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FEEDING ECOLOGY OF HUMMINGBIRDS IN THE SERRA DO MAR, SOUTHEASTERN BRAZIL

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ABSTRACT.– The feeding behaviour of hummingbirds was studied in November and December 1983 at Boracéia, an area of very humid forest in the Serra do Mar, SE Brazil at 800-900 m. Six species of hummingbirds were present in the area, and were recorded taking nectar from 25 native plant species, of which 15 or 16 were considered to be hummingbird-adapted. Both the number of hummingbird species and the number of individuals were small compared with the numbers occurring in humid forest elsewhere in the neotropics. The rate of feeding visits to native plants was low, and the amount of insect-foraging was relatively high. It is argued that low hummingbird diversity and abundance were related to a sparse nectar supply. On the basis of the limited data available, it seems that two plant families that are important for hummingbirds in the Andes and in other montane areas in the neotropics, the Rubiaceae and Ericaceae, provide little nectar for forest hummingbirds in the Serra do Mar, and that this may partly account for the lack of diversity in hummingbird bill lengths. The way in wich the community of hummingbirds living in an area exploits the flowers of that area is of both ornithological and botanical interest. It is also of wider evolutionary interest, as it may throw light on the coevolution of hummingbirds and plants. *Aceptado el 26 de setiembre de 1986.*

RESUMEN.– Comportamiento alimentario de picaflores en la Serra do Mar, sudeste de Brasil.

El comportamiento alimentario de picaflores fue estudiado en noviembre y diciembre de 1983 en Boracéia, una selva muy húmeda en la Serra do Mar a 800-900 m. Seis especies de picaflores estuvieron presentes en el área y fueron registrados tomando néctar de 25 especies de plantas nativas, de las cuales 15 o 16 fueron consideradas estar adaptadas a picaflores. Tanto el número de especies de picaflores como de individuos fue menor comparado con los números ocurridos en otras áreas de selvas húmedas neotropicales. El porcentaje de visitas a plantas nativas para alimentarse fue bajo y la cantidad de consumo de insectos fue relativamente alta. Se argumenta que la baja diversidad y abundancia de picaflores está en relación a una escasa provisión de néctar. Sobre la base de los limitados datos disponibles, parece que dos familias de plantas que son importantes para picaflores en los Andes y otras áreas montañosas neotropicales, como son las Rubiaceae y Ericaceae, proveen poco néctar para picaflores de selvas en la Serra do Mar, y que esto puede parcialmente explicar la ausencia de diversidad en la longitud del pico de los picaflores. La forma en la cual la comunidad de picaflores que viven en un área explotan las flores es de interés tanto desde el punto de vista ornitológico como botánico. Es también de gran interés evolutivo, porque puede explicar la coevolución de picaflores y plantas.

STUDY AREA AND METHODS

Observations were made in the Boracéia forest reserve, about 80 km east of São Paulo, between 9 November and 15 December 1983. All observations were made in primary or old secondary forest, or at the edge of forest, at altitudes of 800-900 m. The climate of Boracéia is typical of the Serra do Mar, extremely humid with much low cloud and fog,

little sunshine, and moderate temperatures. The trees are mainly of moderate height and are heavily loaded with epiphytes, among wich bromeliads are especially abundant. Further details of the environment are given by Camargo (1946) and Filho & Camargo (1958).

A small collection of birds was made at Boracéia by Camargo (1946), and a number of ornithologists have visited the area subsequently. The most comprehensive investigation of the birds of the area involved a trapping programme carried out by the Seção de Vírus Transmitidos por Artrópodos of the Instituto Adolfo Lutz, São Paulo, between the years 1966 and 1983. Hence the list of bird species known to occur in the Boracéia forest reserve is probably not far from complete.

We made a special effort to find all the flowers that were being fed at by hummingbirds at the time of our visit. Flowers were measured (internal length of corolla tube) and measurements were made of nectar concentrations. Nectar was extracted with disposable micropipettes, and sugar concentrations were measured with a Bellingham and Stanley pocket refractometer calibrated from 0 to 50%.

