collected specimens, of an enlargement of the bill obtained by projecting the silhouette of the bill onto a screen. Wing area, and total length and width of the wing, were measured from tracings of the fully spread wings of mist-netted birds (Fig. 2); area was measured by a leaf area meter. Wing length divided by wing width gives the aspect ratio of the wing. Exposed culmen length and wing length were divided by the cube root of body mass to give relative measures of these dimensions, independent of absolute size. Wing loading was computed as body mass divided by twice the wing area. For comparison with previous studies, wing disk loading was first computed from equation (1) of Feinsinger et al. (1979). This equation estimates wing span from wing chord, but because I found significant differences in wing proportions between species (see below), I also computed wing disk loading using twice the wing length (from the wing tracings) to estimate wing span. All of these calculations were performed for each individual bird, to obtain means and standard deviations for each parameter.

Intensive collecting of hummingbirds was carried out in 1971 and 1972 at Hacienda La Trinidad. Stomach and crop contents were obtained from most of these birds, and from others collected occasionally during mist-netting operations in La Selva and El Plástico through 1989. Specimens were deposited in the collections of the Universidad de Costa Rica and the Western Foundation of Vertebrate Zoology. Arthropod prey in stomachs and crops were identified to order or major group (e.g., ants vs. wasps for hymenopterans). Head-body length was estimated for as many prey items as possible, but this was impossible for the majority of items, which were detected from fragments of wings, legs, mandibles, or poison claws. For the same reason, the number of prey items represents a minimum estimate based on the assumption that fragments of different parts of the body, and of approximately the same size, could have come

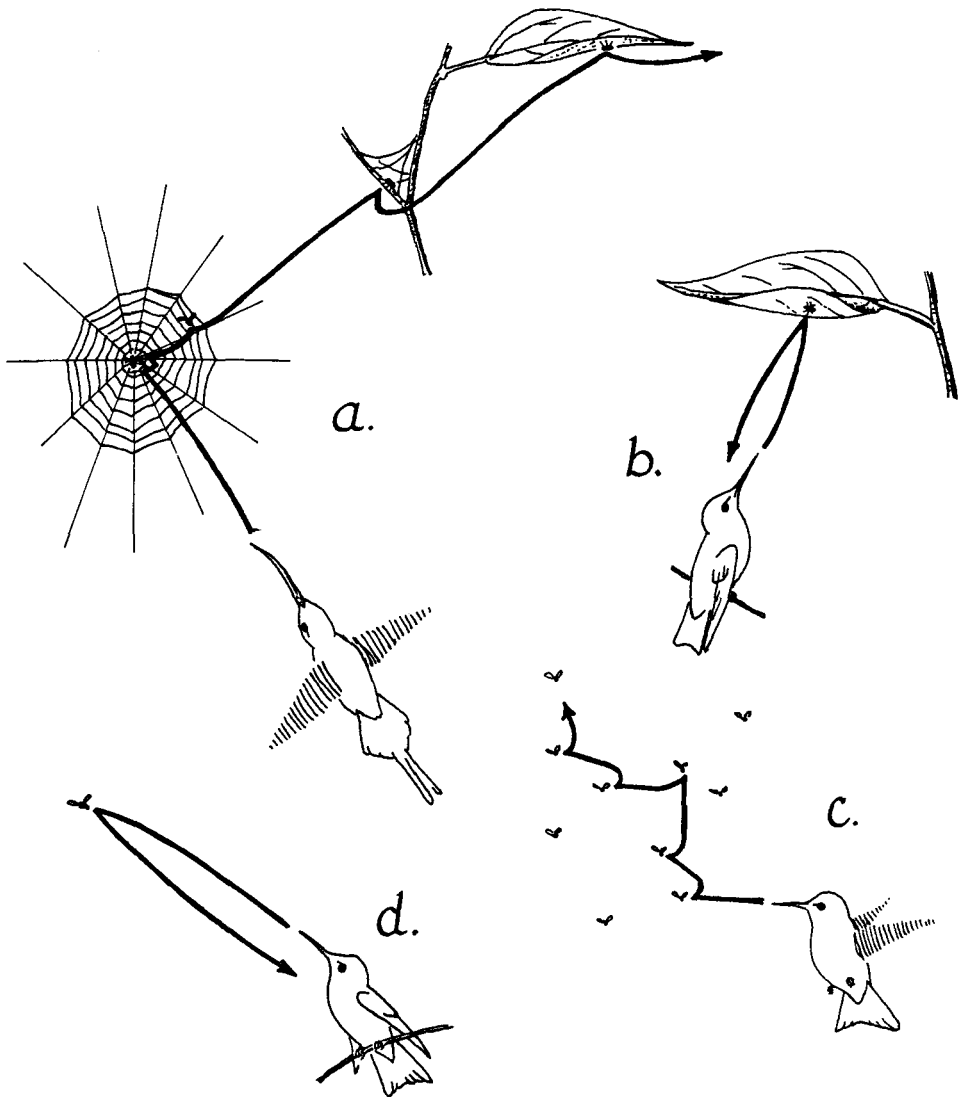


FIGURE 1. Tactics of foraging for arthropods of La Selva hummingbirds. a. hover-gleaning; b. sally-gleaning; c. hover-hawking; d. sally-hawking.

from the same individual. Diet breadth was computed as the antilog of the Shannon-Wiener function, which gives the equivalent number of equally abundant prey types in the diet (Ludwig and Reynolds 1988). Diet overlap was quantified as percent overlap, as computed by Feinsinger (1976); this is the "coefficient of community" of Ricklefs and Lau (1980). Most statistical comparisons employed nonparametrical methods due to the small sample sizes (numbers of species) and nonnormal distributions of most variates.

Observations on time budgets of humming-

birds reported here were made in the Santa Monica Mountains in 1968 and on the Cerro de la Muerte in 1969. The objective of these observations was to compare the time spent foraging for arthropods and nectar by individuals of different sex and breeding status. The most important criteria for including data here were that the birds concerned were under continuous observation for periods of at least 2.5–3 hr, and were out of contact for no more than 5% of this time. Although I have obtained detailed time budgets for males of several species of La Selva hum-

mingbirds that were territorial at flowers, I never succeeded in keeping a nesting female of any species under continuous observation. This necessitated using data from other sites to explore these questions, with the assumption that La Selva hummingbirds would show similar patterns. Similarly, I do not present data on time budgets for trawling species like hermits, because it was impossible to observe the birds continuously.

RESULTS

TACTICS AND SITES OF ARTHROPOD FORAGING BY LA SELVA HUMMINGBIRDS

Tactics and vegetation strata used in foraging for arthropods by 11 species of La Selva hummingbirds are presented in Tables 1, 2, and 3. Overall, the hermits (subfamily Phaethorninae) are hover-gleaners of the understory and gaps in both forest and second growth. The nonhermits (subfamily Trochilinae) include species that virtually always hover, usually sally, or employ different combinations of both to capture prey from the substrate or in the air. In *Thalurania colombica*, seasonal differences in use of tactics and vegetation strata occurred between the sexes (Table 3). The following paragraphs summarize the arthropod foraging behavior of each species (names follow Stiles and Skutch 1989).

Phaethornis superciliosus (Long-tailed Hermit): This species was almost exclusively a hover-gleaner, but occasionally a male on its lek territory would sally to pluck an arthropod from the vegetation near his song perch; I never noted

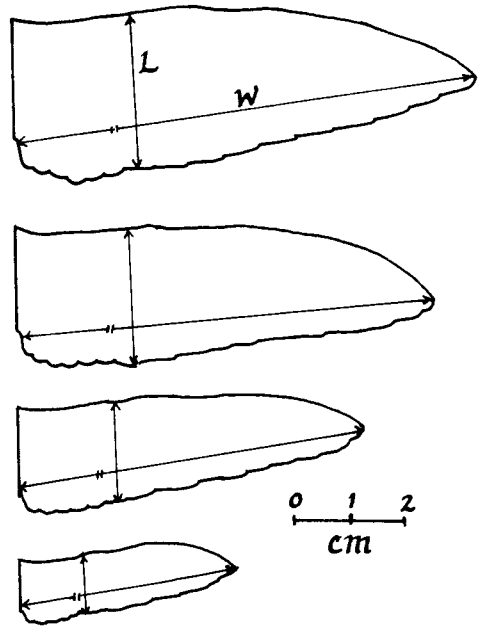


FIGURE 2. Representative wing tracings of four species of La Selva hummingbirds, showing how length and width of wings were measured; the break in the line for wing length corresponds to the division between secondary and primary remiges. Species (top to bottom) are: *Eutoxeres aquila*, *Chalybura urochrysis*, *Thalurania colombica*, and *Phaethornis longuemareus* (all males).

hawking (Table 1). Most prey was evidently gleaned from spiderwebs; large webs, such as those of the giant orb-weaver *Nephila clavipes*, were especially attractive (cf. Young 1971). While

TABLE 1. Tactics employed in foraging for arthropods by 11 species of La Selva hummingbirds: all foraging bouts recorded, 1971–1987.

Species	Tactic and flight mode				Total
	Gleaning		Hawking		
	Hover	Sally	Hover	Sally	
Hermits					
<i>Phaethornis superciliosus</i>	68	3	0	0	71
<i>P. longuemareus</i>	66	2	0	2	70
<i>Glaucis aenea</i>	36	0	1	0	37
<i>Threnetes aenea</i>	36	2	3	2	43
<i>Eutoxeres aquila</i>	17	0	2	0	19
Nonhermits					
<i>Chalybura urochrysis</i>	6	6	6	14	32
<i>Thalurania colombica</i>	19	23	20	40	102
<i>Amazilia tzacatl</i>	14	9	14	11	48
<i>A. amabilis</i>	3	3	3	5	14
<i>Florisuga mellivora</i>	1	2	17	12	32
<i>Helithryx barroti</i>	13	0	9	0	22

TABLE 2. Tactics of foraging for arthropods in forest and second-growth habitats by 11 species of La Selva hummingbirds: data from activity censuses, 1971–1972.

Species	Habitat and tactic			
	Forest		Second growth	
	Glean- ing	Hawk- ing	Glean- ing	Hawk- ing
Hermits				
<i>Phaethornis superciliosus</i>	19	0	14	0
<i>P. longuemareus</i>	21	0	41	0
<i>Glaucis aenea</i>	5	0	18	0
<i>Threnetes aenea</i>	12	1	19	2
<i>Eutoxeres aquila</i>	5	0	6	1
Nonhermits				
<i>Chalybura urochrysis</i>	1	3	3	7
<i>Thalurania colombica</i>	5	15	12	25
<i>Amazilia tzacatl</i>	—	—	4	7
<i>A. amabilis</i>	1	3	1	2
<i>Florisuga mellivora</i>	1	14	0	9
<i>Helithryx barroti</i>	6	3	3	2

gleaning in vegetation, the birds usually started low and moved upward, a technique that probably increased the visibility of spiderwebs by backlighting them against the foliage. Favored locations were along the edges of gaps like stream courses and treefalls. Vine tangles and the masses of dead twigs of fallen branches were examined at length, as were the leaf axils of small understory palms and other monocots, especially when these had trapped debris falling from above. Some prey was also plucked from vegetation, especially the undersides of leaves. Most prey were obtained at 1.5–5 m above the ground, but sometimes a bird continued searching the vegetation upwards to heights of 8–10 m, especially in vine tangles along the edges of gaps or following the aroids (*Monstera*, *Philodendron*) up tree trunks. Occasionally a spider would “bail out” of a web,

falling down on a slender silk thread; the hermit followed the spider down, sometimes catching it before it reached safety.

