POLLINATION AND REPRODUCTIVE BIOLOGY OF THIRTEEN SPECIES OF BEGONIA IN THE SERRA DO MAR STATE PARK, SÃO PAULO, BRAZIL

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Abstract—The reproductive biology of 13 monoecious species of *Begonia* L. (Begoniaceae) that occur in the Serra do Mar State Park, São Paulo, Brazil, was investigated. These species flower annually and present flowers with mostly white tepals, light and sweet odour, pollen as a reward but no nectar, numerous yellow stamens, and coiled yellow styles. Anthesis is diurnal and floral duration is long (6 - 15 days). The unusual appearance of pistillate flowers of these species supports the view that they are intersexual mimics of the staminate flowers. Despite consistently high levels of fruit-set, none of the 11 species tested proved to be apomictic. In contrast to earlier reports of self-compatibility in *Begonia*, self-pollinations of *B. integerrima* and *B. itatinensis* produced no fruits or seeds, and the complete absence of pollen tubes in the styles of self-pollinated flowers of *B. integerrima* suggests that the species is genetically self-incompatible. Flowers pollinated under natural conditions showed many pollen tubes that reached ovules, suggesting that adequate numbers of compatible pollen grains had been transported by pollinators. The principal pollinators were small bees of the Apidae and Halictidae. Ten species of bees were observed to visit eight species of *Begonia*, and pollen collection occurred by means of vibration, except for *Trigona spinipes*. Visits to rewarding staminate flowers were significantly more frequent than visits to unrewarding pistillate flowers. Duration of visits to pistillate flowers also was significantly shorter than the duration of visits to staminate flowers. We conclude that visits to pistillate flowers occur by mistake but with sufficient frequency to allow for successful reproduction in natural populations of these species.

Key words: pollination, Begonia, breeding systems, Atlantic Rainforest, deceit, mimicry

INTRODUCTION

Plant-pollinator interactions involve energy investment in flowers, which offer rewards to facilitate removal and deposition of pollen by visitors (Faegri & Pijl 1979). These interactions, however, are not always mutualistic, as in deceit pollination (Baker 1976). Studies of the interactions between plants and their pollinators and the evolution of morphological characteristics that mediate these interactions can provide useful information to those charged with conserving rare species in threatened habitats (Kearns et al. 1998), such as the Atlantic Rainforest of Brazil (Alves dos Santos 2003).

There are two genera within the family Begoniaceae: *Begonia* and *Hillebrandia* (Forrest & Hollingsworth 2003). *Begonia* is among the largest angiosperm genera, with roughly 1 500 species distributed principally in tropical and subtropical regions (Goodall-Copestake et al. 2009), whereas *Hillebrandia* is monotypic and endemic to the Hawaiian Islands (Clement et al. 2004). Recent estimates put the number of species of *Begonia* in Brazil between 200 to 240, with highest diversity in the Atlantic Rainforest (Silva & Mamede 2001; Jacques 2002). In the Serra do Mar State Park, 24 species have been recorded (Silva & Mamede 2001).

Most species of *Begonia* are monoecious herbs with cymose inflorescences (Givnish 1980; Burt-Utley 1985; Ågren & Schemske 1991). They present staminate and pistillate flowers

in different phases of anthesis (Ågren & Schemske 1993), with staminate flowers usually open before pistillate flowers (Givnish 1980; Jacques 2002). The tepals and the style/stigma of the pistillate flowers typically resemble the tepals and androecium of the staminate flowers, both in size and colour (Schemske & Ågren 1995; Schemske et al. 1995). There exist variations in floral morphology among species, however, that may provide answers to questions regarding their pollination biology and reproduction. For example, the wide variation in tepal length among species of section Pritzelia suggests that some species are pollinated by small bees, such as halictids, whereas other species are pollinated by much larger bees, such as euglossines.

Pollination of *Begonia* by bees was suggested by Seitner (1976), Wiens (1978), Faegri and Pijl (1979), and Givnish (1980), and bees are probably the main pollinator group of Begoniaceae. But pollination by birds occurs in some species, such as *Begonia ferruginea* (section Casparya) of Colombia, whose red, tubular pistillate flowers produce nectar and have been observed to be visited by hummingbirds (Vogel 1998). Species of section Symbegonia also have tubular flowers and are visited by nectarivorous sunbirds (Forrest et al. 2005).

Studies in Central America by Ågren and Schemske (1991), Schemske and Ågren, (1995), Schemske et al. (1995), and Corff et al. (1998) have shown that deceit pollination occurs in some species of *Begonia*, in which bees mistakenly visit unrewarding pistillate flowers. In these species, pistillate

flowers resemble, and possibly mimic, rewarding staminate flowers to attract pollinators (Vogel 1978; Burt-Utley 1985; Ågren & Schemske 1991; Schemske et al. 1995; Jacques 2002). Pollination by mistake (deceit pollination) was first described by Sprengel (1793). Since then, authors have identified three types of deceit pollination: pseudocopulation, interspecific mimicry, and intersexual mimicry (Vogel 1978; Wiens 1978; Dafni 1992). Deceit pollination is common in a diverse array of families in tropical and temperate regions (Renner & Feil, 1993), such as Apocynaceae (Haber 1984), Caricaceae (Baker 1976), Ebenaceae (House 1989), Myristicaceae (Armstrong & Drummond 1986), and Orchidaceae (Cozzolino & Widmer 2005; Pansarin et al. 2008).

We suggest that several factors play a role in the rate of deceit (i.e., the proportion of visits to unrewarding pistillate flowers). First is the ability of different pollinator species to discriminate between staminate and pistillate flowers. There may also be differences within a given species of pollinator between naïve and experienced bees, depending on their ability to learn. The rate of deceit may also be related to the species of Begonia, especially with respect to the timing and presentation of staminate and pistillate flowers. Species of Begonia in which staminate and pistillate flowers are presented simultaneously and which maintain a high ratio of staminate to unrewarding pistillate flowers are expected to show higher rates of deceit.

Little information exists regarding the reproductive biology of Begonia. It has been suggested that the genus is self-compatible (East 1940; Burt-Utley 1985), and Ågren and Schemske (1993) confirmed self-compatibility (geitonogamy) in five species of section Doratometra. Burt-Utley (1985) and Jacques (2002) have reported natural hybrids between some species of Begonia.

We studied pollination and reproductive biology of 13 species of Begonia in Brazil that occur in the Atlantic Rainforest on the coast of the state of São Paulo. The specific objectives were to determine reproductive phenology, breeding system, and reproductive success under natural conditions and to record information on floral biology and floral visitors. The species were selected based on population size in the area of study, length of flowering period, and accessibility of flowers. This approach allowed us to compare and contrast a range of species with respect to a set of basic questions. What are the ratios of staminate to pistillate flowers and how do these change over time? Do these ratios change the behaviour of pollinators and lead to lower or higher levels of pollination and fruit-set? Do pollinators differ in their ability to discriminate between staminate and pistillate flowers?

MATERIALS AND METHODS

This study was conducted in areas of dense, humid forest in the Núcleo Picinguaba (23° 31′ to 23° 34′ S and 45° 02′ to 45° 05′ W), Serra do Mar State Park. The elevation varies between sea-level and 1 340 m. The climate of the region is hot and extremely humid, with average temperatures above 18°C and with a drier period in winter (Nimer 1977). According to Köppen (1948) the local climate is classified as Rainy Tropical type Af, having high precipitation during all months of the year. Part of this study was conducted in an area of dense, humid montane forest in the Núcleo Santa Virgínia (23° 17′ to 23° 24′ S and 45° 03′ to 45° 11′ W), Serra do Mar State Park. The elevation varies between 850 and 1 100 m above sea-level, and the climate is Temperate Tropical (Cwa following the classification of Köppen 1948), with a mean annual precipitation in excess of 2 000 mm. In the driest months, the precipitation never falls below 60 mm (Setzer 1966).

