

## The hummingbird community of a lowland Amazonian rainforest

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Between October 1987 and September 1989, the British Ornithologists' Union Colombia Expedition recorded 16 species of hummingbird at Matamatá in the Amacayacu National Park, Amazonas, Colombia. Most of these species were resident breeders at the study site although two appeared to be local migrants. Six species of hermit hummingbirds (subfamily Phaethornithinae) occurred at Matamatá; although very similar in general morphology and behaviour, they showed different preferences for habitat, food plants and foraging technique. Hermits were predominant in the forest, but in areas of secondary vegetation and along riverine borders, "typical" hummingbirds (subfamily Trochilinae) were more common. The study site consisted of terra firme and várzea forest and an area of riverine secondary vegetation and contained around 60 species of flowering plants visited by hummingbirds. In contrast with most groups of organisms, hummingbirds and hummingbird-pollinated plants had similar species diversity in primary forest and secondary habitats. The overall abundance of hummingbirds and flowers was significantly higher in areas of riverine secondary growth. The hummingbird community at Matamatá is remarkably species rich when compared with study sites elsewhere in North and South America. However, random null model comparisons among Amazonian hummingbird communities reveal that they share many characteristics in their structure and show a high degree of species overlap.

The structure and organization of hummingbird communities have been extensively studied in North and Central America and the Caribbean Islands (Snow & Snow 1972, Lack 1973, Feinsinger 1976, 1978, Wolf *et al.* 1976, Feinsinger & Colwell 1978, Stiles 1981, 1985, Kodric-Brown *et al.* 1984, Brown & Bowers 1985). In contrast, little is known about Amazonian hummingbird communities beyond species lists and taxonomic studies (Johns 1986, Karr *et al.* 1990).

Most tropical hummingbirds overlap extensively in the flowers they exploit and compete aggressively for the available resources (Feinsinger 1978, Gass 1978, 1979); others, such as the hermits, have elongated bills which allow them more or less exclusive access to nectar in long-tubed flowers, which less specialized hummingbirds cannot reach (Snow & Snow 1972, 1980, Stiles 1975). Thus communities of hummingbirds are often considered to be organized on the basis of interference competition at defensible resources and coevolved relationships between bill morphology and flower morphology (Feinsinger 1976, 1978, Wolf *et al.* 1976, Kodric-Brown *et al.* 1984, Brown & Bowers 1985, Stiles 1985). Hinkelmann (1990) examined the geographical separation of hermit hummingbird species in Amazonian lowland rainforest. He found that present-day theories for the distribution of bird species in Amazonia were unable to explain the distributions of many species represented in museum collec-

tions. However, body-mass was apparently of great importance; only one hermit species of each body-mass category (2–4 g, 4–8 g, >8 g) occurred at a given site in terra firme forest. In the cases where species of similar weight occurred in the same site, Hinkelmann suggested that differences in their culmen morphology (and therefore feeding niche) might explain their sympatry.

Lack (1973) noted that the distribution of hummingbird species between Antillean islands appeared to be determined by interspecific competition, with most islands having two or three hummingbird species which differed in their culmen morphology and body size. This observation was confirmed by Brown and Bowers (1985), who tested the morphology and the observed number of species on each island against that predicted by models based on random distributions. The communities studied were relatively simple—most of the 39 islands studied had one to three species of hummingbirds.

Many Amazonian communities are among the oldest on earth and are exceptionally rich in both plant (Gentry 1988) and bird species (Terborgh *et al.* 1990). The hummingbird–plant community of an Amazonian forest might therefore be expected to be exceptionally diverse and to show a high degree of coevolved relationships. Here I report on the first detailed study of an Amazonian hummingbird community and compare the species composition at Matamatá with published reports for other study sites in the Amazon basin.



**Figure 1.** The location of the Amacayacu National Park. The study site, Matamatá, was at the southern end of the park, on the Amazon River ( $3^{\circ}49'S$ ,  $70^{\circ}16'W$ ).

## METHODS

### The study site

Fieldwork was carried out between October 1987 and September 1989 as part of the British Ornithologists' Union Colombia Expedition. The expedition was based at Matamatá ( $3^{\circ}49'S$ ,  $70^{\circ}16'W$ ) in the southern part of the Amacayacu National Park, Amazonas, Colombia (Fig. 1). Matamatá is on the northern shore of the Amazon River and is approximately 100 m above sea level.

The park has been managed since 1975 by the Instituto Nacional de los Recursos Naturales Renovables y del Ambiente (INDERENA) and covers almost 300,000 ha of primary rainforest. Most of the Amacayacu National Park is covered by terra firme (or dry-land) forest, forming a continuous canopy 40–50 m high, occasionally interrupted by emergent trees reaching 60 m. The forest understory is composed largely of tree seedlings, ferns and perennial herbs beneath midlevels containing palms, sapling trees and climbing ferns. There has been little human interference at Matamatá although subsistence hunting and tree felling by local people are permitted within the park.