Phaethornis longuemareus (Little Hermit): Also a hover-gleaner, this small species foraged in a similar manner to the preceding one but usually much lower in the vegetation, often within 0.5 m of the ground (Tables 1, 2). Often a foraging bird would approach understory shrubs or palms from practically ground level, then move upwards, evidently seeking spiderwebs. This species often searched through low herbaceous vegetation in gaps, and like its larger congener often spent lengthy periods hovering through a mass of dead branches and twigs of a fallen tree or vine tangle at a gap, or leaf axils and fronds of understory palms and other monocots.

Glaucis aenea (Bronzy Hermit): This species occurred very infrequently inside forest, and then only at large gaps along streams; it was much more frequent in second growth, where it foraged for arthropods by hover-gleaning in a variety of sites. Like *Phaethornis* species, *G. aenea* showed a strong predilection for gleaning from spiderwebs, and tended to move upwards through dense thickets along streams and edges, and in young second growth. This species also foraged through herbaceous or shrubby vegetation in open swamps and riverbanks, favoring more open sites than did other hermits; it often inspected carefully spiderwebs suspended within or between grass or sedge stems or inflorescences, and like *P. superciliosus* sometimes pursued downwards spiders that had bailed out of their webs. Other prey were gleaned directly from leaves and twigs, especially their undersides.

Threnetes ruckeri (Band-tailed Barbthroat): Although mostly a hover-gleaner, this species also hawked or sallied occasionally (Table 1). *T. ruck-*

TABLE 3. Tactics and vegetation strata used by male and female *Thalurania colombica* foraging for arthropods during dry and wet seasons at La Selva.

Vegetation stratum	Tactics											
	Dry season						Wet season					
	Males		Females		Totals for stratum		Males		Females		Totals for stratum	
	Glean	Hawk	Glean	Hawk	Males	Females	Glean	Hawk	Glean	Hawk	Males	Females
Lower Understory	0	0	4	0	0	4	2	0	2	0	2	2
Upper Understory– Mid-levels	4	2	7	2	6	9	4	9	3	9	13	12
Subcanopy–Canopy	2	8	2	3	10	5	3	8	2	6	11	8
Gaps–Edges	1	4	3	3	5	6	2	4	1	2	6	3
Totals	7	14	16	8	21	24	11	21	8	17	32	25

eri preferred the understory and edges of gaps for foraging for arthropods, usually in dense vegetation where it was very difficult to observe. I occasionally noted it searching between the buttresses or stilt roots of forest trees or palms. It did not appear to seek spiderwebs and tended to move horizontally rather than vertically upwards through the vegetation. Prey were apparently gleaned from both upper and lower surfaces of leaves, especially those of large monocots. Its flycatching appeared rather clumsy; on two occasions I watched a bird sally to capture an insect in the tip of the bill, return to a perch, flip the insect into the air and, with a quick lunge, catch it in its mouth and swallow it.

Eutoxeres aquila (White-tipped Sicklebill): This large species was nearly always observed hover-gleaning, especially along streams and in gaps, often at large spiderwebs (Tables 1, 2). I did not see it working through foliage in the manner of other hermits. It appeared especially adept at catching spiders that had bailed out of their webs, rushing at them with its notably large mouth wide open. Instances of hawking involved similar open-mouthed rushes at insects hovering near *Heliconia* inflorescences (in one instance, the prey was a small *Trigona* bee!); the bird appeared to capture the prey directly in the mouth, rather than with the bill.

Chalybura urochrysia (Red-footed Plumeleater): I usually noted this large nonhermit sally-hawking, typically from a perch in the upper understory. In second growth, a bird would often sally up into the canopy or out into a gap from an understory perch. Gleaning was noted in both hovering birds (mainly females) and in sallies from a perch to the adjacent vegetation (mostly males); prey were plucked from upper and under surfaces of leaves (Tables 1, 2). This species was often shy and difficult to observe, and most of my data are from males that held feeding territories at *Heliconia* flowers; I have very few observations of females.

Thalurania colombica (Purple-crowned Woodnymph): As a whole, this species employed a wider variety of tactics in more levels in the vegetation than any other (Tables 1, 2). During the dry (breeding) season males tended to occupy the canopy while females nested in the understory (Stiles and Skutch 1989), but sometimes foraged higher. Males did more flycatching at this season, females more gleaning; but these differences disappeared during the wet season (Table

3). Gleaning tended to be from leaves at edges and gaps, or from bromeliad leaf axils or other epiphytes. Males in particular often hovered in gaps well up in the canopy, darting to snatch one insect after another. However, this tactic was probably used less, and brief sallies more, than my data indicate since short sallies in the canopy and subcanopy are easy to miss while hover-hawking is more conspicuous.

Amazilia tzacatl (Rufous-tailed Hummingbird): This species appeared to hover-glean more frequently than most other nonhermits, from trunks, stumps, branches, and manmade structures like buildings, electric wires and fences as well as from foliage. It occurred mostly in young or old second growth and around human habitations, very rarely at large gaps inside forest. This species and *G. aenea* were the only ones to regularly seek arthropods in open, grassy areas, although the latter tended to search much more assiduously for spiderwebs. *A. tzacatl* also hawked regularly, somewhat more often continuously (typically hovering and darting in swarms of gnats in open areas, above the vegetation) than by sallying (Tables 1, 2). The sexes are usually indistinguishable in the field, so no comparisons with respect to arthropod foraging were possible.

Amazilia amabilis (Blue-chested Hummingbird): Like its congener, this species employed hawking and gleaning, hovering and sallying tactics with nearly equal frequencies (Table 1); it usually occurred in shadier situations, both in tall second growth and forest where I encountered it mostly at gaps, often well above the ground. I obtained too few observations to evaluate sexual differences in tactics or sites of arthropod foraging.

Florisuga mellivora (White-necked Jacobin): This species was almost exclusively a hawker, using both hovering and sallying tactics frequently (Table 1). I usually observed it well up in the canopy or at gaps; hover (continuous) hawking was especially frequent high in the air above rivers or streams. Females nest in the forest understory, where the few instances of gleaning were observed; however, they were sometimes noted hawking for insects much higher in the vegetation. Because many females have male-like plumage (Stiles and Skutch 1989), no reliable conclusions regarding sexual differences in foraging are possible.

Heliathryx barroti (Purple-crowned Fairy): This species differed from the other nonhermits in

being almost exclusively a hoverer rather than a sallier, and in gleaning more than hawking (Tables 1, 2). In these respects it resembled the hermits, but habitually foraged much higher in the vegetation. Gleaning typically was from the outer foliage of trees and vines well up in the canopy, though the birds sometimes came down to shrub-top level along edges or in gaps. Most hawking occurred as the bird hovered just outside the foliage, evidently in pursuit of insects flushed from the vegetation, perhaps by the bird's own wingbeats. I also occasionally saw this species engage in lengthy bouts of continuous hawking in swarms of gnats over vegetation or in gaps.

In no species was a difference in tactics between forest and second growth habitats evident (Table 2). In the hummingbird community as a whole, gleaning was more frequent in the lower vegetation strata and in dense vegetation, while hawking occurred more often in the higher strata and in more open sites (Fig. 3). The reasons are obvious: the more surface area (e.g., foliage), the more substrate is available for gleaning, while hawking requires open space for maneuvering and a clear view for prey detection. It therefore appears that a given hummingbird species chose the vegetation configuration most appropriate for its preferred tactics in both forest and second growth, rather than changing tactics between habitats.

In general, a hummingbird species used the same vegetation strata for arthropod foraging as for flower visitation (Table 4). The correspondence is somewhat better in forest than in second growth; taking hermits and nonhermits as groups, vertical distribution of the two types of foraging is virtually identical in forest ($\chi^2 = 0.97$ and 0.06 respectively; $P > 0.5$ for both). In second growth the differences are more marked ($\chi^2 = 7.30$, $0.10 > P > 0.05$ for hermits, $\chi^2 = 12.98$, $P < 0.01$ for nonhermits). Here, the difference probably reflects the more restricted distribution of flowers. Whereas in forest there are many canopy epiphytes with flowers visited by hummingbirds (Stiles 1978, 1980), in second growth such epiphytes are rare or absent (cf. Terborgh and Weske 1969). Nonhermits in particular worked the second growth canopy for arthropods, and visited flowers like *Heliconia* in the understory and at gaps. Nonhermits and hermits differed strongly in both habitats with the former more in the canopy, the latter in the understory (for flower visitation $\chi^2 = 15.31$ in forest, $\chi^2 = 14.40$ in

second growth, $P < 0.01$ for both; for arthropod foraging $\chi^2 = 28.47$ in forest, $\chi^2 = 47.55$ in second growth, for both $P < 0.001$). The more pronounced differences for arthropod foraging than for flower visitation reflect a stronger preference by hermits for gaps as well as the understory, with nonhermits more in the canopy (Table 5).

The ratio of arthropod foraging to flower visitation recorded in the activity censuses was slightly higher for hermits than for nonhermits in both forest and second growth (Table 5), but in neither habitat was the difference statistically significant ($P > 0.10$; χ^2 tests). The differences that were noted probably reflect biases in the respective observations, at least in part. The hover-gleaning tactics of hermits are doubtless easier to observe than the brief sallies made by many nonhermits, especially when the latter occur in the canopy. Observations of hummingbirds in the canopy are very difficult to obtain in any case, and because brightly colored flowers constitute a focus of attention for the observer (as well as the hummingbird), the chances of observing a visit to a bromeliad flower are probably higher than those of observing a sally or short gleaning bout in this stratum. Also, several of the second growth areas censused were chosen specifically for their high density of flowers of *Heliconia*, several species of which (e.g., *H. latispatha*, *H. imbricata*) are visited mainly by nonhermits (Stiles 1975). Therefore, I do not believe that the data (Table 5) justify concluding that differences exist in the proportions of nectar vs. arthropod foraging between hermits and nonhermits.

