

Aechmea pectinata: a Hummingbird-dependent Bromeliad with Inconspicuous Flowers from the Rainforest in South-eastern Brazil

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The pollination biology of *Aechmea pectinata* (Bromeliaceae) was studied in a submontane rainforest in south-eastern Brazil. This species has a mainly clumped distribution and its aggregated individuals are likely to be clones. From October to January, during the flowering period, the distal third of its leaves becomes red. The inflorescence produces 1–15 flowers per day over a period of 20–25 d. The flowers are inconspicuous, greenish-white coloured, tubular shaped with a narrow opening, and the stigma is situated just above the anthers. Anthesis begins at 0400 h and flowers last for about 13 h. The highest nectar volume and sugar concentration occur between 0600 and 1000 h, and decrease throughout the day. *Aechmea pectinata* is self-incompatible and therefore pollinator-dependent. Hummingbirds are its main pollinators (about 90 % of the visits), visiting flowers mainly in the morning. There is a positive correlation between the number of hummingbird visits per inflorescence and the production of nectar, suggesting that the availability of this resource is important in attracting and maintaining visitors. The arrangement of the floral structures favours pollen deposition on the bill of the hummingbirds. Flowers in clumps promote hummingbird territoriality, and a consequence is self-pollination in a broader sense (geitonogamy) as individuals in assemblages are genetically close. However, trap-lining and intruding hummingbirds promote cross-pollination. These observations suggest that successful fruit set of *A. pectinata* depends on both the spatial distribution of its individuals and the interactions among hummingbirds.

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Key words: *Aechmea pectinata*, hummingbird-pollination, inconspicuous flowers, nectar production, reproduction, Atlantic forest.

INTRODUCTION

Bromeliaceae is the largest family of plants in the Atlantic forest showing a high degree of endemism (Martinelli, 1997), and its species constitute one of the most important nectar sources available to hummingbirds (Snow and Snow, 1986; Araújo *et al.*, 1994; Sazima *et al.*, 1995, 1996). Sick (1984) suggested that the evolution of bromeliads and hummingbirds is parallel, and according to McWilliams (1974), Bawa (1990) and Sazima *et al.* (2000) hummingbirds have been considered as the major pollinators of these plants.

Hummingbirds are nectar-feeding specialists (Brown and Bowers, 1985), whose visitation behaviour is influenced by the availability of nectar in the flowers (see Heinrich, 1975; Feinsinger, 1976; Roubik, 1989). In addition, the spatial distribution of this resource promotes different foraging strategies in these birds (Feinsinger, 1978; Snow and Snow, 1986; Locatelli and Machado, 1999; Buzato *et al.*, 2000).

Aechmea pectinata Baker (Bromeliaceae) presents an irregular and discontinuous distribution along the south/south-eastern Brazilian coast (Reitz, 1983; Wendt, 1997). It occurs in the 'restinga' scrub, in the mangrove and on rocky shores, either as a terrestrial, epiphytic or saxicolous plant. It grows mainly in assemblages of 10–15 individuals, which

are likely to be clones as asexual reproduction is common in Bromeliaceae (Rauh, 1990; Benzing, 2000), even if isolated individuals also occur (M. B. F. Canela and M. Sazima, pers. obs.). Although cursory reports of the floral features of *A. pectinata* and its visitors were made by Snow and Snow (1986), Sazima *et al.* (1995) and Buzato *et al.* (2000), no detailed information about the floral biology and reproductive system of this species is available.

This study sought to relate data on phenology, floral morphology and biology, as well as breeding system with the composition and dynamics of the pollinators of *A. pectinata*. The main purpose was two-fold: (1) to verify if pollinator visitation is correlated with nectar production, and (2) to evaluate if the reproductive success of this bromeliad species is influenced by its spatial distributions, via pollinator behaviour.

MATERIALS AND METHODS

Study site

This study was carried out in the Atlantic Forest at Picinguaba (Parque Estadual da Serra do Mar, Ubatuba, São Paulo State, Brazil) approx. 23°22'S and 44°50'W, at sea level. The climate is wet tropical ('Af.': see Köppen, 1948), with an annual rainfall of up to 2600 mm, an average annual temperature of 21 °C and no well-defined dry-cold season, even during the so-called dry months, from May to

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September (data source: Instituto Agrônomico de Campinas, Campinas, Brazil).

