

DIVERSITY OF FLOWER VISITORS AND THEIR ROLE FOR POLLINATION IN THE ORNITHOPHILOUS BROMELIAD *VRIESEA FRIBURGENSIS* IN TWO DIFFERENT HABITATS IN SOUTHERN BRAZIL

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Abstract. In order to analyze species richness of flower visitors to the bromeliad *Vriesea friburgensis*, and to relate the visitor spectrum to resource availability and differences in habitat, we studied its floral biology in two habitat types: dune vegetation and secondary Atlantic rain forest on Santa Catarina Island, southern Brazil. Flowering extends from October to February, the anthesis is diurnal. We found the reproductive system to be partially autogamous without the possibility of intra-floral selfing. Therefore the bromeliad is pollinator-dependent, but the flowers do not need to be cross-pollinated. Mean nectar sugar concentration was 20.7% with a high sucrose proportion. Flowers secreted 73.9 µl nectar per day. Although the flowers show ornithophilous features like tubular and scentless flowers and higher energetic nectar in the morning hours, besides two hummingbird species we recorded 28 species of insects and spiders also associated with the flowers of *V. friburgensis*. Species richness of flower visitors was higher in restinga than in secondary forest. In both habitat types hummingbirds and bees were the most frequent visitor groups, but whereas hummingbirds were the most frequent animals visiting flowers in secondary forest, followed by bees, the opposite was the case in the restinga habitats. Because *V. friburgensis* is partially autogamous, small bees might also be pollinators, transferring self-pollen. Thus, there is redundancy in the pollination service provided by birds and bees, leading to a high probability of successful reproduction in this bromeliad species. *Accepted 31 January 2011.*

Keywords: Bees, Bromeliaceae, flowering biology, hummingbird, nectar analysis, ornithophily, Santa Catarina Island, southern Brazil, visitation frequency.

INTRODUCTION

The Neotropical plant family Bromeliaceae comprises about 2800 epiphytic, lithophytic, and terrestrial forms, many with large showy flowers (Benzing 2000). Flower morphology, floral rewards, and flowering phenology constitute so-called floral syndromes, which have an influence on the flower visitor community and have been regarded as signals for specific flower visitor groups that can act as pollinators (Fenster *et al.* 2004). In bromeliads, the ornithophilous syndrome is commonest (Benzing 2000, Kessler & Krömer 2000) and hummingbirds appear to be effective pollinators (Benzing 2000). On the other hand, there are several reports of insects, e.g. bees and butterflies, visiting bromeliad flowers (Ber-

nardello *et al.* 1991, Wendt *et al.* 2001, 2002; Canela & Sazima 2003, 2005; Schmid *et al.* 2011b). In particular, many short-corolla bromeliads with otherwise typical ornithophilous syndrome are frequently visited by a high diversity of bees (Schmid *et al.* 2011a).

Some floral visitors, like hummingbirds, are specialized nectar feeders and depend on it as their most important energy source (Krömer *et al.* 2008). Nectar quality and quantity are important features when it comes to floral choice. There are several studies providing nectar volumes and concentrations for Bromeliaceae (Bernardello *et al.* 1991, Buzato *et al.* 2000, Canela & Sazima 2003, Krömer *et al.* 2008). Bromeliad nectar contains only the three sugars sucrose, glucose, and fructose, and the proportion of sucrose to glucose and fructose is related to pollinator types. Hummingbirds prefer dilute and

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sucrose-rich nectars (Krömer *et al.* 2008). Therefore, the attractiveness of bromeliad flowers to pollinators is strongly influenced by nectar composition and corresponding volume, both features not yet determined for *Vriesea friburgensis*.

Vriesea friburgensis var. *paludosa* (Bromeliaceae) is endemic in Brazil and common in the coastal areas of the southern states Santa Catarina, Paraná, and Rio Grande do Sul (Reitz 1983). Plants reproduce through clonal growth and via seeds, and each rosette produces only one inflorescence. Floral traits like tubular shape and the combination of red and yellow colors suggest the flowers to be adapted to hummingbird visitation (Faegri & van der Pijl 1971, Sick 1993), and two hummingbird species, *Thalurania glaucopis* and *Amazilia fimbriata*, have been previously reported as visitors to *V. friburgensis* flowers in the Atlantic forest in Paraná (Piacentini & Varassin 2007, Cestari 2009). However, in *Aechmea nudicaulis*, a bromeliad species exhibiting an apparently ornithophilous syndrome with the same combination of floral traits, bees can also be regarded as possible pollen vectors (Schmid *et al.* 2011b). The much longer corolla in *V. friburgensis* suggests a more pronounced ornithophily than in *A. nudicaulis*, so we hypothesized that (i) the visitor spectrum of *V. friburgensis* is more restricted, especially in bee species, due to flower morphology, and (ii) that bees do not play a role in pollination.

Studying the species richness of bromeliad flower visitors and the diversity and nature of their animal-plant interactions, this study focused on recording the species spectrum and frequency of floral visitors of *V. friburgensis*. To understand what attracts visitors to the flowers, we (1) analyzed floral phenology and reproductive system, as well as the quality and timing of floral rewards. We further hypothesized that habitat has an influence on species richness and visitation frequency of floral visitors (Tews *et al.* 2004, Schmid *et al.* 2011a), so we (2) compared the species spectrum of flower visitors to *V. friburgensis* between two habitat types, secondary forest and restinga (sand dune habitat).

