



Ipomoea bahiensis pollinators: Bees or butterflies?

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ABSTRACT

Ipomoea bahiensis presents many characters of a psychophilous nectar flower. At the investigated synanthropic site, it is, however, visited and pollinated primarily by pollen-foraging small to medium sized bees that leave the flowers well before the end of anthesis. The busy bees appear to intimidate, probably by their mere existence, butterflies that function as pollinators in early morning, but disappear from the scene after beginning of anthesis. The plant is allogamous. A higher fruit set in hand cross-pollinated flowers as compared to naturally pollinated controls indicates pollen limitation. For the first time, we observed male bees entering the closing flowers as an overnight accommodation even before noon.

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Introduction

Since the time of Darwin (1862) scientists have worked under the perspective that floral characteristics reflect the type of pollinator. Comparative observations of characters of flowers and their pollinators in an evolutionary analysis suggest that certain pollinators can promote the selection of different flower forms that consequently develop and display a variety of pollination syndromes (Fenster et al., 2004).

The syndrome concept, first proposed by Delpino (1868, 1869a,b), was further developed by Müller (1881) and Vogel (1954), amongst others, and finally compiled by Faegri and van der Pijl (1979). Recently, this concept was questioned (e.g., Waser et al., 1996). Some investigations demonstrated that the predictions of pollination syndromes did not correspond to results of empirical tests (Ollerton et al., 2009). Other authors rendered support for the existence of pollination syndromes (e.g., Momose et al., 1998).

The floral biology of certain species of *Ipomoea* has been studied especially because the genus contains weedy species of economic importance (Maimoni-Rodella and Yanagizawa, 2007). Several syndromes were described for the genus: melittophily (Knuth, 1898–1905; Parra-Tabla and Bullock, 1998; Piedade, 1998), psy-

chophily (Machado and Sazima, 1987), and ornithophily (Machado and Sazima, 1987); sometimes, generalized flowers are also mentioned (Stucky and Beckmann, 1982).

Ipomoea bahiensis occurs in arboreal cerrado, caatinga, restingas, dunes, and synanthropic sites like road verges, pastures and fields all over Brazil (Simão-Bianchini, 1993); more detailed information on its natural growing conditions are unknown up to now.

Weedy species often are self-compatible, but when they present self-incompatibility, one expects that they are pollinated by unspecialized visitors or by wind. Usually, their habitats are disturbed (Baker, 1974) so that the pollinator communities are not narrowly circumscribed (Aizen and Feinsinger, 1994).

We studied the relations between *Ipomoea bahiensis* and its guild of flower visitors in a population growing at a synanthropic site. With this aim, (i) flower form and function were described, (ii) the reproductive system studied, (iii) visitor and pollinator activities monitored and (iv) pollination mechanisms examined.

Materials and methods

Data were collected between June and October 2009 in the Parque Botânico do Ceará (3°42'42.81"S–38°38'44.35"W), a conserved area of the Brazilian semi-arid region, near Fortaleza. The experiments were executed in an area of the coastal tabuleiro considerably affected by men, where a shrubby vegetation grows with some emergent trees (Ceará, 1998). The climate of the region is hot tropical, with an average temperature of 26.6 °C. Mean annual precipitation is 1243.2 mm, with rains concentrated between January

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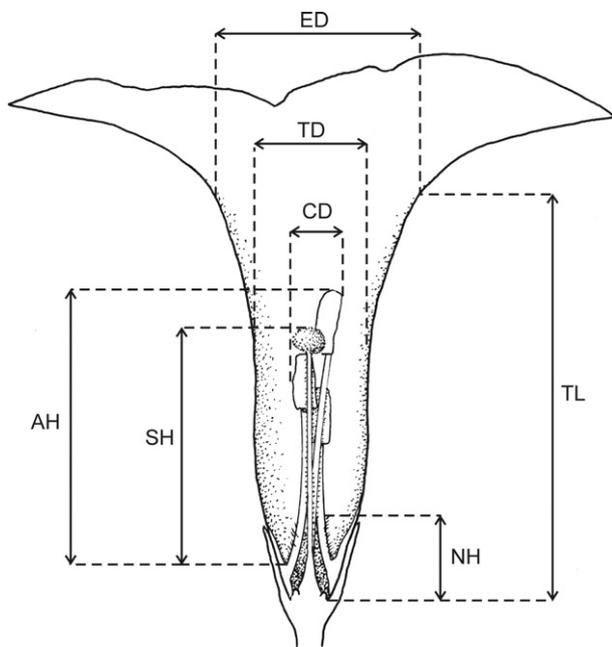


Fig. 1. Schematic longitudinal section of the flower of *Ipomoea bahiensis*, showing the nectar chamber (NH) and indicating the measurements taken: AH, anther height; CD, column diameter; ED, entrance diameter; NH, nectar chamber height; SH, stigma height; TD, tube diameter; TL, tube length.

and May. In 2009, however, rains were more intense (2161.6 mm) and lasted until August (FUNCEME, 2009).