The following species of Begonia were studied: B. caraguatatubensis Brade, B. cucullata Willd. var. cucullata (Fig. 1a, b), B. dentatiloba A. DC., B. fernandocostae (Fig. 1c, d), Irmsch., B. aff. fluminensis Brade (Fig. 1e, f), B. fruticosa A. DC., B. hookeriana Gardner (Fig. 1g, h), B. integerrima Spreng. var integerrima (Fig. 1i, j), B. itatinensis Irmsch., B. lanceolata Vell., B. luxurians Scheidw., B. pulchella Raddi. (Fig. 1k, l), and B. valdensium A. DC.

To determine the flowering phenology of the species studied, flowering periods were recorded for approximately 50 individuals between March 2007 and July 2009. The pattern of flowering of these species was determined according to the phenological patterns defined by Newstrom et al. (1994). Their classification provides a logical system to describe the full range of patterns quantitatively (e.g., annual, subannual, continuous). For B. caraguatatubensis, B. dentatiloba, B. fernandocostae, B. aff. fluminensis, and B. integerrima, the number of flowers opening on a determined day was measured. Floral measurements of both staminate and pistillate flowers were taken from Silva and Mamede (2001) for all species studied. Biological characteristics of the flowers of all species, such as time of anthesis, sequence of staminate/pistillate anthesis and duration, presence of odour, tepal colour, and receptivity of the stigma (tested with 10 M hydrogen peroxide) were determined directly in the field (Dafni 1992; Kearns & Inouye 1993). Pollen viability was tested in B. cucullata and B. aff. fluminensis by observing colouration of the cytoplasm with a 1.2% solution of carminic acid (Radford et al. 1974). Other characteristics such as floral symmetry, number of flowers per inflorescence (mean ± standard deviation), form and size of tepals, stamens, stigma, and capsules were noted.

To gauge the effectiveness of pollinators, pollen tube analysis was done for 12 species of Begonia, using 7 to 20 pistillate flowers collected from natural populations. The analysis of pollen tubes in flowers of B. luxurians was not possible due to the rigidity of the ovary wall tissue. The opened pistillate flowers were collected under natural conditions (i.e., available to pollinators) before tepal senescence and preserved in a solution of 50% ethanol. The gynoecia were washed with distilled water and placed in a 2 % solution of sodium hydroxide, where they remained within an oven at 49°C for 5 to 20 minutes until the stigma, style, and ovary softened and cleared sufficiently (Iara Bressan, pers. com.). Slides were stained using an aniline blue solution (Martin 1959), and an Olympus BX51 fluorescence microscope was used to observe pollen tubes in the stigmas and ovaries. Images were captured using an Evolution®MP digital microscope camera from Media Cybernetics.
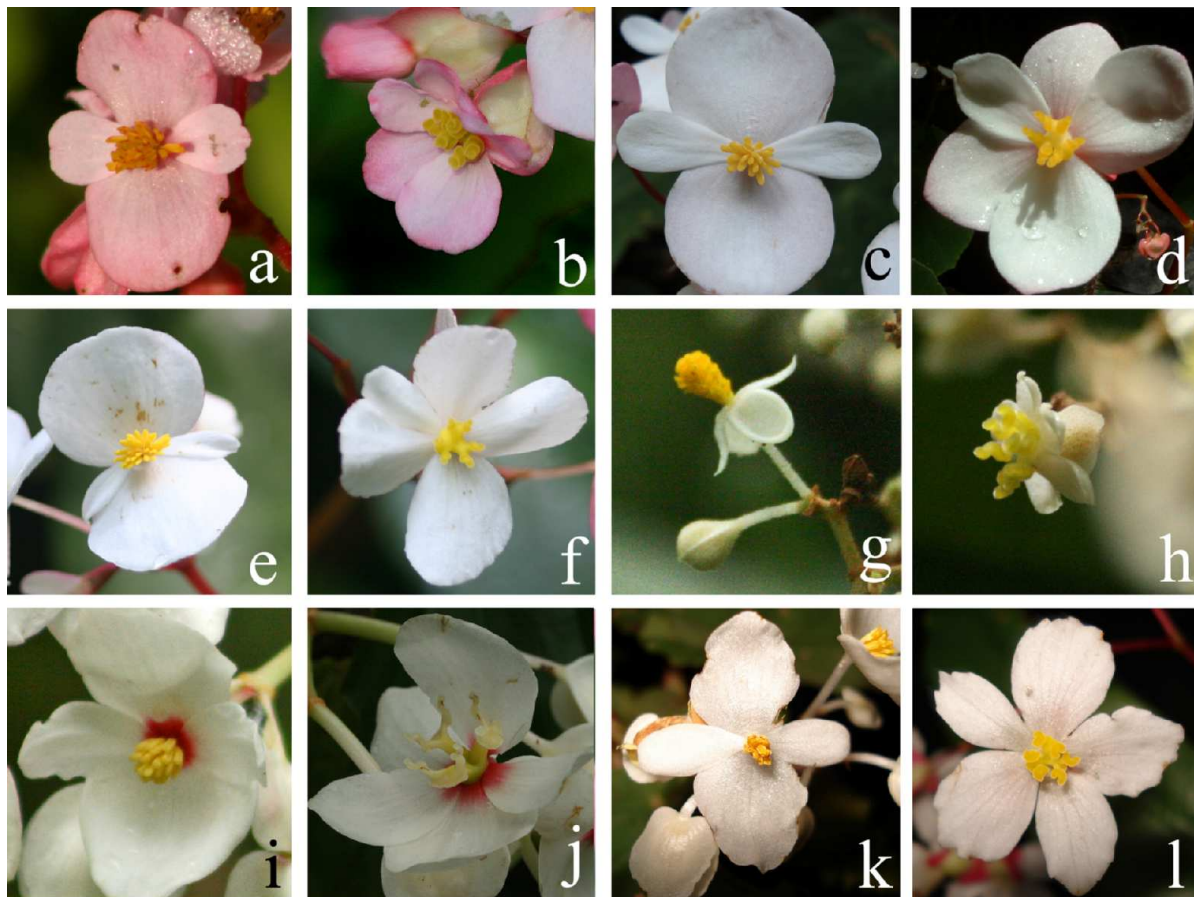
FIGURE 1. Staminate flowers (left) and pistillate flowers (right), respectively for: *Begonia cucullata* (a, b); *B. fernandocostae* (c, d); *B.* aff. *fluminensis* (e, f); *B. hookeriana* (g, h); *B.* integerrima (i, j); *B. pulchella* (k, l).

To test for apomixis, inflorescences were bagged prior to anthesis. Staminate buds or flowers were removed before bagging to prevent self-pollination. *Begonia integerrima* and *B. itatinensis* present open and receptive pistillate flowers at the same time as staminate flowers on the same individual. Therefore, tests for self-compatibility involving self-pollinations (geitonogamy) could be performed on these species. Pollen was transferred from a staminate flower to a pistillate flower on the same plant: four in *B. itatinensis* and nine in *B. integerrima*. In one inflorescence of *B.* aff. *fluminensis* and another in *B. fernandocostae*, one pistillate flower received outcross pollen to serve as a control; both of the inflorescences were bagged until maturation of the capsules. To test the potential for pollination by wind, various pistillate flower buds were bagged with organza bags to exclude visitors and were later examined for presence and growth of pollen tubes. Estimates of fruit-set under natural conditions were obtained for *B. fernandocostae*, *B.* aff. *fluminensis*, and *B. caraguatatubensis* by comparing numbers of pistillate flowers and numbers of developed capsules on marked inflorescences.

Observations of floral visitors were conducted between June 2007 and May 2009 for five species: *B. caraguatatubensis*, *B. dentatiloba*, *B. fernandocostae*, *B.* aff. *fluminensis*, and *B. integerrima*. These species were chosen based on their abundance in the area of study, accessibility of flowers, and presence of floral visitors. Observations were made continuously between 0700h to 1500h, when visitation ceased.

