

# ECOLOGICAL FITTING: USE OF FLORAL NECTAR IN *HELICONIA STILESII* DANIELS BY THREE SPECIES OF HERMIT HUMMINGBIRDS<sup>1</sup>

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**Abstract.** Three species of hermit hummingbirds—a specialist (*Eutoxeres aquila*), a generalist (*Phaethornis superciliosus*), and a thief (*Threnetes ruckeri*)—visited the nectar-rich flowers of *Heliconia stilesii* Daniels at a lowland study site on the Osa Peninsula of Costa Rica. Unlike *H. pogonantha* Cufodontis, a related Caribbean lowland species with a less specialized flower, *H. stilesii* may not realize its full reproductive potential at this site, because it cannot retain the services of alternative pollinators such as *Phaethornis*. The flowers of *H. stilesii* appear adapted for pollination by *Eutoxeres*, but this hummingbird rarely visited them at this site. Lek male *Phaethornis* visited the flowers frequently in late May and early June, but then abandoned this nectar source in favor of other flowers offering more accessible nectar. The strong curvature of the perianth prevents access by *Phaethornis* to the main nectar chamber; instead they obtain only small amounts of nectar that leaks anteriorly into the belly of the flower.

**Key words:** Hummingbird; pollination; mutualism; foraging; *Heliconia stilesii*; nectar.

## INTRODUCTION

Species that expand their distribution following speciation enter novel ecological associations unrelated to previous evolutionary history and face the challenges of adjustment to new settings, called "ecological fitting" (Janzen 1985a). In the case of mutualistic species, such as plants and their pollinators, new ecological settings may include new arrays of species varying in ability to function as partners. Bird-pollinated plants in a new setting, for example, will face new selection pressures on the form of floral display, the accessibility of nectar, and the phenology of flowering, all of which affect ability to compete for the services of hummingbirds (Brown and Kodric-Brown 1979, Kodric-Brown and Brown 1979, Stiles 1980).

Hermit hummingbirds (Trochilidae, Phaethorninae) and *Heliconia* flowers (Zingiberales: Heliconiaceae) provide striking examples of specialized pollination mutualisms (Snow and Snow 1972, 1980; Stiles 1975, 1979; Feinsinger 1983; Dobkin 1984). Promoting the parallel evolution of bills and flowers is the effect of the precise fit between the two on the hummingbird's rate of nectar extraction and the associated probability of pollen transfer (Wolf et al. 1972, Stiles 1980).

Ultimately affected are the hummingbird's choice of flowers and patterns of competition among hummingbird species for nectar (Stiles 1975, 1978; Wolf et al. 1976; Feinsinger 1978; Gill 1978). Use of specific *Heliconia* flowers as sources of nectar by particular species of hermit hummingbirds, however, varies seasonally and geographically (Stiles 1975). Comparative studies of the foraging ecology of hermit hummingbirds and the pollination biology of *Heliconia* flowers could help us to understand the loosening and tightening of mutualistic relationships in different ecological settings.

In this paper I examine the use of nectar in flowers of *Heliconia stilesii* Daniels by three species of hermit hummingbirds at one locality in the Pacific lowlands of southern Costa Rica. Belonging to different genera, the three species of hermit hummingbirds differ strikingly in bill form: *Phaethornis superciliosus* (Long-tailed Hermit) has a long (38 to 39 mm) decurved bill; *Threnetes ruckeri* (Band-tailed Barbthroat) has a shorter (28 to 29 mm) nearly straight, sharp-tipped bill; *Eutoxeres aquila* (White-tipped Sicklebill) has a sharply bent, stout bill (photos in Stiles 1975). The differences in bill form affected their abilities to extract nectar from *H. stilesii* flowers, which were abundant next to a large lek of *P. superciliosus*, and thus an obvious potential source of energy for their breeding efforts. Nectar