Observations of the feeding behaviour of hummingbirds were made with 10 x binoculars, usually at fairly close quarters. Some observations were 'casual', i.e. made during random walks in the area; but most were made during timed watches at nectar sources which we had found to be, or suspected to be, important. Each visit by an individual hummingbird to a plan or (in the case of some herbaceous plants) group of plants was recorded, and was counted as a unit for purposes of analysis. Further records were made for subsequent visits only if they were separated by intervals of at least 5 minutes. Insect-foraging records similarly were treated as separate only if there was an interval of at least 5 minutes between them. A limited number of hummingbirds were caught in mist-nets, weighed and measured.

Specimens of food plants were collected, and have been deposited in the Herbarium of the Royal Botanic Gardens, Kew. Other plants were identified by botanists of the University of São Paulo, and the bromeliads by Dr Lyman B. Smith of the Smithsonian Institution.

RESULTS

THE HUMMINGBIRDS

We usually found six species of hummingbirds in the study area during our visit their measurements are given in Table 1. In addition, we twice saw *Chlorostilbon aureoventris,* an open-country species, in clearings where a road or power-line went through the forest. One other forest hummingbird, *Ramphodon naevius,* has been recorded from the area. It must have been rare, if present at all, during our visit, as we were constantly looking out for it but never saw it. Five other species of hummingbirds have been recorded in or near our study area (Camargo 1946).

With the possible exception of *Ramphodon naevius,* the species listed in Table 1 are almost certainly the full complement of hummingbird species regularly occurring in forest in the study area, and probably in forest in other very humid parts of the Serra do Mar at altitudes around 900m.

In Table 1 the sexes of two species, *Clytolaema rubricauda* and *Thalurania glaucopis,* are treated separately. In these two species, in contrast to the other four, the plumages of males and females are very different, so that they can be easily distinguished in the field; and males and females differ markedly in their feeding habits. It may be noted that in each of them males are larger than females, both in weight and in wing-length, but females differ markedly in their feeding habits. It may be noted that in each of them males

TABLE 1.- Forest hummingbirds, Boracéia.

	Weight	Wing	Bill	Bill as % of wing
Phaethornis eurynome		60	34.9	58
Melanotrochilus fuscus	7.7	81	21.1	26
Leucochloris albicollis	6.4	60	21.3	36
Amazilia versicolor	5.1	49	15.6	32
Clytolaema rubricauda ♂		72	20.1	28
Clytolaema rubricauda ♀	6.7	66	21.2	32
Thalurania glaucopis ♂	6.0	59	19.3	33
Thalurania glaucopis ♀		53	19.7	37

Wing and bill lengths are means of samples of 10; weights are mostly based on smaller samples.

are larger than females, both in weight and in wing-length, but females have both relatively and absolutely longer bills. Similar sex differences are found in many other hummingbird species; they are relevant to feeding ecology and are briefly discussed later (p. 294).

THE PLANTS

The plants at which we saw hummingbirds feeding (25 native and 2 introduced species) are listed, with some of their relevant characteristics, in Table 2. Taking into consideration the general features that distinguish hummingbird flowers (Stiles 1980) and also the special features of some of the flowers in this list, 17 of the 25 native plants may be classified as hummingbird-adapted. Of the other 8, most are probably primarily insect-pollinated (*Inga* sp. probably also by bats) but have nectar accessible to hummingbirds.

A majority of the plants are epiphytes (10 species) or vines, climbers and scramblers (7 species). Of the other 8 species, 5 are herbaceous ground plants, 2 are shrubs, and only one is a canopy tree (*Inga* sp.). In addition to the data given in Table 2, the following points are noteworthy.

Marcgravia polyantha. The highly specialized flowers of this genus, many of them adapted for hummingbird-pollination, have been described by several authors (e.g. Wagner 1946). They have no corolla tubes and no bright colours, the nectar being produced in specially modified, pitcher-shaped sterile flowers. Unfortunately, though a common plant in our study area, the flowers are borne so high above the ground that we were unable to obtain nectar samples.

Manettia cordifolia. This species, a scrambler with long, bright red, tubular flowers, was the only member of the Rubiaceae that we found in flower. In many other neotropical forest areas rubiaceous shrubs with shorter, less specialized flowers are an important nectar source for short-billed hummingbirds, but they seemed to be absent in our study area. See p. 295 for further discussion.