MATERIAL & METHODS

Study site. The study was conducted at Florianópolis on Santa Catarina Island, southern Brazil, during four flowering seasons of *V. friburgensis*, from December to February 2005/2006, 2006/2007, 2007/2008, and 2008/2009. Fieldwork was carried out at three sites, differing in habitat type: dune

vegetation at (1) Joaquina Beach (27°37'37"S, 48°26'59"W) and (2) Campeche Beach (27°40'38"S, 48°28'48"W) ('restinga'; Sampaio *et al.* 2002), and a hillside secondary forest area at (3) Santo Antônio de Lisboa (Zillikens *et al.* 2001; 27°30'26"S, 48°30'28"W, hereafter Sto. Antônio). The distance between the forest and the restinga sites is 14 km. Time specification is given in standard time instead of daylight saving time, because the switch to and from daylight saving time would interfere with our time scales.

Flowering period and analysis of breeding system. Emergence and development of inflorescences were observed weekly from 24 August 2007 to 13 March 2008 at all study sites. Per site, all inflorescences visible along defined trails were counted. Three phenology categories were defined: (i) "new", from first sight of new inflorescences still covered by bracts till bud stage; (ii) "open", with open flowers; and (iii) "withered", with only withered flowers and developing fruits. The ramification pattern as well as the arrangement and orientation of the flowers are shown in Grohme *et al.* (2007).

Total number of flowers per inflorescence was counted for 17 inflorescences (ten from Sto. Antônio, seven from Joaquina). The number of open flowers per day and inflorescence was recorded for seven inflorescences in Sto. Antônio throughout their whole flowering phase. Additionally, the same flowering rate was assessed (without accounting for the developmental state within the flowering phase) for 517 inflorescences in Joaquina on ten days while always walking along the same trail. Because inflorescences flower over a long period, several inflorescences were scored not only once but were always counted as independent inflorescences. The number of days with open flowers for an inflorescence was analyzed for seven plants located in the miconietum vegetation (a pre-forest succession stage; Queiroz 1994, Zillikens & Steiner 2004) in Sto. Antônio.

The breeding system was assessed with hand-pollination treatments on plants taken to the laboratory: autonomous self-pollination, manual self-pollination, and manual cross-pollination ($n = 8$ flowers each treatment) (Dafni 1992). Additionally, flowers in the field ($n = 13$ flowers of 12 plants) were marked as control for natural pollination. The "Index of self-incompatibility" (ISI) and "Index of automatic self-pollination" (IAS) were calculated according to Zapata & Arroyo (1978).

Analysis of nectar composition. Nectar samples were collected with 2- μ l end-to-end micropipettes from 05:00 h to 15:00 h at 2-hour intervals (12 flowers of four plants) and sugar composition and concentration were analyzed by HPLC (Piechowski 2007). The total volume was then determined by measuring the remaining nectar with 5- to 20- μ l micropipettes (Assistant, Germany) and adding this volume to the previously collected 2 μ l. Correlations of the concentrations of the three sugar types, as well as differences between concentrations, were tested with the statistical software package JMP 8.0.1 (SAS Institute Inc. 2009). The total nectar energetic value was calculated by multiplying total sugar weight (μ g) for the three sugars glucose, fructose, and sucrose with the energy-per-mass factors (0.0156 J μ g⁻¹, 0.0157 J μ g⁻¹, and 0.0165 J μ g⁻¹, respectively, Wieser 1986). The products were added together. For the nectar measurements at 05:00 h, the time period of its secretion may exceed or fall below two hours because we did not exactly know the onset of nectar secretion. Sugar concentration was not measured after 15:00 h because almost no nectar was present at that time.

Flower visitor spectrum, visitation frequency, and foraging behavior. In total, 80 inflorescences were observed *in situ* at Joaquina Beach and Sto. Antônio either directly or with binoculars (314 observation hours) to record taxa and frequency of flower visitors. As flowers open only for a single day, one inflorescence observed on different days was counted as two independent observation events because the flowers were different in position and number. We recorded floral visitors in the widest sense, so all animals touching a flower were counted as visitors. For every approaching visitor we recorded species, time of arrival and leaving, and the kind of reward collected. Voucher specimens were deposited in the collection of Josefina Steiner, LANUF-SC, Federal University of Santa Catarina, Brazil.