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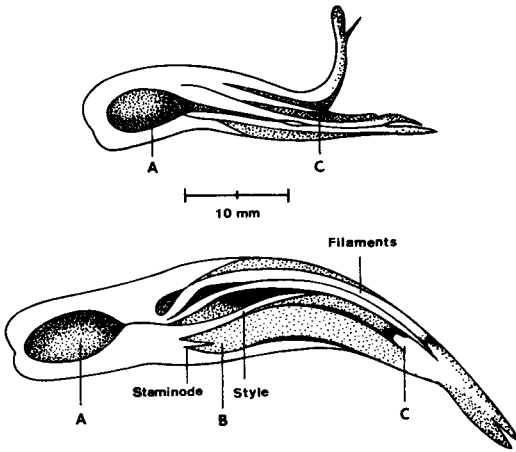


FIGURE 1. Mid-longitudinal section of *Heliconia imbricata* (upper) and *H. stilesii* (lower) flowers. A = main nectar chamber; B = belly of flower where nectar accumulates after overflowing from the main chamber; C = site of bill insertion by *Phaethornis superciliosus* and *Eutoxeres aquila*.

from the quite similar *H. pogonantha* Cufodontis fuels reproduction by *P. superciliosus* at La Selva in the Caribbean lowlands on the opposite side of Costa Rica (Stiles and Wolf 1979). Contrary to expectation, however, the flowers of *H. stilesii* served only as a temporary resource for *P. superciliosus* in our study area.

#### MATERIALS AND METHODS

I conducted this study of color-marked hummingbirds (see Stiles and Wolf 1973 for procedures) in 1980 and 1981 in Corcovado National Park on the Osa Peninsula of Costa Rica. Allen (1956) and Hartshorne (1983: 132–136) describe the forests of this region. Our study site was located on the edge of rain forest near the park headquarters at Sirena at the base of a small ridge next to the park headquarters and adjacent to a lek of *P. superciliosus*. Both *Phaethornis* and *Threnetes* were common at this locality, but *Eutoxeres* was rare, as reflected in the relative abundance of captures during our study, namely 155 *Phaethornis*, 76 *Threnetes*, and 7 *Eutoxeres*.

Table 1 summarizes the floral and nectar characteristics of *H. stilesii*, the principal botanical subject of this study, and of *H. imbricata* (Kuntze) Baker, the main alternative source of nectar used by *Phaethornis* in our study area in May to July. *H. stilesii* is found on the Pacific side of Central America up to 1,000 m elevation from Parrita, Costa Rica south through the Golfo Dulce region

TABLE 1. Floral characteristics of two species of *Heliconia*.

Character	<i>H. imbricata</i> <sup>1</sup>	<i>H. stilesii</i>
Flower (perianth)		
Length (cm)	2.5–3.0	5.5
Curvature	slight	strong
Nectar		
Concentration ± 1		
SD (% sucrose equivalents)	22.4 ± 2.1	29.1 ± 5.4
Energy content ± 1		
SD (J/μl)	3.6 ± 0.3	4.9 ± 0.9
Production <sup>1</sup> (μl/hr)	19	18

<sup>1</sup> Rates of nectar production declined during the day (see Stiles 1975; Gill, in press). The values presented here are average working estimates for early to mid-morning.

into Panama (Daniels and Stiles 1979). It was common at several forest edge localities at Sirena. It was scarce elsewhere in Corcovado National Park. *H. stilesii* flowers throughout the year at Sirena with a general peak of bloom during the rainy season starting in late May. Each flower lasts only half a day, wilting conspicuously by early afternoon. The flowers are long and sharply bent, making access to the main nectar chamber extremely difficult. A tight passageway at the anterior end of the chamber compounds the challenge of nonlinear access to the distant nectar chamber.

*H. imbricata* is an abundant, widespread species in both the Caribbean and Pacific lowlands of Central America, and was one of the dominant plants in the wet second growth habitat at Sirena. The dark red, compact, vertical inflorescence produces short, slightly curved flowers, which allow direct access to the nectar chamber by a straight bill or capillary tube. The anterior opening to the nectar chamber of *H. imbricata* flowers allows easy passage. Both straight-billed hummingbirds, such as *Thalurania furcata* and *Amazilia decora*, and hermit hummingbirds can reach the floral nectar chamber.

