



Bat-pollinated Flower Assemblages and Bat Visitors at Two Atlantic Forest Sites in Brazil

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A comparison between bat-pollinated plant assemblages at two sites in different altitudinal ranges covered by the Atlantic rainforest in southeastern Brazil is presented. The lowlands (5–90 m) harbour ten plant species in seven families, pollinated mostly by three glossophagine bat species. The highlands (1540–1600 m) harbour seven plant species in five families, pollinated by a single species of glossophagine. Bromeliads account for about 30% of the bat-pollinated species at each assemblage. Tube and brush shapes prevail in the flowers at both sites. Corolla lengths averaged 26.8 and 37.2 mm, sugar concentrations in nectar averaged 15.0 and 18.1%, and nectar volumes averaged 150.8 and 167.0 μ l in the lowland and highland assemblages, respectively. The flowers are pollinated mostly by glossophagine bats during hovering visits, and the plants are visited in the trap-line foraging pattern. The plants bloom annually and both assemblages show a staggered continual flowering pattern. Flowering seasonality was found at both sites, with flowering clustering in the drier season at the lowland site and in the wetter season at the highland site. The ratio between bat-pollinated and hummingbird-pollinated species is 0.24 at the lowland site and 0.23 at the highland one. These similar values indicate that additional studies on bat- and bird-pollinated assemblages are merited at other Atlantic rainforest sites.

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Key words: *Abutilon*, bat-pollination, *Dysochroma*, *Eriotheca*, *Hillia*, *Lafoensia*, *Marcgravia*, rainforest, *Siphocampylus*, southeastern Brazil, *Tetrastylis*, *Vriesea*.

INTRODUCTION

Among vertebrate pollinators of flowers in the Neotropical rainforest, phyllostomid bats are second only to hummingbirds in the number of plant species they visit (300 estimated chiropterophilous species, see Dobat and Peikert-Holle, 1985). Rainforest flower-visiting phyllostomid bats comprise about 30 species (Gardner, 1977; Emmons and Feer, 1990) and almost 50% of these are found in the Atlantic rainforest in southeastern Brazil (Marinho-Filho and Sazima, 1998). Studies on bat-pollinated plants in this type of rainforest date back to the pioneering and comprehensive work of Vogel (1969), and were followed by observations focusing mostly on a particular plant species (e.g. Sazima and Sazima, 1980; Buzato, Sazima and Sazima, 1994 and references therein). However, it was not until recently that more broadly-based field studies on bat-pollinated flower assemblages from southeastern Brazil rainforest were started.

This paper reports a medium-term study on bat-pollinated flower assemblages and their flower-visiting bats at two Atlantic rainforest sites, one in the coastal lowlands and the other in the westward highlands (a similar approach has been taken for hummingbird-pollinated flower assemblages; Buzato, Sazima and Sazima, 1999). We examined flower species composition, diversity of flower attributes, and flowering phenology, as well as occurrence and flower-visiting behaviour of the attendant phyllostomid bats. We review the relationship between flowers and bats in the

Atlantic rainforest and evaluate the flowering patterns and their consequent distribution of floral resources for the bats. We also identify patterns in this mutualistic relationship between flowers and bats and compare these to the patterns obtained in similar studies on flowers and hummingbirds from the Atlantic rainforest (Sazima, Buzato and Sazima, 1996; Buzato *et al.*, 1999).

MATERIALS AND METHODS

Study sites

Fieldwork was undertaken during 1 to 5 nights monthly from Sep. 1993 to Jul. 1996, with supplementary data recorded occasionally until April 1998. The two field sites comprise the mountain ranges of the Serra do Mar and the Serra da Mantiqueira in São Paulo, southeastern Brazil (Fig. 1). The site at the Serra do Mar is in the coastal lowlands at Caraguatubá (approx. 23° 35' S, 45° 20' W, 5–90 m alt), and the site at the Serra da Mantiqueira is in the westward highlands at Campos do Jordão (approx. 22° 44' S, 45° 35' W, 1460–1600 m alt). These mountain ranges are included in the Atlantic Forest Domain (*sensu* Ab'Saber, 1977) but the vegetation physiognomy differs between the two study sites. The coastal lowland site is covered by subhumid evergreen broadleaf forest, whereas the highland site is covered by mixed semi-deciduous broadleaf forest with *Araucaria* (Eiten, 1970; Sazima, Buzato and Sazima, 1995a, 1996). Average annual rainfall for the lowland and