RESULTS

Flowering biology and breeding system of *V. friburgensis*. Inflorescences started to appear in October. The flowering period extended from November to February. Bud stage as well as flowering period and presence of infructescences were synchronous at the three sites (Fig. 1). The zygomorph flowers were tubular

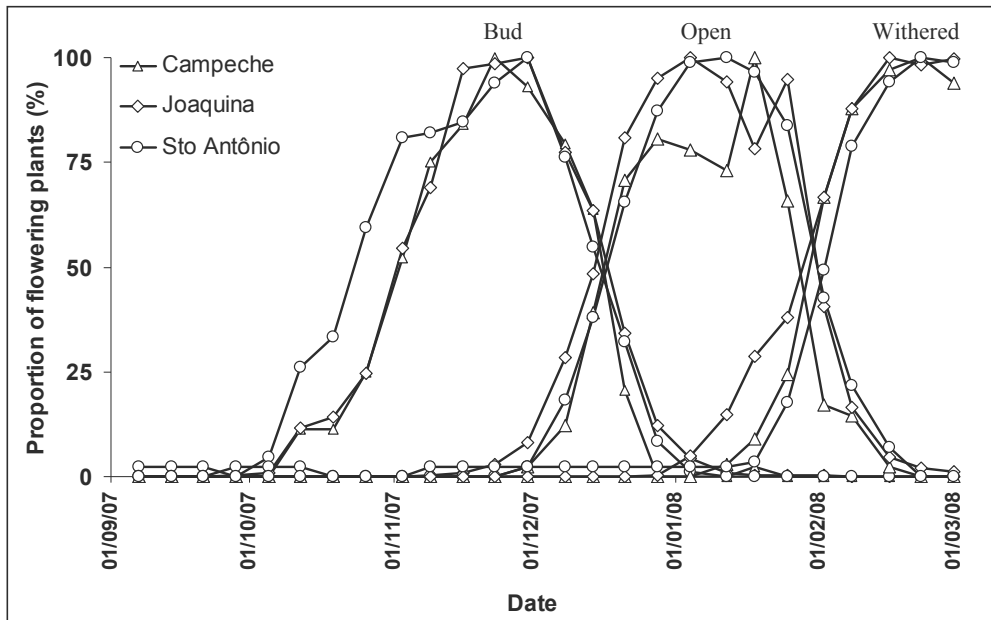


FIG. 1. Period of *Vriesea friburgensis* inflorescences with buds, open, and withered flowers at the three sites Campeche Beach (triangle), Joaquina Beach (diamond), and Sto. Antônio (circle) on Santa Catarina Island, Brazil. Since sample size differed between sites the number of inflorescences with at least one open flower is given in % of the maximum weekly number of flowering plants.

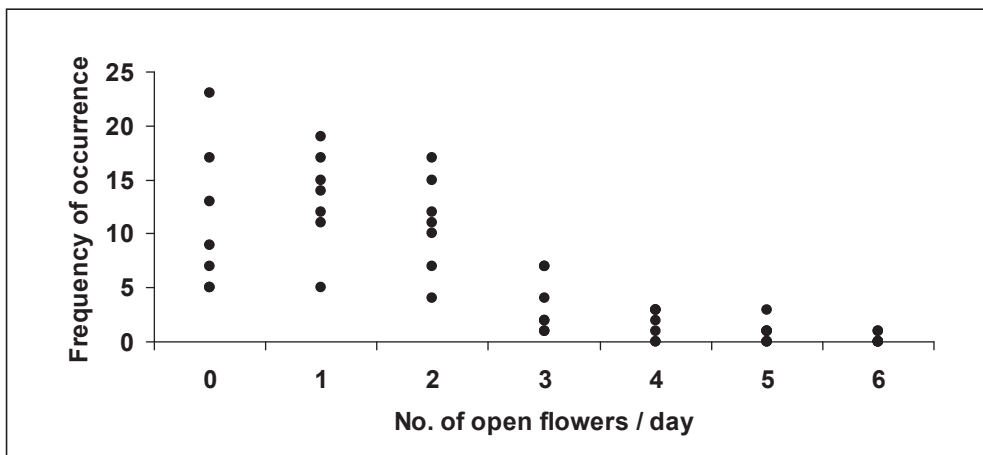


FIG. 2. Frequency distribution of the number of open flowers per inflorescence and day of *Vriesea friburgensis* ($n = 7$ plants) in Sto. Antônio, Santa Catarina Island, Southern Brazil. Each data point represents the number of days with the corresponding number of open flowers (0 – 6 flowers open per day) during the flowering period of one inflorescence.

and without scent. Anthers and stigma protruded from the corolla. Flowers began to open between 01:00 h and 02:00 h. The stigma came out first, followed by the anthers. Around 05:00 h the flower was fully open, but the anthers did not dehisce until 06:00 h with sunrise. Effective depth of flowers (the depth of the corolla which a visitor has to overcome to reach the nectar) was 29 mm (median; $Q1 = 28$, $Q3 = 32$; range 24.8 – 37.5 mm; $n = 33$ flowers, 10 plants). Flower entrance width measured 5 mm (median; $Q1 = 4.5$, $Q3 = 5$, range 3.9 – 6.1 mm; $n = 33$ flowers, 10 plants).