With some 550 species, *Ipomoea* is the largest genus of the Convolvulaceae (Singh, 2004). It consists predominantly of sun-loving creepers thriving in open places and deciduous forests where neighbouring plants of small stature offer adequate support, but permit access of sunlight down to the ground (McDonald, 1991). *Ipomoea bahiensis* Willd. ex Roem. & Schult. is endemic to Brazil (Austin and Huáman, 1996). According to Piedade (1998), it shows characters typical of annuals; it sprouts during the whole rainy season and lasts into the dry period.

Floral morphology of *I. bahiensis* was studied using a dissecting microscope, drawings and photographs; floral parts were measured (Fig. 1) with a digital calliper and the software ImageJ (Abramoff et al., 2004).

To evaluate floral events, 12 individuals were marked and their flower development followed. They were observed from 4.30 h to 14 h, period in which insect visitation occurred. Anthesis was observed studying flowers from pre-anthesis to dropping of floral parts ($n > 50$). Receptivity was tested immersing stigmas in H_2O_2 (10%) in hourly intervals, beginning at 5 h ($n > 50$). Presence and quantity of nectar were measured with microcapillaries of $0.5 \mu\text{l}$ ($n = 261$) in five flowers from different plants in intervals of 1 h. To determine the quantity of nectar accumulated during the day, previously bagged flowers were probed with microcapillaries of $5.0 \mu\text{l}$ ($n = 21$). To describe pollen availability, quantity of grains in/on anthers was ascertained in selected flowers ($n = 40$) at hourly intervals. The quantity of pollen has not been measured, we only documented the decline of its presence at the opened thecae during the day. To observe the moment of anther dehiscence, flower buds were opened during pre-anthesis.

To study the reproductive system, experiments of pollen requirement were carried out and the fruit/flower ratio was calculated. For the first, the following tests were carried out: manual cross-pollination, manual self-pollination, spontaneous self-pollination, geitonogamy and pollination restrict by tulle bagging. Afterwards, fruit production was compared between

treatments and with the control. To assess the fruit/flower ratio from each of six plants five young inflorescences ($n = 30$) were marked and during the following development the numbers of buds, flowers and fruits formed by these inflorescences counted. To calculate the fruit/flower ratio, the total number of fruits produced was divided by the total quantity of flowers developed in the selected inflorescences.

To study flower guests, hourly walks were made amongst the plants in flower to collect the animals during their visits, always following the same trajectory. After gathering the flower visitors, eventual pollen deposits were localized on the bodies and form and size of the animals recorded; finally, the insects were sent to the entomology section of the Universidade Federal da Bahia for identification. On 21 non-consecutive days visitors were observed in order to identify: (1) preferred time for pollen and nectar gathering; (2) resource searched for by every visitor; (3) whether the visitors touched the reproductive parts; (4) and the behaviour shown in the flower ($n = 98$ field hours). Observations of visitor behaviour were made directly and videographed. The following measures of insect bodies were taken: body length (from clypeus frontline to last abdominal segment), thorax height (from ventral side to back), and tongue length. These measurements were made with the aid of photos and the ImageJ software.

Analyses of flower morphology and biology as well as of visitor behaviour were made by means of descriptive statistics. Pollen requirement data should have been analyzed by the Kruskal–Wallis test because of the binomial character of this kind of data; as only cross-pollination and control produced fruits, the exact Fisher test was applied to find out differences in fruit production. To check for differences in nectar availability during the day, an ANOVA was performed. To correlate between nectar availability and visitor frequency, the Pearson test correlation was utilized (Zar, 1984). Data were analyzed with the Statistica7 software (StatSoft, Inc., 2005).

