

Competition between the oligolectic bee *Ptilothrix plumata* (Anthophoridae) and the flower closing beetle *Pristimerus calcaratus* (Curculionidae) for floral resources of *Pavonia cancellata* (Malvaceae)

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Abstract. The flowers of *Pavonia cancellata*, a creeping ruderal half-shrub of northeastern Brazil, open synchronously at 6:00 h with all anthers already dehisced. The oligolectic bee *Ptilothrix plumata* was the most effective pollinator. During 90–180 min, female bees make up to 40 brief pollen collection trips to provision their brood cells. The pollen of about 40 flowers of *P. cancellata* is needed to feed one bee larva. The most frequent flower visitors, however, are the specialized curculionid beetles *Pristimerus calcaratus*, which do not cross-pollinate the flowers. They perforate the epidermis with their mouthparts, provoking dehydration, and then actively close the loose petals with their legs. Two hours after opening, half of the flowers had already been closed by the beetles. We interpret the fast, uninterrupted pollen foraging of *Ptilothrix plumata* bees as a strategy adapted to synchronous pollen presentation of *Pavonia* and to competition with *Pristimerus calcaratus*: the female bees have to provision their brood cells before the beetles succeed in closing the flowers.

Key words: Pollination, *Pavonia cancellata*, Malvaceae, *Ptilothrix plumata*, Anthophoridae, bees, *Pristimerus calcaratus*, Curculionidae, northeastern Brazil, foraging behavior, pollen presentation.

Pavonia is one of the largest genera of Malvaceae, containing between 150 (Cronquist 1981) to more than 200 species (Krapovickas and Cristóbal 1962) distributed in the neo- and paleotropics. Pollination by bees and birds is reported in the genus. Porsch (1929) cites ornithophily in five species of *Pavonia*. Gottsberger (1972) studied six species of *Pavonia*, four of which were pollinated by bees, one was autogamous and one ornithophilous. In the Malvaceae, he considers ornithophily to be primitive and melittophily to be derived. Melittophily is also reported for three species of *Pavonia* from southern Brazil (Schlindwein 1998). Some species of the genus produce small cleistogamous flowers as well as normal-sized chasmogamous ones (Krapovickas and Cristóbal 1962). The flowers of most studied species of *Pavonia* are self fertile (Gottsberger 1972).

Most species of *Pavonia* are shrubs, dwarf shrubs or herbs. *Pavonia cancellata* Cav. is a prostrate, creeping half-shrub, common at ruderal sites on sandy soils in northeastern Brazil. Flowers of *Pavonia* have numerous

stamens with large pollen grains (Barth 1975, Roubik and Moreno 1991). The large size of pollen grains in melittophilous flowers is often cited in relation to behavioral and morphological specializations of pollen-collecting bees, thus explaining their oligolecty (Roubik 1989, Gimenes 1991, Neff and Simpson 1993a; Schindwein and Wittmann 1997).

During our survey of melittophilous plants and their pollinators in northeastern Brazil, we recorded frequent visits of a solitary bee and a curculionid beetle to flowers of *P. cancellata*. We asked: Which flower visitors are effective pollinators? Do flower visitors compete for floral resources of *Pavonia cancellata*? In what ways does the manner of pollen presentation influence pollen collection behavior, and which are the foraging strategies of visitors to *Pavonia* flowers?

Material and methods

Study site. Field studies were carried out from October 1997 through January 1999 on the coastal plain of northeastern Brazil, about 15 km south of João Pessoa, Paraíba State. The study site was located at 7°11'58"S and 34°48'37"W at 30–40 m elevation and about 1 km distant from the coast. The climate is tropical and humid throughout the year, with a maximum of precipitation from May to August. Medium annual rainfall is 1740 mm the mean monthly temperature ranges from 23.9 °C to 26.7 °C (Paraíba 1985).

The local vegetation at the study site consists of ruderal plants and Tabuleiro vegetation, which is a sparsely wooded type of forest of coastal northeastern Brazil, typically characterized by poor, sandy soils and resembling the Cerrado physiognomically. The population of *Pavonia cancellata* studied occupied road margins, coconut plantations and open, deforested sites.

Breeding system. Thirty flower buds of *P. cancellata* were bagged with paper pouches. At anthesis, 10 flowers were self-pollinated by hand, 10 cross-pollinated by hand and the remaining 10 flowers were not treated and kept bagged to test for spontaneous self-pollination. Ten additional flowers were marked and used as open pollinated controls. These flowers received visitors, and pollen

was deposited on the stigmas. Seeds were counted from mature fruits. During the experiment a few marked flowers were lost.