The observations were done on non-consecutive days during the flowering period of each species, for a total of 20 hr of observation for each species. Observation sites were 25 m² and contained between 24 and 1 095 flowers. Observations of visitors to *B. luxurians* and *B. valdensium* were done during one day (3 hr/species) and in *B. cucullata* visitor observations were sporadic, totalling 3 hr. For each visit, the species of visitor, frequency, duration of visit, and sex of the flower being visited were recorded, as well as details on pollen collecting behaviour.

Data from each period of observation were analyzed using BioStat 3. A Mann-Whitney U-Test was used to test statistical differences between duration of visits to staminate flowers and duration of visits to pistillate flowers. Histograms were created using Systat 11. For each species of visitor, the rate of deceit was calculated as the proportion of all visits that are made by mistake (i.e. visits to pistillate flowers rather than rewarding staminate flowers). The importance of each visitor as a pollinator to each species of *Begonia* was determined based on frequency of visits to pistillate flowers and behaviour during these visits.

RESULTS

Phenology, morphology, and floral biology

Three patterns of reproductive phenology were identified among the 13 species of *Begonia*. *Begonia cucullata* is the only species with a continuous pattern of flowering, with a long peak of approximately six months and a reduction in the

number of flowers produced during the rest of the year (Fig. 2). The species that present a sub-annual pattern of flowering are *B. dentatiloba*, *B. fernandocostae*, *B. lanceolata*, *B. luxurians*, and *B. valdensium*, having a distinct flowering peak and one or more shorter periods of flowering throughout the year. *Begonia caraguatatubensis*, *B. fruticosa*, *B.* aff. *fluminensis*, *B. hookeriana*, *B. integerrima*, *B. itatinensis*, and *B. pulchella* are characterized by an annual flowering pattern (Fig. 2).

All 13 species of *Begonia* that were studied have cymose inflorescences with pistillate and staminate flowers in the same inflorescence (Fig. 3a-c) or in separate inflorescences (Fig. 3d). *Begonia lanceolata* has staminate flowers in dichasial cymes and depauperate, subsessile pistillate flowers (Fig. 3d, e). All species are monoecious and present staminate and pistillate flowers in different phases of anthesis, with the exception of *B. cucullata*, *B. integerrima*, and *B. itatinensis*, in which staminate and pistillate phases overlap. In nine of the 13 species studied, staminate flowers open before pistillate flowers. Typically, pistillate flowers open and become receptive only after staminate flowers have senesced. These species may produce more than one inflorescence per individual, but inflorescences always occur in different phases (staminate or pistillate). The species that present staminate and pistillate flowers open synchronously on the same inflorescence are *B. integerrima* and *B. cucullata*. *Begonia itatinensis* also presents synchronously open staminate and pistillate flowers, but the inflorescences are reduced to a single flower (Fig. 3f).

The number of flowers per inflorescence and flower size vary widely among the species studied. *Begonia caraguatatubensis* (Fig. 3a, b), *B. hookeriana*, and *B. luxurians* possess many small (2 - 4 mm; Tab. 1) staminate and pistillate flowers. *Begonia caraguatatubensis* presents 24 ± 28 flowers (n = 10 inflorescences) open per inflorescence in the staminate phase and 57 ± 66 open flowers (n = 10 inflorescences) per inflorescence during the pistillate phase. These species show a temporal separation of open staminate and pistillate flowers, with anthesis of pistillate flowers following the senescence of staminate flowers. On the other hand, *B. fernandocostae*, *B.* aff. *fluminensis*, *B. integerrima*, and *B. valdensium* possess larger

staminate and pistillate flowers (9 - 15 mm; Tab. 1) and relatively fewer flowers per inflorescence than other species. For example, *B. integerrima* has 12 ± 6 flowers per inflorescence (n = 10 inflorescences), but some of the staminate flowers open soon after the pistillate flowers. For this species there is an overlap of the two types of flowers.

The flowers are of the open type (sensu Faegri & Pijl, 1979) and present white, white to pink, white with a red centre, or white to greenish-yellow tepals (Tab. 1). There is no apparent change in colour following anthesis or prior to senescence. In *B. integerrima* the bases of tepals in both staminate and pistillate flowers possess a red colouration (Fig. 1i, j). As with most *Begonia* species, pollen acts as the sole reward to visitors for all species studied. The number and size of the tepals of staminate flowers differ little from pistillate flowers, with the exception of size in *B. itatinensis* (Tab. 1). Aside from minor morphological differences in the tepals, staminate and pistillate flowers (Fig. 1) are quite similar for all species. The stigmas can be localized in strips or spread over large areas covered with papillae, occurring along the branches of the styles, which are yellow in colour (with the exception of the branches of the styles of *B. integerrima*, which are white to pale-yellow; are six in number and have a spiral form (corkscrew; Fig. 4d). Stigmas remain receptive throughout the life of the flower. Stamens may be free (Fig. 3f, 4a) or united to form a column (Fig. 3d, arrow), and the number varies greatly among species (Tab. 1). Anthers are yellow and rimose (Fig. 4a), with the size of the axial aperture varying among species. Poricidal anthers were observed in only one of the thirteen species: *B. integerrima* (Fig. 4b). The pollen in all species studied is diminutive, dry, powdery, and whitish-yellow. Pollen viability is high in *B. cucullata* (82%) and *B.* aff. *fluminensis* (78%). We detected floral odour in nine of the 13 species (Tab. 1). Odours are lightly sweet and seemed identical for staminate and pistillate flowers of a given species. We did, however, detect differences between species. Odour is strongest between 0700 to 1100 hours, corresponding to the peak hours of visitation.
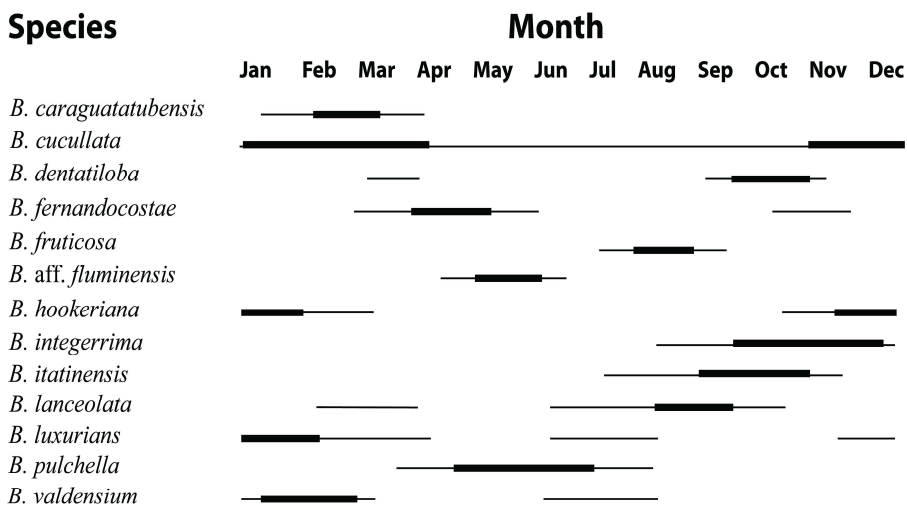

FIGURE 2. Flowering phenology of 13 species of *Begonia* in the Serra do Mar State Park, São Paulo. Thick lines represent flowering peaks and thin lines represent the entire period of observed flowering.