Bromeliaceae. The bromeliad flora of Boracéia is rich in species and in abundance of plants. Seven species were in flower at the time of our visit. Five of them were common, two (*Canistrum giganteum* and *Vriesea pabstii*) much less common. Our observations of *V. pabstii* proved to be only the second record of the species since its discovery (at Boracéia) by Dr Lyman B. Smith in 1968. *Vriesea jonghei,* though regularly visited by

TABLE 2. Plants fed at by hummingbirds, Boracéia, November - December 1983.

Families	Species	Growth form	Corolla tube (mm)	Flower colour	Nectar concentration o/o N	Range	$\bar{x}$
Marcgraviaceae	*Marcgravia polyantha**	V	–	Brown	–	–	–
Leguminosae	*Dahlstedtia pinnata**	S	15	Pink	6	18-22	20.4
	Dioclea sp.	V	–	Mauve	2	23,25	–
	Inga sp.	T	–	White	–	–	–
Onagraceae	*Fuchsia regia**	V	26	Red and Purple	5	15-17.5	16.4
Loganiaceae	*Buddleja* cf. brasiliensis	H	–	Yellow	–	–	–
Loranthaceae	sp. indet.	E	–	Orange	–	–	–
Apocynaceae	*Mandevilla funiformis*	V	21	Yellow	5	31-37	33.8
Labiatae	*Salvia articulata**	S	43	Red	1	27	–
Gesneriaceae	*Nematanthus gregarius**	E	22	Orange	1	22	–
	Nematanthus aff. *fritschii**	E	46	Red	2	30,32.5	–
Acanthaceae	*Jacobinia carnea**	H	39	Pink	9	21 - 27	23.9
	*Mendoncia coccinea**	V	39	Red	2	29, 30	–
Rubiaceae	*Manettia cordifolia**	V	50	Red	3	21-23.5	22.3
Compositae	*Piptocarpa notata*	V	6.5	White	–	–	–
Bromeliaceae	*Aechmea pectinata**	E	23	Green (leaf-tips red)	2	28, 28.5	–
	*Canistrum giganteum**	E	41	Yellow (bracts red)	1	28.5	–
	*Nidularium innocentii**	E	52	White (bracts red)	7	25.5-32.5	30.1
	*Tillandsia stricta**?	E	13	Mauve (bracts pink)	–	–	–
	*Vriesea incurvata**	E	46	Yellow (bracts red)	4	26 - 32	29.6
	Vriesea jonghei	E	50-60	Purple	6	20 - 22	21.5
	Vriesea pabstii	E	–	Yellow	2	17, 18	–
Strelitziaceae	*Heliconia velloziana**	H	39	Green (bracts red)	7	19-23.5	21.6
Amaryllidaceae	*Alstroemeria campaniflora**	H	19	Pink	4	15.5-20	17.2
	Alstroemeria inodora	H	–	Dark red	–	–	–
Agavaceae	*Phormium tenax*	H	29	Orange	4	11 - 18	14.0

NOTES:
* Denotes species considered to be hummingbird - adapted.
Growth forms: E = epiphyte, H = herb, S = shrub, T = tree, V = vine or scrambler.
Nectar concentrations: sugars as percentages of total weight of solute.

hummingbirds, seems not to be primarily adapted for pollination by hummingbirds. It has an open, trumpet-shaped corolla tube, which insects can freely enter; the flowers were constantly visited by small bees (*Trigona* sp). wich seem to be the most likely pollinators. The inflorescence is not brightly coloured, and the flowers themselves are dull purple-brown. The outer surface of the whole inflorescence is extremely sticky, apparently an adaptation preventing insects from climbing up it to take nectar and pollen; even small dragonflies (Odonata) are caught on the gummy surface. Its nectar is less concentrated than the nectars of four bromeliads which are apparently hummingbird-pollinated (Table 2). *V. pabstii* is even less likely to be hummingbird-pollinated. The flowers are pale yellow and no part of the plant is red or brightly coloured. The flowers, like those of *V. jonghei*, have open trumpet-shaped corollas, and the nectar is even more dilute than that of *V. jonghei*. The single visit by a hummingbird recorded in 4.9 hours of observation was very brief and may have been only exploratory. Possibly this species is pollinated by night-flying insects.