Procedure

Fieldwork was performed during two consecutive flowering seasons of *A. pectinata*, from October 2000 to January 2001 and from December 2001 to February 2002. Epiphytic, terrestrial and saxicolous individuals ($n = 91$) were sampled in the mangrove, the restinga scrub and on rocky outcrops. Inflorescences were observed *in situ* to determine the

TABLE 1. Fruit-set of autonomously self-pollinated, hand-pollinated and pollinated under natural conditions *Aechmea pectinata* flowers

Treatments	Fruit set (%)
Autonomous self-pollination	0 (0/171)
Manual self-pollination – same flower	0 (0/37)
Cross-pollination	96 (24/25)
Natural conditions (control)	56 (398/716)

Numbers in parenthesis are the number of fruits/flowers, respectively.

number of open flowers per day, features of anthesis, visitation frequency and foraging behaviour of flower visitors. Floral and vegetative structures related to attraction were also recorded. The internal length of corollas was measured from base to opening ('effective length'; Wolf *et al.*, 1976).

Nectar sugar concentration ($n = 20$) was measured with a pocket refractometer and its volume ($n = 50$) with microlitre syringes (Dafni, 1992). These measures were made throughout anthesis, at 2-h intervals, on previously bagged flowers of 18 individuals. The accumulated nectar volume ($n = 46$) and its respective sugar concentration ($n = 42$) were also measured on bagged flowers of nine individuals, at the end of anthesis. Pollen viability ($n = 10$ flowers, 10 individuals) was estimated by cytoplasmic staining, using the acetocarmine technique (Radford *et al.*, 1974). Stigmatic receptivity ($n = 70$ flowers, 24 individuals) was tested using the H_2O_2 (10 V) catalase activity method (Zeisler, 1938).

Visits were observed directly or through binoculars for 36 individuals from 0400 to 1800 h, totalling 112 h in 19 days. Some visits were photographed and videotaped. The identification of hummingbirds was made according to Ruschi (1982) and confirmed by a specialist. The bill length of the hummingbirds is as given in Grantsau (1989).