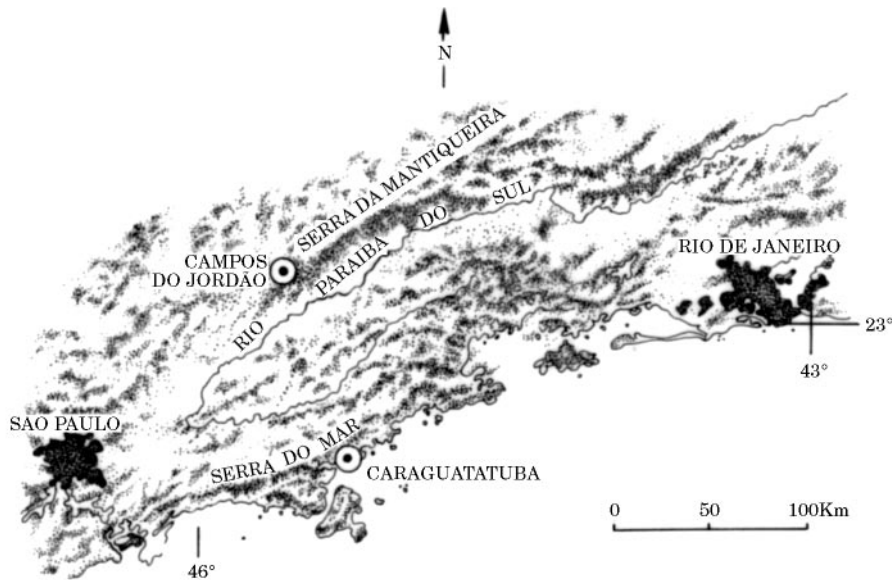


FIG. 1. Map of the Serra do Mar and Serra da Mantiqueira ranges in southeastern Brazil showing the two study sites: Caraguatatuba (lowland) and Campos do Jordão (highland). Modified from Suchantke (1982).

highland site, respectively, during the study period was 2526 and 1401 mm, and average annual temperature was 22.7 and 15.3 °C. From May to August there is a drier, cooler season at the highland site, when rainfall drops to 100 mm and temperatures may fall below zero (Nimer, 1977).

Procedures

Observations of plants and bats were made in about 3 km of trails used as transects at each study site, and included the forest understorey up to 6–10 m, stream banks, forest edges and clearings, and covered both closed and open habitats. We recorded all bat-pollinated flowers in view to estimate the number of plant species and their flowering phenology throughout the year. At the same time, we recorded the plant growth habit and flower features including morphology, volume and concentration of nectar (cf. Faegri and Pijl, 1980; Buzato *et al.*, 1994; Sazima *et al.*, 1996). In Tables 1 and 2 flower colour is ground colour (when present, venation is darker), and colour names follow Kornerup and Wanscher (1963). The internal length of flower corollas was measured from base to opening (effective length cf. Wolf, Stiles and Hainsworth, 1976) with the exception of the *Marcgravia* species, for which we recorded the distance from the lid to the bottom (internal length) of the pitcher-like extrafloral nectary. Nectar concentration and volume were measured within 2 h of flower opening and/or nectar production (visitors excluded from measured flowers), with a pocket refractometer and microlitre syringes, respectively (cf. Kearns and Inouye, 1993). In Table 3 nectar volume for *Marcgravia* is averaged for one extrafloral nectary (four–five nectaries per inflorescence). Flower shape nomenclature follows Faegri and Pijl (1980). Bat species composition at each site was studied mostly by watching bat visits to selected flowering plants, combined with mistnetting in front of the plants. Bats were photographed on flowers

during visits (recognition at a given site is possible at the species level; see Sazima and Sazima, 1977; Sahley, 1995), mistnetted, and sometimes visually recorded (this latter method allows recognition at the subfamilial level at best; see Sazima and Sazima, 1975, 1977). Photographs of bat visits to flowers, as well as morphology of flowers and bats, were used to assess pollen placement on the body parts of bats.