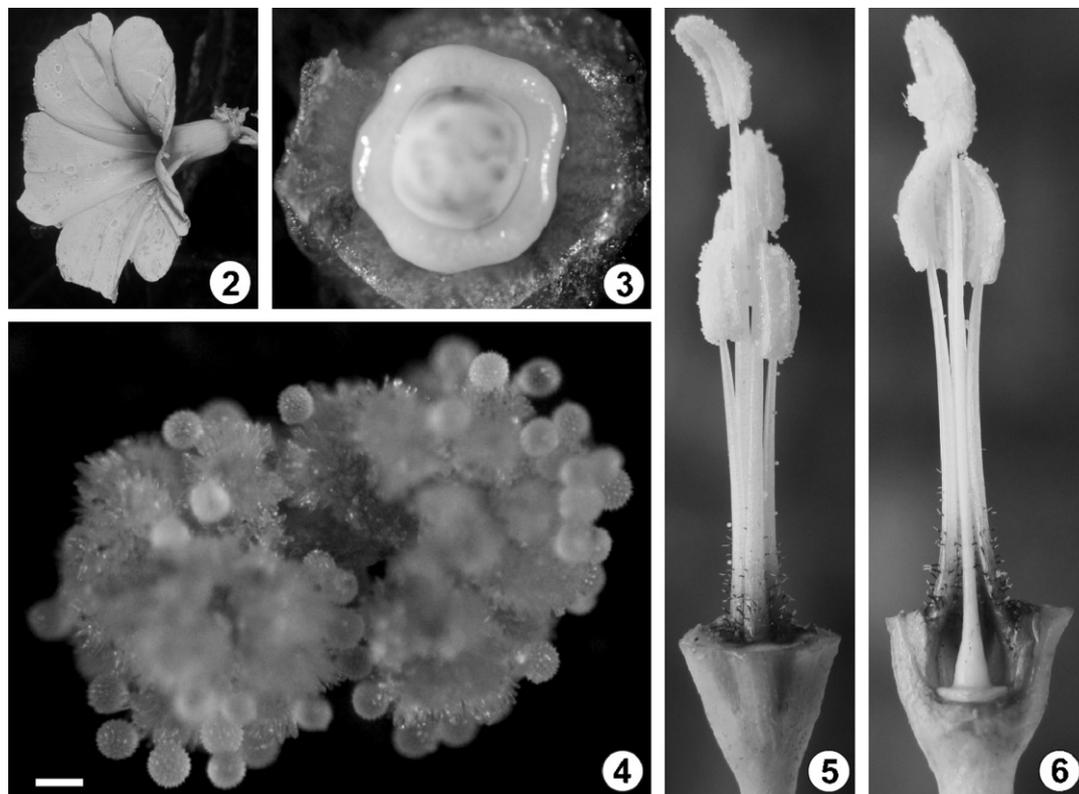
Results

Flower: form and function

The flowers of *Ipomoea bahiensis* develop from condensed cymose inflorescences of 5–15 buds (average 9.2, $n = 30$), one to three of which open per day. The free sepals of the pentamerous flowers are of different lengths and provide extranuptial nectaries on their outer surfaces; subapically, they are armed with recurved conical structures, typical for this species (Fig. 2).

The sympetalous corolla is funnel-shaped (Figs. 1 and 2): a >7 cm-wide flat area with short free lobes deepens into a 22 mm long and 8 mm wide tunnel. Basally, it forms a staped, a sturdy fusion zone between petal and filament bases (Fig. 6). The area of the median vein of each petal is widened and has a different surface structure. In sum this results in a star-shaped nectar guide (Fig. 2), emphasizing the centre of the radial symmetric flower. The flat part of the corolla has a pink-magenta coloration, with the star-shaped medians slightly darker. Beginning at the transition to the tubular part, the tone is blending into a darker violet.