Section Species	Tepals n/length (mm)		Tepal Colour	Stamen Number	Odour
	Staminate	Pistillate			
Begonia					
B. cucullata	4/6	5/5	white to pink	>15	present
Pritzelia					
B. caraguatatubensis	4 /3--4	5/3	white	<15	present
B. dentatiloba	4/5--6	5/4--6	white to pink	>10	present
B. fernandocostae	4/11--15	5/9--12	white to pink	>20	present
B. aff. fluminensis	4/8--10	5/10--15	white	>20	present
B. hookeriana	4/2--4	5/2--3	white	>15	absent
B. itatinensis	4/4--6	5/10--12	white	>10	absent
B. pulchella	4/11	5/8	white	>10	absent
B. valdensium	4/10--15	5/5--8	white	>20	absent
Scheidweileria					
B. luxurians	4/3--4	5/4--5	white	>25	absent
Solananthera					
B. integerrima	4/15--16	5/13--14	white, red	>15	absent
Trachelocarpus					
B. lanceolata	2/4--9	3/5--10	white	>20	absent
Trendelenburgia					
B. fruticosa	4/4	5/1	white to greenish-yellow	>10	absent

TABLE 1. Floral characteristics of the species of *Begonia* studied in the Serra do Mar State Park, São Paulo (n = tepal number). Tepal number and length taken from Silva and Mamede (2001).
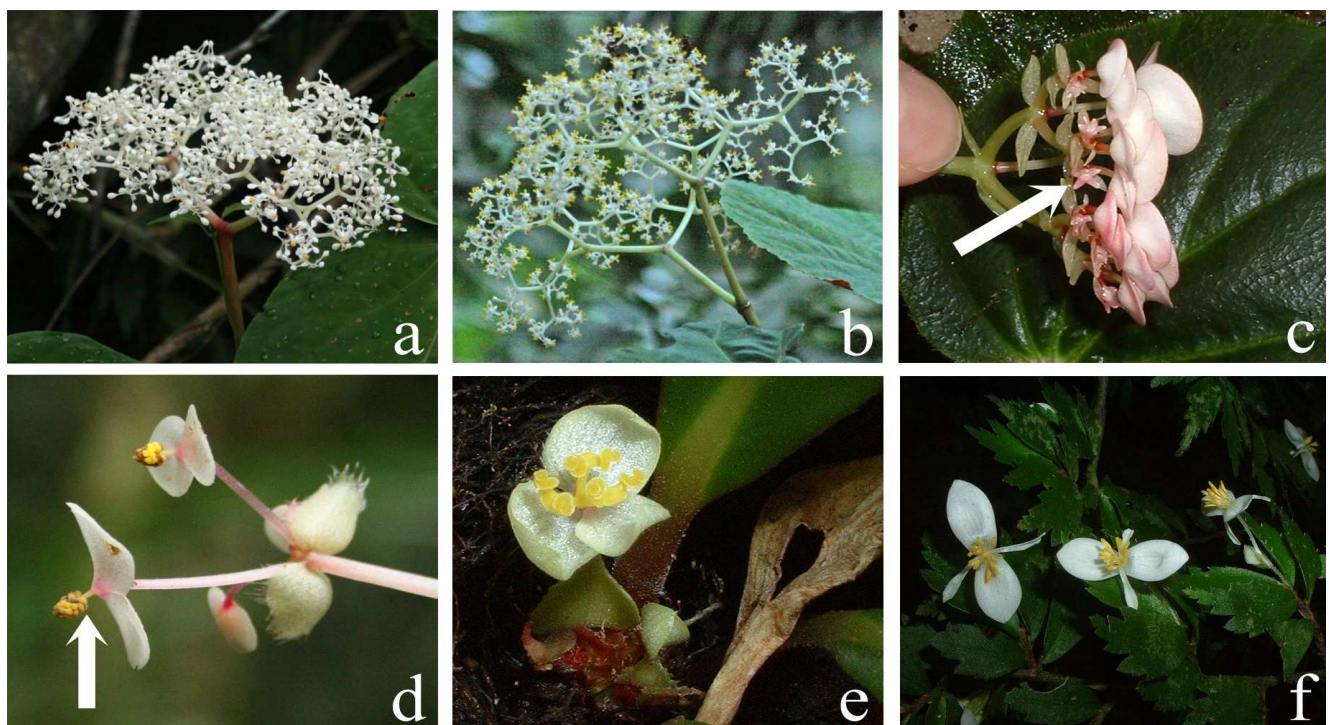

FIGURE 3. Inflorescences and flowers: Inflorescence in staminate phase of *Begonia caraguatatubensis* (a); Inflorescence in pistillate phase of *B. caraguatatubensis* (b); Inflorescence of *B. fernandocostae* with staminate flowers and pistillate flower buds (arrow) (c); Inflorescence of staminate flowers of *B. lanceolata* (note fused stamens forming a column at arrow) (d); Pistillate flower of *B. lanceolata* (e); Staminate flowers of *B. itatinensis* (f).
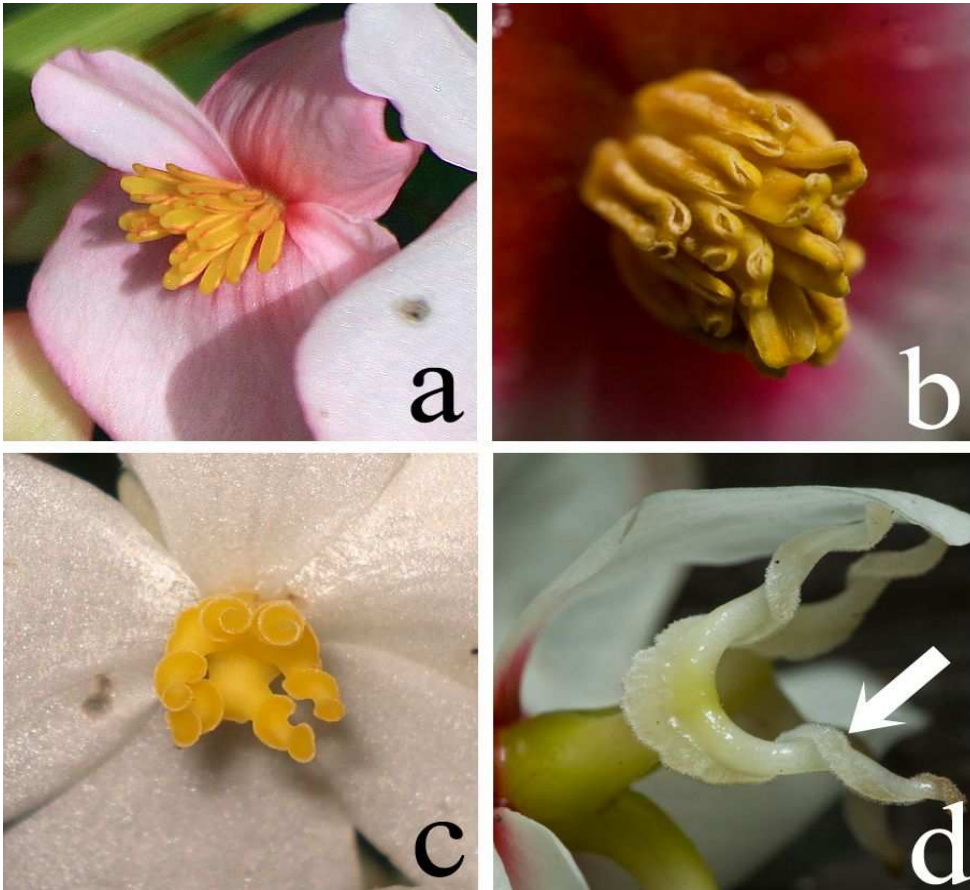
FIGURE 4. Rimose stamens of *Begonia cucullata* flower (a) and poricidal stamens of *B. integerrima* (b). Branches of the style and stigmatic surfaces of *B.* aff. *fluminensis* (c) and of *B. integerrima* (tepal removed) (d). Note the spiral form of the branches and the papillae on the stigmatic surfaces (arrow).