Foraging activity was most intense early in the morning and declined through the day for both hermits and nonhermits, in both forest and second growth, and for both flower visitation and arthropod foraging (Table 5); all χ^2 tests comparing hermits and nonhermits gave $P > 0.10$. However, there is a tendency for arthropod foraging to be more evenly distributed through the day than flower visitation ($\chi^2 = 6.08$, $P < 0.05$, 2 df, hermits and nonhermits combined). The decline in flower visitation through the day doubtless reflects a decline in nectar production through the day (Stiles 1975, Stiles and Wolf 1979). Much of the late-afternoon visitation is to flowers of Gesneriaceae, which show peaks of nectar production later in the day (Grove 1979), and to species pollinated by nocturnal visitors (e.g., *Inga* spp., Salas 1974), whose flowers open and begin to produce nectar at dusk. On the other

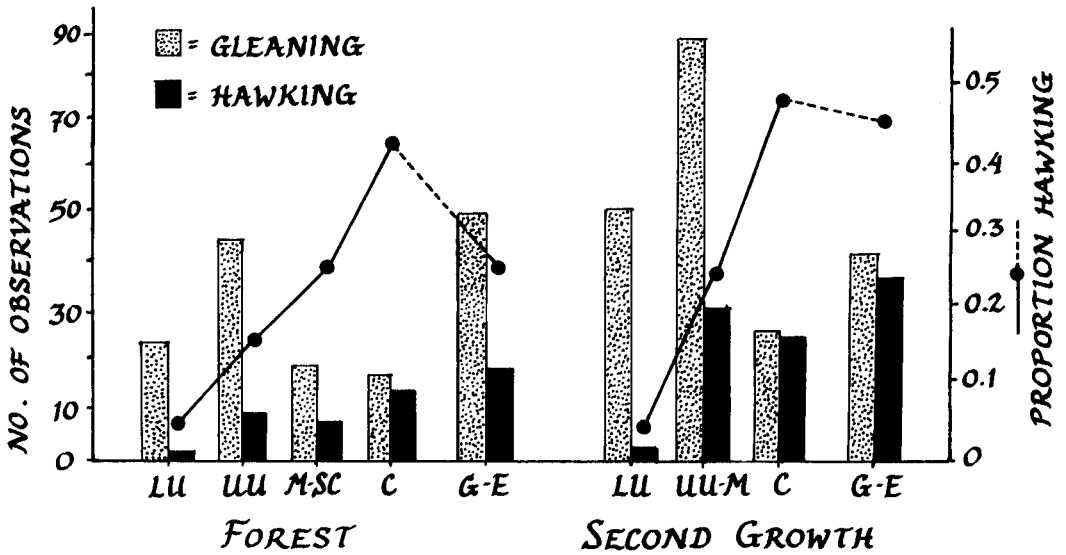


FIGURE 3. Relative amounts of gleaning and hawking by La Selva hummingbirds in different vegetation strata of two habitats. Abbreviations: LU = lower understory; UU = upper understory; M = mid-levels; SC = subcanopy; C = canopy; G-E = gaps and edges.

hand, activity of small arthropods extends through the day except during heavy rains. Many spiders most actively spin webs during the morning hours, and small flying insects tend to be more active in midmorning and late afternoon in open areas, but during the hottest hours in shaded areas (personal observations). Because these patterns might affect the success of gleaning vs. hawking through the day, the occurrence of these two tactics was examined among the non-hermits (not for hermits because they did so little hawking). For all habitats combined, hawking was somewhat more evenly distributed through the day than was gleaning, although the difference was not quite significant ($\chi^2 = 5.16, 0.10 > P > 0.05, 2 \text{ df}$; Table 5).

ARTHROPOD PREY OF LA SELVA HUMMINGBIRDS

The numbers of individuals of major taxa of arthropod prey found in the crops and stomachs of 76 individuals of 11 species of La Selva hummingbirds are presented in Table 6. Sample sizes ranged from 3 to 14 stomachs, and 24 to 299 total arthropods, per hummingbird species. The mean number of prey items per stomach ranged from 7 to 45 among hummingbird species; although the smallest species (*P. longuemareus*) did have the fewest prey items per stomach, no relation between hummingbird size and mean number of prey per stomach was evident over the entire sample of 11 species (Spearman $r_s = 0.079$). In spite of much variation in the types

TABLE 4. Distribution of records of flower visitation vs. foraging for arthropods among vegetation strata in forest and second growth habitats, for hermit and nonhermit hummingbirds at La Selva.

Species—Activity	Habitat and stratum ¹									
	Forest					Second growth				
	LU	UU	M-SC	C	G-E	LU	UU-M	C	G-E	
Flower visitation										
Hermits	6	11	2	0	23	36	116	5	70	
Nonhermits	2	10	7	10	13	11	107	43	72	
Arthropod foraging										
Hermits	13	18	2	0	29	27	38	3	33	
Nonhermits	2	13	9	13	15	3	26	29	17	

¹ Vegetation strata: LU = Lower understory; UU = Upper understory; M = mid-levels; Sc = Subcanopy; C = Canopy; G-E = Gaps and Edges.

TABLE 5. Distribution of records of flower visitation and arthropods foraging over different times of day by La Selva hummingbirds in forest and second growth; and for nonhermits, records of gleaning vs. hawking at different times of day data from activity censuses.

Species—Activity	Habitat, time of day ¹					
	Forest			Second growth		
	EM	LM	AF	EM	LM	AF
Flower visitation						
Hermits	24	13	5	112	73	42
Nonhermits	25	12	5	111	81	41
Arthropod foraging						
Hermits	28	19	15	43	35	23
Nonhermits						
Gleaning	8	5	1	13	6	4
Hawking	14	13	11	18	20	14
Total	22	18	12	31	26	18

¹ Time of day: EM = early morning, 06:00–09:00; LM = Late morning-midday, 10:00–13:00; AF = Afternoon, 14:00–17:00.

of prey consumed, stomachs of most species contained a mean of about 20 prey items, usually belonging to at least five different species, often of different orders.

From 70 to 95% of the prey individuals taken by the different species of hermits were spiders; largely for this reason, the median prey diet breadth B' was significantly narrower for hermit than for nonhermit species (Mann-Whitney $U = 29$, $P = 0.01$; see Table 6). The nonhermits took a wider variety of prey, but for nearly all species the dominant group, in terms of numbers of individuals, was the Diptera. Some species (*F. mel-*

livora, *C. urochrysia*, *T. colombica*) also took many small wasps, and *Amazilia* species, especially *A. tzacatl*, also took many ants. Only *H. barroti* differed from the other nonhermits to a marked degree, taking more spiders than flies (Table 6).

Percent overlap in major prey taxa was uniformly high among all species of hermits (coefficients of 0.761–0.943), due to the pronounced preference of all species for spiders (Table 7). Among the nonhermits, overlap was moderately high (0.628–0.866) among the species specializing most on flies (*T. colombica*, *C. urochrysia*, *F. mellivora*, *A. amabilis*); most of these species showed less overlap with *A. tzacatl* (0.543–0.501) because of the many ants taken by the latter. However, *A. amabilis* also took ants and overlapped more (0.667) with its congener. The most divergent nonhermit was *H. barroti*, which overlapped more with the various hermits (0.611–0.683) than with the other nonhermits (0.250–0.453) due to its high consumption of spiders. Except for this species, overlap between hermits and nonhermits was extremely low (0.035–0.185). Thus, it appears that the La Selva hummingbirds can be divided into spider-hunters (hermits) and flycatchers (most nonhermits); only *H. barroti* is intermediate in prey choice.

These data, based upon classifying prey only to the ordinal (or subordinal) level, give only an approximate idea of overlap at other taxonomic levels. Among the spiders, family determinations are available for many prey items of four species

TABLE 6. Numbers of individuals of different prey taxa in stomachs and crops of 76 individuals of 11 species of La Selva hummingbirds, and prey niche breadth of each hummingbird species.

Species	No. of stomachs	Prey taxa ¹														Σ	x/ Stomach	B'
		Sp	Mt	Ps	Cl	Is	He	Ho	Or	Lp	Ha	Hw	Di	Co	Un			
Hermits																		
<i>Phaethornis superciliosus</i>	14	174	2	0	0	0	0	0	0	0	1	2	2	2	0	183	13.1	1.315
<i>P. longuemareus</i>	4	22	3	0	2	0	0	0	0	0	2	0	1	0	0	30	7.5	2.543
<i>Glaucis aenea</i>	13	250	10	0	0	0	0	1	2	0	11	3	4	0	0	282	21.7	1.675
<i>Threnetes aenea</i>	7	115	0	0	1	0	0	0	8	0	0	0	8	0	1	133	18.9	1.712
<i>Eutoxeres aquila</i>	3	49	0	0	0	0	0	0	0	0	1	1	2	1	0	54	18.0	1.540
Nonhermits																		
<i>Chalybura urochrysia</i>	12	6	0	5	0	5	4	10	0	0	18	102	144	1	3	299	24.9	3.818
<i>Thalurania colombica</i>	10	10	0	1	0	0	0	4	0	1	2	38	131	1	0	188	18.8	2.572
<i>Amazilia tzacatl</i>	4	22	0	1	0	0	0	5	0	0	81	3	66	2	0	180	45.0	3.424
<i>A. amabilis</i>	3	5	0	0	1	1	3	0	0	10	8	30	0	1	59	19.7	4.409	
<i>Florisuga mellivora</i>	5	1	0	0	0	1	0	1	0	0	1	21	102	0	16	142	28.4	2.474
<i>Heliophryx barroti</i>	2	14	0	0	0	0	0	1	0	0	3	0	4	1	1	24	12.0	2.746

¹ Prey Taxa: Sp = spiders; Mt = mites; Ps = psocids; Cl = Collembola; Is = Isoptera; He = Hemiptera; Ho = Homoptera; Or = Orthoptera; Lp = Lepidoptera; Ha = Hymenoptera—ants; Hw = Hymenoptera—wasps; Di = Diptera; Co = Coleoptera; Un = Unidentified.

² B' = niche breadth = $\text{antilog} - \Sigma (P_i \log P_i)$ where P_i = proportion of items of taxon i .

TABLE 7. Pairwise coefficients of percent overlap of taxa in stomach content samples of La Selva hummingbird species (data of Table 6).

Species	Species										
	P.s.	P.l.	G.a.	T.r.	E.a.	C.u.	T.c.	A.t.	A.a.	F.m.	
P.l.	0.761		Hermit-Hermit								
G.a.	0.933	0.822	Overlaps								
T.r.	0.847	0.773	0.886	Hermit-Nonhermit							
E.a.	0.943	0.784	0.937	0.902	/Overlaps						
C.u.	0.051	0.113	0.087	0.087	0.096	Nonhermit-Nonhermit					
T.c.	0.086	0.153	0.092	0.113	0.124	0.756	Overlaps				
A.t.	0.161	0.222	0.189	0.182	0.205	0.501	0.479				
A.a.	0.112	0.185	0.154	0.145	0.158	0.628	0.729	0.66			
F.m.	0.035	0.041	0.042	0.081	0.069	0.669	0.866	0.405	0.689		
H.b.	0.611	0.683	0.639	0.650	0.656	0.293	0.257	0.453	0.436	0.230	

of hermits (Table 8). These data yield a striking ($\chi^2 = 75.6, P < 0.001$) separation of *T. ruckeri* from *P. superciliosus*, *G. aenea*, and *E. aquila*: the latter three species take almost exclusively web-building spiders, the former nearly all jumping spiders. Working at the ordinal level may well obscure differences in prey families (let alone species!) for other groups as well, but much larger samples of prey in a better state of preservation (especially recently-captured items from crops rather than more digested prey from stomachs) would be required to evaluate this. A considerable proportion of the Diptera that were identified to family in the stomachs or crops of several species of nonhermits belonged to families of relatively slow-flying flies like craneflies (Tipulidae) and mosquitoes (Culicidae).