Directly above the free filament bases are strong and hirsute (Figs. 5 and 6). Since the hairs intermingle, no space is left between them (Fig. 5). Their color is the same as that of the inner side of the corolla base. Above, they come close to the central style, their diameter slightly diminishes and the color changes into white. As a consequence of the greater anther diameter, longitudinal clefts are forming between them (Fig. 6). Because of the differing lengths of the filaments, the anthers are exposed at different heights – forming a spiral around the pistil (Fig. 5). The bitheous anthers open longicidally (Fig. 5); they are extrorse. As a result, pollen is presented all-around the androecium. An amphitribical flower results,



Figs. 2–6. Flower of *Ipomoea bahiensis*. Fig. 2. General view of the flower; notice the typical subapical cones on the sepals. Fig. 3. Disc nectary, with ovary removed. Fig. 4. Two stigma lobes with highly subdivided surface, covered by many echinate pollen grains (bar = 100 μm). Fig. 5. Outside view of central column of androecium and gynoecium; notice the nectarostegium formed by the hairy bases of the filaments. Fig. 6. Nectar chamber, enclosed by the strong staped, opened up to display the disc nectary surrounding the superior ovary; notice the tight (dark colored) nectar cover and the access holes between the ends of the filaments, immediately below the anthers.

with pollen distributed over more than the distal half of the central column.

The large white spheroidal pollen grains are echinate (Fig. 4); they are not very sticky – neither to the thecae nor between each other.

The bicarpellary gynoecium forms a small superior ovary (Fig. 6; with 4 ovules). The diameter of the style is similar to that of the surrounding filaments. The bilobed stigma (Fig. 4), located between three lower and two higher anthers, is deeply fissured so that a rugged ball-shaped papillary surface results presenting receptivity all over.

Gynoecium and androecium jointly form a white central column which results in a strong color contrast with the dark violet corolla centre.

A ring-shaped nectary (Fig. 3) surrounds the base of the ovary (Fig. 6). Nectar accumulates in a resistant nectar chamber with the staped as basement (Fig. 6) and locked by the widened filament bases with their interlacing hair cover (Figs. 5 and 6). Access is only given from above by the longitudinal slits between the distal parts of some of the filaments. Flower position varies between perpendicular (Fig. 1) and horizontal (Fig. 2) relative to the shoot axes and all stages in between.

Buds burst begins around 4.30 h and at 5.30 h the flowers are fully open. At 9.30 h (arrow in Fig. 7), the petals start to gradually curl inwards. 24 h after beginning of anthesis flowers commence to shed their organs. If fertilized, ovary and calyx are left over; if not fertilized, the flower is dropped entirely.

Anthers liberate pollen one or two days before anthesis, the pollen even adhering to the stigma (Fig. 4). Anther dehiscence occurs simultaneously. Thus, all pollen is available at 5.30 h; from this time onwards it diminishes rapidly. At 9 h, next to no pollen is

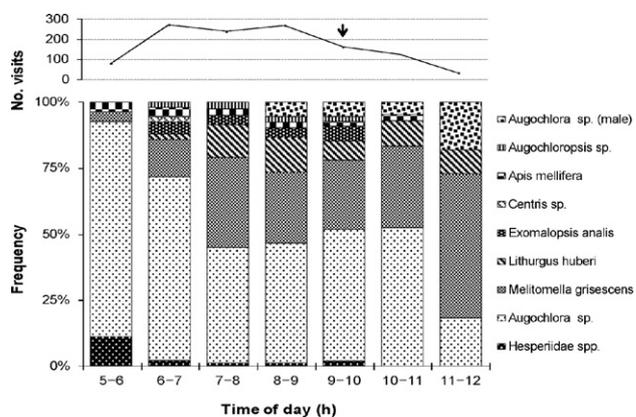


Fig. 7. Number of visitors to the *Ipomoea bahiensis* flowers (above) and the percentual specific composition of visitors (below) at hourly intervals during anthesis. The arrow indicates the beginning of flower withering with petal infolding.

left over. Sometimes, pollen falls from the anthers and accumulates below – especially in flowers poorly visited.

The stigma is receptive from the beginning of anthesis until 12 h; bubbling intensity of H_2O_2 did not vary during this time.

Nectar secretion is continuous during anthesis; the quantity available per flower varies between 0 and 1.5 μl . Low quantities were measured between 7 h and 8 h, while the major volume was available between 11 h and 12 h. After noon, an abrupt reduction of nectar availability was observed. Beside of these extremes, however, nectar quantities did not significantly differ ($p > 0.10$) at different hours. Accumulated nectar varied between 2.2 and 19.8 μl

per flower (average $7.3 \pm 4.4 \mu\text{l}$, $n = 21$). A Pearson test showed no correlation between visitation and nectar production.

On average, every inflorescence produced 8.1 flowers, 44.3% of which resulted in fruits. The fruit/flower ratio thus was 0.44.