RESULTS AND DISCUSSION

Composition of the flower assemblages

We recorded 17 native species of bat-pollinated plants, distributed over ten families and ten genera, at the two sites (Tables 1 and 2). The species richness decreased as altitude increased (Tables 1 and 2), a trend already detected for hummingbird-pollinated flower assemblages of the Atlantic rainforest (Buzato *et al.*, 1999). Bromeliaceae account for about 30% of plant species in each of the bat-pollinated assemblages we studied, this value being close to that found for hummingbird-pollinated assemblages (36%) at the same sites (Sazima *et al.*, 1996; Buzato *et al.*, 1999). Bromeliads may thus be qualified as the most representative and important family in both bat- and bird-pollinated flower assemblages of the Atlantic rainforest in southeastern Brazil.

At each site only two plant genera are represented by more than one species (Tables 1 and 2), a pattern similar to that found for hummingbird-pollinated flower assemblages (Buzato *et al.*, 1999). We suggest that this pattern, besides being based on historical events (see Grant, 1994), is related to the promiscuous foraging behaviour of glossophagine bats (Heithaus, Fleming and Opler, 1975; Sazima, Sazima and Buzato, 1994b), which results in widely spread and opportunistic relationships between bats and flowers in a given bat-pollinated flower assemblage in the rainforest. There is no floristic similarity between the two flower assemblages, and this difference may be due mostly to

TABLE 1. Ten native bat-pollinated plants from a lowland rainforest at Caraguatatuba, Serra do Mar, southeastern Brazil

Plant species	Plant habit	Corolla colour	Flower shape	Recorded pollinator*	Pollen placement†
Bombacaceae					
<i>Eriotheca pentaphylla</i>	Tree	Pale yellow	Brush	unG	win, che, sho, thr
Bromeliaceae					
<i>Vriesea</i> aff. <i>bituminosa</i>	Epiphyte	Greyish orange	Tube	Anc	chi, thr
<i>Vriesea gigantea</i>	Epiphyte	Yellowish white	Tube	Anc, unG	fac, thr
<i>Vriesea longiscapa</i>	Epiphyte	Orange white	Tube	Anc, Ang	chi, thr
Fabaceae					
<i>Mucuna urens</i>	Vine	Greyish green	Flag	Anc, Gls	che, bel
Lythraceae					
<i>Lafoensia glyptocarpa</i>	Tree	Yellowish white	Brush	Pla, unG	win, sho, che, bel
Marcgraviaceae					
<i>Marcgravia polyantha</i>	Vine	White	Brush	Anc, unG	win, che, sho
<i>Marcgravia</i> aff. <i>polyantha</i>	Vine	White	Brush	Anc	win, che, bel, leg
Passifloraceae					
<i>Tetrastylis ovalis</i>	Vine	Light green	Dish	Anc, Ang	cro, sho
Rubiaceae					
<i>Hillia illustris</i>	Epiphyte	Yellowish green	Tube	Anc	chi, thr

* Abbreviations: Anc, *Anoura caudifer*; Ang, *Anoura geoffroyi*; Gls, *Glossophaga soricina*; unG, unidentified Glossophaginae (any of the three precedent species); Pla, *Platyrrhinus lineatus*.

† Site of pollen deposition on bat visitor's body parts: bac, back; bel, belly; che, chest; chi, chin; cro, crown; fac, face; leg, legs; sho, shoulders; thr, throat; win, wings.

TABLE 2. Seven native bat-pollinated plants from a highland rainforest at Campos do Jordão, Serra da Mantiqueira, southeastern Brazil

Plant species	Plant habit	Corolla colour	Flower shape	Recorded pollinator*	Pollen placement*
Bromeliaceae					
<i>Vriesea bituminosa</i>	Epiphyte	Brownish red	Tube	Anc	chi, thr
<i>Vriesea sazima</i>	Epiphyte	Light yellow†	Tube	Anc	chi, thr
Lobeliaceae					
<i>Siphocampylus sulfureus</i>	Herb	Sulfur yellow	Tube	Anc	cro
Lythraceae					
<i>Lafoensia</i> aff. <i>replicata</i>	Tree	Yellowish white	Brush	Anc	win, sho, che, bel
<i>Lafoensia</i> aff. <i>vandelliana</i>	Tree	Yellowish white	Brush	unG§	win, sho, che, bel
Malvaceae					
<i>Abutilon</i> aff. <i>regnelli</i>	Treelet	Purplish pink‡	Bell	Anc	chi, thr
Solanaceae					
<i>Dyssochroma viridiflora</i>	Epiphyte	Yellowish green	Bell	unG§	bel, che, win

* As for Table 1.