The ease of measuring floral nectar contents facilitates study of energetic rewards available to hummingbirds. Nectar concentrations in *H. stilesii* flowers were measured in terms of percent sucrose equivalents with a temperature-compensated hand refractometer and converted to J/flower based on grams of solute per 100 ml (Bolten et al. 1979). The nectar contained fructose, sucrose, glucose, and unidentified amino

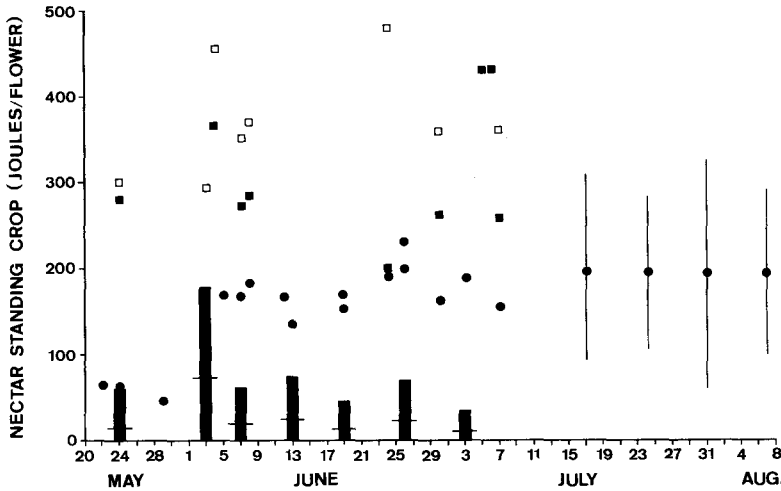


FIGURE 2. Standing crops of nectar energy in *Heliconia stilesii* (squares) and in *H. imbricata* (closed circles). Black squares = mean total nectar per *H. stilesii* flower at 06:00; white squares = mean total nectar per *H. stilesii* flower at 10:00; black circles = mean total nectar per *H. imbricata* flower  $\pm 1$  SD indicated for values after mid-July (deviations in May and June were similar but omitted to simplify figure). Nectar energy available as overflow in the belly of *H. stilesii* flowers is shown at the bottom left of the figure: horizontal bars = mean; vertical black bars =  $\pm 1$  SD.

acids (Gill, unpubl. data). Nectar volumes in plucked flowers were measured using 100  $\mu$ l capillary tubes, first from the belly of the flower anterior to the staminode and then separately from the main chamber (Fig. 1). The presence of insect larvae or ants in the nectar chamber was noted. Most flowers also contained floral mites (see Colwell 1973, Dobkin 1984). In this paper the term "standing crop" refers to nectar present in flowers open to visitors of all kinds. Nectar production was estimated as the accumulation in flowers bagged with mesh cloth before dawn.

To establish the temporal patterns of flower visitation, we undertook continuous vigils at stands (= presumed clones) of *H. stilesii*. We monitored all visits by hummingbirds to these flowers from 07:00 to 12:00, and into the late afternoon on some days. On certain days in 1981, we numbered 80 to 90% of the bracts with fresh flowers, which enabled us to record the specific flowers that a hummingbird visited. The cohort sizes of the monitored flowers were 131 on 26 May, 140 on 27 May, 131 on 28 May, 97 on 11 June, 88 on 12 June. Data in this paper are based on 167 monitor hours from June 6 to July 8, 1980 and 100 monitor hours from May 22 to July 9, 1981. One large stand (designated "I") with >40 inflorescences was the focus of our

studies. One lek male, color-marked Pink-White-Red (PWR), accounted for 83% of the visits to "I" in 1981.

To determine the patterns of nectar removal from *H. stilesii* flowers by *Phaethornis*, we bagged bracts with new flowers at dawn and then removed the netting in midmorning to await hummingbird visits. Bagged flowers remaining on an inflorescence served as controls. Flowers with beetle or fly larvae were excluded from the analysis of nectar removal; such flowers typically were rejected by *Phaethornis*. Brief or aborted flower visits (less than 5% of total) also were discarded to insure that the flower contained substantial nectar and that the hummingbird fed without interference from larvae inside the flower or from *Trigona* bees.