Alstroemeria. The two species occur close to but not inside the forest, *A. campaniflora* in wet, semi-open second growth and *A. inodora* beside forest streams. *A. inodora*, with dark red flowers, a rather open, trumpet-shaped corolla, and apparently little nectar (none could be obtained for measurement), may not be adapted for hummingbird-pollination; *A. campaniflora*, with pink flowers and a well-formed corolla tube, is a more typical hummingbird flower.

Phormium tenax. This plant, native to New Zealand, grew locally in a wet area of second growth. It is not, of course, a hummingbird-adapted plant, but its flowers were much visited by hummingbirds.

HUMMINGBIRD FEEDING RECORDS

The main results of our observations are summarized in Table 3. Table 4 summarizes data on the hourly rates of hummingbird feeding visits to the more important plants.

It is apparent from Table 4 that a great deal of watching was necessary in order to obtain many feeding records. For example, watches of an hour at the bromeliad *Vriesea incurvata* (usually two or three plants visible from the observation point), at times when this species was known to contain nectar, in most cases yielded not a single record. Equally few and far between were hummingbird visits to two other bromeliads and to *Jacobinia carnea*, with hourly rates of only 0.2-0.3. For no native plant except *Piptocarpa notata* (2.4 per hour) and *Marcgravia polyantha* (2.7 per hour), neither of which qualifies for inclusion in Table 4, did the rate of feeding visits reach 2 per hour. By contrast, an hourly rate of 7.7 was recorded for *Phormium tenax*, an introduced plant which on this criterion was more attractive to hummingbirds than any native plant. *P. tenax* is a very large herbaceous plant and was growing in marshy ground. Although its nectar was not very concentrated it was produced throughout the day, probably in copious quantities.

Table 3 shows that there were differences in the feeding behaviour of males and females of *Clytolaema rubricauda* and *Thalurania glaucopis*. In both species, females were recorded insect-foraging more often than taking nectar. Males of *C. rubricauda* were mainly recorded taking nectar (31 nectar, 9 insect-foraging records) and males of *T. glaucopis* were only seen taking nectar. The males of these two species were aggressive in defence of nectar sources. Males of *C. rubricauda* defended the flowers of *Marcgravia*, which seemed to be their most important nectar source at the time of our visit (17 records, cf. 14 records for all other flowers combined). *Heliconia* clumps provided one of the most important nectar sources for males of *T. glaucopis*, and they apparently defended these

TABLA 3 - Summary of hummingbird feeding records, Boracéia, November - December 1983.

	P.e.	M.f.	L.a.	A.v.	C.r.♂	C.r.♀	T.g.♂	T.g.♀	Total
Marcgravia polyantha					17	1		1	19
Dahlstedtia pinnata	3		5			1	7		16
Dioclea sp.			4				1	1	6
Inga sp.		5	1		2				8
Fuchsia regia					3	4	2	1	10
Loranthaceae sp.						1		1	2
Buddleja cf. *brasiliensis*				1					1
Mandevilla funiformis		6	8						14
Salvia articulata	1								1
Nematanthus gregarius			1			1		1	3
Nematanthus aff. *fritschii*	1								1
Jacobinia carnea	4						1	1	6
Mendoncia coccínea			3		3	2	3	2	13
Manettia cordifolia	3	2	3						8
Piptocarpa notata				3			3		6
Aechmea pectinata	2								2
Canistrum giganteum	6								6
Nidularium innocentii			1			1			2
Tillandsia stricta				2					2
Vriesea incurvata	3								
Vriesea jonghei	5	5	4	7	3	10	1	5	40
Heliconia velloziana.	7					6	11	4	28
Alstroemeria campaniflora			3	1					4
Alstroemeria inodora	2								2
Phormium tenax		24	13		3		6	1	47
Total nectar records	37	42	46	14	31	27	35	18	250
Insect-foraging: gleaning	8	3	5	3	3	18		26	66
Insect-foraging: hawking		13	18	10	6	12		5	64
Total insect-foraging	8	16	23	13	9	30		31	130

P.e. = *Phaethornis eurynome,*
A.v. = *Amazilia versicolor*
M.f. = *Melanotrochilus fuscus*
C.r. = *Clytolaema rubricauda,*
L.a. = *Leucochloris albicollis*
T.g. = *Thalurania glaucopis.*

clumps against intruders, behaving aggressively even to human observers and, on one occasion, to a small flycatcher, *Platyrinchus mystaceus.* Although females of *T. glaucopis* were present in the study area throughout the whole period of observation, males were not seen until 20 November, which suggests a local migratory movement.