Anthesis is diurnal, occurring in the first hours of daylight, between 0600 and 0700 hours. The duration of pistillate flowers depends in part on pollination success. A single pistillate flower of *B. lanceolata*, maintained in a greenhouse and not visited by any insect, remained functional for 15 days. On this same individual, a different pistillate flower that was pollinated manually with cross-pollen on the first day of anthesis showed the senescence of tepals on the second day, followed by development of the ovary. Similar patterns were observed in the field for flowers of other species that were bagged. Flowers excluded from visitors of *B. fernandocostae, B.* aff. *fluminensis, B. hookeriana,* and *B. integerrima* had an estimated duration of 15 days. Staminate flowers in natural conditions showed shorter durations than those of pistillate flowers, estimated between 6 - 9 days.

Breeding Systems

In *Begonia caraguatatubensis, B. cucullata, B. dentatiloba, B. fernandocostae, B.* aff. *fluminensis, B. hookeriana, B. integerrima, B. itatinensis, B. lanceolata, B. pulchella,* and *B. valdensium,* pollen tubes were observed in naturally pollinated pistillate flowers (Fig. 5), both in the stigmas and through the styles reaching the ovules (Fig. 5a, c, e, arrows). The tubes are very dense and exhibit callose plugs, allowing them to be easily differentiated from lignified vessel elements, which are also visible in the stigmas and styles under fluorescent light.

Tests showed no evidence of apomixis in any of the species of *Begonia* studied (Tab. 2), as no ovaries enlarged or thickened into fruits and no ovules developed into seeds. Moreover, these ovaries senesced prematurely when compared with ovaries of flowers under natural conditions. Self-pollinated flowers (geitonogamy) of *B. integerrima* and *B. itatinensis,* which regularly present pistillate flowers synchronously with staminate flowers, failed to develop into fruits (Tab. 2). In addition, there was no development of pollen tubes in self-pollinated flowers of *B. integerrima*. The pistillate flowers of *B.* aff. *fluminensis* and *B. fernandocostae* that received hand cross-pollination developed fruits (Tab. 2), whereas the rest of the bagged flowers of that inflorescence, which received no treatments, senesced prematurely and the ovaries failed to increase in size. Fruit-set under natural conditions was high for *B. caraguatatubensis, B. fernandocostae,* and *B.* aff. *fluminensis*. The other species studied also had high fruit-set (80 - 90%). No fruits developed nor were any pollen or pollen tubes present in bagged flowers tested for wind pollination. Because the mean of greatest width of the pollen grains of *B. cucullata* is 14.4 ± 1.37 μm, and the weave of the fabric used to bag flowers is approximately 206 μm, wind movement of pollen should have been possible.
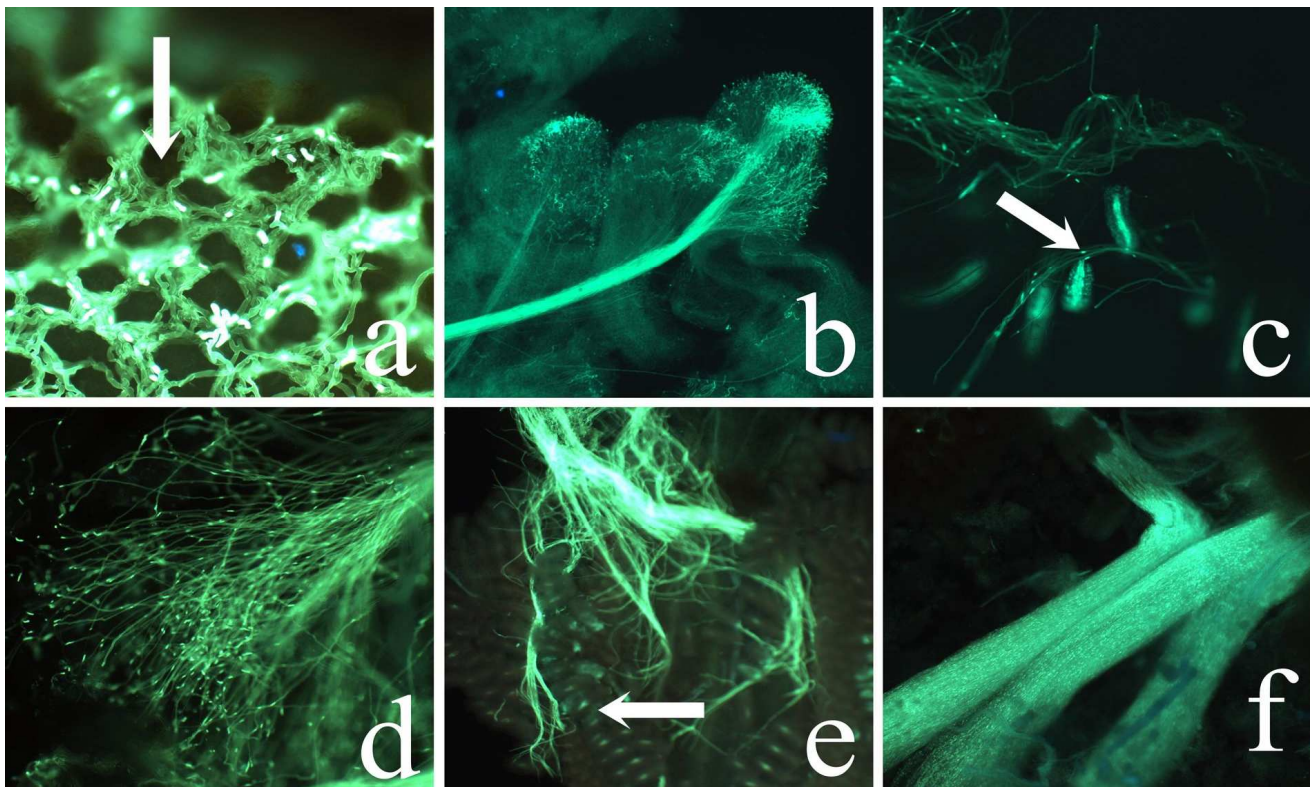
FIGURE 5. Details of pollen tubes around ovules of *Begonia caraguatatubensis* (arrow) (a); Branches of the style of *B. dentatiloba* (b); Ovules of *B. integerrima* with pollen tubes exhibiting callose plugs (arrow) (c); Pollen tubes in the style of *B. pulchella* (d); Pollen tubes among the ovules (arrow) of *B. pulchella* (e); Pollen tubes in the styles of *B. valdensium* (f).

Species	Apomixis	Self-pollination (geitonogamy)	Cross-pollination	Natural conditions
B.caraguatatubensis	0 (0/142)			88 (112/128)
B. cucullata	0 (0/14)			
B. dentatiloba	0 (0/14)			
B. fernandocostae	0 (0/39)		100 (1/1)	84 (54/64)
B. aff. *fluminensis*	0 (0/30)		100 (1/1)	77 (20/26)
B. hookeriana	0 (0/43)			
B. integerrima	0 (0/16)	0 (0/9)		
B. itatinensis	0 (0/7)	0 (0/4)		
B. lanceolata	0 (0/6)			
B. pulchella	0 (0/53)			

TABLE 2. Percentage of fruits resulting from experimental pollination of the species of *Begonia* in the Serra do Mar State Park, São Paulo. The number of fruits / flowers is in parentheses.

Visitors: Hymenoptera

Ten species of bees were observed, collected, and identified visiting flowers in various species of *Begonia*. These were all Halictidae (*Augochlorodes* sp., *Augochloropsis* sp. 1 and sp. 2, *Neocorynura* sp. 1 and sp. 2) or Apidae (*Paratetrapedia* sp., *Trigona spinipes*, *Euglossa* sp., *Melipona bicolor*, *Melipona quadrifasciata*), and small to medium in size (0.3 to 1 cm). In addition, bees of large size, belonging to the genera *Bombus*, *Xylocopa*, *Centris* and *Epicharis* were observed visiting flowers of *B. fernandocostae* and *B. integerrima*, but these visits were rare and it was not possible to make collections.