Due to the fact that the numbers of flowers per inflorescence in the two habitats Joaquina and Sto. Antônio were not normally distributed and also significantly different (Mann-Whitney U-test, JMP 8.01, SAS Institute Inc, 2009; $\chi^2 = 11.6667$, d.f. = 1, $p = 0.0006$), medians for Joaquina and Sto. Antônio

were computed separately. Number of flowers per inflorescence was 54 in Sto. Antônio (median; $Q1 = 46.5$, $Q3 = 72.5$; range 26 – 53) and 113 in Joaquina (median; $Q1 = 85.75$, $Q3 = 152.75$; range 80 – 172). Number of open flowers per day was 1 (median; $Q1 = 1$; $Q3 = 2$; range 0 – 7; $n = 517$ infl.). Between zero and two open flowers per day were most frequently observed (see Fig. 3). Median number of days with open flowers was 44 ± 10.3 ($Q1 = 36.5$; $Q3 = 49$; range 26 – 53; $n = 7$ infl.).

There was seed set in the two treatments manual self- and manual cross-pollination as well as in naturally pollinated flowers (Table 1). The ISI resulted in 0.61 ($n = 16$) and the IAS was 0 ($n = 16$). Induction of seed set, tested with manually cross-pollinated flowers, was possible during the whole phase of anthesis (from flower opening till closure, see Fig. 3).

TABLE 1. Seed numbers resulting from pollination experiments to analyze the breeding system of *Vriesea friburgensis* on Santa Catarina Island, southern Brazil.

Pollination treatment	N	Mean no. of seeds per fruit	Range	SD
manual cross-pollination	8	188.1	0-316	094.5
manual self-pollination	8	115.4	0-242	106.0
autonomous selfing	8	0	0	0
natural pollination	13	361.62	237-442	071.79

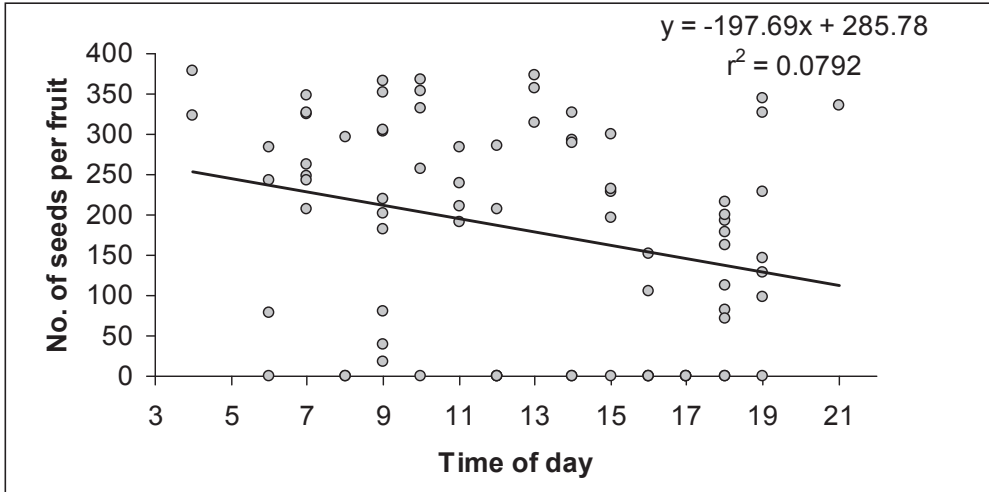


FIG. 3. Temporal pattern of the possibility of ovule fertilization in flowers of *Vriesea friburgensis*, Santa Catarina Island, southern Brazil.

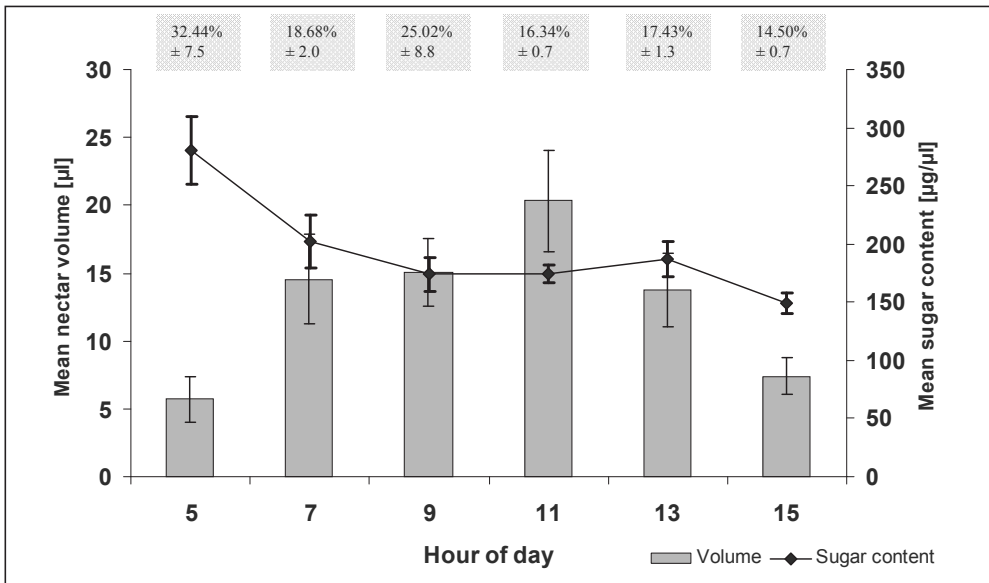


FIG. 4. Diel pattern of mean nectar volume (columns), nectar sugar content (diamonds), and sugar concentration (gray boxes) every two hours of anthesis in flower of *Vriesea friburgensis*, Santa Catarina Island, southern Brazil. Standard error bars or values are given for each mean.