Floral morphology and anthesis. Floral diameter, diameter of the throat of the corolla, column length and stylar length were measured in 20 flowers. Pollen reference slides were prepared using fresh pollen. Pollen grains were picked up on a small piece of glycerine gelatine and transferred to a microscope slide. The glycerine gelatine was gently melted, mounted with a cover glass and sealed with paraffin wax.

The total pollen content of an anther was transferred to a microscope slide and prepared for counting of pollen grains. Twenty anthers were prepared. The average pollen number per flower was calculated by multiplying the average pollen content of an anther by the average number of stamens per flower.

Effective pollinators and foraging strategy. We used a hand lens to determine whether a flower visitor left conspecific pollen on a stigma head. The large, red pollen of *P. cancellata* contrasted strongly with the light yellow stigma heads and could easily be detected in the field. Females of *P. plumata* were captured at nest entrance when coming back from pollen collection flights with full scopae. The composition of the pollen loads was analyzed to evaluate flower constancy during foraging. In addition, we excavated nests of *P. plumata* to analyze the pollen composition of the brood cells. To quantify the pollen collected by a female during a pollen collection flight, we counted all pollen grains collected from eight females. Pollen adhering to the surface of the bees body was dabbed with small blocks of glycerine gelatine.

Flight activities of individual females were recorded at their nesting sites during total period of pollen collection and nest closure. We noted the times of departure and arrival of the female at the nest entrance and whether or not the bee came back with filled scopae. When there were puddles near the nesting sites after rainfalls, we could follow the flight course of some bees from the nest entrance to the water. The bees were observed using a Zeiss 6X telescope for short distances.

Eighty-four flowers of *P. cancellata* were marked individually. Every 30 minutes we checked the flowers, noting presence of *Pristimerus calcaratus* beetles and stage of flower closure.

SEM-photographs of *P. calcaratus* were made with a Zeiss DSM 940. The objects were sputter-coated with gold using a Balzers Union SCD 040.

Vouchers of bees, beetles and plants are housed in the entomological collection and herbarium, respectively, of the Department of Botany of the Federal University of Pernambuco, Recife, and the Department of Systematics and Ecology, Federal University of Paraíba, João Pessoa.

Results

Floral morphology and anthesis of *Pavonia cancellata*

Pavonia cancellata has light yellow, campanulate, erect flowers with a dark-violet throat. Floral diameter is 35 (29–42) mm and diameter of the throat is 10 (7–12) mm. The style is enclosed in a column formed by fused filaments and terminates in ten free, visible, filiform stylar lobes, each ending in a globose, papillous stigmatic head (Fig. 1). Column length is 9 (7–12) mm and stylar length is 14 (12–19) mm. The ovary is 5-locular, with each locule containing one ovule. The anthers are monothebate and contain echinate pollen grains (diameter without spines 116.0 μm , standard deviation (s) = 4.5, including spines 160.3 μm , s = 6.0, n = 25) with a dark red-colored exine. The grains are covered with sticky, yellow pollenkitt.



Fig. 1. Transverse section of a flower of *Pavonia cancellata* soon after beginning of anthesis. All anthers are dehiscent and present pollen. The stigma heads are not yet pollinated

Pavonia cancellata flowered from June (wet season) until February (dry season) with peak flowering from September to December. Only 1–3 flowers open per plant per day. Intervals between flowering of each creeping twig was generally larger than four days. Only 15 of 35 marked twigs opened a second flower during a ten-day observation period. Before blooming, the floral buds are protected by long, hairy, filiform sepals of the outer calyx. One day before anthesis the yellow corolla becomes visible, forming a tip that exceeds the sepals by about 4–5 mm. Flowers open simultaneously between 5:30 h and 6:00 h in the morning and close between 12:00 h and 12:30 h; on rainy days, anthesis may continue until 16:00 h. Each flower lasts a single day. The anthers dehisce before or during opening of the flowers and pollen presentation coincides with the beginning of anthesis. Therefore, all flowers of *P. cancellata* blooming on the same day present their pollen at the same time.