Mean spider size shows a perfect (rank) correlation with hummingbird size (mass) among

eight species of hummingbirds ($r_s = 1.0, P < 0.01$; Tables 9, 11). Mean size of flies taken by four species of flycatchers also increases with mean bird mass ($r_s = 0.60$), but too few species are available to permit statistical significance. For three hummingbird species that took both spiders and flies, and for which five or more of each prey type could be measured, no significant differences in median prey sizes of spiders and flies were found by Mann-Whitney *U*-tests.

On the whole, there was good agreement between the data on prey choice and foraging behavior for all hummingbird species. As expected for specialized hover-gleaners, hermits took almost exclusively substrate-based prey. The degree to which different hermits appeared to seek out spiderwebs corresponded closely to the types

TABLE 8. Numbers of individuals of different families of spiders identified in stomachs and crops of four species of hermit hummingbirds.

Spider families ¹	Hummingbird species			
	<i>P. superciliosus</i>	<i>G. aenea</i>	<i>T. ruckeri</i>	<i>E. aquila</i>
Araneidae*	12	5	0	18
Theridiinae*	11	1	0	0
Linyphiidae*	2	0	0	0
Uloboridae*	5	1	0	1
Pholcidae*	2	0	0	0
Clubionidae	1	0	0	0
Mimetidae	2	0	0	0
Salticidae	0	1	31	0
Scytodidae	0	0	3	0

¹ Families marked with an asterisk are web weavers; Mimetidae do not make webs but are often found as parasites on orb webs. Salticidae and Clubionidae occur on vegetation, Scytodidae in sheltered spots like tree buttresses.

TABLE 9. Mean, standard deviation, and range of head-body lengths of spiders, and of flies and wasps, taken by several species of La Selva hummingbirds.

Prey type and hummingbird species	<i>n</i>	Mean, standard deviation, range (in mm)
Spiders		
<i>P. superciliosus</i>	26	3.23 ± 1.31 (1.2-6.2)
<i>P. longuemareus</i>	10	1.71 ± 0.78 (0.7-3.2)
<i>G. aenea</i>	31	2.27 ± 1.30 (1.1-5.7)
<i>T. ruckeri</i>	12	2.98 ± 1.10 (1.6-5.0)
<i>E. aquila</i>	13	4.01 ± 1.65 (1.8-7.8)
<i>C. urochrysia</i>	3	3.33 ± 0.47 (2.8-4.0)
<i>T. colombica</i>	6	1.86 ± 0.42 (1.2-2.3)
<i>A. tzacatl</i>	7	2.26 ± 0.72 (1.2-3.4)
Flies		
<i>C. urochrysia</i>	24	2.81 ± 1.11 (1.5-5.8)
<i>T. colombica</i>	21	2.35 ± 0.87 (1.2-4.2)
<i>A. tzacatl</i>	6	2.09 ± 0.32 (1.6-2.5)
<i>F. mellivora</i>	38	2.53 ± 1.04 (1.2-6.5)

TABLE 10. Bill morphology of La Selva hummingbirds. Means and standard deviations or ranges are given, depending on sample sizes.

		<i>n</i>	Exposed culmen (mm)	Relative bill length ¹	<i>n</i>	Bill curvature ²
<i>Phaethornis superciliosus</i>	♂	32	37.68 ± 1.01	20.59	5	1.050 (1.033–1.068)
	♀	29	36.10 ± 1.23	20.01	3	1.091 (1.065–1.113)
<i>P. longuemareus</i>	♂	13	21.48 ± 0.61	15.70	3	1.032 (1.027–1.037)
	♀	10	21.78 ± 0.51	15.78	4	1.036 (1.030–1.042)
<i>Glaucis aenea</i>	♂	18	30.17 ± 0.69	17.18	2	1.047 (1.040–1.054)
	♀	17	30.24 ± 1.00	17.40	3	1.066 (1.052–1.072)
<i>Threnetes ruckeri</i>	♂	14	29.57 ± 1.02	16.29	4	1.040 (1.028–1.054)
	♀	10	29.40 ± 1.11	16.33	2	1.051 (1.045–1.057)
<i>Eutoxeres aquila</i>	♂	11	27.38 ± 0.67	12.16	3	1.221 (1.211–1.229)
	♀	15	27.22 ± 0.77	12.60	4	1.243 (1.225–1.261)
<i>Chalybura urochrysia</i>	♂	64	22.69 ± 0.79	11.83	4	1.021 (1.012–1.029)
	♀	41	23.58 ± 0.82	12.89	2	1.024 (1.023–1.025)
<i>Thalurania colombica</i>	♂	84	19.28 ± 0.55	11.62	5	1.022 (1.014–1.031)
	♀	80	20.38 ± 0.61	12.83	5	1.017 (1.006–1.029)
<i>Amazilia tzacatl</i>	♂	19	20.32 ± 0.80	11.65	2	1.025 (1.019–1.030)
	♀	16	21.38 ± 0.74	12.53	3	1.029 (1.021–1.033)
<i>A. amabilis</i>	♂	21	18.15 ± 0.55	11.34	3	1.017 (1.010–1.022)
	♀	19	18.80 ± 0.65	12.12	1	1.013
<i>Florisuga mellivora</i>	♂	9	17.88 ± 0.98	9.22	2	1.026 (1.022–1.030)
	♀	16	18.74 ± 1.08	10.01	2	1.027 (1.023–1.031)
<i>Heliothryx barroti</i>	♂	5	16.65 ± 0.53	9.36	1	1.002
	♀	6	16.86 ± 0.40	9.46	2	(1.000–1.002)

¹ Exposed culmen divided by the cube root of body mass.

² Arc: Chord ratio of exposed culmen.

of spiders taken; in particular, the one species that did not search for spiderwebs (*T. ruckeri*) but rather gleaned leaf surfaces and tree buttresses took nearly all jumping spiders. This species engaged in more flycatching than most hermits, and more flies were found among its prey than in any other hermit. *T. ruckeri* was also the only hermit to take Orthoptera regularly, and these insects were probably gleaned from leaf surfaces (Tables 1, 6, 8).

Among the nonhermits, the amount of glean-ing vs. hawking observed in a given species agreed fairly well with the proportion of nonvolant vs. volant prey found in its digestive tracts (Tables 1, 6). The only species to glean more than it hawked was *H. barroti*, which was also the only one found to take more spiders than flies. Among the other species, those that gleaned more often (*Amazilia* spp., especially *A. tzacatl*) took the highest proportion of their prey from the substrate. Conversely, the species observed to hawk almost exclusively (*F. mellivora*, *C. urochrysia*) took the highest proportions of volant prey. Unfortunately, I lacked sufficient material to deter-

mine whether the differences in foraging behavior between the sexes of *T. colombica* during the dry season (Table 3) resulted in the capture of different prey. Only one of three stomachs of females, and two of seven males, were taken in the dry season. That of the female contained nine flies, two spiders, and an ant; those of the males contained 17 flies and two spiders. Clearly more data are needed to evaluate possible prey differences between the sexes of this species.

Taking the 11 species as a group, there was a strong rank correlation between the proportion of spiders and ants in the diet and the proportion of all foraging observations that involved glean-ing rather than hawking ($r_s = 0.921$, $P < 0.001$; Tables 1, 6). Conversely, the proportion of flies and wasps among all prey items was closely correlated with the proportion of hawking observed in the foraging repertoire ($r_s = 0.957$, $P < 0.001$). The proportions of spiders and ants was negatively correlated with the proportions of flies and wasps ($r_s = -0.921$, $P < 0.001$), emphasizing the dichotomy between spider hunters and fly-catchers.

TABLE 11. Body mass and wing morphology of La Selva hummingbirds. Means and standard deviations are given. Only birds for which wing tracings exist are included in these samples.

Species	Sex	n	Body mass (g)	Wing chord (mm)	Wing length (mm)	Relative wing length ¹	Aspect ratio ²	Wing area (cm ²)
<i>Phaethornis superciliosus</i>	♂	17	6.19 ± 0.30	60.82 ± 1.29	68.78 ± 1.56	12.55 ± 0.39	2.99 ± 0.06	12.43 ± 0.55
	♀	12	5.82 ± 0.19	57.68 ± 0.86	65.28 ± 1.96	12.22 ± 0.34	2.97 ± 0.05	11.62 ± 0.60
<i>P. longuemareus</i>	♂	9	2.49 ± 0.17	36.80 ± 0.69	40.64 ± 0.99	9.21 ± 0.35	3.28 ± 0.10	4.37 ± 0.18
	♀	7	2.62 ± 0.17	38.37 ± 0.89	42.79 ± 1.14	9.56 ± 0.40	3.25 ± 0.12	4.84 ± 0.22
<i>Glaucis aenea</i>	♂	11	5.46 ± 0.29	55.41 ± 1.15	63.89 ± 1.52	12.53 ± 0.30	2.89 ± 0.06	10.90 ± 0.61
	♀	8	5.16 ± 0.20	51.82 ± 1.49	60.05 ± 2.05	12.21 ± 0.55	2.85 ± 0.06	9.99 ± 0.49
<i>Threnetes ruckeri</i>	♂	9	6.01 ± 0.26	57.98 ± 1.19	65.78 ± 2.43	12.64 ± 0.43	2.86 ± 0.05	11.64 ± 0.52
	♀	9	5.92 ± 0.26	56.24 ± 1.61	64.13 ± 2.22	12.45 ± 0.31	2.86 ± 0.08	11.43 ± 0.64
<i>Eutoxeres aquila</i>	♂	9	11.92 ± 0.81	74.67 ± 2.06	87.48 ± 2.28	13.29 ± 0.29	2.87 ± 0.60	20.69 ± 1.06
	♀	6	10.40 ± 0.66	69.87 ± 1.84	81.55 ± 2.44	13.13 ± 0.17	2.85 ± 0.05	18.30 ± 0.92
<i>Chalybur urochrysis</i>	♂	15	7.06 ± 0.29	68.49 ± 0.94	76.55 ± 1.41	12.63 ± 0.28	3.16 ± 0.06	14.98 ± 0.85
	♀	6	6.13 ± 0.26	62.62 ± 0.93	69.33 ± 1.01	11.90 ± 0.33	3.19 ± 0.05	12.30 ± 0.52
<i>Thalurania colombica</i>	♂	13	4.59 ± 0.22	52.75 ± 1.68	60.72 ± 1.86	11.26 ± 0.27	3.24 ± 0.07	8.74 ± 0.45
	♀	9	4.04 ± 0.15	49.24 ± 1.45	56.59 ± 1.12	10.85 ± 0.39	3.26 ± 0.06	7.65 ± 0.38
<i>Amazilia tzacatl</i>	♂	10	5.22 ± 0.28	55.79 ± 1.33	63.48 ± 1.71	11.98 ± 0.29	3.07 ± 0.06	10.21 ± 0.49
	♀	9	4.91 ± 0.19	53.61 ± 1.49	60.47 ± 1.29	11.70 ± 0.37	3.04 ± 0.07	9.42 ± 0.43
<i>A. amabilis</i>	♂	5	4.13 ± 0.15	52.10 ± 0.98	59.34 ± 1.47	11.79 ± 0.50	3.14 ± 0.09	8.39 ± 0.25
	♀	4	3.80 ± 0.16	49.60 ± 0.55	56.60 ± 1.60	11.62 ± 0.50	3.12 ± 0.04	7.82 ± 0.27
<i>Florisuga mellivora</i>	♂	5	7.02 ± 0.38	67.70 ± 1.22	78.12 ± 1.60	12.43 ± 0.19	3.27 ± 0.05	15.33 ± 1.10
	♀	5	6.48 ± 0.26	64.76 ± 1.14	72.76 ± 1.14	12.16 ± 0.29	3.29 ± 0.06	13.75 ± 0.75
<i>Heliothryx barroti</i>	♂	2	5.60 ± 0.28	65.55 ± 0.92	74.80 ± 0.77	13.61 ± 0.19	3.09 ± 0.42	13.70 ± 1.45
	♀	3	5.55 ± 0.26	66.23 ± 0.67	73.97 ± 1.56	13.52 ± 0.35	3.09 ± 0.50	13.82 ± 0.62

¹ Wing length divided by the cube root of body mass.² Wing length divided by wing width.