The floodplain of white-water rivers, the várzea, is highly productive but usually is less diverse than terra firme forest. Between January and June, changes in the level of the Am-

azon River flooded the várzea at Matamatá to a depth of up to 2 m. As a result of these prolonged annual floods, the várzea has very little herbaceous ground cover, but the mid-layers are rich in shrubs, palms, epiphytes and hemiepiphytes. The várzea canopy is lower and less continuous than in the terra firme forest although emergents, such as Silk-cotton Trees *Ceiba pentandra*, rise above the canopy to over 50 m. At Matamatá, the várzea forest extends from the Amazon River's banks for about 1 km to where it meets terra firme forest. The transition is abrupt, with a dense ground cover of ferns and seedlings replacing the bare floor of the várzea.

An area close to the river at Matamatá was cleared of forest for cattle grazing but had been allowed to regenerate naturally since 1975. Many large trees, originally left to provide shade, now form a highly discontinuous upper level approximately 25–30 m high. The midlevel comprises less mature trees and old plantations of cacao. Although most of the riverine habitat is seasonally inundated, there is a narrow levee covered with perennial herbs which is not normally flooded. The wetter soils along river banks and in low-lying riverine areas are dominated by grasses with some shrubs.

Matamatá has a tropical humid climate with little seasonal variation. At a weather station situated in a clearing near the forest edge, we recorded a mean monthly shade temperature of  $27.5^{\circ}C$ , with a range of less than  $3^{\circ}C$ . Daily variation in temperature was more marked; the mean range was  $10^{\circ}C$  and the maximum  $15^{\circ}C$ .

Amacayacu is located almost in the geographical centre of the Amazon basin and is one of the wettest areas. At Matamatá, we recorded an average annual rainfall of 3377 mm. July and August had the lowest rainfall (127 mm) and January to March the highest (339 mm). There was little seasonal variation in relative humidity at 06.00 h (97%) although the daily range was up to 50%.

### Mist netting

Between 25 August 1987 and 10 September 1989, I conducted a total of 308 bird-ringing sessions at Matamatá. Half of these sessions were in the riverine secondary vegetation, the others were split evenly between the várzea and terra firme forests. All hummingbirds caught were marked with an individually numbered aluminium ring and many with a small spot of coloured acrylic paint on the tail feathers. Standard measurements of weight, wing-length and culmen length were taken, and in addition, I collected samples of pollen from the bill and head feathers. All species names given follow Hilty and Brown (1986). There were no taxonomic difficulties with identification, but all biometrics were checked against specimens in the British Museum.

### Flower watches and monthly records

Flowering phenology was recorded using three standard transects along footpaths to census approximately equal ar-

eas (1.7–2.0 ha) in the riverine, várzea and terra firme habitats every 2 weeks. In addition, a census of over 120 individually marked plants was made every 2 weeks to record their flowering and fruiting cycles. I recorded the nectar production for the 20 most frequently visited species.

Every month I spent at least 7 h watching each species of hummingbird-visited plant which was flowering. For each visit by a bird, I recorded the time of day, species, sex, colour marks, number of flowers or inflorescences visited and the duration of the visit. Behaviour, such as territorial defence, courtship singing or mating, was also recorded.

### Collection and identification of plants

I collected specimens of all plants visited by hummingbirds and sent them for identification to Dr José Vicente Rodríguez, INDERENA, Bogotá, Colombia, and Dr Ray Harley, Royal Botanic Gardens, Kew, UK. Botanical collections were also made by Dr Al Gentry, Missouri Botanic Gardens, USA, and Rodolfo Vásquez, La Universidad de Amazonas, Iquitos, Peru. Voucher numbers and determinations for the specimens, as well as descriptions of their habitat, morphology, phenology and visitors are given in P. Cotton (1993, unpublished DPhil thesis, University of Oxford).

### Niche parameters

I calculated species diversity and niche breadth using Simpson's diversity index,  $D$ , which ranges from 0 (low diversity) to a maximum of 1.0 (Simpson 1949). Niche overlap between two species was calculated using Pianka's index (Pianka 1973). The frequency of occurrence of a species in a particular habitat was assessed as a preference index (Jacobs 1974). This preference index ranges from  $-1$  (total avoidance) to  $+1$  (exclusive use), with a score of zero indicating habitat use in proportion to availability.

## RESULTS

### The hummingbird guild

I recorded 16 species of hummingbirds at Matamatá (Table 1), most of which were resident throughout the year and are known or suspected to breed at Matamatá. Two additional species, Black-bellied Thorntail *Popelairia langsdorffi* and Olive-spotted Hummingbird *Leucippus chlorocercus*, were recorded in the region but were not seen at Matamatá.