† About 30% of individuals display greyish red flowers.

‡ Some individuals display reddish lilac flowers (see Fig. 2 and Buzato *et al.*, 1994).

§ Probably *Anoura caudifer*, the only glossophagine recorded at this study site.

historical colonization (in the sense of Grant, 1994) in the Atlantic rainforest. For instance, the two known species of *Tetrastylis* occur at lowland sites (Buzato and Franco, 1992; pers. obs.), whereas most, if not all, species of *Siphocampylus* are distributed at higher altitudes (Godoy, 1992; Sazima *et al.*, 1994a).

Plant types and flower features

Most plant species of the two bat-pollinated assemblages are epiphytes and vines (about 65%) with a predominance of the former which account for about 41% of the overall plant habits (Tables 1 and 2). The predominance of herbs and vines among bat-pollinated plants in southeastern

Brazil was pointed out by Vogel (1969), and these plants also dominate the hummingbird-pollinated flower assemblages studied at the same two sites as reported here (Buzato *et al.*, 1999).

The flower colour of most studied species agreed with the chiropterophilous syndrome (cf. Faegri and Pijl, 1980) except for some bromeliads and *Abutilon* aff. *regnelli* (Tables 1 and 2). Reddish and purplish-pink flowers presented by this species are features of bird-pollinated flowers (Faegri and Pijl, 1980) and, indeed, flowers of these colours were also visited by hummingbirds at both studied assemblages (Buzato *et al.*, 1994; Sazima, Buzato and Sazima, 1995b).

Flower morphology at the two bat-pollinated assemblages



FIG. 2. Bat-pollinated flowers and their hovering glossophagine bat visitors in the Atlantic rainforest of southeastern Brazil. A, *Vriesea longiscapa* visited by *Anoura geoffroyi* during a hovering visit—note whitish pollen of *Marcgravia* on bat's wings, belly, and legs. B, *Tetrastylis ovalis* visited by *Anoura caudifer*—note anthers touching bat's head and shoulders. C, *Hillia illustris* visited by *A. caudifer*. D, *Marcgravia* aff. *polyantha* visited by *A. caudifer*—note pollen spread over bat's wings, legs and belly. E, *Abutilon* aff. *regnellii* visited by *A. caudifer*—note bunch of stamens touching bat's throat. F, *Siphocampylus sulfureus* visited by *A. caudifer*—note yellowish pollen of *Vriesea* on bat's throat, and whitish pollen of *Dysochroa* on belly.

varied (Fig. 2, Tables 1 and 2), but the brush and tube shapes prevailed (76.5%). Once again bromeliad flowers influenced this, as they accounted for 71% of the tube-shaped flowers. The dominance of tube-shaped flowers is related to the fact that bromeliads belong to the subclass Zingiberidae, where tubular flowers are a systematic character (Cronquist, 1988) independent of the kind of pollinator. Thus, tube shape in some species of glossophagine-pollinated flowers should be viewed from both phylogenetic and ecological perspectives. A similar view for hummingbird-pollinated flowers was advanced in Buzato *et*

al. (1999), and we think that the adaptive radiation of some groups within the Zingiberidae and hovering vertebrates may be linked.