Breeding system

The flowers of *P. cancellata* are self-compatible. Seed set in hand self-pollinated flowers did not differ from hand cross-pollinated or open pollinated flowers (Table 1). Nevertheless, the flowers did not show spontaneous self-pollination and none of the bagged flowers set seed. The pollen/ovule ratio is 451, suggesting that the breeding system of *P. cancellata* may be facultative autogamy or facultative xenogamy (Cruden 1977).

Table 1. Breeding system, seed and fruit set: spontaneous self-pollination, hand self-pollination, hand cross-pollination, open pollinated controls

Mode	n	Fruits	Seeds	Seed/ Fruit
Spontaneous self-pollination	10	0	0	0
Hand self-pollination	6	6	22	3.7
Hand cross-pollination	7	7	25	3.6
Open pollinated controls	7	7	27	3.9

Table 2. Characteristics of pollen foraging trips of 6 females of *Ptilothrix plumata*. The females start pollen collection soon after beginning of anthesis of the flowers of *Pavonia cancellata* and stop pollen collection when the brood cell is provisioned. One brood cell is provisioned per day

Bee	Foraging period	Number foraging trips	Total foraging time (min)	Total time spent in nest (min)	Total time collecting pollen (min)
A	6:33–8:05	32	92	37	55
B	6:31–7:56	28	85	31	54
C	6:27–8:39	40	132	48	84
D	6:27–9:23	35	176	116	60
E	6:34–9:17	40	133	38	95
F	6:26–8:21	29	115	23	92
G	6:44–8:58	30	134	17	117

cell with pollen, 28–40 pollen collection trips of 143 sec average duration ($s = 82$, $N = 232$) were made (Table 2). Between collection trips the females stayed an average of 58 sec inside the nest ($s = 34$, $N = 182$). After each of these trips the females entered the nest forwards with full pollen loads. To fill their scopae they needed only a few minutes; 88% of all pollen collection trips were shorter than 4 min (Fig. 3). The durations of pollen collection trips were similar throughout the period of pollen collection (Fig. 4). After the final

pollen collection trip, females made a long flight, lasting up to half an hour, and returned to the nest with empty scopae. They then remained in the nest for up to 35 min to oviposit.

After provisioning of brood cells and oviposition, females started to collect water. Each water collection trip lasted from 12 to 50 sec, depending on the distance from accessible water. When rainfall left puddles in the vicinity of the nesting site, water collection trips were short (12–20 sec). To

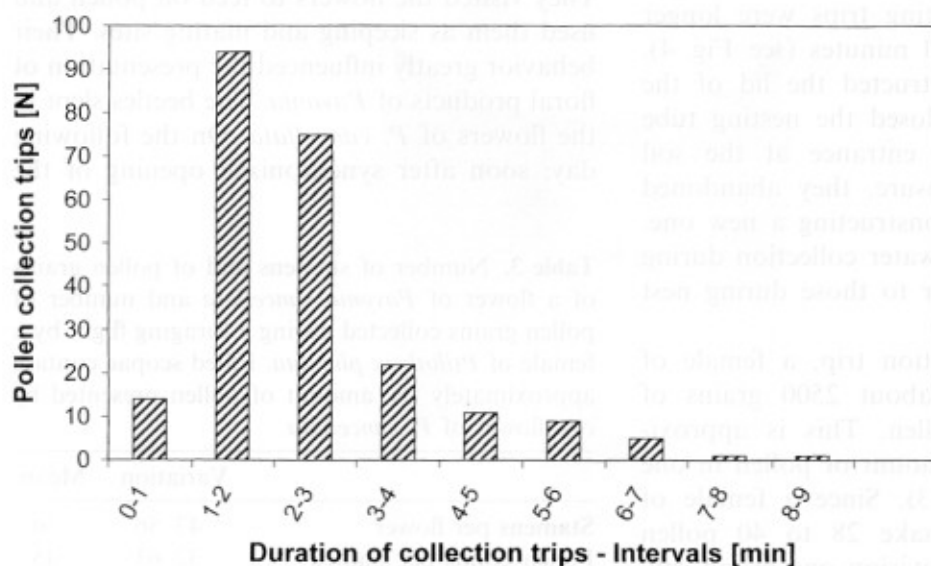


Fig. 3. Duration of pollen collection trips of *Ptilothrix plumata*. The females rapidly fill their scopae. Most frequent are collection trips of 1 to 2 min. Eighty-eight percent of all pollen collection trips were shorter than 4 min ($N = 232$)