I recorded six species of hermit hummingbirds (subfamily Phaethornithinae) in the study site, most of which were relatively common and showed largely overlapping ranges. All hermits are specialized trapliners that visit isolated and undefended flowers (Feinsinger & Colwell 1978); only Rufous-breasted Hermits *Glaucis hirsuta* were observed defending territories. Hermit hummingbirds primarily occur in the lower levels of the forest (Hilty & Brown 1986), and it is reasonable to assume that the frequency of observation and capture (see Table 2) reflects their actual abundance.

Of the ten species of typical hummingbirds recorded, most were found holding territories in riverine vegetation and were recorded only rarely in the forest (Table 2). Three species (Fork-tailed Woodnymph *Thalurania furcata*, Gould's Jewelfront *Polyplancta aurescens*, Black-eared Fairy *Heliothryx aurita*) occurred regularly in the forest and were not usually observed to hold feeding territories. Two species of typical hummingbirds (Grey-breasted Sabrewing *Campylopterus curvipennis*, Blue-tailed Emerald *Chlorostilbon mellisugus*) were apparently local migrants which moved along the banks of the Amazon River following the flowering patterns of their food plants.

### The hermit subcommunity

Compared with other locations in the Neotropics, the hummingbird community at Matamatá is species rich, with a strikingly large number of coexisting hermit species. Hinkelmann (1990) found that only one hermit species of each body-mass category (2–4 g, 4–8 g, >8 g) inhabited a given site in Amazonian lowland rainforest. At Matamatá, only the Reddish Hermit *Phaethornis ruber* is in the 2–4-g category, the other five species all weigh between 4 g and 8 g (Table 1). Some species are separated by their habitat preferences, but at least two 'medium-sized' species were frequently recorded in each habitat (Table 2).

Hermit hummingbirds are often considered to be segregated into specific feeding niches because their long bills are believed to have coevolved with their food plants (Stiles 1978, Snow 1981, Gill 1987). Morphologically and behaviourally, there is little to distinguish the five larger hermit species (Table 1). Some species (e.g. Straight-billed Hermit *Phaethornis bourcieri*, Pale-tailed Barbthroat *Threnetes leucurus*) are unlikely to be competitors for resources because their ranges do not usually overlap (Fig. 2), but where similar hermit species are common within the same habitat, it appears likely that there is potential for severe interspecific competition.

Long-tailed Hermits *Phaethornis superciliosus* and Rufous-breasted Hermits are similar in size and culmen morphology and share 11 food plants out of a total of 13 for the Rufous-breasted Hermit. However, analysis of the niche overlap between the two species showed that they have only 10.5% overlap in their diet (Table 3). Only two pairs of species, Rufous-breasted Hermit–Reddish Hermit and Straight-billed Hermit–Long-tailed Hermit, had a dietary overlap greater than 50%.

### The plant guild

Hummingbirds at Matamatá visited the flowers of over 60 species. At least 40 of these species were considered ornithophilous (adapted for pollination by birds), having brightly coloured, tubular flowers and copious quantities of nectar (Feinsinger 1983); 30 were visited primarily by traplining hermits. The majority of the hummingbird-adapted plants were herbaceous perennials, vines or epiphytes; only a few

**Table 1.** Biometrics (mean  $\pm$  s.d.), habitat use and abundance of the 16 species of hummingbirds recorded at Matamata