ARTHROPOD FORAGING IN THE TIME BUDGETS OF MALE AND FEMALE HUMMINGBIRDS

Because female hummingbirds must gather many arthropods to satisfy the protein requirements of the growing young, as well as their own for egg production, one might expect them to dedicate more of their time to arthropod foraging than do males. Unfortunately, I could not test this hypothesis with hummingbirds at La Selva because, despite a number of attempts with nests of various species, I could never maintain females under continuous observation during the time they were off their nests. It is my impression that females of tropical forest hummingbirds avoid foraging near their nests. They are usually very furtive when departing from or arriving at their nests, probably to avoid attracting predators, which take a heavy toll of such nests (Skutch 1966, Stiles 1992). In all of my observations of hummingbirds, I have obtained adequate time budgets for only two nesting females: a *Calypte anna* in California (Stiles 1973), and a *Panterpe insignis* on the Cerro de la Muerte, Costa Rica (Wolf and Stiles 1970). Although neither species occurs at La Selva, in the absence of contrary evidence it seems reasonable to assume that the same patterns hold in La Selva hummingbirds.

As predicted, both nesting females engaged in more foraging for arthropods than did territorial males observed in the same areas, times of day, dates, and weather conditions (Fig. 4). The female *C. anna* was observed both while incubating eggs and while feeding young for up to a week after hatching. Time spent foraging for arthropods increased during this period. When feeding young, the female spent 3–4 times more time seeking arthropods than did males. Time spent foraging for arthropods by the female *P. insignis* was nearly six times that spent by a male in the same territory (Wolf and Stiles 1970). In each case, females spent more time visiting flowers than foraging for arthropods, and their times in this respect differed little from time spent by males. The increment in flower visitation between incubation and feeding young was much less than the corresponding increment in time spent foraging for arthropods by the female *C. anna*; no data are available for feeding young by the female *P. insignis* (Fig. 4). Incubation is probably energetically the least expensive part of the nesting cycle because the insulative value of the nest doubtless reduces the female's thermoreg-

ulatory costs, and she is not yet incurring the high expenditures associated with feeding the young.

In conclusion, these female hummingbirds differed much more from males in the time spent foraging for arthropods than in that spent foraging for nectar, at least during the breeding season. Assuming that this also holds in La Selva hummingbirds, one can hypothesize that adaptations for arthropod foraging will be more important for females than for males. In particular, to the extent that foraging behavior is an important selective force upon hummingbird morphology, one might predict that sexual differences in morphology related to foraging might reflect arthropod foraging more than flower visitation. This prediction can be evaluated in the light of the morphological data for male and female La Selva hummingbirds.

BILL MORPHOLOGY AND ARTHROPOD FORAGING AMONG LA SELVA HUMMINGBIRDS

As a group, the hermits differed most strongly from the nonhermits studied in their more strongly curved bills on average, which were also relatively (and in most cases, absolutely) longer than bills of the nonhermits (Table 10). Bills of female hermits were more curved than those of males in all species, and longer relative to body mass in all but *P. superciliosus*. Bills of nonhermits were straight to very slightly curved (curvature less than 1.03), and in all species females had longer bills than males, although there was no consistent sexual difference in bill curvature. Relative to body mass, the difference in bill length between the sexes was much greater for the nonhermits (except for *H. barroti*) than for the hermits (Tables 10, 11).

Considering the 11 species as a group, there was a strong positive correlation between bill curvature (mean of males and females) and the proportion of spiders in the diet ($r_s = 0.766$, $P < 0.01$) and a negative correlation with the proportion of flies and wasps in the diet ($r_s = -0.713$, $P < 0.02$). Bill curvature was also positively correlated with the proportion of gleaning, as opposed to hawking, in the observations of foraging tactics ($r_s = 0.671$, $P < 0.05$). The most divergent species with respect to the relation between bill morphology and arthropod foraging was *H. barroti*, which combined a very straight, rather short bill with a high consumption of spiders and ants

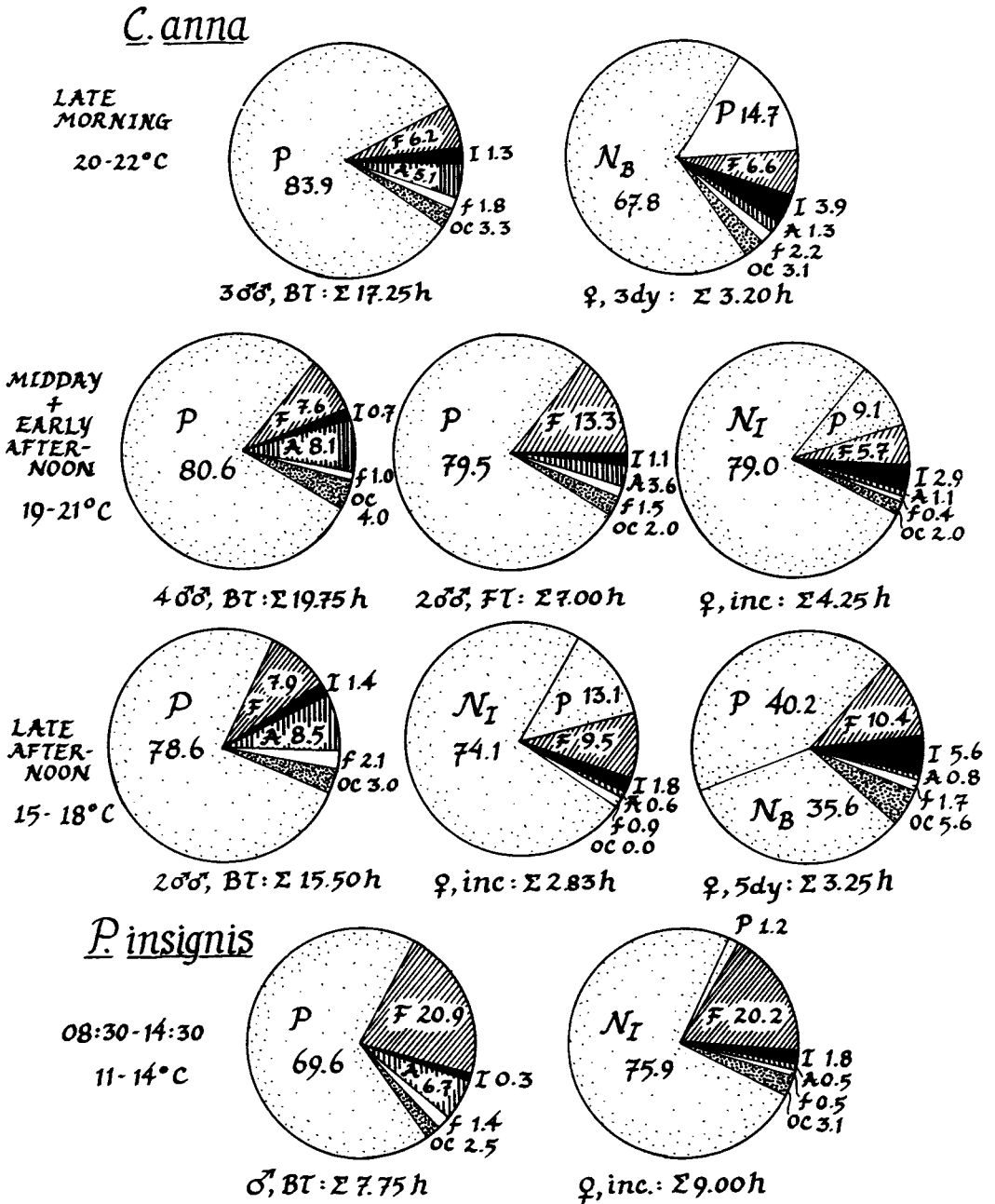


FIGURE 4. Time budgets of males and breeding females of Anna (*Calypte anna*) and Fiery-throated (*Panterpe insignis*) Hummingbirds. Data for *C. anna* are for March–April 1968 and 1969, except for males on feeding territories (July–August 1968); data for *P. insignis* are for July 1969. Numbers are percentages of total time observed. Abbreviations: BT = breeding territories; FT = feeding territories; inc = incubating eggs; 3dy, 5dy = feeding-brooding 3- or 5-day-old nestlings; P = perched; NI = incubating (on nest); NB = brooding (on nest); F = flower visiting; I = foraging for arthropods; A = aggressive behavior (chases, aerial displays); f = miscellaneous flying; OC = out of contact.

obtained by hover-gleaning. The bill of this species is also unique in its fine, needle-sharp point, which is used to pierce the bases of many flowers to rob nectar (Stiles 1980 and unpublished data, Stiles and Skutch 1989). Excluding this species from the analysis raises of all of the above values to around 0.9.

Aside from its possible value in flower visitation, a slight increase in bill length could be advantageous in foraging for arthropods. For gleaners, a longer bill not only provides a longer reach, but also increases the distance between the point of capture (the bill tip) and the body and wings of the bird. Vibrations of similar frequencies and intensities to the wingbeats of hummingbirds produce escape reactions in some spiders (C. Valderrama, pers. comm.). For hawkers that capture prey in the bill tip, a longer bill might increase the bird's ability to capture agile flying prey by increasing the linear velocity of the closing bill tip relative to its angular velocity, as was suggested for fish-eating terns by Ashmole (1968). This effect would be greatest for birds with long, narrow bills with slender, light weight points like many hummingbirds or jacamars, which are well known for their ability to catch fast-moving butterflies and bees (Chai 1986). This might partly explain why female hummingbirds have relatively longer bills than males. The most exceptional species among La Selva hummingbirds in this respect was *P. superciliosus*, in which males had relatively as well as absolutely longer bills. Given the importance of the bill in the lek displays of this species (Stiles and Wolf 1979), the longer bill of males may result from sexual selection; males of several other species of large *Phaethornis* with lek social systems also have longer bills than females (pers. observ.).