## RESULTS

### NECTAR AVAILABILITY

Large amounts of energy were present in *H. stilesii* flowers. Standing crops averaged 200 to 300 J/flower in the early morning and 300 to 500 J/flower by midmorning (Fig. 2). Some flowers contained over 842 J and one (unvisited) flower contained 1,374 J by 14:00. Variations among flowers in accumulated nectar reflected consumption by insects and birds as well as variable

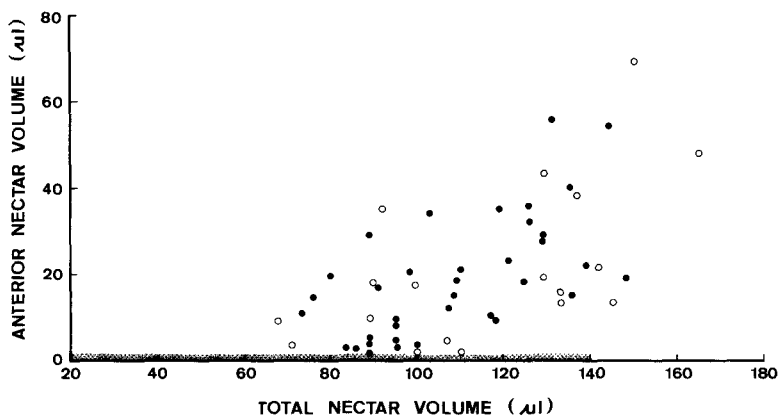


FIGURE 3. The amount of nectar that overflows from the main nectar chamber anteriorly to the belly of *Heliconia stilesii* flowers increases with total production. Sixty flowers with 22 to 142  $\mu\text{l}$  of nectar in the rear chamber had no nectar anterior to the chamber (baseline stippling) in the belly of the flower. Open circles = unbagged flowers; closed circles = bagged flowers.

nectar production per se. Nectar volumes of less than 100  $\mu\text{l}$  were restricted to the main nectar chamber in most flowers. As production continued, however, nectar flowed forward into the belly of some flowers, causing their anterior nectar volumes to increase with total accumulation (Fig. 3). Flowers with more than 115  $\mu\text{l}$  total had 10 to 60  $\mu\text{l}$  available anteriorly. The average amount of nectar available anteriorly at 10:00 most mornings in 1981 was less than 6  $\mu\text{l}$  per flower.

*H. stilesii* flowers offered more nectar (total) than did *H. imbricata* flowers, which (in late May) contained only 42 to 80 J/flower at 10:00 and accumulated up to 417 J/flower by midday. As *H. imbricata* flower abundance increased, mid-morning nectar volumes also increased to stable levels of 150 to 200 J/flower for the rest of the summer. Although much less than the total nectar energy content of *H. stilesii* flowers, the nectar energy content of *H. imbricata* flowers was about eight times that available anteriorly in the belly in *H. stilesii* flowers.

TABLE 2. Flower visitation by a lek male (PWR) *Phaethornis superciliosus* during the morning and as nectar volumes increased in the accessible belly of *Heliconia stilesii* flowers. Values are mean number of flowers visited per hour ( $\pm 1$  SD) for three successive days in late May 1981.

Early morning (07:00–08:00)	Midmorning (08:00–10:00)	Late morning (10:00–12:00)
16.6 $\pm$ 6.1	56.2 $\pm$ 13.7	74.2 $\pm$ 9.6

#### HUMMINGBIRD VISITS

Visits to *H. stilesii* flowers increased during the morning. *Phaethornis* rarely visited these flowers before 07:00 and only occasionally before 08:00, but visited over 70 flowers per hour from 10:00 to 12:00 (Table 2). Such increased feeding activity in late morning corresponded to the increasing amount of nectar in the belly of the flower.

Despite continued availability of nectar in *H. stilesii* flowers, use of the nectar by *Phaethornis* declined dramatically in late June. *Phaethornis* visited *H. stilesii* stands up to four times an hour in late May and early June in 1980 and up to six times an hour in 1981. After mid-June *Phaethornis* visited the stands less than three times per hour, usually less than once per hour (Fig. 4). Visits to stand "I" virtually ceased after mid-June 1981, even though there was no obvious decline through July in the number of new flowers available each day. Decreased use in terms of the number of flowers visited per hour after mid-June was especially pronounced (Fig. 5). By late June, we observed *Phaethornis* feeding primarily on increasingly abundant *H. imbricata* flowers.