Species	Number caught	Weight <sup>a</sup> (g)	Wing <sup>a</sup> (mm)	Culmen <sup>b</sup> (mm)	Bill curve <sup>c</sup>	Habitat <sup>d</sup>	Abundance <sup>e</sup>
<b>Hermits (Phaethornithinae)</b>							
Rufous-breasted Hermit <i>Glucis hirsuta</i>	186	6.3 $\pm$ 0.7	60.3 $\pm$ 3.5	29.3 $\pm$ 1.0	M	R, V, TF	A
Pale-tailed Barbthroat <i>Threnetes leucurus</i>	75	6.0 $\pm$ 0.6	60.9 $\pm$ 3.2	28.5 $\pm$ 1.3	S	<u>R</u> , V, TF	C
Long-tailed Hermit <i>Phaethornis superciliosus</i>	54	6.3 $\pm$ 0.5	60.7 $\pm$ 2.2	37.7 $\pm$ 2.1	V	R, V, TF	C
White-bearded Hermit <i>Phaethornis hispidus</i>	41	5.0 $\pm$ 0.4	57.2 $\pm$ 3.2	31.6 $\pm$ 1.9	M	<u>R</u> , V	C
Straight-billed Hermit <i>Phaethornis bourcieri</i>	30	4.4 $\pm$ 0.4	57.3 $\pm$ 2.4	29.2 $\pm$ 0.6	O	V, TF	F
Reddish Hermit <i>Phaethornis ruber</i>	2	2.6 $\pm$ 0.1	40.5 $\pm$ 0.6	21.9 $\pm$ 0.8	S	R, V, TF	U
<b>Typical hummingbirds (Trochilinae)</b>							
Grey-breasted Sabrewing <i>Campylopterus largipennis</i> <sup>f</sup>	0	8.5	73.2	25.8 $\pm$ 1.5	S	<u>R</u> , V	U
White-necked Jacobin <i>Florisuga mellivora</i>	1	6.3	62.0	18.5 $\pm$ 1.0	S	<u>R</u> , V	F
Black-throated Mango <i>Anthracoceros nigricollis</i>	1	7.0	67.0	23.5 $\pm$ 0.8	S	<u>R</u>	F
Blue-chinned Sapphire <i>Chlorestes notatus</i>	3	3.7 $\pm$ 0.1	51.0 $\pm$ 1.4	17.4 $\pm$ 1.2	O	<u>R</u>	U
Blue-tailed Emerald <i>Chlorostilbon mellisugus</i>	1	2.6	45.0	14.9 $\pm$ 0.7	O	<u>R</u>	F
Fork-tailed Woodnymph <i>Thalurania furcata</i>	20	4.3 $\pm$ 0.2	55.5 $\pm$ 2.0	20.6 $\pm$ 0.8	S	R, V, TF	C
Golden-tailed Sapphire <i>Chrysura oenone</i>	12	4.3 $\pm$ 0.4	51.9 $\pm$ 1.5	17.6 $\pm$ 0.7	S	<u>R</u> , V	F
Glittering-throated Emerald <i>Amazilia fimbriata</i>	76	4.9 $\pm$ 0.4	54.8 $\pm$ 2.4	20.5 $\pm$ 0.7	S	<u>R</u> , V	A
Gould's Jewelfront <i>Polyplanta aurescens</i>	2	6.2 $\pm$ 0.6	60.5 $\pm$ 3.5	18.5 $\pm$ 0.7	O	V, TF	U
Black-eared Fairy <i>Heliothryx aurita</i> <sup>f</sup>	0	5.4		17.2	O	V, TF	R

<sup>a</sup> Mean values; sexes grouped. Data from mist-net captures.<sup>b</sup> Exposed culmen, length. Measurements from mist-net captures (species with  $n > 20$ ) and museum specimens (species with  $n < 20$  captures).<sup>c</sup> Bill curvature: V = very curved; M = moderately curved; S = slightly curved; O = straight.<sup>d</sup> Habitat: R = riverine secondary vegetation; V = várzea forest; FT = terra firme forest. Preferred habitats are underlined.<sup>e</sup> Abundance: A = abundant, 10–100 records/day; C = common, 1–10 records/day; F = frequent, 10–20 records/month; U = uncommon, <10 records/year; R = rare, 1 record in several years.<sup>f</sup> Biometric data from Feinsinger *et al.* (1979) and Dunning (1993).

**Table 2.** The number of mist-net captures, the proportion of foraging observations<sup>a</sup> and the number of plant species visited in each habitat<sup>b</sup> by the 16 hummingbird species recorded at Matamatá. The diet breadth for each species was calculated using Simpson's index

Species	Number of mist-net captures			Foraging observations (%)			Number of plant species visited			Diet breadth, D <sup>c</sup>
	R	V	TF	R	V	TF	R	V	TF	
Hermits										
Rufous-breasted Hermit	181	8	5	88	9	3	7	3	3	0.61
Pale-tailed Barbthroat	55	11	11	98	0	2	7	0	1	0.73
Long-tailed Hermit	11	10	36	19	20	61	7	3	9	0.88
White-bearded Hermit	36	6	0	61	39	0	7	1	0	0.73
Straight-billed Hermit	1	4	25	0	30	70	0	1	6	0.63
Reddish Hermit	0	8	0	30	30	40	2	2	2	0.83
Typical hummingbirds										
Grey-breasted Sabrewing	0	0	0	96	4	0	1	1	0	0.08
White-necked Jacobin	0	0	1	80	20	0	3	1	0	0.47
Black-throated Mango	1	0	0	100	0	0	3	0	0	0.21
Blue-chinned Sapphire	3	0	0	100	0	0	3	0	0	0.59
Blue-tailed Emerald	1	0	0	100	0	0	3	0	0	0.26
Fork-tailed Woodnymph	7	4	10	18	27	55	3	2	2	0.70
Golden-tailed Sapphire	15	0	1	97	3	0	7	1	0	0.75
Glittering-throated Emerald	79	1	0	99	0	0	13	1	0	0.84
Gould's Jewelfront	0	2	1							
Black-eared Fairy	0	0	0							

<sup>a</sup> The total number of independent foraging observations (i.e. territorial defence by an individual treated as one observation).

<sup>b</sup> R = riverine, V = várzea, TF = terra firme.