WING MORPHOLOGY AND ARTHROPOD FORAGING

Absolute wing length (from wing tracings) varied widely in accord with the fourfold variation in body mass among the 11 species. Relative wing length was remarkably constant however, between about 0.35 and 0.40 for nearly all species. Most divergent was the tiny *P. longuemareus* with its very short wing, especially in males. The longest-winged species, *H. barroti* and *F. mellivora*, differed much less from the rest (Table 11). Wing of males were longer with respect to body mass in all species except *P. longuemareus* (females longer). All hermits except *P. longuema-*

reus had relatively broad wings (aspect ratio less than 3) and in all, wings of females averaged slightly broader wings than those of males. Most nonhermits had narrower wings, especially *F. mellivora* and *T. colombica*; only in these two and *C. urochrysia*, did females have narrower wings than males.

Wing loading of most species averaged between 0.23 and 0.27 g/cm², with sexual differences mostly slight and not statistically significant. The highest wing loadings were those of *E. aquila*, reflecting its great mass, and male *P. longuemareus*, due to their very small wings. Only *H. barroti* had a very low wing loading. No consistent pattern of sexual differences in wing loading were found (Table 12).

When wing disk loading was calculated according to the equation of Feinsinger et al. (1979), the relative positions of several species were markedly affected ("A" values in Table 12). *P. longuemareus* was now lowest among the hermits and *F. mellivora* no longer showed a particularly low wing disk loading, as might have been expected from its long wing (Table 11); rather, *A. amabilis* was now second lowest after *H. barroti*. Nevertheless, wing loading and wing disk loading were significantly correlated ($r_s = 0.693$, $P < 0.05$). This measure of wing disk loading involves estimating wing span from wing chord, which entails assuming that the proportion of wing span represented by wing chord is constant across all species. To test this assumption, I measured the percent of total wing length represented by the secondaries vs. the primaries in all wing tracings where the primary-secondary break could be clearly discerned (Fig. 2). Among six species for which four or more such measurements could be made, significant differences in this percentage existed (Kruskal-Wallis non-parametric analysis of variance, ANOVA, $H = 12.74$, $P < 0.05$), with the lowest median percentage of wing length comprised by the secondaries being precisely that of *P. longuemareus* (21.16%); the highest, that of *C. urochrysia* (24.10%). It thus appears that the assumption of constant proportionality of wing parts is invalid, and that previous calculations of wing disk loading may be biased for comparative purposes. Another problem with this procedure is that wing chord effectively measures only the length of the outermost, longest one or two primaries. When these feathers are modified for sound production, as in many *Selasphorus* species (Stiles 1983), fur-

TABLE 12. Wing loading and wing disk loading of La Selva hummingbirds (means and standard deviations, sample sizes are those of Table 11). Units are g/cm².

Species		Wing loading	Wing disk loading-A ¹	Wing disk loading-B ²
<i>Phaethornis superciliosus</i>	♂	0.249 ± 0.012	0.0380 ± 0.0018	0.0417 ± 0.0020
	♀	0.251 ± 0.012	0.0386 ± 0.0012	0.0435 ± 0.0014
<i>P. longuemareus</i>	♂	0.283 ± 0.019	0.0380 ± 0.0020	0.0479 ± 0.0019
	♀	0.271 ± 0.016	0.0373 ± 0.0023	0.0458 ± 0.0026
<i>Glaucis aenea</i>	♂	0.251 ± 0.009	0.0392 ± 0.0018	0.0426 ± 0.0022
	♀	0.258 ± 0.013	0.0414 ± 0.0023	0.0454 ± 0.0018
<i>Threnetes ruckeri</i>	♂	0.258 ± 0.009	0.0395 ± 0.0015	0.0442 ± 0.0022
	♀	0.261 ± 0.012	0.0414 ± 0.0031	0.0457 ± 0.0028
<i>Eutoxeres aquila</i>	♂	0.288 ± 0.013	0.0488 ± 0.0030	0.0495 ± 0.0026
	♀	0.284 ± 0.014	0.0482 ± 0.0018	0.0497 ± 0.0021
<i>Chalybura urochrysis</i>	♂	0.237 ± 0.016	0.0342 ± 0.0012	0.0383 ± 0.0014
	♀	0.265 ± 0.019	0.0350 ± 0.0020	0.0407 ± 0.0019
<i>Thalurania colombica</i>	♂	0.263 ± 0.017	0.0360 ± 0.0020	0.0396 ± 0.0021
	♀	0.265 ± 0.016	0.0362 ± 0.0026	0.0403 ± 0.0029
<i>Amazilia tzacatl</i>	♂	0.258 ± 0.019	0.0369 ± 0.0016	0.0412 ± 0.0023
	♀	0.261 ± 0.010	0.0374 ± 0.0016	0.0426 ± 0.0015
<i>A. amabilis</i>	♂	0.246 ± 0.013	0.0332 ± 0.0019	0.0372 ± 0.0017
	♀	0.245 ± 0.007	0.0334 ± 0.0012	0.0378 ± 0.0014
<i>Florisuga mellivora</i>	♂	0.230 ± 0.019	0.0345 ± 0.0014	0.0366 ± 0.0013
	♀	0.236 ± 0.006	0.0347 ± 0.0017	0.0378 ± 0.0014
<i>Heliodytes barroti</i>	♂	0.205 ± 0.011	0.0293 ± 0.0023	0.0319 ± 0.0020
	♀	0.199 ± 0.004	0.0282 ± 0.0011	0.0323 ± 0.0021

¹ Calculated according to equation (1) of Feinsinger et al. (1979).

² Calculated using 2× wing length (Table 11) to estimate wing span.

ther bias may be introduced into the calculations of wing span.

I accordingly recalculated wing disk loadings using twice the total wing length (Fig. 2, Table 11) as my estimate of wing span (the "B" values in Table 12). This procedure probably underestimates wing span slightly by neglecting the proximal, unfeathered part of the wing, but given the very short humerus of hummingbirds any error should be slight, and affect interspecific comparisons far less than assuming constant proportionality of flight feathers. The resultant values are in far better accord with other measures of wing morphology: in particular, the correlation with wing loading improves ($r_s = 0.852$, $P < 0.01$) and the small wing of male *P. longuemareus* is again evident, as is the long one of *F. mellivora*. *E. aquila* again shows the highest wing disk loading and *H. barroti*, the lowest (Table 12). Hermits as a group show high wing disk loading, approached among the nonhermits by that of *A. tzacatl*. Wing disk loading of females averages higher than that of males in nearly all species but few sexual differences are significant, the major exception on both counts being *P. lon-*

guemareus. Wing disk loading is inversely correlated with aspect ratio ($r_s = 0.830$, $P < 0.01$) when this species is excluded, but not when it is included ($r_s = 0.536$, $P = 0.10$).

Clearly, the most unusual species with respect to wing morphology was the diminutive *P. longuemareus*, which like many other tiny (<3 g) hummingbirds showed reversed sexual size dimorphism. The very small wing of males in particular may be related to their courtship displays, in which a loud wing-buzz is produced (Skutch 1964, Snow 1968). This appears to result from an increase in wingbeat frequency, perhaps accompanied by a decrease in amplitude (personal observation). A small, narrow wing might produce less inertial drag (Pennycuik 1975) in such a situation.

Relationships between wing morphology and arthropod foraging are also complex. Relative wing length is not significantly correlated with any aspect of foraging tactics or diet. Aspect ratio is inversely related to the proportion of spiders and ants in the diet ($r_s = -0.791$, $P < 0.05$) among all 11 species. However, when *P. longuemareus* is excluded, this correlation is

strengthened ($r_s = -0.903$, $P < 0.001$), and strong correlations are revealed between aspect ratio and the proportions of sallying ($r_s = 0.691$, $P < 0.05$) andhawking ($r_s = 0.867$, $P < 0.01$) in the foraging repertoire (with the corresponding inverse correlations with hovering and gleaning, respectively), and with the proportion of flies and wasps in the diet ($r_s = 0.897$, $P < 0.005$). The association of narrow wings with flycatching is further reinforced by the fact that only in the three species that flycatch most (*C. urochrysis*, *F. mellivora*, and *T. colombica*) do females have narrower wings than males. In fact, the ratio of female to male aspect ratios is correlated with the proportion of sallying in the foraging repertoire ($r_s = 0.691$, $P < 0.05$), and *P. longuemareus* is not unusual in this respect (Tables 1, 6, 11, 12).

In spite of being inversely correlated with aspect ratio ($r_s = -0.664$, $P < 0.05$), wing loading shows no significant correlations with any aspect of foraging or diet. Wing disk loading, however, is significantly correlated with the proportion of gleaning ($r_s = 0.716$, $P < 0.05$) but not hovering ($r_s = 0.536$, $P = 0.10$) among foraging tactics, with the proportion of spiders and ants in the diet ($r_s = 0.689$), and inversely with the proportion of flies and wasps ($r_s = -0.647$, both $P < 0.05$). Excluding *P. longuemareus* from the analysis, wing disk loading shows a strong inverse correlation with aspect ratio ($r_s = -0.830$, $P < 0.01$). This suggests that narrow-winged species (flycatchers) may sweep out a wider disk area with respect to body weight than do broad-winged species (gleaners); there might be trade-offs between wing shape and wingbeat amplitude that impinge upon foraging tactics. I should note here that most of the same correlations emerge when wing disk loading is calculated according to the equation of Feinsinger et al. (1979), but their magnitudes (and in some cases, significance levels) are somewhat reduced.

DISCUSSION

Observations by other authors on arthropod foraging by hummingbirds have been neither as quantitative nor as systematic as those reported here, but nevertheless many of the same tendencies were noted. In both Trinidad and Dominica, hermits or other curve-billed hummingbirds (e.g., *Eulampis*) tended to seek arthropods by hover-gleaning in the understory, while straighter-billed species did more flycatching in the canopy or open habitats (Snow and Snow 1972, Feinsinger

et al. 1985, Chávez-Ramírez and Tam 1993). Flycatching, both by sallying and during continuous hovering, was the predominant mode of arthropod foraging by the straight-billed Mexican hummingbirds observed by Wagner (1946), though larger and longer-billed species (*Eugenes*, *Lampornis*) also gleaned regularly. Young (1971) described web-gleaning by *P. superciliosus*.

Reports of the arthropod prey of hummingbirds are scattered; many early, largely anecdotal reports were summarized by Bent (1940). Lucas (1893) and Cottam and Knappen (1939) provide more detailed data for several North American species. As I found at La Selva, hummingbirds with medium-length, straight bills take a variety of arthropod prey with flies and wasps usually predominating, while larger or longer-billed species take more spiders. The most detailed information on the arthropod prey of tropical hummingbirds was obtained by Poulin et al. (1994c) in the dry coastal lowlands of Venezuela. Three straight-billed species (*Chlorostilbon mellisugus*, *Leucippus fallax*, and *Amazilia tobaci*) all took principally volant prey with flies and wasps predominating, but all also showed substantial intake of spiders. *Leucippus* also consumed many beetles, an exceedingly unusual prey type for La Selva hummingbirds. More limited information for five other species generally agreed well with tendencies noted here, in particular *Thalurania furcata* (a close relative of *T. colombica* and very similar in morphology) took almost all flies, while the hermit *Glaucis hirsuta* (larger than but otherwise similar to *G. aenea*) also took mostly substrate-based prey, especially spiders. Prey sizes also agreed well with those reported here. The emetic technique of Poulin et al. (1994c) has the advantage that the bird need not be collected, but I am struck by the threefold decrease in number of prey items per emetic sample compared with stomachs. It might be desirable to collect several hummingbirds after obtaining emetic samples to determine how thoroughly this technique samples gut contents.