The proportion of available *stilesii* flowers that were visited once by 12:00 declined with the change in *Phaethornis*' feeding preferences, from 80% in late May to 12% in mid-June 1981 (Fig. 6). Fifty-five to 60% of the flowers received two or more visits by midday in mid-May and 20% received four or more visits. No flowers were visited twice by midday on 12 June.

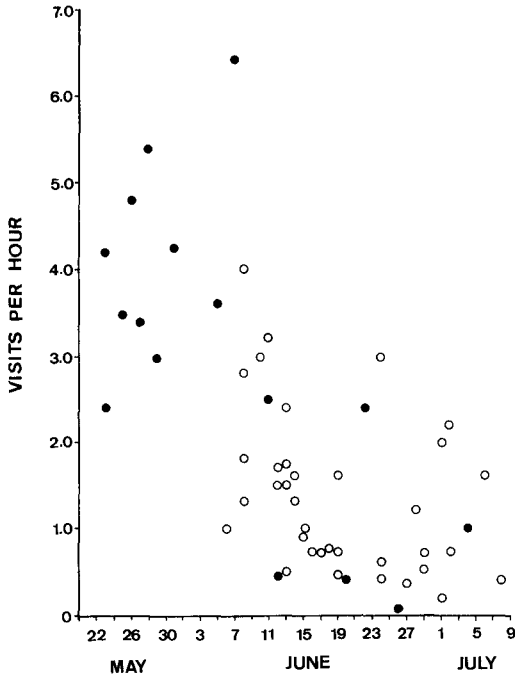


FIGURE 4. *Phaethornis superciliosus* visited stands of *Heliconia stilesii* less frequently during the morning (before 12:00) as the rainy season progressed and other sources of nectar became available. Open circles = 1980,  $r = -0.40$ ; Closed circles = 1981,  $r = -0.47$ .

*Threnetes* regularly visited *H. stilesii* flowers, especially soft wilted flowers in the afternoon. They accounted for 18 to 20% of all flower visits before 12:00 on May 26 to 28, 1981, and for 54 to 65% of all flower visits in the afternoon on these same days. Visit rates by *Threnetes* were below those of *Phaethornis* (Fig. 5).

*Eutoxeres* rarely visited the abundant *H. stilesii* flowers in May to July. We recorded no visits during our regular monitoring, but did observe two visits at other times. We noted this hummingbird at *H. stilesii* flowers primarily during the dry season in February to March, when we recorded a total of 43 site visits and 119 flower visits during 25 hr of morning hour monitors (06:00 to 11:00) at two different stands of *H. stilesii*. Rates of site visitation varied from 0.8 to 3.2 times per hour and rates of flower visitation varied from 2.2 to 7.6 flowers per hour. One of the *Eutoxeres* responsible for these data was territorial at a large stand of *H. stilesii*.

#### NECTAR REMOVAL

Feeding *Phaethornis* insert their bill through the anterior opening in the perianth of *H. stilesii*

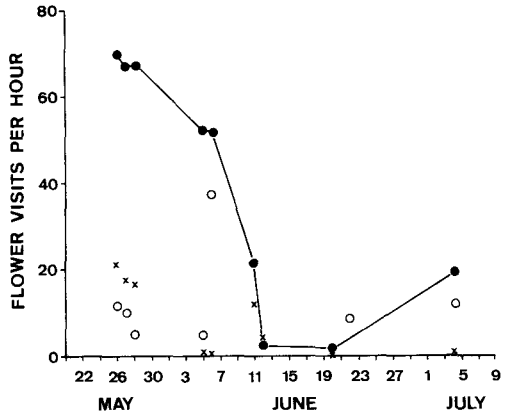


FIGURE 5. The number of marked *Heliconia stilesii* flowers hummingbirds visited each hour declined sharply in June 1981. Closed circles = visits by a lek male (color-marked PWR) *Phaethornis superciliosus*; open circles = visits by other *P. superciliosus*; X = visits by *Threnetes ruckeri*.