Mean number of seeds per successfully developed fruit after natural pollination was 361.6 ± 71.8 and the percentage of undeveloped fruits under natural field conditions was $62.2\% \pm 16.7$, of which $26.1\% \pm 15.6$ were found to be parasitized by eurytomid wasps.

Nectar analyses. Nectar volume per flower and hour was 6.4 ± 5.3 µl (mean \pm SD). Nectar production was not evenly distributed over anthesis but peaked at 11:00 h (Fig. 4). Sugar concentration over the day was $19.5 \pm 6.8\%$ (w/w, mean \pm SD); highest concen-

SUPPLEMENTARY TABLE 1. Spearman correlations between pairs of sugars contained in floral nectar of *V. friburgensis* on Santa Catarina Island, southern Brazil. Bonferroni correction yields a significance level of $\alpha = 0.05/18 = 0.0028$. Significant p values are designated by an asterisk (*). G: glucose, F: fructose, S: sucrose.

Hour of day	F – S		G – S		G – F	
	Spearman ρ	p	Spearman ρ	p	Spearman ρ	p
05:00	-0.2909	0.3855	-0.1727	0.6115	0.9455	<0.0001*
07:00	-0.1727	0.6115	-0.1636	0.6307	0.9636	<0.0001*
09:00	-0.3636	0.2453	-0.0559	0.8629	0.8531	<0.0004*
11:00	-0.2168	0.4986	-0.3007	0.3423	0.9091	<0.0001*
13:00	-0.1469	0.6488	-0.1329	0.6806	0.9021	<0.0001*
15:00	-0.0061	0.9867	-0.1394	0.7009	0.9515	<0.0001*

tration was measured at 05:00 h (Fig. 4). Sucrose secretion was higher than that of the hexoses and most of the time the nectar was sucrose-dominant. Overall sucrose/hexose ratio $[S/(F+G)]$ was 1.65 ± 0.62 (mean \pm SD). Mean sucrose proportion per hour was high in the first hour of secretion and decreased steadily during anthesis from 71.4% (05:00 h) to 43.1% (15:00 h), while those of fructose and glucose remained more or less unchanged. Total sugar secreted per flower and day was $14\,565.7\,\mu\text{g} = 14.5 \pm 0.9\,\text{mg}$ (mean \pm SD). Fructose values were significantly higher than those of glucose (Wilcoxon Signed-Rank Test Statistic 1173.000, $p < 0.0001$) and both hexoses were significantly correlated with each other (Spearman correlation) whereas sucrose concentration was not significantly correlated with concentration of both hexoses (Suppl. Table 1).

Energy value per flower was $218.3 \pm 104.3\,\text{J}$. Multiplication by the median number of flowers per

inflorescence (Sto. Antônio: 54; Joaquina: 113) resulted in an average caloric nectar value per inflorescence of 9.6 kJ for Sto. Antônio and 24.7 kJ for Joaquina.

Flower visitor species spectrum, frequency, and foraging behavior. We recorded a total of 30 species as visitors, in the widest sense, to flowers of *V. friburgensis* (Table 2). The restinga habitat had a higher species richness (21 species, $n = 1073$ visitors) than the secondary forest (14 species, $n = 304$ visitors). Secondary forest and restinga sites shared 6 species. One species, the hummingbird *Eupetomena macroura*, was only observed attending flowers in an urban area. In both habitats the most frequent visitors were hummingbirds and bees. Whereas hummingbirds were the commonest animals visiting flowers of *V. friburgensis* in secondary forest followed by bees, it was the opposite on flowers in the restinga habitats (Fig. 5).

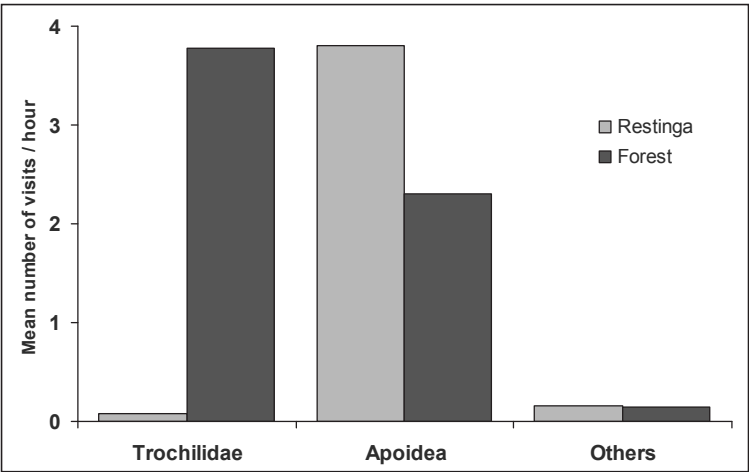


FIG. 5. Visitation frequency (mean number of visits per hour) of flower-visitor groups on *Vriesea friburgensis* in restinga and secondary forest habitat on Santa Catarina Island, southern Brazil.