NECTAR VS. ARTHROPODS IN HUMMINGBIRD DIETS

The relative frequency of flower visitation vs. foraging for arthropods by hummingbirds has been controversial. As noted above, there are inherent biases in observing both types of foraging that rarely have been taken into account by previous authors. Flowers are conspicuous,

and visits to them are more likely to be noted by a casual observer than gleaning or sallying in vegetation. However, flowers are often highly patchy or localized in space, and observations in a limited area where flowers are scarce or absent might underestimate flower visitation relative to arthropod foraging—especially as hummingbirds may commute to or trapline nectar sources over distances of 1 km or more (e.g., Stiles 1973, Stiles and Wolf 1979). Conversely, observations in areas of high flower density probably overemphasize flower visitation relative to arthropod foraging, especially if the birds visit the area specifically for nectar. These biases can be reduced by careful censuses over wide areas, in which every effort is made to determine the activities of every hummingbird detected. Even with this method some bias is probably unavoidable, for instance when dealing with activities of hummingbirds of the forest canopy (see above).

Data presented here (Table 4) suggest that arthropod foraging comprises ca. 60% of all foraging attempts in forest by hermits, and 55% by nonhermits; the corresponding values for second growth are 30% and 25%. Differences between hermits and nonhermits could reflect biases in detecting different tactics of arthropod foraging at different levels in the habitat; the great difference between habitats is due at least in part to the high flower density of the particular sites selected for censusing in second growth. Perhaps the only safe conclusion that a major portion, perhaps about one-half, of the foraging attempts of most or all species of hummingbirds are for arthropods. However, this need not reflect the time spent nor the relative energetic yields of the two types of foraging (see below).

Snow and Snow (1972) reported that 8–14% of feeding observations of Trinidad hummingbirds consisted of arthropod foraging, except for 31% in *Glaucis hirsuta*. This species, however, regularly hover-gleaned along a stream and trail where observer activity was frequent. As the Snows specifically state that their observations were opportunistic rather than systematic, underestimation of arthropod foraging relative to flower visitation would be likely, with *G. hirsuta* perhaps least affected by this bias. At the opposite extreme is the statement of Young (1971) that in the dry season at La Selva, flowers are scarce and *P. superciliosus* is mainly insectivorous. In fact, the dry season includes the peak blooming period of the most important flower

in the annual cycle of this hummingbird, *Heliconia pogonantha* (Stiles and Wolf 1979, Stiles 1980). Evidently Young's observations were made near the field station, while the nearest large clones of this *Heliconia* are 200–300 m away! Similarly, Chávez-Ramírez and Dowd (1992) reported that 94% of foraging attempts by *Eulampis jugularis* on Dominica were for arthropods, but of these 63% were from the *corollas of heliconia flowers* (italics mine). I have never seen concentrations of arthropods on *Heliconia* flowers in quantities that would justify such behavior, and suspect that they were misled by an unusual technique of flower visitation by this curve-billed hummingbird.

Reports of hummingbirds existing for extended periods in the wild without access to flower nectar (Kuban and Neill 1980, Montgomerie and Redsell 1980) may be similarly biased, particularly as the great mobility of the birds was not considered. The latter authors concluded that an incubating female *Selasphorus platycercus* consumed only arthropods because they found no flowers within 500 m of the nest. However, they surveyed only 15% of the total area, and the bird was out of contact for over 75% of the time she was off the nest. Their data do not preclude the possibility that this female commuted to a distant nectar source, or used alternative sugar sources like sapsucker drillings (Miller and Nero 1983). At best, the case for wild hummingbirds going for extended periods without nectar remains to be proven.

Poulin et al. (1994a, 1994b, 1994c) also used emetic sample data to evaluate the relative importance of nectar vs. arthropods in hummingbirds' diets. Unable to recognize nectar as such in these samples, they used presence of pollen as their indicator of flower visitation. However, there are no reliable reports of hummingbirds specifically consuming pollen, and it is doubtful if they could digest it (Paton 1981). In examining stomach contents of hummingbirds, I rarely find more than a grain or two of pollen, even when there is nectar in the crop. Most of the pollen in the emetic samples may have come from the ramphotheca via bill-wiping on the substrate following vomiting. In examining numerous samples of pollen from the bills and plumage of various hummingbird species, I have been impressed with the great variation in the amount of pollen according to plant species, time of day, weather, and other factors: presence and amount

of pollen is often not a reliable indicator of visitation of many flower species (personal observation). The method of Poulin et al. is thus probably biased against detecting flower visitation in relation to arthropod foraging, and their conclusions regarding a preponderance of the latter for most species may be overstated.

NECTAR VS. ARTHROPODS IN TIME AND ENERGY BUDGETS OF HUMMINGBIRDS

Another source of information regarding the relative use of nectar and arthropods by hummingbirds is time budgets of individuals kept under essentially continuous observation. Data summarized by Pyke (1980) suggest that most foraging time is devoted to flower visitation, with only around 15% being devoted to foraging for arthropods. However, nearly all these data were for males defending territories at flowers, which might not be representative of hummingbirds in general. The need to guard their flowers probably restricted these males to short sallies from lookout perches while on their territories, which might not have included sites with high densities of arthropods. Much foraging for arthropods could have taken place off territory, when the birds were generally out of contact. Time budgets for breeding females include only those of Hainsworth (1977) for *Colibri coruscans*, and those presented here. A higher proportion of time was devoted to arthropod foraging by these females, especially when feeding young, but flower visitation still comprised 65–70% of total foraging time.

Much of the controversy regarding the impact of foraging for arthropods on hummingbirds' time and energy budgets may reflect failure to take foraging tactics into account. Sallying for passing insects is likely to be highly time-efficient, in that searching can be done from a perch and, for territorial birds, subsumed into vigilance time. Only the actual sally (commenced when the prey has been located and presumably is within effective capture range) will be counted as foraging time. Continuous hawking would also be feasible only at very high prey densities, such that after pursuing one prey item, another can be detected immediately (at least, in less time than it would take to return to a perch). Most of the foraging for arthropods included in the time budgets reported by Wolf and Hainsworth (1971), Hainsworth (1977), Pyke (1980), and in this study (Fig. 4) was of these types. Gleaners, on the other hand, must search for prey mostly or entirely on

the wing, which will increase the amount of time spent overtly in arthropod foraging. For trapliners like hermits, this expense could be mitigated were they to interrupt the circuits of their foraging routes to engage in bouts of gleaning at favorable sites encountered in passing.

Disagreement also stems from use of different caloric values for "typical" insects (e.g., Brenner 1967, Ricklefs 1974), often easily obtained species or laboratory strains rather than those that actually comprise the natural diet, as well as assumptions regarding assimilation efficiencies. For instance, Scheithauer (1966) reported a mean wet mass of 1.5 mg for *Drosophila melanogaster*; Hainsworth (1977) used this same value for dry mass. Since a *D. melanogaster* is ca. 60% water (Scheithauer 1966), this difference alone would yield a twofold variation in estimates of the energetic yield of arthropod foraging. Assimilation of soft-bodied spiders might well be higher than that for many insects with higher chitin content, making spiders a more favorable prey for hover-gleaners like hermits. Data for capture rate per unit of time, or per foraging attempt, are also lacking. Until many of these assumptions can be replaced by reliable data, the safest general conclusion is that the energetic efficiency of foraging for nectar is probably considerably higher than that of foraging for arthropods, but that the difference will vary according to foraging tactics and, probably, prey types. In any case, the energetic impact of arthropod foraging is far from negligible. For hover-gleaners in particular, the energetic costs might be quite high—requiring in turn specializing on energy-rich prey (spiders?) and/or more flower visitation to balance their energy budgets. It therefore is not unexpected that the flowers specialized for pollination by hermits have the highest nectar volumes of any lowland hummingbird-pollinated flowers (Stiles and Freeman 1993).

NECTAR VS. ARTHROPODS AS DETERMINANTS OF BREEDING SEASONALITY

Numerous studies have concluded that hummingbirds breed when their preferred flowers are most abundant, in a variety of habitats (reviews in Stiles 1973, 1985). Indirect evidence suggested that arthropod abundance was not limiting in some cases, but detailed data on arthropod availability were not obtained in any study. Recent work on avian seasonality in dry forest and thorn scrub in Venezuela led Poulin et al. (1992) to

conclude that hummingbirds there nested in the rainy season because insects, rather than flowers, were more abundant. However, problems exist with their methods for monitoring both nectar and arthropod resources. Following the flowering of several marked plants per species is at best an indirect indicator of flower availability in the habitat and might give seriously misleading results where plants in a population flower asynchronously (cf. Stiles 1992). Trapping methods such as Malaise, pitfall, and light traps often show large variations in capture rates from hour to hour and day to day; cloudiness and moon phase also greatly affect captures at light traps. The precise location of the trap can also be important: moving a Malaise trap a few meters can dramatically change the numbers and kinds of insects captured (P. A. Hanson, pers. comm.). Sweep samples are subject to most of these biases, and can vary enormously according to the technique of the person doing the sweeping; obtaining a representative idea of the arthropods even in simple vegetation requires a very intensive sampling effort (Janzen 1973). Presenting results as total insect biomass or numbers may mask patterns at the level of particular groups. I therefore am uncertain of the extent to which the techniques of Poulin et al. (1992) give a representative picture of arthropod availability to hummingbirds over the annual cycle.

Poulin et al. (1992) also suggested that availability of insects, rather than flowers, might be the main factor inducing hummingbirds to breed in the early wet season in tropical areas with less than 1,500 mm annual rainfall. However, in other dry tropical areas such as Guanacaste, Costa Rica (annual rainfall 1,200 mm) and Chamela, Jalisco, Mexico (750 mm), different hummingbird species nested in wet or dry seasons, according to blooming periods of their preferred flowers (Wolf 1970, Arizmendi 1987, Stiles and Skutch 1989). On present evidence, the major ecological impact of arthropod foraging by hummingbirds is at the daily, rather than seasonal, level; and flower availability is the major, though not necessarily the only, ultimate factor governing seasonal rhythms in these birds.