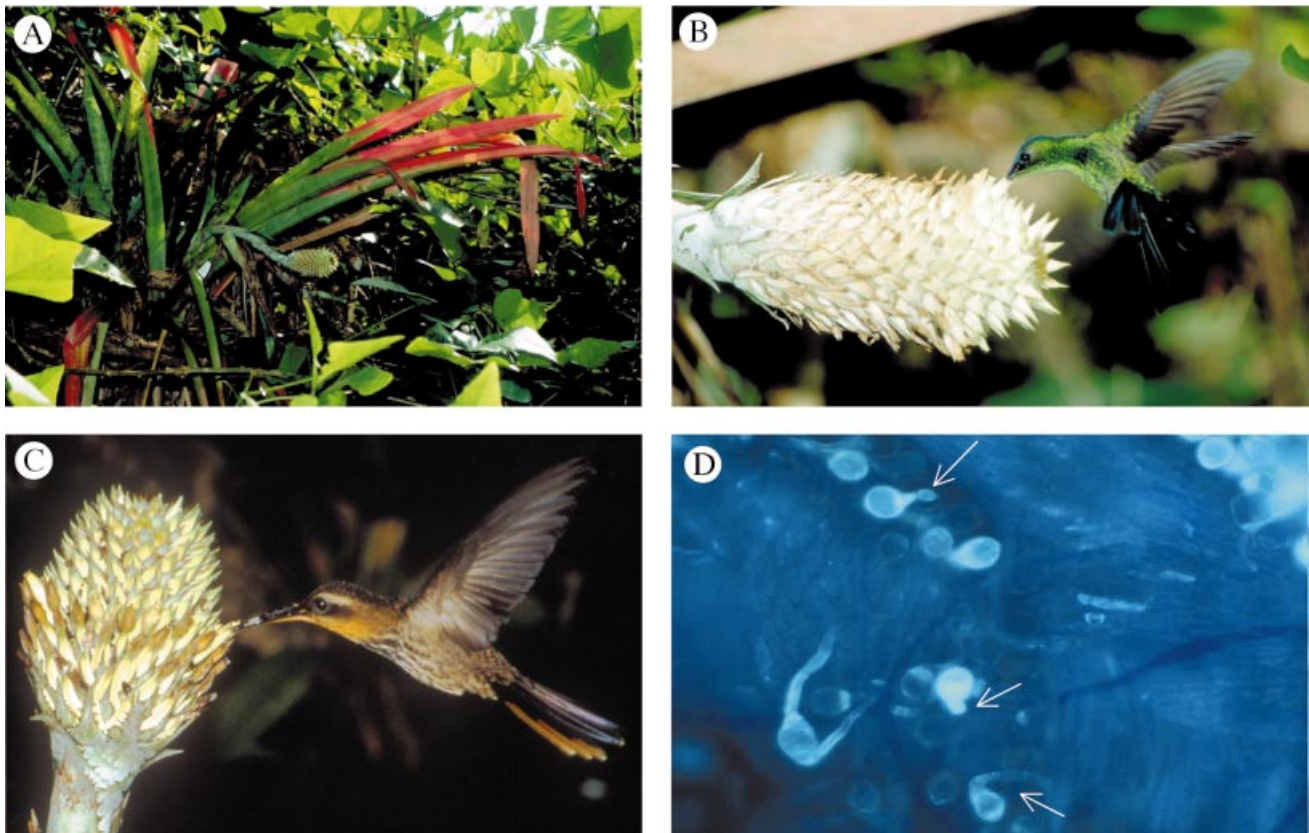


FIG. 1. Individual, pollinators and pollen tubes of *Aechmea pectinata* in the rainforest, south-eastern Brazil. A, Individual showing highly visible red coloured leaf tips and a bent inflorescence; note that the inflorescence is very inconspicuous. B, A male *Thaluranium glaucopsis* visiting a flower on the upper side of a bent inflorescence. C, *Ramphodon naevius*, a trap-liner hummingbird, visiting an erect inflorescence; note the pollen load on its bill tip. D, Signs of incompatibility such as curvature and thickening of the callose deposit on the extremity of the pollen tubes (arrows) on a flower fixed 12 h after manual self-pollination.

The breeding system was assessed by hand-pollination treatments on previously bagged flowers of 17 individuals: manual self-pollination, cross-pollination (previously emasculated flowers) and autonomous self-pollination (bagged

buds); flowers under natural conditions of pollination were marked as control (see Table 1). Fruit set for all treatments was determined approx. 2 months after pollination. Pistils of self- and cross-pollinated flowers ($n = 5$ flowers for each treatment, 14 individuals) were fixed in FAA 12, 24, 36, 48 and 72 h after pollination, and pollen tube growth was analysed by fluorescence microscopy (Martin, 1959). To compare the fruit set per plant resulting from activity of pollinators in clumped individuals vs. isolated ones, data were recorded from 22 randomly chosen individuals of four assemblages and of eight isolated individuals.

Daily nectar production and hummingbird visitation were evaluated for normality through the Kolmogorov–Smirnov test (BioEstat 2.0). As our data are non-parametric, the median (M) was calculated and variations were analysed through box-plot graphs (Systat 8.0), Kruskal–Wallis test (H), Mann–Whitney test (U), Spearman correlation and a regression analysis (BioEstat 2.0).

RESULTS

Flowering phenology and floral features

Aechmea pectinata flowers continuously from late October to mid-January. During the flowering period, the distal third of the leaves' length becomes red (Fig. 1A), which makes each individual very showy. This coloration gradually fades away during the fruiting season, which occurs from February to March.

The inflorescence is strobiliform, 10–15 cm long and 6–8 cm wide; it bears 150–250 flowers, and is supported by a 40–60 cm long stalk (Fig. 1A) that makes flowers more accessible to visitors. The inflorescence is usually erect, although bent ones may occur in epiphytic (Fig. 1A) or saxicolous individuals. In each inflorescence, 1–15 flowers open per day over a period of 20–25 days. Flowers are sessile, actinomorphic, with a tubular-shaped 30 mm long corolla and a narrow opening. The flowers are inconspicuous: bracts are greenish, sepals are greenish white, and petals are yellowish white (Fig. 1C), making it difficult even to distinguish the inflorescences from the foliage (Fig. 1A).

Prior to bud opening the style lengthens so that the stigma slightly exceeds the anthers. Anthesis of the *A. pectinata* flowers begins at 0400 h, and is characterized by discrete separation and outward curvature of petal tips, resulting in an approx. 2 mm wide opening. In open flowers, the apex of the stigma slightly extends out of the corolla. The stigma is receptive throughout the flower life. Anthers are juxtaposed, included in the corolla, extrorse and open longitudinally. The somewhat sticky pollen is available from the first hour of anthesis and it presents high viability (93 %). Nectar accumulates at the base of the corolla tube. Flowers remain open for approx. 13 h.