TABLE 2. Species spectrum and frequency with resource collected by flower visitors to *Vriesea friburgensis* on Santa Catarina Island, southern Brazil. N = number of visits observed in field experiments are given in parentheses. Visitation aims: n = nectar, p = pollen, o = oviposition, h = herbivory, pr = predator. Because bees of the taxon Augochlorini could not be identified to species during flower visits, frequency and number of visits are given as sum and x in the table show the species occurrence in the habitats.

Taxon	Visitation frequency			Aims
	Total % (N)	Forest % (N)	Restinga % (N)	
Trochilidae	15.0 (207)	60.9 (185)	2.1 (22)	n
<i>Amazilia fimbriata</i>	10.3 (142)	46.7 (142)	-	n
<i>Thalurania glaucopis</i>	4.7 (65)	14.1 (43)	2.1 (22)	n
<i>Eupetomena macroura</i> *				n
Apoidea	81.6 (1121)	37.1 (113)	93.9 (1008)	p+n
Apidae	11.1 (151)	1.9 (6)	13.6 (145)	
<i>Apis mellifera</i>	3.3 (45)	-	4.2 (45)	p
<i>Ceratina (Crewella)</i> sp.1	0.4 (5)	1.6 (5)	-	p+n
<i>Plebeia droryana</i>	0.1 (1)	0.3 (1)	-	
<i>Trigona spinipes</i>	6.9 (95)	-	8.9 (95)	p+n
<i>Xylocopa brasiliatorum</i>	0.4 (5)	-	0.5 (5)	p+n
Halictidae	70.4 (969)	35.2 (107)	80.3 (862)	p+n
<i>Augochlora (A.) amphitrite</i>		-	x	
<i>Augochlora (A.)</i> sp.2		x	x	
<i>Augochlora (A.)</i> sp.3		x	-	
<i>Augochlorella ephyra</i>		x	x	
<i>Augochloropsis</i> cfr. <i>cleopatra</i>		-	x	
<i>Augochloropsis</i> cfr. <i>patens</i>		-	x	
<i>Dialictus</i> cfr. <i>opacus</i>		-	x	
<i>Thectochlora hamata</i>		-	x	
Apoidea n.i.	0.1 (1)		0.1 (1)	
Lepidoptera	-	0.1 (1)	-	n+o
Lepidoptera n.i.*		0.1 (1)	-	n
<i>Strymon serapio</i> *	-	x	-	n+o
Coleoptera	0.7 (9)	-	0.8 (9)	h
Diptera	1.3 (18)	0.7 (2)	1.5 (16)	-
Diptera n.i.		(2)	(16)	-
Saltatoria	0.1 (2)	-	0.2 (2)	pr
Saltatoria n.i.				pr
Mantidae	0.1 (1)	-	0.1 (1)	pr
Mantidae n.i.	(1)		(1)	pr
Vespidae	0.8 (11)	0.3 (1)	0.9 (10)	pr + n
Vespidae sp.1		-	x	pr + n
Vespidae sp.2		-	x	pr + n
<i>Eurytoma</i> sp.1	0.4 (6)	0.3 (1)	0.5 (5)	o
Blattaria	0.1 (1)	0.3 (1)	-	h
Blattaria sp.1	-	x (1)		h
Blattaria sp.2	-		x	h
Araneae	0.5 (7)	0.7 (2)	0.5 (5)	pr
Araneae n.i.		(1)		pr
Thomisidae n.i.*			x	pr
Salticidae n.i.		(1)	(5)	pr
Total	100 (1378)	100 (305)	100 (1073)	

* Individuals were observed as visitors but not during regular observation sessions so there is no frequency available.

Hummingbirds inserted their bills into open flowers and touched the anthers and stigmata while hovering in front of the flowers (Fig. 6A-B, Video S1). One individual of the bee species *Xylocopa brasiliatorum* was observed piercing the corolla tube to reach the nectar chamber (Fig. 6C). *Trigona spinipes*, *Ceratina* sp., and halictid bees collected pollen with their forelegs while hanging upside down on the anthers (Fig. 6D-F, respectively). They then stored the pollen in corbiculae (Fig. 6D) or the ventral abdominal and hind leg scopae (Fig. 6D-F). Individuals of these bee species were also slender enough to enter the flowers to collect nectar. *Trigona spinipes* individuals also sometimes gnawed holes in the corolla base when the tube was too narrow for them. Halictids were the most frequent flower visitors in restinga sites (Table 2) and collected pollen during 50% of their visits, mainly in the first hours

of anthesis. Occasionally the augochlorine bees touched the stigma while foraging for pollen. One individual was observed expanding a regurgitated nectar droplet between hypostomal fossa (Engel 2000) and the proximal section of the proboscis (cardines and hypopharynx) (Krenn *et al.* 2005) after the visit (Fig. 6G). Beetles and cockroaches were observed on the inflorescences feeding on open and withered flowers. Flower mites gathered on the anthers to feed on pollen (Fig. 6H). Vespid wasps were observed walking on the inflorescences, one individual tried to enter an open flower. Jumping spiders, crab spiders (Fig. 6I), and praying mantises lurked at the inflorescences for potential prey, for example ants (Fig. 6I). Ants at the flowers were not recorded systematically but they were observed regularly on and in flowers (Fig. 6J), preying on other animals, and collecting nectar inside the flowers.