Flower shape accounts for pollen placement on different body parts of the bats (see Vogel, 1969; Helversen, 1993 for reviews). Pollen loads on the throat and chest prevailed at the two studied assemblages, these two placements being related to tube and brush-shaped flowers, respectively (Tables 1 and 2). The size of the flower also influenced this placement, as pollen spread on the ventral side of the bat's body and wings is related mainly to large, brush-shaped

TABLE 3. Floral features of ten bat-pollinated plants from a lowland rainforest at Caraguatubá, southeastern Brazil

Plant species	Flowers per plant nightly	Corolla length (mm) (x ± s.d.)	Sugar concentration (%) (x ± s.d.)	Nectar volume (µl) (x ± s.d.)
Bombacaceae				
<i>Eriotheca pentaphylla</i>	12 ~ 80	19.7 ± 1.6 (n = 7)	10.4 ± 1.3 (n = 3)	259.0 ± 83.0 (n = 3)
Bromeliaceae*				
<i>Vriesea</i> aff. <i>bituminosa</i>	1–2	43.4 ± 2.7 (n = 5)	18.2 ± 2.4 (n = 5)	196.0 ± 28.1 (n = 5)
<i>Vriesea gigantea</i>	6–7	34.1 ± 0.7 (n = 6)	17.8 ± 1.1 (n = 6)	152.8 ± 40.0 (n = 6)
<i>Vriesea longiscapa</i>	1–2	27.4 ± 0.9 (n = 5)	19.2 ± 1.2 (n = 5)	116.6 ± 5.7 (n = 3)
Fabaceae				
<i>Mucuna urens</i>	1–16	23.0 ± 1.2 (n = 6)	17.7 ± 0.6 (n = 10)	102.6 ± 28.5 (n = 9)
Lythraceae				
<i>Lafoensia glyptocarpa</i>	6 ~ 100	12.0 ± 0.6 (n = 6)	17.0 ± 1.0 (n = 6)	107.0 ± 5.9 (n = 6)
Marcgraviaceae				
<i>Marcgravia polyantha</i>	3–10	20.5 ± 2.1 (n = 6)	10.2 (n = 1)	68.0 (n = 1)
<i>Marcgravia</i> aff. <i>polyantha</i>	6–29	12.7 ± 1.0 (n = 8)	10.6 ± 0.8 (n = 10)	49.8 ± 6.9 (n = 5)
Passifloraceae				
<i>Tetrastylis ovalis</i>	1–8	11.8 ± 0.8 (n = 5)	14.9 ± 1.4 (n = 12)	280.9 ± 92.5 (n = 11)
Rubiaceae				
<i>Hillia illustris</i>	1–4	63.6 ± 2.3 (n = 6)	13.9 ± 1.2 (n = 6)	175.5 ± 26.5 (n = 4)

* Data from Sazima *et al.* (1995b).

TABLE 4. Values of four floral features of six bat-pollinated plants from a highland rainforest at Campos do Jordão, southeastern Brazil

Plant species	Flowers per plant nightly	Corolla length (mm) (x ± s.d.)	Sugar concentration (%) (x ± s.d.)	Nectar volume (µl) (x ± s.d.)
Bromeliaceae*				
<i>Vriesea bituminosa</i>	1–2	50.6 ± 0.5 (n = 5)	19.6 ± 0.1 (n = 5)	235.0 ± 21.7 (n = 5)
<i>Vriesea sazima</i>	1–2	36.7 ± 2.9 (n = 10)	18.7 ± 1.2 (n = 10)	200.2 ± 20.5 (n = 10)
Lobeliaceae				
<i>Siphocampylus sulfureus</i> †	1–16	25.1 ± 11 (n = 10)	14.2 ± 8.9 (n = 22)	11.5 ± 3.9 (n = 29)
Lythraceae				
<i>Lafoensia</i> aff. <i>replicata</i>	1–28	19.5 ± 1.5 (n = 6)	18.2 ± 0.9 (n = 5)	408.8 ± 70.1 (n = 5)
Malvaceae				
<i>Abutilon</i> aff. <i>regnellii</i> ‡	1–12	34.2 ± 2.2 (n = 10)	16.6 ± 7.3 (n = 5)	18.3 ± 1.3 (n = 5)
Solanaceae				
<i>Dysochroa viridiflora</i>	1–6	57.4 ± 1.0 (n = 10)	21.6 ± 0.0 (n = 2)	131.0 (n = 1)

* Data from Sazima *et al.* (1995b).

† Data from Sazima *et al.* (1994b).