<sup>c</sup> Simpson's index ranges from 0 (low diversity) to a maximum of  $(1 - 1/S)$ , where S is the number of species (Simpson 1949).

shrubs (*Palicourea* and *Sanchezia* spp.) and two tree species (*Quararibea lasiocalyx* and *Palicourea* aff. *lasiantha*) appeared to be adapted for hummingbird pollination. One tree, *Erythrina fusca*, was probably the most important nectar source to non-hermit hummingbirds during the dry season (July and August); however, hummingbirds did not appear to reliably pollinate the flowers and rarely carried *Erythrina* pollen. Pollen samples collected from hummingbirds at Matamatá indicated that hummingbirds transfer pollen of most of the flower species they visit (P. A. Cotton, unpubl. data).

### Hummingbird-plant associations

Hummingbirds often show a striking fidelity to particular species or size categories of flowers (Snow & Snow 1980). The specificity of legitimate visits of large hummingbirds to long-tubed flowers and small hummingbirds to short-tubed flowers appears to be maintained by a relatively precise matching of the corolla and nectar secretion rates of flowers to the bill lengths and foraging economics of hummingbirds (Feinsinger 1978).

At Matamatá, this pattern generally occurred although Rufous-breasted Hermits and Long-tailed Hermits fed from a wide variety of plants with corollas ranging from 15 mm to 70 mm (Table 2). The more abundant hummingbird species were observed feeding from 6–19 species of plants; however, some hummingbirds were uncommon (e.g. Grey-

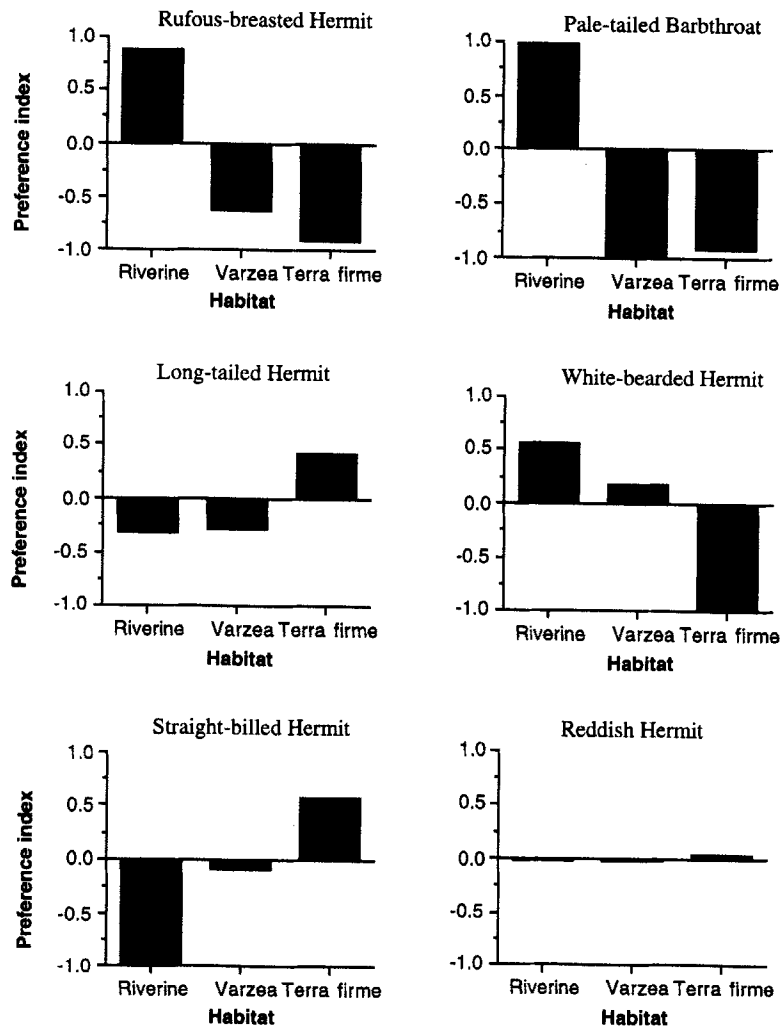
breasted Sabrewing) or fed high in the canopy (e.g. White-necked Jacobin *Florisuga mellivora*, Black-throated Mango *Anthracothorax nigricollis*), and the small sample size of foraging observations may have caused the dietary niche breadth to be underestimated.

The primary food sources for hermits were herbaceous plants (especially Acanthaceae, Musaceae, Zingiberaceae) and Passifloraceae vines. The Trochilinae fed predominantly from the flowers of vines (Cucurbitaceae), bushes (Rubiaceae) or trees (Fabaceae, Myrtaceae, Rubiaceae).

### Habitat differences in the hummingbird-plant community

The hummingbird-plant guilds in terra firme forest and the noninundated areas of riverine secondary growth were dominated by perennial herbs, especially Cucurbitaceae, Musaceae and Zingiberaceae. In the várzea and low-lying areas of the riverine habitat forest, where herbaceous plants were scarce, epiphytes (Bromeliaceae), shrubs (*Palicourea* spp.) and vines (Passifloraceae) were of greater importance.