flowers, probe deeply into the flower to extract nectar, and, while doing so, brush their foreheads against the anthers and stigma, conspicuously coating their foreheads with whitish *H. stilesii* pollen. These hummingbirds typically remove most of the nectar from the belly of the flower, but little (8%) from the main nectar chamber. The average residual nectar volume in the bellies of visited flowers was only  $1.1 \mu\text{l}$  compared to  $12.7 \mu\text{l}$  in controls ( $P < .01$ ; Wilcoxon's Matched Pairs Signed-Rank Test,  $n = 12$ ). The average residual volume ( $73.9 \mu\text{l} \pm 17.9 \text{SD}$ ) in the main chamber of visited flowers was only slightly less than that ( $80.2 \mu\text{l} \pm 18.7 \text{SD}$ ) in unvisited controls ( $0.01 < P < 0.025$ ; Wilcoxon's Matched Pairs Signed-Rank Test, one-tailed,  $n = 23$ ). Possibly some of the nectar in the main chamber is drawn forward as the hummingbird removes the overflow.

Unlike *Phaethornis*, both *Eutoxeres* and *Threnetes* extract nectar from the main nectar chambers of the *H. stilesii* flowers they visit, but in different ways. *Eutoxeres* probes the flower directly as does *Phaethornis*, but does so while clinging to the bract instead of hovering in front of the flower. Prolonged contact with the anthers causes pollen to be deposited in the groove on their foreheads. The nectar chambers of the four flowers we checked immediately after sicklebill feeding visits were completely empty. *Threnetes* does not usually probe the flowers directly through the anterior opening in the perianth, but instead

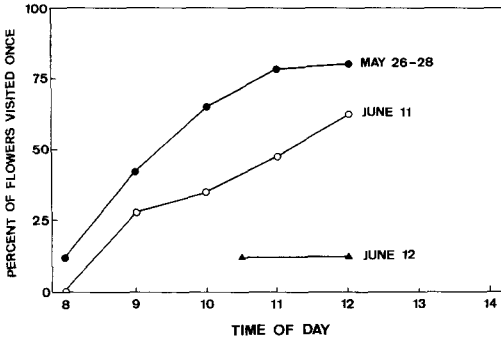


FIGURE 6. Cumulative probability of a *Heliconia stilesii* flower being visited once by *Phaethornis superciliosus* during the morning in late May and June 1981. A switch by these hummingbirds to other flowers in mid-June caused the majority of the flowers to remain unvisited.

pierces the lower side of the perianth and drinks directly from the main nectar chamber without making contact with a flower's reproductive structures. No or little nectar remained in the rear chamber of 11 of 13 visited flowers. Substantial nectar volumes (69 and 83  $\mu$ l) were left in two flowers, but these were less than in the paired control (109 and 89  $\mu$ l). In contrast to six control flowers, only one visited flower contained some nectar anterior to the main nectar chamber. I conclude that pirating *Threnetes* extract much of the nectar available in *H. stilesii* flowers. In summary, access to the main nectar chamber of *H. stilesii* flowers potentially yields much more nectar to *Eutoxeres* and *Threnetes* than *Phaethornis* can get from the belly of the flower.

FORAGING EFFICIENCY

Differences among the three hermits in average times per *H. stilesii* flower visit and in their foraging costs determine each species' net energy gain (Table 3). Extraction time is the total time that a hummingbird takes to insert its bill into a flower, to extract nectar, and then to remove its bill from the flower (Wolf 1975). *Phaethornis* fed more quickly at *H. stilesii* flowers than did *Eutoxeres* or *Threnetes*. The rapid flower visits by *Phaethornis* are consistent with the uptake of small leakage nectar volumes only compared to the entire contents of the nectar chamber and, for *Threnetes* only, the time required to pierce the flower tissue.

To determine if *Phaethornis* achieved the same net gain as the other hermits by rapidly visiting more flowers each with less nectar, we recorded average times per flower visit achieved during 72 foraging bouts of variable lengths. The times included extraction time at a flower plus time spent moving between flowers. In these foraging bouts, which were restricted to flowers within one large stand of *H. stilesii*, *Phaethornis* averaged  $4.38 \pm 1.53$  (SD) sec per flower visited. Thus, *Phaethornis* potentially visits four flowers in the same amount of time (17.3 sec) *Eutoxeres* takes to visit one flower, obtaining a net energy gain of 72 J compared to 345 J for *Eutoxeres*.

DISCUSSION

The roles of the three hermit hummingbirds that visit the flowers of *H. stilesii* are not unique to this assemblage of species. Combinations of specialists, generalists, and thieves are characteristic

TABLE 3. Foraging efficiencies of three hermit hummingbirds at *Heliconia stilesii*.