Both nectar volume ($H = 134.00$, $P < 0.001$) and sugar concentration ($H = 80.41$, $P < 0.001$) varied significantly throughout the day. This variation was most evident between the morning and afternoon periods (Fig. 2A and B). At the onset of anthesis (0400 h), flowers have no nectar ($M = 0 \mu\text{l}$, $n = 30$, four individuals), but production begins soon after and reaches its peak at 0800 h ($M = 21.5 \mu\text{l}$), after

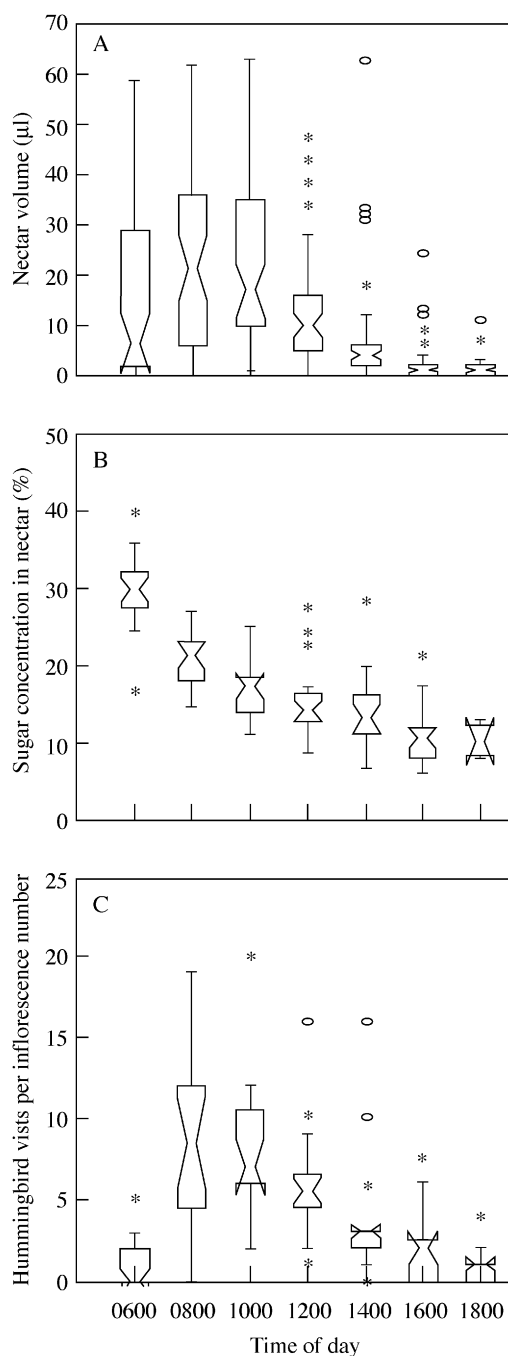


FIG. 2. Nectar features and number of visits in *Aechmea pectinata*. A, Variation in nectar volume. B, Sugar concentration in nectar. C, Number of hummingbird visits per inflorescence. The boxes represent the inter quartile range and their centres the medians. The interval between the slanted lines around the medians is the 95 % confidence limit. Inferior and superior vertical lines represent the total range of the distribution (25 and 75 %). Extreme values are represented by asterisks, and outliers by open circles. Overlap between boxes indicates no statistical difference.