Small light gaps in the forest, caused by single tree falls, were quickly closed by saplings and plants growing from the soil seed bank, but multiple tree falls and human disturbance created large light gaps and allowed colonization by herbaceous hummingbird-pollinated plants. Where gaps remained open, usually for agricultural crops, dense stands of



**Figure 2.** Habitat preference indices for hermit hummingbirds (Phaethornithinae) at Matamá. The indices are based on foraging observations only and were calculated using Jacobs' index.

*Costus* spp. or *Heliconia* spp. often formed in undisturbed patches. Crop plants such as Pineapples *Ananas comosus* and Plantain *Musa paradisiaca* provided additional nectar sources in these areas.

Hummingbirds visited almost equal number of plant species in the riverine secondary vegetation (30) and the terra firme forest (31). The várzea forest had considerably fewer

species of hummingbird-visited flowers (11) and had the lowest diversity of flower species recorded on monthly transects ( $F_{2,72} = 33.8$ ,  $P < 0.001$ ,  $\sqrt{\text{arc sine transformed}}$ ). Flower density recorded on monthly transects was low in várzea and terra firme forest (<50 open flowers/ha) but significantly higher (416) in riverine secondary vegetation ( $F_{2,72} = 29.2$ ,  $P < 0.001$ , log transformed).

**Table 3.** The dietary niche overlaps<sup>a</sup> of the six species of hermit hummingbirds (Phaethornithinae) recorded at Matamá

Species	Pale-tailed Barbthroat	Long-tailed Hermit	White-bearded Hermit	Straight-billed Hermit	Reddish Hermit
Rufous-breasted Hermit	0.09	0.11	0.15	0.02	0.52
Pale-tailed Barbthroat		0.20	0.35	0.00	0.00
Long-tailed Hermit			0.26	0.59	0.17
White-bearded Hermit				0.00	0.36
Straight-billed Hermit					0.15

<sup>a</sup> Pianka's niche overlap.

**Table 4.** Features of the plant–hummingbird communities of riverine secondary vegetation, várzea forest and terra firme forest

	Riverine	Várzea	Terra firme
Plants			
Number of species visited	30	11	31
Species diversity, $D^a$	0.62	0.27	0.54
Mean flower density (flowers/ha $\pm$ s.d.)	416 $\pm$ 153	58 $\pm$ 26	28 $\pm$ 5
Mean number of flowers per plant ( $\pm$ s.d.)	306 $\pm$ 121	24 $\pm$ 12	17 $\pm$ 8
Hummingbirds			
Number of species caught	11	9	8
Number of individuals caught	390	48	90
Diversity, $D^a$	0.72	0.84	0.73

<sup>a</sup> Simpson's index.

Many plant species in riverine secondary vegetation showed "high-density" flowering, with some individuals producing over 1000 open flowers at one time. Forest species produced significantly fewer open flowers per plant ( $F_{2,56} = 7.34$ ,  $P < 0.01$ , log transformed), most individuals having less than five flowers open at any one time. The low flower density in the forest precluded territorial defence and probably accounts for the observation that very few typical hummingbirds regularly occurred in the forest. Fork-tailed Woodnymphs were the main exception to this, although Gould's Jewelfront and Black-eared Fairy were primarily forest species (Table 2). All other non-hermit hummingbirds showed a marked preference for the riverine areas.

In all three habitats, c. 80% of the plant species visited by hummingbirds were ornithophilous; there was no significant difference between habitats in the proportions of plants visited which were adapted for pollination by all hummingbirds ( $\chi^2_2 = 0.18$ , n.s.) or by specialized traplining hermit hummingbirds ( $\chi^2_2 = 1.06$ , n.s.).

Habitats did differ significantly in the mean number of

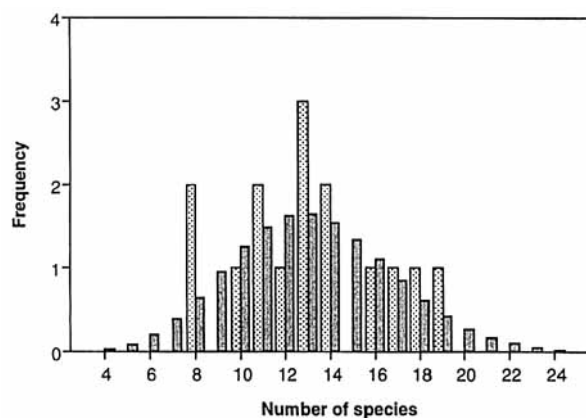
individuals caught per mist-netting session per month ( $F_{2,70} = 23.9$ ,  $P < 0.001$ , log transformed) and the mean number of species caught per session per month ( $F_{2,70} = 23.1$ ,  $P < 0.001$ , log transformed). For both measures, the mean for the riverine habitat was significantly higher than for the forest habitats.