	Long-tailed Hermit ( <i>Phaethornis superciliosus</i> )	Band-tailed Barbthroat ( <i>Threnetes ruckeri</i> )	White-tipped Sicklebill ( <i>Eutoxeres aquila</i> )
Weight (g)	6.0	6.5	10.0
Metabolism (J/sec) <sup>1</sup>	1.0 (hover)	1.1 (hover)	0.3 (sit)
Foraging costs <sup>2</sup>			
Extraction time	2.0 $\pm$ 1.0	6.5 $\pm$ 4.2	17.3 $\pm$ 11.2
(n)	(85)	(33)	(11)
Energy (J/flower)	2.1	7.2	5.2
Net gain <sup>2</sup>			
Anterior at 20 J/flower	17	13	15
Total at 350 J/flower	—	343 <sup>2</sup>	345

<sup>1</sup> Assumes hovering costs = 0.175 J/g·sec and sitting at 30°C = 0.03 J/g·sec (DeBenedictis et al. 1978, Gill 1985).  
<sup>2</sup> Assumes removal of all nectar; does not account for residual volumes.

of several well-studied hummingbird assemblages (Colwell et al. 1974, Feinsinger 1976, Wolf et al. 1976, Feinsinger and Colwell 1978). The three montane species of sunbirds that often feed together at *Leonotis* mint flowers in East Africa (Gill and Wolf 1978) provide a striking analogue, in which differences in the fit between bill and flower affect rates of nectar uptake and patterns of flower use. In this case, the largest species, *Nectarinia reichenowi* has a strongly decurved bill and pollen-carrying groove similar to those of *Eutoxeres*. Like *Eutoxeres* at certain *Heliconia* flowers, *N. reichenowi* is a specialized mutualist of the *Leonotis* flowers. Resembling *Phaethornis* at *H. stilesii* flowers, the sunbird *N. famosa* has a long straight bill that fails to negotiate the flower curvature and to probe accurately into the basal nectar chamber. Like *Threnetes*, the sunbird *N. venusta* is a thief that pierces floral tissue directly into the nectar chamber and performs little or no pollination service. The use of *Leonotis* flowers by *N. famosa* and *N. venusta* depends on whether *N. reichenowi* is the primary visitor of the flowers and on the local availability of other flowers yielding higher foraging efficiency.

Hummingbirds are sensitive to subtle variations in net energetic rewards, and quickly shift to the best available sources of nectar (Wolf et al. 1972, Feinsinger 1978, Wolf and Hainsworth 1983, Montgomerie 1984, Montgomerie et al. 1984). Even though *H. stilesii* produces flowers rich in nectar throughout the year and primarily during the 6-month rainy season, *P. superciliosus* only uses them for a several week period and then shifts to other, higher-yield nectar sources. This abbreviated seasonal interest reflects *Phaethornis*' inability to remove the majority of nectar available; the length and severe curvature of the perianth of *H. stilesii* flowers prevented access to the main nectar chamber. The abandonment of *H. stilesii* flowers contrasts with this hummingbird's sustained 6 to 7 month relationship with *H. pogonantha* in the lowlands of northeastern Costa Rica (Stiles 1975, 1979; Stiles and Wolf 1979). The difference lies in the fact that *Phaethornis* extracts the full nectar reward from the basal chamber of *H. pogonantha* flowers and thus is not restricted to anterior overflow in these flowers (Stiles, pers. comm.). The accessible nectar also attracts a large, territorial hummingbird, *Chalybura urochrysis*, which defends some clumps of *H. pogonantha* against traplining

*Phaethornis* (Stiles and Wolf 1979; Gill, pers. observ.).

Diffuse mutualisms characterize pollination systems (Janzen 1980, 1983, 1985a; Feinsinger 1983; Schemske 1983a). Most pollinators visit a variety of flowers on a nonexclusive basis; most flowers attract a variety of visitors that vary greatly in their effectiveness as pollinators (Schemske 1983b, Jennersten 1984, Schemske and Horvitz 1984). Because the distributions and abundances of partners independently reflect varied historical and ecological factors, the participants in pollination mutualisms also vary radically in time and space. New associations form and old bonds break, preventing the development of stable equilibria (Janzen 1985a, 1985b).