Only flowers manually cross-pollinated ($n = 60$) and those of the control ($n = 60$) resulted in fruits. The percentage of fruit set was 87% in the first group and 65% in the second. Hand-crossed flowers thus presented significantly ($p = 0.0098$) more fruits than the control. All other pollination treatments did not result in fruits, neither manual self-pollination ($n = 60$), nor spontaneous self-pollination ($n = 55$), nor wind pollination ($n = 60$).

Visitors

Bees (Table 1) were the most abundant visitors (97.9%), followed by butterflies – with a very low frequency early in the morning and afterwards diminishing rapidly (Fig. 7). The most frequent species was *Augochlora* sp. (females; 50.6%), followed by *Melitomella grisescens* (27.7%) and *Lithurgus huberi* (9.1%). Fig. 7 shows the visit frequencies per species (*Augochlora* sp. separated into males and females) per hour.

The visits began at 5.30 h, with highest frequency between 6 h and 9 h. After this time, the visits diminished continuously until coming to an end around midday. Two periods could be distinguished: one of pollen collecting (from beginning of anthesis until 9 h) and one of nectar drinking (9–12 h). In the first period, occasional nectar visits were observed, while pollen collection was virtually absent in the second phase.

To consume nectar, bees (*Exomalopsis*, *Augochloropsis*, *Apis*) enter the flower below the central column; with their dorsal side they touch the reproductive parts. The principal nectar consumers, *Augochlora* males, however, were too small to contact pollen and stigma.

Pollen foragers entered the floral tube walking along the central column of style and stamens touching pollen and stigma – both accessible on all sides of the column. *M. grisescens* and *L. huberi* walked straightforward, while *Augochlora* sp. described a spiral along the central column. *M. grisescens* and *Augochlora* sp. removed pollen with their forelegs and mouthparts; the first species moistens the grains during uptake. In *M. grisescens* and *Augochlora* sp. pollen is accumulated in hindleg scopas. *L. huberi* voluntarily messes up its body with pollen that afterwards is groomed and transferred to the ventral scopa where it is stored in dry condition. Even after grooming, pollen grains remained on the bees' bodies – ready for pollination. This was especially obvious for pollen accumulated in the ventral scopa of *L. huberi* that always contacted the stigma when the bee entered the floral tube until the base.

As of 11 h, males of *M. grisescens* were observed entering the closing flowers of *I. bahiensis*. They remained therein for the remainder of the day and the following night and were encountered here early next morning.

Butterflies of the HesperIIDae landed on the corolla and introduced their mouthparts into the corolla tube. While searching for an entrance and while drinking nectar they presumably touched the reproductive parts.

Discussion

Reproductive system

A low fruit/flower ratio indicates that *Ipomoea bahiensis* is allogamous (Sutherland, 1986). This is corroborated by the results of our pollination tests that demonstrated self-incompatibility. There are several hypotheses to explain low fruit/flower ratios (Parra-Tabla and Bullock, 1998), amongst them predation on flowers, fruits and

seeds as well as pollen limitation. In *I. bahiensis* a constant predation on buds and flowers could be observed. The consequences were not measured, but these herbivory effects might have influenced fruit/flower ratio, resulting from the abortion of buds and flowers.

Also pollen limitation could explain the low fruit/flower ratio in our study. According to the theory of sexual selection applied to reproductive ecology and evolution in plants, female reproductive success is generally limited by resource availability and not by missing partners, i.e. pollen reception (Bateman, 1948). If this assumption is right, fruit and seed production should not increase if more pollen were added, as no additional resources would be available to mature additional fertilized ovules (Ashman et al., 2004). An opposite result would indicate pollen limitation. The significant difference in fruit production between control and manually cross-pollinated flowers gives evidence that pollen availability indeed is a limiting factor.

According to Knight et al. (2005), reproductive success can be diminished by low quantity or quality of pollen deposited on the stigma. As pollinators were abundant in the area and visited the flowers frequently and the stigmas of *I. bahiensis* carried more grains than necessary after Cruden's (2000) pollen per ovule estimate, we assume that fruit production was conditioned more by quality than by quantity of pollen. Compatibility limitations are obviously a common reason for low fruit set in tropical plants with great floral exhibition and self-incompatibility (Bullock et al., 1989). According to these authors, predominant intra-plant pollinator movements cause this limitation when incompatible pollen is deposited on the stigma.