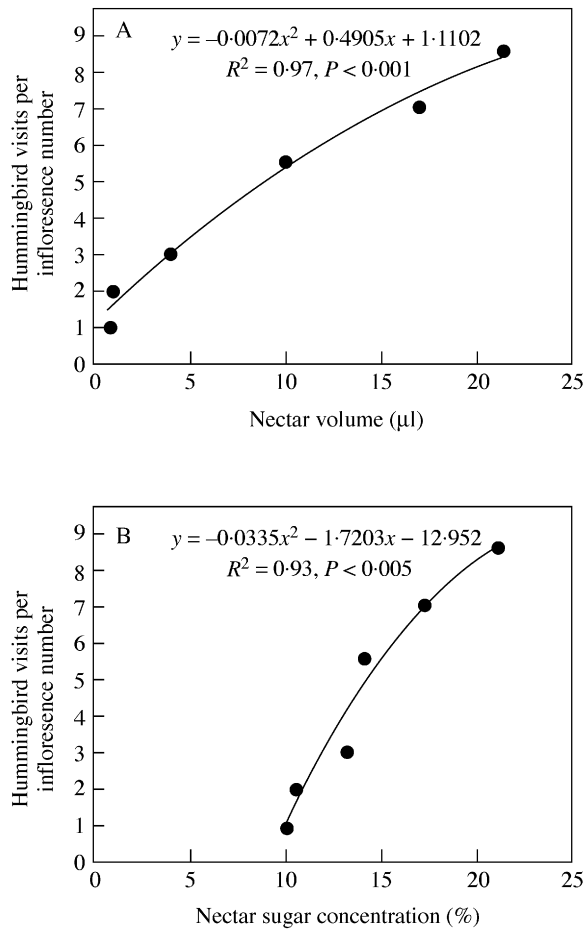


FIG. 3. Positive correlation between the number of hummingbird visits per inflorescence and nectar offered by *Aechmea pectinata* flowers: A, Nectar volume; B, sugar concentration. The values of nectar production from 0400–0600 h were excluded from this analysis as they correspond to a period of low hummingbird activity.

which it gradually decreases until late afternoon (Fig. 2A). Sugar concentration was also greatest in the early morning, at 0600 h ($M = 30\%$, $n = 20$); it decreased to half this value between 1000 and 1200 h, and continued decreasing gradually until late afternoon when it stabilized (Fig. 2B). Nectar volume is positively correlated with sugar concentration ($r = 0.85$, $P < 0.01$). The accumulated nectar volume throughout the day ($M = 79.5\ \mu\text{l}$, $n = 46$) and the sum of its partial values ($M = 67.0\ \mu\text{l}$, $n = 43$) did not differ significantly ($U = 959.50$, $P > 0.05$), indicating that nectar production is continuous and reabsorption does not occur. Sugar concentration in accumulated nectar ($M = 26.7\%$, $n = 42$) was also similar ($U = 756.00$, $P > 0.05$) to the concentration registered in the first hours of anthesis ($M = 25\%$, $n = 40$).

Floral visitors

Of the 535 visits to *A. pectinata* flowers, 489 were made by hummingbirds (91%) and the remaining ones by insects, namely bees and butterflies. The most frequent

hummingbird visitor, *Thalurania glaucopsis* Gmelin (Trochilinae) was accountable for approx. 42% of the visits ($n = 489$), 83% of which were made by males (Fig. 1B). *Amazilia fimbriata* Elliot (Trochilinae) made 36% of the visits, and *Ramphodon naevius* Dumont (Phaethornithinae) 20% (Fig. 1C). *Phaethornis ruber* Linné and *Melanotrochilus fuscus* Vieillot (Phaethornithinae) were rarely observed (only 1% of the visits).

Most of the hummingbird visits (55%) occurred between 0600 and 1000 h ($\bar{x} = 3.8$ visits $\text{plant}^{-1}\ \text{h}^{-1}$), the others occurring throughout the rest of the day at a diminishing frequency (Fig. 2C). This variation in the number of hummingbird visits throughout the day ($H = 72.02$, $P < 0.001$) is correlated with nectar production, for both volume ($r^2 = 0.97$, $P < 0.001$; Fig. 3A) and sugar concentration ($R^2 = 0.93$, $P < 0.005$; Fig. 3B).

Although periods of 30–40 min between visits were common, intervals were highly irregular and the longest ones occurred mainly in the afternoon. Visit duration at each flower varied from 1 to 10 s. When taking nectar, hummingbirds contacted anthers, receiving pollen on their bill (Fig. 1C).

Thalurania glaucopsis and *Amazilia fimbriata* were more frequent on clumped individuals of *Aechmea pectinata* than on isolated ones, being often found on the most conspicuous inflorescences or on those with the greatest number of flowers. They visited every flower on each inflorescence before moving to another one, and sometimes returned to one they had previously visited. Between visits, the hummingbirds commonly remained perched nearby. *Thalurania glaucopsis* (mainly males) and *Amazilia fimbriata* frequently showed aggressive behaviour and interacted agonistically with intruding hummingbirds, be these of another or the same species; they also excluded and chased bees. *Ramphodon naevius* (both males and females) visited *Aechmea pectinata* inflorescences in a trap-line fashion, sometimes interacting agonistically with other visitors. Individuals of these hummingbird species commonly alternated their roles when visiting *A. pectinata*, becoming territory intruders.