The pollination biology of *H. stilesii* Daniels at Sirena in 1981 doubtfully resembles the conditions under which this plant originally evolved. My study area was in abandoned pasture at the edge of rain forest. Much of the surrounding region had been clearcut for livestock or banana crops, favoring an abundance of second-growth plants, such as *H. imbricata*, and an abundance of opportunistic hummingbirds and insects, including *Trigona* bees. The attraction of such opportunists and robbers to unharvested nectar can thwart visits by pollinators and depress seed set (Lyon and Chadek 1971, Carpenter 1979, McDade and Kinsman 1980, Willmer and Corbet 1981, Gill et al. 1982, Roubik 1982, Snow 1982, Inouye 1983). Studies of seed set by *H. stilesii* at Sirena in relation to pollinator visitation at different times of the year would be of interest. Unless autogamy or self pollination by floral mites (Dobkin 1984) prevails, we expect that the ratio of fruits/flowers declines markedly during the rainy season at Sirena. Even if autogamous fruits are formed, the effects of inbreeding depression on seed quality may be profound (Schemske 1983b). Also, the probability of pollination and seed set will depend on the exact times of hummingbird visits during the morning in relation to temporal patterns of stigma receptivity and anthesis, details of which are not known for this species.

Many species of *Heliconia* have evolved floral attributes that exclude casual foragers and attract regular visits by traplining hermit hummingbirds (Snow and Snow 1972, Stiles 1979, Feinsinger et al. 1982). The species of *Heliconia* with pen-

dant inflorescences in the *H. pogonantha* assemblage, including *H. stilesii*, have coevolved with sicklebills to varying degrees (Stiles 1979, also Kress 1982 for taxonomic issues). *H. vellerigera* Poeppig and *H. ramonensis* Daniels and Stiles, which have long (45 to 55 mm) perianths bent 90° in the middle, are the most specialized for *Eutoxeres* visitation. The sharply bent flowers of *H. stilesii* Daniels and *H. curtispatha* Petersen flowers are intermediate in length, but still seem geared primarily for *Eutoxeres*. *H. pogonantha*, on the other hand, has a short (40 cm), moderately curved, less specialized perianth. The varying degrees of specialization correspond to the distribution of *Eutoxeres* in Central America. *Eutoxeres* is most common at moderate elevations in the wet foothills, but ranges seasonally into the lowlands (Slud 1964, Ridgely 1976). The severely curved *H. vellerigera*, which is restricted to a narrow band of 800 to 1,000 m on the Caribbean slopes of the Cordillera Central, occupies prime sicklebill habitat. Likewise, *H. ramonensis* also occupies prime sicklebill habitat up to 1,200 m on the southwestern slopes of Costa Rica. The less-curved *H. pogonantha* is restricted to the Caribbean lowlands below 350 m and thus below the primary distribution of *Eutoxeres*, and it also ranges north to Honduras, where sicklebills do not occur. The slightly curved flowers of *H. pogonantha* attract generalized hermit hummingbirds, such as *P. superciliosus*, throughout the flowering season. *Eutoxeres* visits the Caribbean lowlands at Finca La Selva only irregularly, apparently descending there to feed at *H. pogonantha* and other flowers during periods of food shortage at higher elevations on the Caribbean slopes.

*E. aquila*, one of the pollinators with which *H. stilesii* probably coevolved, rarely visits Sirena, a coastal locality. Stiles and Wolf (unpubl. data) observed that when the primary mutualist does not visit the flower and harvest the nectar, overflow of nectar from the chambers of the specialized species of *Heliconia* with long flowers provides a "fail-safe" mechanism for the attraction of generalized pollinators, such as *P. superciliosus*. A survey of geographic variation in *H. stilesii* floral morphology in relation to *Eutoxeres* pollination service would be most interesting. *H. stilesii* at Sirena is at the fringes of its range and partnership with *Eutoxeres*. Here, perhaps, it faces new selection pressures to bring its mutualistic relationships into better accord with the Long-tailed Hermit, including shortening and

straightening of the corolla to allow easier access to the nectar chamber i.e., convergence towards floral morphology of *H. pogonantha*.

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