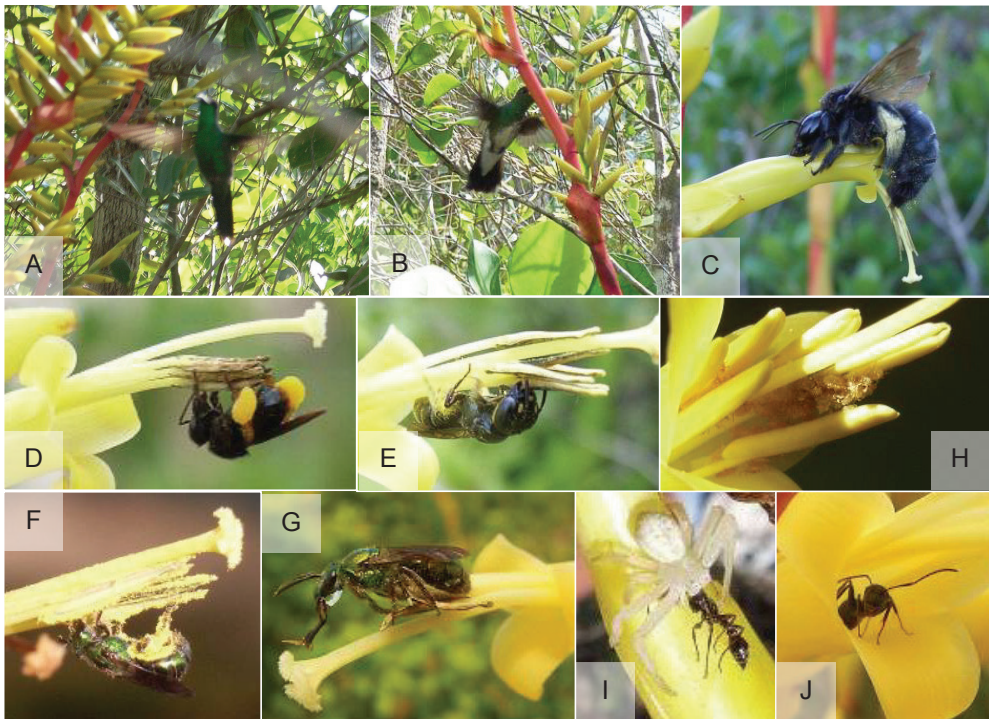


FIG. 6. Visitors on flowers of *Vriesea friburgensis* on Santa Catarina Island, southern Brazil. (A) *Thalurania glaucopis* and (B) *Amazilia fimbriata* hovering in front of flowers. (C) *Xylocopa brasiliatorum* acting as nectar robber. (D) *Trigona spinipes* collecting pollen. (E) *Ceratina* female collecting pollen at the anthers. (F) Pollen-collecting augochlorine bee, (G) and an individual sitting on the stigma while “dehydrating” a nectar droplet. (H) Flower mites on the anthers. (I). Crab spider (Thomisidae) feeding on a *Pseudomyrmex gracilis* worker ant. (J) *Camponotus* worker ant guarding the flower entrance.

DISCUSSION

Flowering phenology and nectar production favor hummingbird visits. The bromeliad species *Vriesea friburgensis* has an annual flowering pattern (Newstrom *et al.* 1994). Rosettes flower over a longer period, having a more synchronous and extended flowering period and less open flowers per day than sympatrically growing bromeliads of the genus *Aechmea* (Schmid *et al.* 2011b, Dorneles *et al.* in press, Kamke *et al.* 2011). A long flowering period and few open flowers per day lead to a low standing crop per plant, which in turn stimulates hummingbirds to forage by trap-lining along the *V. friburgensis* individuals. To collect enough nectar the hummingbirds have to visit many inflorescences, thereby enhancing cross-pollination.

The temporal pattern of nectar production and concentration throughout anthesis of *V. friburgensis* is adapted to attract hummingbirds, because features like high volume and sucrose content in the early morning, as well as sucrose-dominant nectar, seem to be common in hummingbird-pollinated flowers (Baker 1975, Heinrich 1975, Freeman *et al.* 1984, Bernardello *et al.* 1991, Stiles & Freeman 1993, Krömer *et al.* 2008). Also, floral traits (long tubular flowers, anthers and stigma exposed, stigma slightly in front to touch the bird's forehead first) match with the morphology of hummingbirds with straight and rather short bills. Therefore, based on nectar and morphological properties, we assume the visiting hummingbirds to be the main pollinators of *V. friburgensis*, but pollination experiments are needed to confirm this assumption.

Large bees of genera like *Bombus* and *Xylocopa*, or long-tongued bees of the genus *Euglossa*, are able to drink high quantities of floral nectar and they can reach the nectar even in flowers with moderately ornithophilous features. These bees were reported as visitors of *A. nudicaulis* (Schmid *et al.* 2011a) and *A. lindenii* (Dorneles *et al.* in press) but they cannot exploit, at least not in a legitimate way, *V. friburgensis* flowers and can only be considered nectar thieves. Therefore more nectar is available for the hummingbirds. This might make visits to *Vriesea* flowers more profitable for the birds than visits to *Aechmea* flowers.