Reproduction

Aechmea pectinata is hermaphroditic, homogamic and self-incompatible. In flowers fixed 12 h after manual self-pollination, some pollen had germinated, tubes were short and showed evidence of incompatibility (see Murray, 1990), such as curvature and thickening of the callose plugs on their tips (Fig. 1D). Flowers fixed 48 h after manual self-pollination did not show developed pollen tubes. In cross-pollination experiments, flowers fixed 12 h after pollination showed high quantities of germinated pollen and well-developed tubes up to two-thirds of the style length; fertilization occurred after 24 h. Under natural conditions fertilization occurred after a similar period.

None of the autonomously or manually self-pollinated flowers produced fruits, which contrasts with the fruiting of 96% of the manually cross-pollinated flowers and 56% of the flowers under natural conditions (Table 1).

Of the clumped individuals ($n = 22$), only 23 % produced fruits, whereas 88 % of the isolated individuals ($n = 8$) produced fruits. Fruits are highly apparent because they become reddish when ripe. In erect inflorescences most of the flowers set fruit, whereas in bent ones only the flowers accessible to hummingbirds (Fig. 1B) developed fruits.

DISCUSSION

The annual flowering pattern (Newstrom *et al.*, 1994) of *A. pectinata* at the population level, as well as the individual flowering strategy, characterized as 'steady-state' type by Gentry (1974), are common in ornithophilous species of Bromeliaceae (e.g. Araújo *et al.*, 1994; Sazima *et al.*, 1996; Martinelli, 1997; Buzato *et al.*, 2000). A well-defined and synchronized blooming period, as observed for *A. pectinata*, indicates specialization to a given kind of pollinator (Stiles, 1978; Fleming, 1982), and hummingbirds prefer plants that offer regular and constant resources (Wolf *et al.*, 1976; Real and Rathcke, 1991).

Aechmea pectinata presents some floral features related to ornithophily, such as tubular shaped flowers, abundant nectar, absence of odor and long distance between nectar and sexual organs (see Faegri and van der Pijl, 1980; Proctor *et al.*, 1996). Since its flowers are inconspicuous, showing an unusual colour for hummingbird-pollinated species (Faegri and van der Pijl, 1980), the red-coloured leaves are responsible for attracting hummingbirds. Coloured leaves and bracts, and not flowers, that attract pollinators are common in other ornithophilous species of Bromeliaceae, as well as in Gesneriaceae and Heliconiaceae (see Stiles, 1981; Araújo *et al.*, 1994; Sazima *et al.*, 1995, 1996, 2000; Martinelli, 1997; Benzing, 2000).

The morphology of *A. pectinata* flowers favours legitimate access to nectar by visitors with long and stiff mouth parts, namely hummingbirds, and excludes other types of visitors (see Proctor and Yeo, 1972; Faegri and van der Pijl, 1980). The moderately long floral tube allows visits of either short-billed Trochilinae (11–24 mm bill length) or long-billed Phaethornithinae (22–46 mm bill length) (see Feinsinger and Colwell, 1978). In addition to their corolla length and shape, the anther arrangement in *A. pectinata* promotes pollen deposition on the bill of the hummingbird. Pollen deposition on the bill is particularly frequent in Bromeliaceae visitors (see Sazima *et al.*, 1995, 1996; Buzato *et al.*, 2000). This seems to be an efficient way of transferring pollen, as the pollen of most Bromeliaceae species is somewhat sticky (Percival, 1969; see Wanderley and Melhem, 1991; Halbritter, 1992) and hummingbirds usually visit a certain number of flowers before cleaning their bill (Grant and Grant, 1968; Sick, 1984; M. B. F. Canela, pers. obs.).