‡ Data from Buzato *et al.* (1994).

flowers (Fig. 2, Tables 1 and 2). Plant species with brush-type flowers are mainly trees, they bear many flowers at a time, and each flower offers large amounts of pollen and nectar (Tables 1 and 2, also Dobat and Peikert-Holle, 1985). These plants are regarded as generalist bat-pollinated species and are visited by a larger array of species and sizes of bats, as opposed to the more specialized flowers visited exclusively by hovering glossophagine bats, the so-called 'glossophagine flowers' (Helversen, 1993). The latter place their pollen selectively on the bat visitor, mostly over the head (see Vogel, 1969; Helversen, 1993 for numerous examples). Localized deposition of pollen on different parts of the bat's body reduces mixture in the pollen load deposited on stigmas, a favourable trait for the pollination process, as the bats may visit several flower species during their nightly feeding (Fig. 2, also Howell, 1977). At each studied assemblage we found one species with a very long flower tube (Tables 3 and 4). In both cases glossophagines are well suited to exploit these, as the bats are able to protrude their

tongue deep into the flower corolla (see Helversen, 1993 for morphological adaptations of glossophagine bats and flowers).

Sugar concentration in nectar averaged 15.0% in the lowland assemblage and 18.1% in the highland one (Tables 3 and 4), values close to the medial range of most neotropical bat-pollinated flowers (Helversen, 1993). The nectar of the studied flowers is scented, and flowers with no nectar are scentless. Scented nectar probably advertizes the potential of a given flower's resource to the bats (see below). Knudsen and Tollsten (1995) demonstrated that different bat-pollinated plant species have a number of floral scent chemicals in common and regarded this as an example of convergent evolution. Our results support the conclusions of Knudsen and Tollsten (1995), as the scent of the nectar of several studied flower species was very similar, such as the weak cabbage-like scent of *Abutilon*, *Lafoensia*, *Marcgravia* and *Mucuna*, or the strong garlic-like scent of *Hillia* and *Vriesea* (see Bestmann, Winkler and Helversen, 1997 for

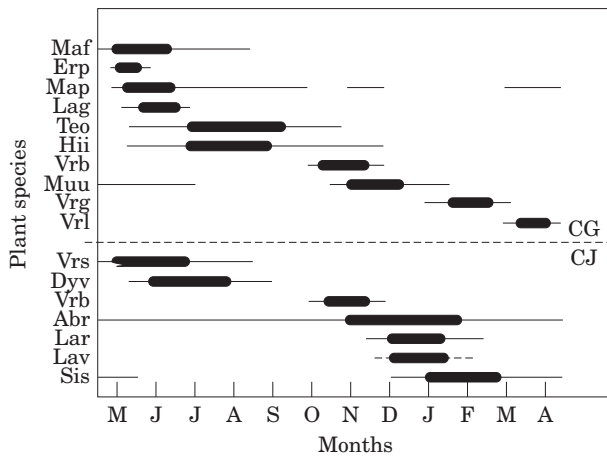


FIG. 3. Flowering period (thin lines) and blooming peaks (thick lines) of bat-pollinated plants at a lowland site (upper—CG) and a highland site (lower—CJ) in the Atlantic rainforest of southeastern Brazil (abbreviations refer to initials of plant generic and specific names in Tables 1 and 2).

presence of sulphur compounds of flower scent of *Vriesea gladioliflora*). Mushroom-like scent, one of the types discussed by Knudsen and Tollsten (1995), is found in the nectar of *Dysochroma*. The flowers of *Siphocampylus* emit a strong musky scent reminiscent of that of foxes (Sazima et al., 1994b).

Flowering phenology and flower resource supply for the bats

The flowers of all but four species last 1 night, a pattern recorded for most bat-pollinated plants (Vogel, 1969; Dobat and Peikert-Holle, 1985 and references therein), whereas flowers of *H. illustris*, *D. viridiflora* and *A. aff. regnellii* last 2 nights, and those of *S. sulphureus* last 3 nights. Daytime hummingbird pollination was recorded for the latter two species (Buzato et al., 1994; Sazima et al., 1994b).