There were marked differences between some of the hummingbirds in their insect-foraging. *Phaethornis eurynome,* like other hermit hummingbirds elsewhere, gleaned for small arthropods from leaves and twigs near the forest floor. Females of *C. rubricauda* and, especially, *T. glaucopis* also foraged for insect mainly by gleaning. These two hummingbirds are inconspicuous while foraging in this way among the vegetation in the

TABLE 4. Hourly rates of hummingbird feeding visits to different plants.

	Hours of observation	N° humming-bird visits	Hourly rate
Dahlstedtia pinnata	6.3	12	1.9
Fuchsia regia	8.2	8	1.0
Mandevilla funiformis	9.1	11	1.2
Jacobinia carnea	11.9	3	0.3
Manettia cordifolia	12.9	8	0.6
Canistrum giganteum	5.9	6	1.0
Nidularium innocentii	5.6	1	0.2
Tillandsia stricta	5.3	1	0.2
Vriesea incurvata	12.3	3	0.2
Vriesea jonghei	24.7	33	1.3
Heliconia velloziana	8.8	17	1.9
Phormium tenax	6.4	48	7.7

The table includes only plants watched for more than 5 hours. In some cases the number of visits is less than in Table 3, because Table 3 includes a few records obtained casually, i.e. not during timed watches.

middle strata of the forest, and the number of records is almost certainly too low in relation to records of nectar-feeding. We often heard them feeding in this way without being able to see them. For the other hummingbirds, aerial hawking was the principal method used. *Melanotrochilus fuscus* and *Leucochloris albicollis* frequently hawked in the air above the treetops, *Amazilia versicolor* mainly at lower levels, among open vegetation.

DISCUSSION

SOME GENERAL COMPARISONS WITH OTHER AREAS

The number of hummingbird species in our Boracéia study area was rather small compared with the number of species occurring within limited areas in other forested parts of the neotropics. Comparable figures are as follows:

La Selva, Costa Rica (wet tropical)	13 species	(Stiles 1980)
Arima Valley, Trinidad (moist tropical)	12 species	(Snow & Snow 1972)
Cerro Fonté, Colombia (upper subtropical)	9 species	(Snow & Snow 1980)
Cerro Carare, Colombia (subtropical)	12 species	(Snow & Snow 1980)

Furthermore, not only was the number of different species low, but also the number of individuals was low, compared with other neotropical areas where we have studied hummingbirds.

The much higher rate of visits to an introduced plant that provided abundant nectar, *Phormium tenax*, suggests that the native plants were not, in aggregate, providing a quantity of nectar capable of sustaining a very high hummingbird density. Two independent arguments support this suggestion. First, nectar sources were rather widely scattered and

individually comparatively small. Thus we found only four plants of *Manettia cordifolia* in flower in the course of seven weeks during which we were out in the forest every day, and similarly, only three plants of *Dahlstedtia pinnata* and three clumps of *Salvia articulata.* Many of the epiphytes were common, but they were sparsely distributed in the trees, not providing any concentrated nectar sources, with the exception of *Vriesea jonghei,* which was locally abundant but, as already mentioned, was visited by bees as well as hummingbirds and may be primarily a bee-pollinated plant. Secondly, the relative number of insect-foraging records that we obtained (34% of the total; Table 3) was much higher than we have obtained in other neotropical forest areas. Not many data are available from other areas for comparison, but such as they are, they suggest that lower percentages are more usual:

Arima Valley, Trinidad (moist tropical)	9% (Snow & Snow 1972)
Guyana (seasonal tropical), hermit hummingbirds only	11%(Snow1973)
Cerro Fonté, Colombia (upper subtropical)	7% (Snow & Snow 1980)
Cerro Carare, Colombia (subtropical)	26 %(11 %if one set of atypical data is excluded; Snow & Snow 1980).