The somewhat short anthesis period of *A. pectinata* flowers is a feature common to several bromeliad species (e.g. Araújo *et al.*, 1994; Sluys and Stotz, 1995; Martinelli, 1997; Siqueira, 1998; Sluys *et al.*, 2001; Wendt *et al.*, 2002), which may be related either to homogamy or to the efficiency of pollinators that effect pollination after just a few visits (Ramirez *et al.*, 1990). The same may be true for *Bromelia antiacantha* Bertoloni (M. B. F. Canela and

M. Sazima, pers. obs.) and for *Hohenbergia ridleyi* (Baker) Mez (Siqueira, 1998).

Nectar volume and sugar concentration in *A. pectinata* were similar to the data of Snow and Snow (1986), Sazima *et al.* (1995) and Buzato *et al.* (2000) for this species, and to those of ornithophilous species in general (Arizmendi and Ornelas, 1990; Sazima *et al.*, 1996; Locatelli and Machado, 1999). In addition, major nectar production early in the day is a consistent tendency in ornithophilous flowers (Feinsinger, 1976), matching the period of hummingbird activity (Benzing, 1980; Sick, 1984). The positive correlation between nectar production and hummingbird visits to *A. pectinata* suggests that both the quantity and quality of nectar are important factors in attracting and maintaining bird visits (see Percival, 1969; Baker, 1975).

The behaviour of *Thalurania glaucopis* and *Amazilia fimbriata* at *A. pectinata* may be classified as territorial (Feinsinger and Colwell, 1978). *Ramphodon naevius* is regarded here as a typical high-reward trap-liner with no extensive territorial behaviour (cf. Stiles, 1975; Stiles and Freeman, 1993), although it can behave aggressively along its routes and exclude hummingbird intruders which it may come across (see Sazima *et al.*, 1995). Phaethornithinae species are known to occasionally hold temporary flower-centred territories (Stiles, 1975; Feinsinger and Colwell, 1978), a 'patrolling' behaviour that may be regarded as a specific resource defence (cf. Wolf *et al.*, 1976). Although hummingbirds are especially suited to a primary role, some individuals of the visiting species of *A. pectinata* frequently acted as territory parasites (Feinsinger and Colwell, 1978) and became intruders. The temporary alternation between different roles may be due to shifts in nectar availability of *A. pectinata* or to the spectrum of hummingbirds at a given site (see Sazima *et al.*, 1996; Locatelli and Machado, 1999; Buzato *et al.*, 2000).

As a self-incompatible species, *A. pectinata* is pollinator-dependent. Although incompatibility is not common in Bromeliaceae, even several genetically self-compatible species depend on pollinators because of different floral mechanisms (dichogamy, herkogamy) that hinder autonomous self-pollination (see Gardner, 1986; Araújo *et al.*, 1994; Martinelli, 1997; Siqueira, 1998; Wendt *et al.*, 2001, 2002). In addition to self-incompatibility, the low fruit set of *A. pectinata* individuals in large assemblages in comparison with the high fruit set of isolated plants is probably related to the territorial behaviour of the hummingbirds, which is favoured by the clumped distribution of the individuals and the long flowering period. Aggregated individuals concentrate the nectar source, thereby reducing the energy costs of the pollinator while searching for food (Locatelli and Machado, 1999) and promoting territoriality among visiting hummingbirds (Feinsinger, 1978; Snow and Snow, 1986; Buzato *et al.*, 2000). Territoriality prevents the visits of trap-liner hummingbirds carrying pollen from distant plants and, in the case of *A. pectinata*, it promotes self-pollination in a broader sense (geitonogamy) since individuals in assemblages are thought to be genetically close. Although less attractive to pollinators, isolated plants have a great chance of being effectively cross-pollinated (Janzen, 1971; Stiles, 1975).

The irregular intervals between hummingbird visits to *Aechmea pectinata* suggest that intruders were frequent, and sometimes not excluded by primary territory holders. Areas of significant aggregated resources attract territory parasites (Wolf and Stiles, 1970), and the hummingbirds that successfully manage to invade such territory have increased possibilities of carrying out cross-pollination in aggregated individuals. Therefore, intruder individuals of *Thalaurania glaucopsis*, *Amazilia fimbriata* and, mainly, *Ramphodon naevius* potentially play an important role in the fruit set of *Aechmea pectinata*.

Due to the high number of individuals and flowers available over a long and continuous period, *A. pectinata* represents a highly important floral resource for its visitors. The dependency of *A. pectinata* on a pollinator, in spite of its inconspicuous flowers, is related to such characteristics as leaf coloration, floral morphology and nectar availability, which attract and maintain hummingbird visits. However, successful fruiting is also related to other factors such as the spatial distribution of its individuals and the dynamics of the hummingbird community.

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