The flower visitors of Vriesea friburgensis. From a Natural Heritage Site in Paraná state, Piacentini & Varassin (2007) reported solely *T. glaucopsis* and *Am. fimbriata* as visitors to *V. friburgensis*, the same hummingbird species observed by us. In contrast to their

findings, and to our own expectations considering the ornithophilous floral syndrome, we recorded a highly diverse arthropod assemblage, especially insects, on Santa Catarina Island. This assemblage was similar to the visitor spectrum of *A. nudicaulis* in the same habitats (Schmid *et al.* 2011a). Comparing the bee spectrum of *V. friburgensis* with that of the sympatrically growing *A. nudicaulis*, *A. lindenii*, and *A. caudata*, there is also some overlap, namely in the Apidae and Halictidae (Schmid *et al.* 2011a, Dorneles *et al.* in press, Kamke *et al.* 2011). Clearly, these bromeliad species partly share the same visitor species, and, flowering sequentially (*A. lindenii*: August to October, *A. nudicaulis*: September to December, *V. friburgensis*: November to February, and *A. caudata*: March to June) support the local hummingbird and bee fauna over an extended period.

Contrary to the findings on flower-visiting ant species on inflorescences of *A. nudicaulis* and *A. lindenii* (Schmid *et al.* 2010), the species richness of floral visitors to *V. friburgensis* was higher in the restinga than in the secondary forest. In restinga, flowers were almost exclusively visited by bees, most of them augochlorine sweat bees, whereas visitation frequency of hummingbirds was much lower than in secondary forest. This may be due to the fact that Joaquina and Campeche are low-vegetation restingas which provide poorer environmental conditions (for example nesting sites or nectar supply) for hummingbirds than for bees. In the early morning hours, the pollen-loaded anthers were especially attractive for bees. Additionally the low frequency of hummingbirds on *V. friburgensis* flowers resulted in a high nectar standing crop which was then available to bees small enough to crawl into the flowers. The exploitation of both of these rich resources explains the high bee visitation frequency.

Pollination biology of V. friburgensis. In the self-compatible flowers of *V. friburgensis* there is a spatial separation of stamina and stigma. Due to this "approach herkogamy" (Barrett 2003) pollen is not automatically transferred to the stigma and intra-floral selfing without an animal pollen vector is not possible. Consequently, pollination can take place when hummingbirds, forced to insert their bills deep into the corolla, touch the stigma with their foreheads dusted with pollen (see Video S1 and S2). Pollination by bees would have to occur in a different way. Pollen gathered by sweat bees (Halictidae) and small carpenter bees (Ceratinini) is stored in the scopae of the hind legs and the abdomen, and is not, as in the

corbiculate bees (Apinae), mixed with nectar to stick together as compact pellets. In fact, the rather loosely packed pollen may be transferred to the stigma while the bee is climbing over it. Therefore even small bees with short tongues (Halictidae and *Ceratina*), only engaged in pollen collection, may be capable pollinators. Individuals of these species-rich taxa are among the most abundant bees on Santa Catarina Island (Steiner *et al.* 2010). They occur all over the Neotropics, are abundant in forest as well as restinga, in natural as well as modified habitats, and are active almost all year round (multivoltine) (Michener 2000). Both taxa are similar in their ecotype and therefore belong to the same functional group (Fenster *et al.* 2004).

It appears that *V. friburgensis* uses both strategies – xenogamy and autogamy – to ensure successful pollination. Xenogamy is favored by forcing hummingbirds to perform trap-lining by offering, on average, only one open flower per plant so that pollen from unrelated plants is transferred with almost every flower visit. On the other hand, autogamy could be performed by a species-rich group of generalist bees characterized by a distinct mode of pollen collection and storing. Our results suggest that in places where hummingbirds are rare visitors or even absent, bees can fill the gap and pollinate the flowers. Even if, from the plant's point of view, xenogamy is more desirable than autogamy, the second strategy eliminates the risk of a total failure of pollination in the absence of the legitimate pollinators. The high seed set per flower observed indicates that, at present, natural pollination is sufficient to ensure the persistence of this bromeliad in the two habitats studied, even though there is loss of seeds due to parasitism by *Eurytoma* wasps (Grohme *et al.* 2007).

Although we did not measure individual pollinator effectiveness, the short-billed hummingbirds occurring on Santa Catarina Island are supposedly the most effective pollen vectors of *V. friburgensis*. Somewhat unexpectedly for this bromeliad species with such a pronounced ornithophilous syndrome, bees may also be a crucial part of the visitor assemblage, and not just pollen and nectar thieves. Araujo *et al.* (1994) also reported halictid bees to be visitors of three *Vriesea* species with similar flower morphology as *V. friburgensis*, but they do not give information about the bees' role in pollination. To what extent these bees provide pollination service for bromeliads with long and tubular flowers

like *V. friburgensis* has to be further investigated in carefully executed pollination experiments. In any case, our study points to the high importance of *V. friburgensis* flowers as food resource for the local bee fauna.

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