These figures cannot do more than suggest the need for further, more detailed research. If it is typical of the wet southeastern Brazilian forests that nectar sources for hummingbirds are poor in comparison with what is found in other neotropical forest areas, it would go some way towards explaining the correspondingly small number of hummingbird species.

RELATIONSHIP BETWEEN BILL – LENGTH AND FLOWER CHOICE

On the basis of bill-length the six hummingbird species fall into three groups: (1) *P. eurynome,* with a very long (34.9mm) and decurved bill; (2) *M. fuscus, L. albicollis, C. rubricauda* and *T. glaucopis,* with bills of intermediate length averaging around 20 mm (range 19.3 – 21.2 mm); and (3) *A. versicolor,* with a short bill (15.6 mm). Although there was much overlap between the species in their choice of flowers, there was a clear relationship between bill-length and flower choice. All but two of the 11 species of flowers visited by *P. eurynome* have long corolla tubes (39-50 mm), and four of them were not seen to be visited by any other hummingbird. The second group of hummingbirds, with bills of intermediate length, were recorded feeding at flowers with a wide range of corolla-tube lengths, but the great majority of records (81 %) were from flowers with short corolla-tubes or no tubes. *A. versicolor* was seen feeding only at flowers with short corolla-tubes (13-19 mm) or no tubes.

It has been widely recognized, from recent research on the feeding ecology of hummingbirds, that there are two very different feeding strategies: defence of a nectar source, and 'trap-lining'. It may be energetically efficient to defend a nectar source which is spatially concentrated and adequate to satisfy an individual hummingbird's nectar requirements; but small, scattered nectar sources cannot be defended, and a hummingbird feeding at such nectar sources must visit a large number of them, thus covering a wide area in its foraging activities. Hummingbirds that defend nectar sources generally have high wing-loading (Feinsinger & Chaplin 1975) and bills that are relatively short in relation to their wing-length (Snow & Snow 1980). Trap-liners tend to have low wing-loading and relatively long bills. Without very accurate mean weights, for which large samples are needed, wing-loading cannot be satisfactorily calculated; but relative bill-lengths can easily

be obtained; they are listed for the Boracéia hummingbirds in Table 1. It will be noted that *Phaethornis eurynome* has relatively and absolutely a far longer bill than the other species. It appeared to be the most pronounced trap-liner, as other *Phaethornis* species are, feeding on sparsely scattered nectar sources, mainly near the forest floor. Relative bill-lengths of the other species are all in the range 26-37%. In the two sexually dimorphic species, *Clytolaema rubricauda* and *Thalurania glaucopis*, males have relatively shorter bills than females. The males of these two species were markedly aggressive in defence of nectar sources, whereas the females were unaggressive, inconspicuous foragers. This undoubtedly influenced their flower-choice; thus females of *C. rubricauda* were effectively excluded from feeding at *Marcgravia*, a moderately concentrated nectar source defended by the males, and females of *T. glaucopis* were largely prevented from feeding at *Dahlstedtia* and *Heliconia*, two concentrated nectar sources defended by the males.

NECTAR CONCENTRATIONS

A general relationship has been established from studies in other neotropical areas between nectar concentrations of different flower species and the degree to which they are adapted for pollination by hummingbirds. Most hummingbird flowers have rather dilute nectar, averaging about 20%(nectar weight/total weight of solution), but the more specialized hummingbird flowers tend to have higher concentrations. Bolten & Feinsinger (1978) argued that the dilute nectar typical of hummingbird flowers may have evolved to deter bees, which need more concentrated nectar, and that once a flower has evolved adaptations to exclude bees, selective pressure from feeding hummingbirds (which prefer the most concentrated nectar if given a choice; Hainsworth & Wolf 1976) may lead to a return to more concentrated nectar. Our data from Boracéia are too few for a thorough discussion of this question in relation to the hummingbird flowers of southeastern Brazil, but the differences in nectar concentration which we found were broadly in agreement with Bolten and Feinsinger's suggestion. The nectar concentrations of most of the flowers in Table 2 average 15-25%. Those with higher concentrations are long-tubed, specialized hummingbird flowers (*Salvia articulata, Nematanthus* aff. *fritschii, Mendoncia coccinea*, four bromeliads) with the exception of *Mandevilla funiformis*, whose yellow open trumpet-shaped flowers may be primarily insect-pollinated.