Incompatibility can avoid inbreeding depression and increase genetic variability favoring cross-pollination (Barrett, 2002). On the contrary, self-incompatibility can limit the number of possible mating partners, especially in populations with small numbers of individuals. This may end in a low seed production and even in local extinctions (Byers and Meagher, 1992).

The absence of fruits in the tulle bagging experiment is not surprising: the pollen grains are too large for aerial transport. Their spiny (echinate) surface is also typical for animal pollen transfer (Ferguson and Skvarla, 1982). Insect pollination is, however, a general trait in the genus *Ipomoea* (incl. *I. bahiensis*, Jones and Jones, 2001; Vital et al., 2008).

Visitors and their fit to the flower

Two groups of visitors were observed (Fig. 7). In their great majority they were small to medium-sized bees, but there also were few butterflies. As the flowers of *Ipomoea bahiensis* produce nectar as attractant and possess several structures for nectar accumulation and access screening, they obviously belong to the so-called nectar-flowers (Endress, 1994; Müller, 1881).

Nectar is produced by a ring-shaped nectary surrounding the superior ovary; it accumulates in situ in a nectar-chamber (nectarotheca). This is formed by the strong stapet – much more resistant than the remainder of the corolla. It is plugged by a well-closing nectar-cover (nectarostegium): the violet-colored bases of the free filaments are thickened and covered by interlacing hairs. Thus, an access directly above the stapet is impossible without the application of much force.

Openings are offered, instead, higher up between the white distal parts of the filaments. As the anthers occupy more space than the thin filaments, the filament ends are separated from each other and provide longitudinal slits amongst them (see the gaps between the filaments below the stigma in Figs. 1, 5 and 6). These lengthwise access holes are distant (NH: ~5 mm) from the nectar and only accessible for long, slender mouthparts. The great distance between nectar and the reproductive region is also in

Table 1
Visitor species, body measurements, locality of pollen deposit, resource utilized, and visitor frequency.

Family	Species	BL	TD	TL	PD	RU	%
Anthophoridae	<i>Melitomella grisescens</i> Ducke, 1907	9.53	3.09	4.9	All over ^a	Pollen ^b	27.68
Megachilidae	<i>Lithurgus huberi</i> Ducke, 1907	11.09	3.26	7.28	All over ^c	Pollen ^b	9.07
Halictidae	<i>Augochlora</i> sp.	7.12	1.69	3.27	All over	Pollen ^b	50.60
Halictidae	<i>Augochlora</i> sp. (males)	6.33	1.43	2.59	Missing	Nectar	2.86
Anthophoridae	<i>Exomalopsis analis</i> Spinola, 1853	7.44	2.4	3.75	Dorsum	Nectar	3.10
Anthophoridae	<i>Centris</i> sp.	13.37	3.98	5.63	Missing	–	0.48
Apidae	<i>Apis mellifera</i> Linnaeus, 1758	10.8	–	5.6	Dorsum	Nectar	2.39
Halictidae	<i>Augochloropsis</i> sp.	7.95	1.93	–	Dorsum	Nectar	1.67
Hesperiidae	Spp.	–	–	–	–	Nectar	2.15

BL, body length; TD, thorax diameter; TL, tongue length; PD, pollen deposit; RU, resource utilized; %, visit frequency.

^a Especially on abdominal venter.

^b Occasionally also nectar.

^c Deposition of greater pollen quantity as compared to *Melitomella grisescens* and *Augochlora* sp.

favor of elongated mouthparts of pollinators (Machado and Sazima, 1987).

Nectar production parallels stigma receptivity during the entire anthesis, while pollen is rapidly depleted after flower opening – another argument in favor of the nectar-flower hypothesis. The abrupt reduction of nectar availability in the early afternoon – in the absence of any visitors – could be explained in several non-exclusive ways: end of nectar production, dehydrating environmental conditions, and re-absorption of nectar (Búrquez and Corbet, 1991).

The tubular part of the sympetalous corolla is not as narrow as in stiel-teller-type flowers. A butterfly, however, cannot enter it entirely. With the head accessing the tube mouth, entry of light from above into the lower parts of the flower is also barred. In the relative darkness of the tube the mouthparts erratically are striving for an entrance towards nectar. Until encountering one of the lengthwise gaps by circular probing movements, there are many chances to be contaminated with pollen from one of the anthers, located at different heights that make the narrow central column amphitribic. As the stigma is \pm ball-shaped, it is receptive on all sides and thus also takes advantage of any erratic tongue movements of the insects.