FORAGING FOR NECTAR VS. ARTHROPODS AND HUMMINGBIRD BILL MORPHOLOGY

The lengths and curvatures of the bills of many hummingbirds have been shown to correspond closely to the sizes and shapes of the corollas of

their preferred flowers (e.g., Snow and Snow 1972, 1980; Stiles 1975, 1985; Wolf et al. 1976). Even small differences in bill-corolla 'fit' can produce major differences in the efficiency of nectar extraction (Wolf and Hainsworth 1971; Wolf et al. 1972, 1976; Temeles and Roberts 1993), which in turn can influence flower choice (Stiles 1981). By contrast, bill morphology appears related to arthropod foraging in a much more general way: species with straight bills take a variety of prey, with flies usually predominating; the more curved the bill, the more a species appears restricted to a diet of spiders. That a curved bill is not a requirement for taking spiders is shown by the many spiders consumed by straight-billed species like *H. barroti*. Rather, such a bill apparently precludes efficient flycatching, as the hermits that flycatch most have either the least curved bills (*T. ruckeri*) or a very large mouth, the bill being practically an impediment (*E. aquila*). Straight bills of moderate length (ca. 15–25 mm) permit a variety of prey types and foraging tactics to be exploited, especially flycatching, perhaps the most efficient in terms of time and energy (see above). A small increase in bill length for such species might increase the effectiveness of flycatching, especially if the prey is captured in the bill tip; as noted above, this might help to explain the longer bills of most female hummingbirds, especially flycatchers. A slightly longer bill could also improve the efficiency of nectar extraction at flowers with longer corollas, although it might actually decrease extraction efficiency at flowers much shorter than the bill (Hainsworth 1973, Temeles and Roberts 1993). Detailed data on flower choice by males and females in relation to bill and flower morphology will be required to explore these possibilities.

FORAGING AND WING MORPHOLOGY IN HUMMINGBIRDS

Selection pressures on the wing morphology of hummingbirds are less easy to separate. As noted above, broad wings are associated with hovergleaning, narrow wings with flycatching. The greater lift provided by broader wings might reduce hovering costs, while the lower drag of narrow wings might facilitate the rapid maneuvers of flycatching (Weis-Fogh 1972, 1973; Penny-cuick 1975). By contrast, no clear association between wing shape and patterns of flower visitation is evident among La Selva hummingbirds. Hermits are invariably trapliners (both sexes), but foraging tactics of nonhermits vary

with species and sex. Territorial defense of flowers is frequent in male *C. urochrysis*, *A. tzacatl*, and *T. colombica*; rare in male *A. amabilis* and *F. mellivora*, and absent in both sexes of *H. barroti*. Among females, only *A. tzacatl* regularly defends flowers, mostly outside the breeding season; such territoriality is rare in *C. urochrysis* and has not been reported in the other species. Females of these species may employ traplining, poaching from flowers defended by other hummingbirds, commuting to good feeding areas and showing aggressiveness (but not defense of flowers) there, or other tactics—as may males in the absence of defendable flowers (Stiles 1975, 1980, and unpubl. data). The broad wings of hermits might suggest an association with traplining, but the relation breaks down among the nonhermits: males of *C. urochrysis* and *F. mellivora* are among the most and least territorial species, respectively, and both have wings broader than those of their females. Conversely, the only female that regularly defends flowers, *A. tzacatl*, has a considerably broader wing than the male.

The situation with respect to wing loading is also unclear. A high wing loading could be associated with higher optimum flight speeds (Pennycuik 1975), a low wing loading with reduced hovering costs. However, I can find no clear relation between wing loading and parameters of either arthropod foraging (see above) or flower visitation among La Selva hummingbirds. Wing loading of highly territorial species varied from fairly low (*C. urochrysis*, males lower than females) to moderately high (*A. tzacatl*, males higher than females), with *T. colombica* intermediate (females slightly higher). Wing loading of *F. mellivora* was notably low, slightly higher in females, but in this species the sexes differ much less in territorial behavior than do those of *T. colombica*. Among the hermits both sexes trapline; males of all except *G. aenea* sometimes (*T. ruckeri*) or regularly associate in leks (Stiles and Wolf 1979), but no sexual differences in wing loading seem associated with either flower visitation or social system. It may be significant that the two species with lowest wing loading, *H. barroti* and *F. mellivora*, are also those most restricted to the canopy; perhaps wing loading reflects the height in the vegetation at which a species normally flies, at least in part.

Previous attempts to relate wing morphology to feeding behavior in hummingbirds have dealt exclusively with wing disk loading and strategies

of nectar foraging (Feinsinger and Chaplin 1975, Feinsinger and Colwell 1978, Feinsinger et al. 1979). These authors suggested that territoriality should reduce foraging time at flowers, and thus relax selection for efficient hovering (low wing disk loading), relative to trapliners. Instead, territorial species should be under selection for the ability to execute high-speed maneuvers in territorial chases; therefore, territorial species or sexes should show higher wing disk loading than nonterritorial species or sexes. The most obvious incompatibility of data with this hypothesis, the high wing disk loading of hermits, was explained by Feinsinger et al. (1979) as an adaptation for the lek behavior of most hermits, which often involves chases (Stiles and Wolf 1979).

These arguments are not supported by patterns of wing disk loading among La Selva hummingbirds. In nonhermit species in which males frequently are territorial at flowers but females are not (*C. urochrysis*, *T. colombica*), wing disk loadings of the latter are higher (as they are in *A. tzacatl*, in which females are territorial during the nonbreeding season only, while males may defend territories at any time of year). A lekking nonhermit, *A. amabilis*, has a notably low wing disk loading despite engaging in numerous chases on the lek (Stiles and Skutch 1989, pers. observ.), such that high wing disk loading need not be associated with lek behavior. This is further evidenced among the hermits where a nonlek species, *G. aenea*, has a wing disk loading comparable to that of most lekking species. In any case, the higher wing disk loading of females of most lekking species is incompatible with the argument of Feinsinger et al. (1979). Part of the problem lies in the assumption that both flower-centered and lek territoriality necessarily involve much high-speed chasing. Lengthy chases are an inefficient method of expelling an intruder from a territory, which perforce must be left unguarded for the duration of the chase. In fact, most intruders are ejected from feeding territories of La Selva hummingbirds by vocalizations, brief rushes or bouts of hovering, or short chases of only a few seconds' duration (Stiles, unpubl. data) and lengthy chases on the leks of *P. superciliosus* are mostly restricted to a short period at dawn (Stiles and Wolf 1979). The amount of fast forward flight is probably far greater for species like *P. superciliosus*, which must make several circuits of a trapline often 1 km or more in length each day, than for a male nonhermit localized

on a small feeding territory. Female nonhermits not so localized might also have to cover much greater distances in foraging than their territorial males, depending upon patterns of flower availability. High-speed maneuvering is in any case arguably more important for flycatching than for any aspect of foraging for nectar.

Given the facultative rather than obligate nature of strategies of nectar foraging, especially among the nonhermits, it might be illusory to expect close correlations of these with wing morphology. Because various aspects of wing morphology (including wing disk loading) show clearer relationships with arthropod foraging than with nectar foraging, the former might well have been the primary selective force upon wing morphology. Selection on wing morphology might indeed ultimately derive from flower visitation, but via the constraints placed upon arthropod foraging by bill morphology more than through any direct influence of strategies of nectar exploitation per se.

ARTHROPOD FORAGING AND THE EVOLUTION OF THE HUMMINGBIRDS

The notion that the hermits (subfamily Phaethorninae) are primitive, insectivorous hummingbirds is over a century old (e.g., Ridgway 1891); its justification appears to be that hermits lack the brilliant iridescence of most other hummingbirds, and that this brilliance is somehow related to flower visitation. Johnsgard (1983) even considered the long, curved hermit bill to be "... the generalized hummingbird bill type ... with a moderate degree of elongation for probing into flowers ... and a limited ability for grasping and extracting insects from them." Data presented here and in other recent studies (e.g., Snow and Snow 1972, Stiles and Wolf 1979, Remsen et al. 1986, Poulin et al. 1994b) should make it clear that hermits are no less nectarivorous than other hummingbirds. The long, curved bills of the hermits are highly specialized not for insectivory, but for extracting nectar from the long, curved corollas of the flowers of large monocots, especially *Heliconia*. The degree of coincidence in the ecological and geographic distributions of the hermits and the genus *Heliconia* also suggests an intimate evolutionary, as well as ecological, association between these groups (Stiles 1979, 1981).

Certain structures of the skull, humerus, and musculature of the hermits show greater resem-

blances to the condition in the swifts than do the corresponding structures in trochilines (Zusi and Bentz 1982). These similarities presumably represent retentions of the ancestral condition that antedated the divergence of the hummingbirds and swifts, which possibly occurred in the late Cretaceous (Sibley and Ahlquist 1989). The condition in the Trochilinae is therefore the derived state, but this does not necessarily imply that the trochilines are derived from the hermits as such. The divergence of the two subfamilies probably occurred early in the Miocene (Bleiweiss et al. 1994; see also Gill and Gerwin 1989, Sibley and Ahlquist 1989). The present-day hermits rather constitute a separate radiation within the family Trochilidae, centered in wet tropical lowland forest understory (Stiles 1981). The Trochilinae, on the other hand, include several evolutionary lines, several of which apparently diversified in the mid-Miocene, when the Andes first attained elevations of 2,000 m or more (Van der Hammen and Cleef 1986, Bleiweiss et al. 1994). The center of trochiline diversity is the middle elevations of the Andes and perhaps, the mountains of southeastern Brazil (Stiles 1981). The dull colors of nearly all hermits are better viewed as an adaptation to their dimly lit habitat, where brilliant iridescent colors have little signal value compared to the contrasting pale markings that most possess on the head and tail, and where most species have lek social systems in which vocal communication is more important over distances much greater than 1–3 m (Stiles and Wolf 1979).

It has often been supposed that hummingbirds originally visited flowers to obtain insects (e.g., Ridgway 1891, Wagner 1946, Johnsgard 1983). This idea was supported by Wetmore (1916) and Wagner (1946), who found little or no nectar but many arthropods in stomachs of hummingbirds they collected. However, it is now known that most nectar passes from the crop directly to the intestine, where it is absorbed rapidly (Hainsworth and Wolf 1972). Moreover, relatively few of the arthropods found in hummingbird stomachs in this and other studies inhabit flowers. This is as true of the hermits, with their predilection for web-building or jumping spiders, as for the nonhermits. Although such groups as mites and thrips could have been extracted from flowers, they make up only a very small fraction of the arthropod food of hummingbirds. There is thus no basis for the statement that humming-

birds visit flowers mainly to obtain insects, nor any reason to infer that their bills are specialized for extracting insects (rather than nectar) from flowers. Hummingbirds have probably visited flowers specifically to obtain nectar throughout most or all of their evolutionary history (Stiles 1981). Conversely, many species of flowers have developed morphological specializations that both favor visitation and pollination by hummingbirds, and exclude insects.

In conclusion, the specialized bills of hummingbirds probably evolved for nectarivory, which then required the daily consumption of many small arthropods for nutrition. The foraging tactics and choice of arthropod prey have, in turn, been constrained by the bill specializations required for efficient nectar extraction. Strategies of flower exploitation may vary from day to day or place to place according to patterns of flower availability, but tactics and prey choice in arthropod foraging do not appear to vary with habitat, although some variation in relative use of different tactics according to sex and season may occur in some species. Thus, the daily need to forage for arthropods might have provided the primary selective forces upon hummingbird wing morphology. I emphasize, however, that these conclusions derive from the study of only a single hummingbird assemblage and should be considered as hypotheses to be tested with data from other such assemblages.

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