The flowering phenological pattern of the two bat-pollinated assemblages is mostly annual (cf. Newstrom, Frankie and Baker, 1994), except for *Abutilon* aff. *regnellii*, which has a continual pattern, and *Marcgravia polyantha* and perhaps *Mucuna urens* as well, with a subannual pattern (Fig. 3). At both study sites we recorded staggered continual

flowering (Fig. 3), a pattern already known both for hummingbird- and bat-pollinated flower assemblages (Heithaus et al., 1975; Stiles, 1975; Newstrom et al., 1994; Buzato et al., 1999). This flowering pattern is of utmost importance to resident bats as they thus have flower nectar resources available year-round. Flowering seasonality was found at both studied sites (Fig. 3), the lowland site had a flowering peak during the dry season (May–July), and the highland site had a peak during the wet season (December–February). Heithaus et al. (1975) also recorded flowering seasonality in bat-pollinated plants in Costa Rica.

The richest nectar supply for the bats at both studied assemblages comes from the flowers of the Bromeliaceae and Lythraceae, as they produce rich nectar and large amounts of it, respectively (Tables 3 and 4). Most of the studied bat-pollinated plants produce one to a few flowers per plant in 1 night (Tables 3 and 4), a trait which promotes the trapline mode of foraging and seems widespread amongst bat- and hummingbird-pollinated assemblages (e.g. Heithaus et al., 1975; Stiles, 1975; Sazima et al., 1996; Buzato et al., 1999).

Species composition of bat visitors to flowers

We recorded four species of phyllostomid bat visiting flowers at the two study sites (Tables 1 and 2), namely three glossophagine long-tongued bats and one stenodermatine fruit bat (Table 5). Additionally phyllostomid fruit bats, which occasionally visit flowers for nectar, occur at both sites but were not recorded visiting flowers during our study. For instance, at the lowland site the carolinee *Carollia perspicillata*, the stenodermatines *Sturnira lilium* and *Artibeus lituratus*, as well as the phyllostomine *Phyllostomus discolor*, are potential pollinators, especially of large flowers with exposed nectar (e.g. Heithaus et al., 1975; Sazima and Sazima, 1977; Sazima et al., 1994a). At the highland site we recorded only *C. perspicillata* and *S. lilium* as being potential pollinators.

Bat features and flower use

Glossophagines are small, light bats well suited for hovering visits to take nectar from flowers on delicate stalks

TABLE 5. Wingspan, body mass, flower visiting, and foraging mode of four phyllostomid bats in the Atlantic rainforest in Brazil

Bat species	Wingspan* (cm)	Body mass* (g)	Visits to flowers†	Foraging mode†
Glossophaginae				
<i>Anoura caudifer</i>	24–27	9–13	Hovering‡	Traplining
<i>Anoura geoffroyi</i>	26–30	10–16	Hovering	Traplining
<i>Glossophaga soricina</i>	22–25	8–13	Hovering‡	Traplining
Stenodermatinae				
<i>Platyrrhinus lineatus</i>	31–35	22–26	Clinging	Commuting

* Source: Sazima and Sazima (1975); Taddei (1975); this study.

† Source: Sazima and Sazima (1975); Fleming (1982); this study.

‡ Clinging visits to *Dysochroma viridiflora* and occasionally to *Mucuna urens*.

(Fig. 2), whereas stenodermatines are larger and heavier (Table 5), being well suited for clinging visits to take fruits from sturdier branches (Heithaus, 1982). Accordingly, the stenodermatine *Platyrrhinus lineatus* exploits the open and accessible flowers of *Lafoensia* only during clinging visits (Table 5; also Sazima and Sazima, 1975; Dobat and Peikert-Holle, 1985). However, even the light and highly manoeuvrable glossophagines have to cling in order to take nectar from the long-tubed flower of *Dysochroma viridiflora* due to its pendulous position (compare the size of the flowers of this species and *Hillia illustris* in Tables 3 and 4). Also, for the initial visit to a flower of *Mucuna urens*, a glossophagine bat may have to cling and force the flower open (Table 5, also Dobat and Peikert-Holle, 1985).

Before the first visit to a flower the bat usually makes a flight pass close to it. As nectar is scented in the studied flowers, the bat may be able to use the scent as a clue to assess whether a visit to a given flower would be profitable (Sazima *et al.*, 1995b; Machado, Sazima and Sazima, 1998). The reconnaissance pass may be repeated over the night, interspersed with several actual visits to the sampled flower. The actual visit to a flower is exceedingly short-lasting (from 200 to 500 ms, see Helversen, 1993; Machado *et al.*, 1998). Even clinging visits are short-lasting and hardly exceed 1 s (Sazima and Sazima, 1975). During its nightly foraging a given bat may visit two to several flower species, as demonstrated by mixed pollen loads (Fig. 2). This promiscuous foraging on flowers is recorded both for bats and hummingbirds, especially for trapliners (e.g. Heithaus *et al.*, 1975; Howell, 1977; Sazima *et al.*, 1994b; Sazima *et al.*, 1995a, 1996).