As there are only four ovules, there is need for only few pollen grains – coinciding with the small carrying area of a butterfly tongue and the poor sticking capacity of the grains.

The flattened part of the radial corolla is very large, offering a great advertisement area (Dafni, 1993) and a huge landing platform, obviously directed at larger animals like butterflies. The star-shaped nectar guide formed by the augmented median nerves converges at the tube entrance – also a typical figure encountered in many flowers that attract Lepidoptera as pollinators (Vogel, 1954).

The far greater group of visitors was composed of certain species of small and medium-sized bees (Fig. 7 and Table 1) that in their majority visited the flower for pollen. The flower, however, does not belong to the pollen-only-flowers (Müller and Müller, 1883) that are said to offer a surplus of pollen to their visitors (Vogel, 1978). The bees instead forage for pollen in a nectar-blossom. A similar case was described by Schlindwein et al. (2005) in *Campánula rapunculoides*, where 95.5% of the pollen was removed by pollen-collecting bees while only 3.7% contributed to pollination. Bees even may develop oligolecty on pollen of nectar flowers (e.g., *M. grisescens* on *Ipomoea*; Schlindwein, 2004), even without any pollination relationship (e.g., *Oenothera*-bees on sphingophilous *Oenothera* species; Linsley et al., 1963a,b, 1964).

Ipomoea bahiensis does not even show any character typical for bee-pollinated flowers: nectar is not normally available to the short bee tongue (in relation to the height of the nectar chamber, Fig. 1: NH). It can only be reached using force to perforate the nectar cover. The flower does not show the dorsiventral construction typical for the majority of bee flowers (keel blossoms: Westerkamp, 1997;

bilabiate blossoms: Westerkamp and Claßen-Bockhoff, 2007), but instead is radially symmetric with a corolla gigantic in relation to the small bees.

The bees do not show a uniform behaviour as is typical for flowers specialized in them as pollinators. Some use the corolla to enter the flower, others walk along the central column – either in a straight or in a spiral line. Moreover, no mutual fit was observed between (certain) bees and the flower of *I. bahiensis*. So, there is no reason to call it a bee flower.

The high frequency of bees on *I. bahiensis* able to collect the coarse-grained pollen once having discovered this source is simply explained: the great need of pollen per offspring (Müller et al., 2006) lets them return to this plant as long as pollen is available. In spite of the low number of pollen grains per flower, the high number of flowers available in an *I. bahiensis* population makes the species a reliable resource. Maybe, the presence of great numbers of busy bees impedes the access of butterflies and even expels the few of them present at the flowers in early morning.

It is not uncommon that male bees utilize flowers as a retreat, especially during the night (Alves-dos-Santos et al., 2009). The fact that *Melitomella grisescens* males enter their accommodation already at the end of the morning to our knowledge is new. Probably the chance to encounter females for the day is ending at noon; so the only chance is to wait until next morning in a safe retreat. As Schlindwein (2004) observed, copulations of this species at the flower itself are extremely rare.

The low numbers of the exotic *Apis mellifera* which approach *I. bahiensis* shows that these flowers do not offer an alternative worth being exploited by this bee (e.g., Visscher and Seeley, 1982). The few bees observed probably were scouts testing for resource quality that after their visit did not recruit other bees to this plant.

Conclusions

All details of the *Ipomoea bahiensis* flower are in strong favor of the psychophilous syndrome. The overwhelming majority of visitors, however, are not butterflies but small to medium-sized bees. They visit this nectar-flower for pollen while nectar is accumulating and finally disappearing after anthesis. After removing all pollen – and obviously pollinating – the number of bees is decreasing continuously; only some nectaring bees remain. Around midday, even these bees have disappeared. The few butterflies observed at the very beginning of anthesis rapidly leave the flowers, probably displaced by the great number of pollen foraging bees. Quarrelling between the two insect groups was never observed, but certainly, the butterflies were negatively affected by the great bee activity.

The illegitimately pollen foraging bees pollinate in reasonable amount this psychophilous nectar flower that does not present any adaptations to bees. It remains still open, whether the observed

pollen limitation is indeed a result of the pollen removed by the bees or does it reflect a high amount of self pollen transferred to the stigma. This question eventually can be tested in a more natural habitat, where *Ipomoea bahiensis* does not behave as a weed and the pollinator guild might be different.

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