The hermit hummingbirds displayed distinct patterns of habitat preference (Fig. 2, Table 4). Rufous-breasted Hermits, Pale-tailed Barbthroats and White-bearded Hermits *Phaethornis hispidus* all showed a strong preference for the riverine habitat, Long-tailed Hermits and Straight-billed Hermits showed a preference for the terra firme forest, whilst Reddish Hermits showed no distinct habitat preference. Only White-bearded Hermits showed a preference for the várzea forest although all hermit species were recorded there.

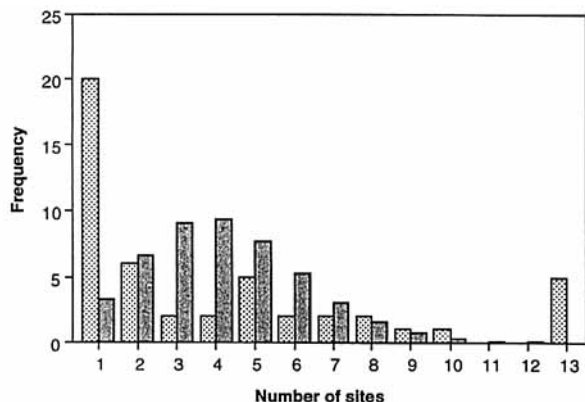
### Comparison with other rainforest hummingbird communities

For 14 hummingbird communities widely spaced throughout the Amazon basin, I obtained a comprehensive avifaunal survey (Gilliard 1941, Blake 1950, Terborgh & Weske 1969, Novaes 1970, Pearson 1972, 1975, O'Neill & Pearson 1974, Willis 1977, Terborgh *et al.* 1984, Moskovits *et al.* 1985, Johns 1986, Karr *et al.* 1990, Willard *et al.* 1991, P. Donahue, T.A. Parker and B. Sorrie, unpubl. report). Following the method outlined in Brown and Bowers (1985), I tested the observed distribution of the number of hummingbird species within each community against a Poisson distribution. The null hypothesis is that there is independent distribution of species between the communities.

There was no significant difference between the observed and predicted distributions of the number of species between communities ( $G_{14} = 18.3$ , n.s.; Fig. 3), so unlike the Antillean communities (Lack 1973, Brown & Bowers 1985), the number of species in Amazonian hummingbird communities is apparently relatively unpredictable. However, a relatively high proportion of species were shared between Matamatá and other communities (range 0.5–1.0, mean = 0.71). The similarity between Matamatá and lowland rain-



**Figure 3.** Comparison between the observed number of hummingbird species at 15 sites in Amazonian forest and that predicted by a Poisson distribution. There is no significant difference ( $G_{14} = 18.3$ , n.s.).  $\square$ , observed;  $\square$  expected.



**Figure 4.** Comparison between the observed number of sites inhabited by a given species of hummingbird and that predicted by a Poisson distribution. The difference is significant ( $G_{14} = 114$ ,  $P < 0.001$ ). ▨, observed; □, expected.

forest sites outside Amazonia is much lower (Arima Valley, Trinidad, 0.33; La Selva, Costa Rica, 0.14) and is no different from a sample drawn at random (0.33).

Six species (Pale-tailed Barbthroat, Long-tailed Hermit, Reddish Hermit, Grey-breasted Sabrewing, White-necked Jacobin, Fork-tailed Woodnymph) occurred at at least 10 of the 15 sites, and all were found at Matamatá. These species appear to represent the "core species" of Amazonian hummingbird communities. In contrast, 20 species occurred only at one location and a further six species were restricted to two sites (Fig. 4). There was no significant difference between hermits and typical hummingbirds in the mean number of sites at which they occurred (Mann-Whitney,  $n = 48$ ,  $U = 169$ , n.s.).

If species occurred at sites independently of one another (i.e. species assemblages were constructed at random), then the frequency of occurrence of the 48 species should have followed a Poisson distribution (Brown & Bowers 1985). However, this was not the case for Amazonian hummingbird communities; there were more restricted and widespread species than would be expected by chance ( $G_{14} = 114$ ,  $P < 0.001$ ; Fig. 4).

## DISCUSSION

### Spatial variation

Contrary to initial expectations and the trend in most groups of organisms, there was no evidence that the hummingbird and plant communities of terra firme forest were richer than those of riverine secondary vegetation. The floral resources in the terra firme forest were neither significantly more diverse nor more specialized than in the riverine habitat, and flower density was significantly higher in the riverine habitats. Although the riverine area is a secondary successional habitat, many of the plants and birds recorded there are typical of primary succession in Amazonian riverine habitats (Remsen & Parker 1983). Riverine commu-

nities are relatively diverse and make an important contribution to Amazonian species richness (Remsen & Parker 1983, Rosenberg 1990).