The two bromeliads that are apparently not hummingbird-pollinated had much lower nectar concentrations than the other four (means of 21.5 and 17.5, compared with means of 28.3-30.1%). One of these two, however, was probably bee-pollinated, thus going against what would be predicted from Bolten & Feinsinger's hypothesis. The Bromeliaceae should be a good family for further investigation; much more complete data are needed on nectar concentrations and pollinating agents.

TAXONÔMIC COMPOSITION OF THE SE BRAZILIAN HUMMINGBIRD – ADAPTED FLORA

A thorough comparison, from the taxonomic point of view, of the hummingbird flowers of southeastern Brazil (and adjacent parts of northern Argentina) with other parts of the neotropics must await further field work. On the basis of the plants listed in Table 1, with additions from three other areas in the coastal montane forests of São Paulo and Rio de Janeiro (Snow & Teixeira 1982), a preliminary comparison may be made with the hummingbird flowers in three more or less thoroughly studied forested areas to the north, two tropical and one subtropical: Trinidad (Snow & Snow 1972, Feinsinger et al.

1982), La Selva, Costa Rica (Stiles 1978, 1979), and the Eastern Andes of Colombia at subtropical levels (Snow & Snow 1980). A few points which seem significant may be briedfly discussed.

The family Bromeliaceae is represented by several species in all four areas. But whereas the list for Trinidad (9 species) and La Selva (8 species) includes probably all the locally important species in the study areas concerned, the Boracéia list (7 species) is certainly very incomplete, being based on the species in flower during only 7 weeks of the year; the E. Andes list (4 species) is similarly incomplete. More complete data may well show that bromeliads provide a greater proportion of the nectar resources for hummingbirds in the very humid southeastern Brazilian forests than elsewhere in the neotropics.

The family Rubiaceae is important in all three of the other areas, for each of which at least 5 species are fed at by hummingbirds. They are mainly under-story shrubs or small trees, and their flowers have corolla tubes of lengths suitable for short-billed hummingbirds. We found no rubiaceous shrubs or small trees of this sort in our stydy area and none were recorded by Snow & Teixeira (1980), but two species with white scented flowers were visited by insects. Our only records for the family were from *Manettia cordifolia,* a climber sparsely distributed in the study area. It seems probable that a lack, or scarcity, of hummingbird-pollinated rubiaceous shrubs may be general in the southeastern Brazilian coastal forests. If so, this would help to explain the small number of short-billed forest hummingbirds.

The southeastern Brazilian list of forest hummingbird flowers differs strikingly from the subtropical Andean list in having no members of the Ericaceae, a very important family in the Andes (6 species in Snow & Snow 1980). In the Serra dos Orgâos, Rio de Janeiro, Dr M. de L. Brooke obtained records of *Stephanoxis lalandi* feeding on the flowers of *Gaultheria eriophylla* at 1800 m, a much higher altitude than our study area. Another ericaceous genus that is probably hummingbird-pollinated, *Gaylussacia,* occurs in the southeastern Brazilian mountains. All ericaceous plants probably occur mainly above 1200 m in the Serra dos Orgâos and are commoner in open vegetation than in forest (Dr James L. Lutyen, pers. comm.). *Stephanoxis lalandi,* the only high-altitude hummingbird and a bird of mainly open country, may be the only hummingbird that regularly feeds at them. In the Andes and higher mountains of Central America ericaceous plants are a main nectar source not only for open-country hummingbirds but also for the hummingbirds of subtropical forest; in the Andes, many of these plants have flowers with long corolla tubes, and are fed at by long-billed hummingbirds such as *Coeligena* spp. It seems likely that the lack of forest hummingbirds with long straight bills and the comparative poverty of the ericaceous flora in the SE Brazil mountains may be interrelated.

To summarize, it seems possible that the comparative lack of diversity of the southeastern Brazilian forest hummingbirds species - that is, the small number of species, most of which have straight bills of intermediate length – may be related to some characteristics of the hummingbird-pollinated flora, two of which we suggest may be: the few species of Rubiaceae with hummingbird flowers, and the complete or virtual absence of members of the Ericaceae in forest at subtropical levels.

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