The most common bee visitor to flowers across all species was *Trigona spinipes*, which was recorded on six species (Tab. 3). On staminate flowers, this species was observed using legs and mandibles to remove pollen from stamens. On pistillate flowers *Trigona spinipes* made short visits, consisting of a brief landing and occasionally longer visits in which a similar behaviour to staminate flower visits was observed: gathering movements elicited by the similar floral display which resulted in pollen deposition and/or removal of pollen deposited from earlier visits. Visit durations to staminate flowers varied from 1 to 107 seconds, whereas visits to pistillate flowers varied from 1 to 36 seconds. *Trigona spinipes* made visits in irregular intervals, with a flower-to-flower movement slower than the

other bee species observed, visiting only 2 to 5 flowers per trip. In total during one five-hour period, 53 staminate flowers and six pistillate flowers of *B.* aff. *fluminensis* (Fig. 7a) were visited. For *T. spinipes* there was no significant difference in duration of visits to staminate versus pistillate flowers (U = 135, Z = 0.6, *P* = 0.55).

Paratetrapedia sp., from the group Tapinotaspidini, was the second most common visitor, being recorded on staminate and pistillate flowers of four species of *Begonia*. This bee was most frequent on *B. caraguatatubensis* and *B. dentatiloba* and the second most frequent visitor to flowers of *B. fernandocostae* and *B.* aff. *fluminensis*, where vibration was performed to facilitate collection of pollen. In general, this species made regular visits during the period of observation, having made for example, visits to 150 staminate flowers and 40 pistillate flowers of *B. caraguatatubensis* during a five-hour period (Fig. 7b). The rate of deceit of *Paratetrapedia* sp. in flowers of *B. caraguatatubensis* was 16.9% (Tab. 3). In this case, the staminate flowers were visited 4.35 times more often than pistillate flowers, even when there were fewer staminate than pistillate flowers (448:647). One month later, when there were almost four times as many pistillate flowers as staminate flowers (1:3.95), the rate of deceit diminished to 4.17%. Similarly, the total number of visits also diminished over this period (Fig. 7c). Statistical analysis revealed a significant difference between visit duration to staminate versus pistillate flowers, when the ratio of staminate to pistillate flowers was 1:1.44 (U = 1216, Z = 5.62, *P* < 0.001; Fig. 7c). Moreover, considering all visits during the entire flowering period, there is a significant difference in visit duration of *Paratetrapedia* sp. to staminate versus pistillate flowers (U = 1216, Z = 6.11, *P* < 0.001).

Bees of the genus *Melipona* were only observed on flowers of *B. integerrima*, and represent the most abundant and regular visitor to this species (Tab. 3; Fig. 6a, b), principally on individuals in the canopy. These bees collected pollen by vibration. The two species of *Melipona* made visits to 180 staminate flowers and 11 pistillate flowers during four hours of observation. *Melipona bicolor* was more discriminating than *M. quadrifasciata*, with a percentage of deceit of 2.07%, whereas *M. quadrifasciata* had a percentage of deceit of 16.7% (Tab. 3). Duration of visits to staminate flowers was significantly longer than on pistillate flowers (U = 286, Z = 3.97, *P* < 0.001; Fig. 7d).

Although *Euglossa* sp. was not a common visitor to these species of *Begonia*, it was the third most frequent visitor to *B. integerrima* and the fourth most frequent to *B.* aff. *fluminensis*. Pollen was collected by vibration, and this species visited only the largest-flowered species of *Begonia*. This pattern also was observed among bees of larger size, such as *Bombus*, *Xylocopa*, *Centris*, and *Epicharis*, which visited only the larger-flowered *B. fernandocostae* and *B. integerrima*. The other species of bees observed in this study showed low visitation frequencies, but all made visits to both staminate and pistillate flowers.

Although we were not able to control for all factors that may play a role in rates of deceit, our data show that rate of deceit tends to decrease with increasing frequency of visits made by a species of pollinator. Moreover, the rate at which a species of pollinator is deceived seems to be consistent across species of *Begonia* visited (Tab. 3). The number of prior visits by an individual pollinator may also play a role in its ability to discriminate between pistillate and staminate flowers, thereby also affecting frequency of visits to unrewarding pistillate flowers.

Pollination by vibration

In the species of *Begonia* studied, staminate flowers open before pistillate flowers, and pollen serves as the only reward. Bees therefore become habituated to visiting staminate flowers, in which vibration is used to collect pollen (except for *Trigona spinipes*). At pistillate flower anthesis, the bees make "mistake" visits, being deceived by the similarity between the branches of the style/stigma of the pistillate flowers and the stamens of the staminate flowers. Deceit is evidenced by the attempt to collect pollen during visits to pistillate flowers: vibration and manipulation of the style by the legs and mandible of the visitor (Fig. 6). When the bees vibrate on the pistillate flowers, grains of pollen on the body are released in a visible cloud and adhere to the stigma.

| Pollinator species | *Begonia* species | | | | | | | |
	car	*cuc*	*den*	*fer*	*flu*	*lux*	*int*	*val*
Augochlorodes sp.	33.3% (21)							
Augochloropsis sp. 1		X					X	
Augochloropsis sp. 2							42.9% (7)	
Euglossa sp.					40.0% (5)		62.5% (8)	
Melipona bicolor							2.07% (145)	
Melipona quadrifasciata							16.7% (48)	
Neocorynura sp. 1	23.9% (159)							
Neocorynura sp. 2					4.76% (21)			
Paratetrapedia sp.	16.9% (236)		12.5% (24)	X	16.7% (12)			
Trigona spinipes		X		X	10.2% (59)	X		X

TABLE 3. Percentage of visits to pistillate flowers (rate of deceit) for pollinators of eight species of *Begonia* in the Serra do Mar State Park, São Paulo, Brazil. The total number of visits observed is in parentheses. "X" indicates observed visits by that pollinator to that species of *Begonia*, but no quantitative data were collected. Species of *Begonia* are designated by the first three letters of the specific epithet.

Other visitors

Besides bees, species of Diptera (Syrphidae), Coleoptera, and Lepidoptera were observed visiting both staminate and pistillate flowers of Begonia, but with lower frequency of visits (Diptera and Lepidoptera), shorter visits (Lepidoptera), and a general failure to pick up and deposit pollen (personal observations). On staminate flowers, Syrphids removed pollen directly from the anthers and also collected pollen that had fallen onto the tepals. A single visit from a Syrphid fly had a duration of 16 minutes and five seconds to a staminate flower of *B. fernandocostae*. On pistillate flowers, Syrphid flies behaved similarly, possibly removing pollen deposited by earlier visits. Species of Coleoptera were very common on *Begonia* flowers, especially on staminate flowers, where they consumed pollen. The infrequent visits of Lepidopterans were always short (<1 sec) and each of the five individuals observed made only one visit.

DISCUSSION

Phenology and Floral Biology

The 13 species of *Begonia* show a range of phenological patterns, from annual, to subannual, to continuous, as defined by Newstrom et al. (1994). Differences in reproductive phenology are evident even between closely related species, such as *B. fernandocostae* and *B.* aff. *fluminensis*, both of which belong to section Pritzelia.

Large differences in flower size also occur among taxonomically closely related species: *Begonia caraguatatubensis* and *B. hookeriana*, which produce many small flowers, versus *B. fernandocostae*, *B.* aff. *fluminensis*, and *B. valdensium*, which produce few, large flowers, all belong to section Pritzelia (Doorenbos & de Wilde, 1998). These differences are probably the result of selective forces imposed by pollinators. On the other hand, differences in size and number of flowers could be phylogenetically fixed (Schemske & Ågren 1995). Schemske and Ågren (1995) speculated that a decrease in the number of flowers per inflorescence in exchange for larger individual flowers may be disadvantageous, because number of flowers per inflorescence may be critical in attracting pollinators. Nevertheless, both large-flowered (small inflorescence) and small-flowered (large inflorescence) species studied attracted similar numbers of pollinators and frequencies of visits, resulting in high reproductive success.