Spatial variation in flowering plants at Matamatá appeared to be determined by two physical factors, light intensity and flooding. In areas which have fewer trees, the herb layer receives considerably more sunlight than in forest habitats and can afford to produce larger amounts of nectar and more flowers than shade-tolerant forest plants. Terborgh and Weske (1969) and also Blake and Loiselle (1991) reported higher numbers and greater diversity of hummingbirds in areas of neotropical lowland secondary growth.

### Competition and coexistence

In spite of the large number of hummingbird species and their comparatively uniform morphology, there is apparently very little overlap in feeding niches. Since MacArthur and Levins (1967) first posed the question, ecologists have asked how much overlap of adjacent utilization curves is compatible with stable coexistence? On the basis of observational data alone, it is impossible to measure competition; however, most hummingbird species at Matamatá had a dietary niche overlap of much less than 50%, indicating that competition for resources was not normally intense. Among the hermits, resource segregation appeared to be initially by habitat preference and secondarily by food choice, possibly determined by the energetics of foraging and the relationship between culmen and corolla morphology. The typical hummingbirds occurred mainly in the riverine habitat and were territorial. Two species, Gould's Jewelfront and Black-eared Fairy, were nonterritorial forest specialists and appeared to be ecologically separated from the similar-sized hermits by having shorter bills and foraging at higher levels in the forest.

### Comparison with other hummingbird communities

Compared with hummingbird communities in North and South America, Matamatá was very diverse, with 16 species occurring sympatrically and another two species found locally. This diversity is equalled at only a few other sites in tropical forest, such as La Selva, Costa Rica (Stiles 1980); La Montura, Costa Rica (Stiles 1985); and Cocha Cashu, Peru (Terborgh *et al.* 1984).

Unlike Antillean communities (Brown & Bowers 1985), the number of species in Amazonian hummingbird communities is relatively unpredictable. This observation is not surprising, given the general trend in Amazonian communities of other taxa for species composition to be highly variable and unpredictable (Capparella 1991). However, a relatively high proportion of species were shared between Matamatá and other Amazonian localities.

Although species composition was variable, the structure of Amazonian hummingbird communities was constant. Most of the 15 communities analysed contained four or five hermit species (Phaethornithinae) and eight or nine "typi-



cal" hummingbird species (Trochilinae). Amazonian hermit subcommunities were generally composed of (1) Rufous-breasted Hermit, (2) Pale-tailed Barbthroat, (3) one large *Phaethornis* species (Long-tailed Hermit, White-bearded Hermit or Sooty-capped Hermit *P. augusti*), (4) one straight-billed *Phaethornis* species (Straight-billed Hermit or Needle-billed hermit *P. phillippi*) and (5) one small *Phaethornis* species (Dusky-throated Hermit *P. squalidus*, Reddish Hermit, White-browed Hermit *P. stuarti*, Gray-chinned Hermit *P. griseogularis* or Little Hermit *P. longuemareus*). At Matamatá, the only difference in hermit subcommunity was the presence of both the Long-tailed Hermit and the White-bearded Hermit. Both species were common, but they were segregated in part by their habitat preferences.

The subcommunity of "typical" hummingbirds at sites in Amazonian lowland forest, although usually larger than the hermit subcommunity, nevertheless had a predictable structure: (1) Grey-breasted Sabrewing, (2) White-necked Jacobin, (3) an *Anthracothorax* species (usually Black-throated Mango), (4) Blue-tailed Emerald, (5) Fork-tailed Woodnymph, (6) an *Amazilia* species and (7) Black-eared Fairy. This accurately describes the Trochilinae subcommunity of Matamatá.

Of the 16 hummingbird species found at Matamatá, only three were not included in this "typical Amazonian community"; even these (Blue-chinned Sapphire *Chlorestes notatus*, Golden-tailed Sapphire *Chrysuronia oenone*, Gould's Jewelfront) were widespread in Amazonia and occurred in at least five of the 14 sites. Only two hummingbird species (Black-bellied Thorntail, Olive-spotted Hummingbird) which I recorded were rare or had restricted ranges. The Black-bellied Thorntail had a large range but was uncommon throughout (Hilty & Brown 1986). The Olive-spotted Hummingbird occurred mainly on small riverine islands in Upper Amazonia (Hilty & Brown 1986).

This research was supported by the David Lack Studentship, awarded by the British Ornithologists' Union, and the British Ornithologists' Union Colombia Expedition. I thank the Instituto Nacional de los Recursos Naturales Renovables y del Ambiente (INDERENA), especially José Vicente Rodríguez, Carlos Castaño, Oscar Pinto, Antonio Villa and their staff in Leticia and Matamatá. Fellow members of the expedition, Martin Kelsey, Alan and Hilary Tye, Claudia Campos and Marta Gomez, all provided valuable assistance during the fieldwork. I thank Chris Perrins, Peter Jones and Matthew Evans for comments and discussion.

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Submitted 25 March 1997; revision accepted 2 June 1997