Glossophagine bats forage mostly following a trapline route (Baker, 1973; Fleming, 1982; Lemke, 1984), a pattern already recorded in several studies on bat-pollinated flowers in the Atlantic rainforest (Sazima and Sazima, 1980; Sazima *et al.*, 1994b; Machado *et al.*, 1998). Traplining is well suited for visiting scattered, small to medium-sized plants with few and long-tubed flowers with plenty of nectar (Tables 3 and 4). Trapline foraging by bats leads to a regular revisitation of plant individuals dispersed over a given area (e.g. Lemke, 1984; Machado *et al.*, 1998), and favours cross-pollination and gene flow between adjacent populations (see Webb and Bawa, 1983 for a discussion). Stenodermatine bats usually forage commuting from one food source to another, and may feed in groups on plants with plenty of flowers (Sazima and Sazima, 1975; Fleming, Heithaus and Sawyer, 1977). The only plants which fit a stenodermatine foraging mode recorded at both study sites are species of *Lafoensia*, trees with plenty of flowers with copious and accessible nectar (Tables 3 and 4).

The mainly nectarivorous glossophagines use flowers as a food source throughout the year, whereas the frugivorous stenodermatines tend to use flowers during the dry season, when fruits are scarce (Heithaus *et al.*, 1975; Sazima and Sazima, 1975). Accordingly, we recorded *Platyrrhinus lineatus* on flowers only during the dry season, when *Lafoensia glyptocarpa* flowers (Fig. 3). However, at a strongly seasonal site in southeastern Brazil, *Platyrrhinus lineatus* was found to feed on nectar only during the wet season (Pedro and Taddei, 1997), which indicates that this

bat species may differ in its use of flower and fruit resources in the lowland Atlantic forest and the upland xeromorphic forest of the Planalto.

The long-tongued glossophagine bats are the major pollinators at both the lowland and highland site (Tables 1 and 2), and this may be related to the predominance of epiphytes and vines or herbs in the two bat-pollinated assemblages. These plant types bear so-called glossophagine-flowers, whose nectar is largely inaccessible to flower-visiting bats other than glossophagines (Helversen, 1993). The occurrence of a single flower-visiting bat species, namely *A. caudifer*, at highland sites in the Atlantic forest is noteworthy and there seems to be a trend in the altitudinal distribution of glossophagine bats in southeastern Brazil (Marinho-Filho and Sazima, 1989; Buzato *et al.*, 1994; Sazima *et al.*, 1994b).

Bat- and hummingbird-pollinated flower assemblages in the Atlantic forest

We noted several similarities between bat- and hummingbird-pollinated flower assemblages in the Atlantic rainforest. For instance, bromeliads are an important nectar source and account for about 30–35% of the vertebrate-pollinated plant species in both assemblages (Buzato *et al.*, 1999; present study). Epiphytes and vines or herbs bearing a few flowers at a time prevail both in bat- and hummingbird-pollinated plant assemblages in the Atlantic rainforest (Buzato *et al.*, 1999; present study). Accordingly, trapline foraging is the prevailing mode recorded both for glossophagine bats and hermit hummingbirds, the major pollinators of vertebrate-pollinated assemblages in lowland and highland sites of the Atlantic forest in southeastern Brazil (Sazima *et al.*, 1995a, 1996; Buzato *et al.*, 1999). The ratio between bat-pollinated and hummingbird-pollinated flower species is 0.24 at the lowland site and 0.23 at the highland one (Buzato *et al.*, 1999; present study). These similar values indicate that further studies on bat and hummingbird pollination are merited at additional Atlantic rainforest sites, especially in eastern and northeastern Brazil where knowledge on vertebrate-pollinated plants is sparse (e.g. Machado *et al.*, 1998).

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