The morphology of all species with respect to number and size of tepals in staminate versus pistillate flowers helps to deceive pollinators due to the high similarity between both types of flowers. The one exception is *B. itatinensis*, the tepals of whose pistillate flowers are twice the length of the tepals of the staminate flowers. Bees visiting *Begonia* have been observed to prefer larger flowers (Schemske & Ågren 1995). The number of observed visits to pistillate flowers is always less than to staminate flowers. This is possibly related to the ability of bees to learn to recognize unrewarding flowers and avoid them. This ability exists not only in honeybees, but also in other social and solitary bees as well (Menzel 2001). Yet even with a lower number of visits, pistillate flowers of each species appear to receive sufficient visits to ensure high fruit-set.
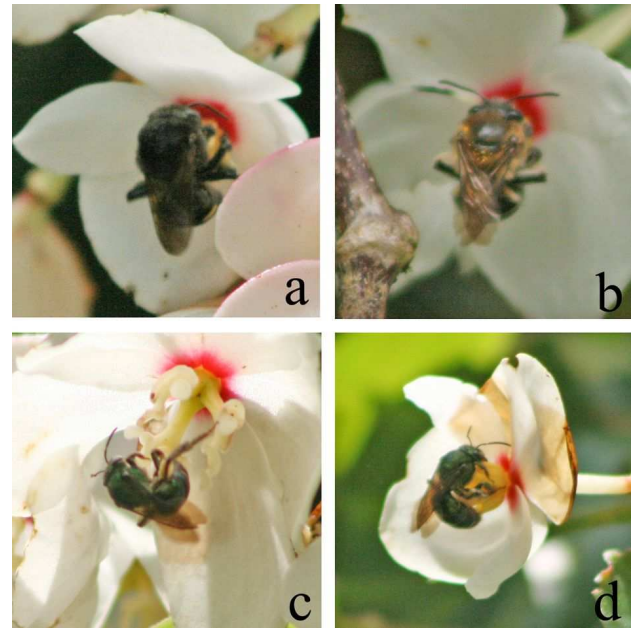

FIGURE 6. Pollination by vibration in *Begonia integerrima*. *Melipona quadrifasciata* in vibration posture on a staminate flower (a); *M. bicolor* adopting vibration posture on a staminate flower (b); Pistillate flower being visited by *Augochloropsis* sp. 2, in vibration posture (c); *Augochloropsis* sp. 2 in vibration posture on staminate flower (d).

Staminate flowers open and become available to pollinators before pistillate flowers in most of the species studied. This likely promotes cross-pollination (Burt-Utley 1985; Ågren & Schemske 1993; Jacques 2002). It may also promote visits to pistillate-phase inflorescences because visitors become habituated to visiting staminate flowers and when the pistillate flowers open, due to their similarity to staminate flowers, the visitors are easily deceived. It was hypothesized by Schemske and Ågren (1995) that species with staminate and pistillate flowers open at the same time would more easily deceive visitors than species with only pistillate flowers open. Our data indicate, however, that species of pollinator may play a larger role in determining visits to pistillate flowers.

Prolonged receptivity of stigmas and long lifespan of flowers likely allow the plant to weather low pollinator visitation, as in *B. gracilis* (Castillo et al. 2002). Additionally, the long duration and receptivity of pistillate flowers may facilitate pollination, since greater floral longevity would likely mean a greater chance of attracting and deceiving visitors if they are open and receptive for a long period (Schemske et al. 1995; Jacques 2002). Since pistillate flowers depend entirely on mistake visits by pollinators, floral odour should have an important role (Ågren & Schemske 1991; Schemske & Ågren 1995). The similarity of odour between staminate and pistillate flowers detected in this study would be expected to facilitate deceit. The spiral branches of the style increase the stigmatic area and therefore the probability of pollen deposition, similar to stigmas of wind pollinated species (Faegri & Pijl 1979). Since the studied *Begonia* species are not pollinated by wind the increase of the stigmatic area may reflect an adaptation regarding the unpredictability of visitors to unrewarding flowers. The stigmatic papillae also increase
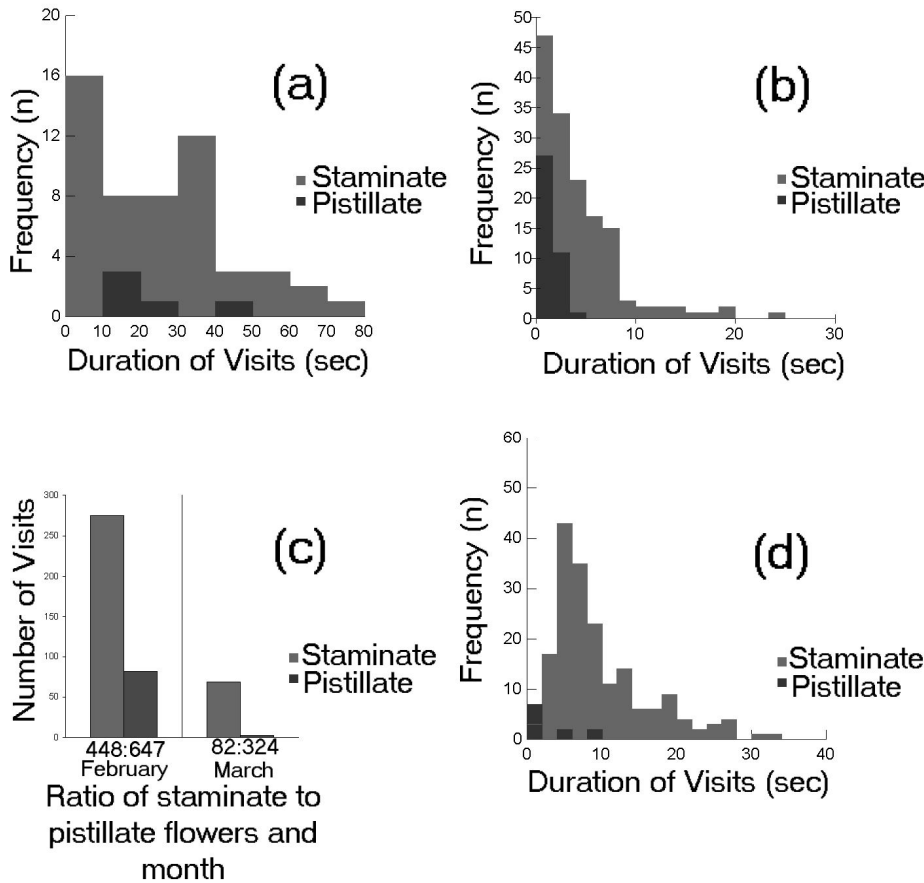
FIGURE 7. Frequency histogram of visit duration of *Trigona spinipes* to flowers of *Begonia* aff. *fluminensis* (a). Frequency histogram of visit duration of *Paratetrapedia* sp. to flowers of *B. caraguatatubensis* (b). Number of visits by *Paratetrapedia* sp. to staminate and pistillate flowers of *B. caraguatatubensis* during two periods of observation (c). Frequency histogram of visit duration of species of *Melipona* on flowers of *B. integerrima* (d).

the receptive area and facilitate adherence of pollen grains through direct contact with the pollinators or during vibration when pollen grains are liberated from the pollinator's body.

The position of rimose anthers, grouped in large numbers, facilitate the collection of pollen by vibration. The anthers of *B. integerrima* and other species of section Solananthera (Buchmann 1983; Silva & Mamede 2001; Jacques 2002) are poricidal. We suggest that this type of anther may help to exclude pollen-robbing insects, which commonly remove large numbers of grains from open, longitudinally dehiscing anthers. Poricidal anthers also ensure that pollen is released more slowly over the life of the flower. Finally, pollen is effectively dispersed from pores only when insects buzz at a special frequency that causes anther contents to be released, often as a clump. High pollen viability is expected in all species of *Begonia*, although we were only able to confirm it for *Begonia cucullata* and *B.* aff. *fluminensis*. Even though production of large numbers of viable pollen grains represents a large energetic cost, it may be especially important in *Begonia* and similar plants in which visits to pistillate flowers depend on deceit.

Breeding Systems

The large numbers of pollen tubes observed in flowers collected from natural populations suggest that pistillate flowers receive many visits and/or that the visitors are efficient

pollen vectors. Because visits to pistillate flowers generally are less frequent than to staminate flowers, it is likely that in one visit to a pistillate flower, a large load of pollen will be transferred. Visits to pistillate flowers where vibration is performed by the visitor probably result in more pollen being transferred than in visits where little contact is made with stigmas, especially taking into account that *Begonia* pollen is small and powdery. A single brief visit may be sufficient to guarantee deposition of large pollen loads. The abundance of pollen tubes in stigmas, styles, and ovaries indicate that pollinators are effective, which is also confirmed by high fruit-set observed in natural populations. Ågren and Schemske (1991) also observed high fruit-set in natural populations of *B. involucrata* in Costa Rica.

The absence of apomixis and geitonogamy (in species with inflorescences with flowers of both sexes open synchronously) suggests an absolute dependence on floral visitors for reproduction by these species of *Begonia*. Earlier researchers have considered the entire genus to be self-compatible (East 1940; Burt-Utley 1985). The only experimental studies of breeding systems in *Begonia* showed five species from section Doratometra in Central America to be self-compatible (Ågren and Schemske 1993). Moreover, Ågren and Schemske (1993) found extremely low (<5%) rates of outcrossing in natural populations of *B. hirsuta* and *B. semiovata*. In contrast, our results indicate that at least two species from Brazil are self-

incompatible. More crossing studies of species of *Begonia* from different sections of the genus are needed.

Hymenoptera

The bees that we observed visiting the eight species of *Begonia* studied are of suitable body size and exhibit behaviour fitting to effect pollination of pistillate flowers. Moreover, their behaviour, frequency, and duration of visits reveal these bees as the principal pollinators of all eight species of *Begonia* investigated.

Trigona spinipes, the most abundant visitor, is known for its opportunistic behaviour, frequently acting as a robber of floral rewards in many species of plants (Roubik 1989; Sazima & Sazima 1989). In our study these bees occasionally made visits of long duration to pistillate flowers, possibly enhancing pollen deposition and/or removal of pollen that had already been deposited on the stigmas. For this species of visitor only, duration of visits to pistillate flowers did not differ significantly from the duration of visits to staminate flowers. The slow movement of *T. spinipes* between flowers probably is compensated by its high frequency of visits.

Paratetrapedia sp. is one of the most important pollinators of the species of *Begonia* studied, due to its frequency of visits and the diversity of species of *Begonia* visited. Due to the varied floral morphology and reproductive phenology of the species of *Begonia* visited by this bee, *Paratetrapedia* sp. probably visits many of the other 16 species of *Begonia* in the study area.

Species of *Melipona* are probably important pollen vectors for species of *Begonia* that occur high in the canopy, like *B. integerrima*, because these bees frequently forage at high levels of the forest (Nieh 1995; Ramalho 2004). Taking into account that the percentage of mistake visits was greater in *Melipona quadrifasciata* than *Melipona bicolor*, the former is probably a more efficient pollinator of flowers of *B. integerrima*, despite the fact that it makes fewer visits.

Euglossa spp. are probably important pollinators of *B.* aff. *fluminensis* and *B. integerrima*, promoting cross-pollination as these bees forage over long distances (Janzen 1971). This fact may be very important for *B.* aff. *fluminensis*, which is endemic to the Ubatuba municipality and occurs in small, isolated populations. It is likely that the observed species of *Euglossa* visits other species of *Begonia* with flowers similar to *B.* aff. *fluminensis* and *B. integerrima*, such as *B. fernandocostae*, which is sympatric with *B.* aff. *fluminensis*, has a similar reproductive phenology and floral morphology, and nearly identical floral odour. Other examples would be *B. solananthera* and *B. radicans*, which are also vines with very similar floral morphology to *B. integerrima*. These species occur in the area of study but were not studied. Visits by *Euglossa* sp. were characterized by a high percentage of mistake visits to pistillate flowers.

Pollination by vibration

Collection of pollen by vibration is characteristic of all the species of *Begonia* in our study. Pistillate flowers also benefit from vibration, as this behaviour favors deposition of more pollen on stigmas than those deposited by contact with the body of a visitor alone. It is likely that, during vibration, many pollen grains adhered to the abdomen of the bee fall on to the stylar branches. This would explain the large pollen loads on stigmas and the high levels of fruit-set under natural conditions that we observed. This study confirms Roubik's (1989) inclusion of *Begonia* on a list of genera with species characterized by poricidal anthers (*B. integerrima*), as also reported by Silva and Mamede (2001). *Trigona spinipes*, the only bee incapable of vibration, was notably absent from *B. integerrima* flowers. We suggest that pollination by vibration predominates in those species of *Begonia* pollinated by bees that present staminate flowers with connivent rimose or poricidal anthers. Poricidal anthers do not appear to be widespread in the genus, as this was observed in only one of the 13 species studied.

Other visitors

Non-hymenopteran visitors are not considered principal pollinators of *Begonia*. The fact that these insects visit both staminate and pistillate flowers, however, suggests that they may occasionally effect pollination. Butterfly visits probably were made by immatures that had not yet learned that *Begonia* flowers lack nectar.

Diversity of pollinators

The diversity of pollinators observed and recorded in this study differs from other studies, which reported low diversity of visitors to flowers of *Begonia* (Ågren & Schemske 1991; Schemske & Ågren 1995; Corff et al. 1998). Ågren and Schemske (1991) reported that a single species of *Trigona* made 98% of all observed visits to *B. involucrata*. Similarly, Schemske et al. (1995) reported that one species of *Bombus* made 97% of all visits to *B. oaxacana*. Corff et al. (1998) observed that *Trigona fulviventris* made 95% of visits to *B. tonduzii*. The high diversity of visitors to the species of *Begonia* studied in Brazil is similar to that recorded on the flowers of *B. urophylla*, a member of section Gireoudia (Corff et al. 1998). That species was visited by seven species of bees from four genera (*Augochloropsis, Melipona, Neocorynura, Trigona*), all represented by visitors to the species of *Begonia* in this study. The high diversity of bee visitors to the eight species of *Begonia* studied appears to be related to their presentation of open flowers with readily accessible pollen. The diversity of visitors, including other functional types, such as Diptera and Coleoptera, may indicate a tendency to generalization of floral type in these species of *Begonia*.

Future directions

This study confirms for a number of previously unexamined species the role of intersexual mimicry in the deceit pollination system of *Begonia*. It also shows that there is wide variation in ratios of staminate to pistillate flowers and in the timing of flowering. It remains to be shown how phenology and flower ratios influence pollinator behaviour and the rate of deceit. In any case, the rate does appear to differ depending on the species of pollinator, yet overall levels of pollination appear to be adequate to maintain high levels of fruit-set in natural populations. More detailed studies of individual species of *Begonia* may reveal greater differences in the behaviour of

individual pollinators, including the possibility of learning on the part of individual pollinators.

This study also reports that two species of *Begonia* from Brazil are genetically self-incompatible. Previous work has found Central American species of *Begonia* section Doratometra to be self-compatible, with very high levels of selfing in natural populations. Apparently, breeding systems in *Begonia* are more diverse than previously thought, and it will prove interesting to map these transitions on a phylogenetic tree of the genus. Moreover, examination of other floral characteristics in a phylogenetic context should prove informative regarding the evolution of *Begonia* in relation to its pollinators.

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