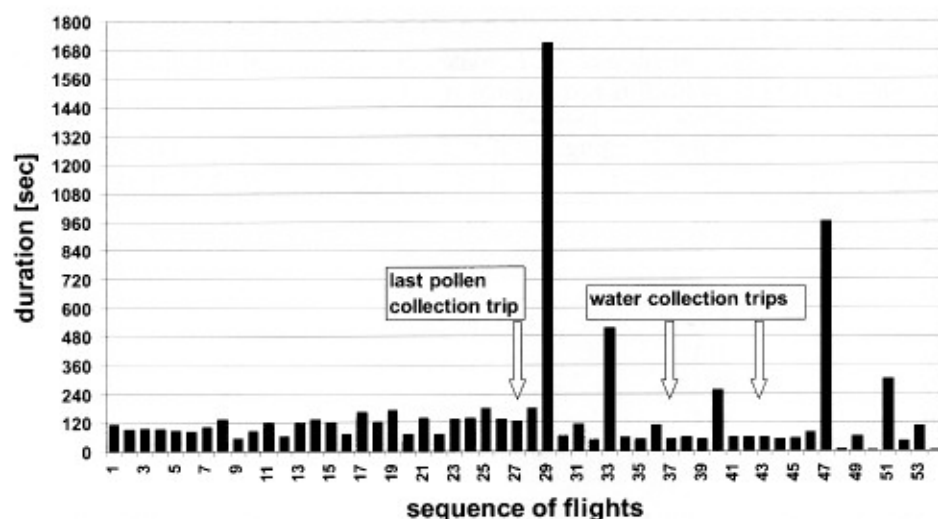


Fig. 4. Flight activity of a female of *Ptilothrix plumata*, while provisioning the brood cell and closing the nest (one morning, 23.10.1998). The bee made 28 pollen collection trips and returned to the nest after short intervals of 2–3 min. After flight number 29 the female stayed in the nest for about half an hour. Then she made water collection trips to close the nest with soil. Note the long lasting flights (n° 33, 36, 40, 47) intercalated among several water collection trips

take up water with their proboscis, the females alighted on the soil at the margin of a puddle or directly on the surface of the water for 5–6 sec. At the nesting site they regurgitated the water and moistened the soil to model the substrate. Intercalated among the short water collecting trips were longer journeys lasting several minutes (see Fig. 4). The females first constructed the lid of the brood cell and then closed the nesting tube with mud up to the entrance at the soil surface. After nest closure, they abandoned the nest and started constructing a new one. The characteristics of water collection during nest closure are similar to those during nest construction.

On a pollen collection trip, a female of *P. plumata* collected about 2500 grains of *Pavonia cancellata* pollen. This is approximately equal to the amount of pollen in one *Pavonia*-flower (Table 3). Since a female of *P. plumata* had to make 28 to 40 pollen collection flights to provision one brood cell, about the same number of flowers of *Pavonia cancellata* were required to feed one bee larva of *Ptilothrix plumata*.

Active flower closing by the curculionid beetle Pristimerus calcaratus

The tiny curculionid beetles *Pristimerus calcaratus* (body length 4.1 mm, N = 6) were abundant visitors on *P. cancellata* flowers. They visited the flowers to feed on pollen and used them as sleeping and mating sites. Their behavior greatly influenced the presentation of floral products of *Pavonia*. The beetles slept in the flowers of *P. cancellata*. On the following day, soon after synchronized opening of the

Table 3. Number of stamens and of pollen grains of a flower of *Pavonia cancellata* and number of pollen grains collected during a foraging flight by a female of *Ptilothrix plumata*. Filled scopae contain approximately the amount of pollen presented by one flower of *P. cancellata*

	Variation	Mean
Stamens per flower	43–56	50
Pollen grains per stamen	32–63	45
Pollen per flower		2250
Pollen grains in a filled scopa of <i>Ptilothrix plumata</i>	2103–3091	2596

new flowers, the beetles left the old flowers in which they were sleeping by pushing outwards between the dry petals. At about the same time, when female bees of *Ptilothrix plumata* started pollen collection, *Pristimerus calcaratus* beetles looked for fresh flowers of *Pavonia cancellata*. In the flowers, we noticed no aggressive interaction between bee and beetle.

When the beetles left their sleeping places, no pollen adhered to their smooth body surface and as they did not move between flowers of *Pavonia*, they did not provoke cross-pollination. Once a fresh flower was localized, the beetles stayed in the flower the whole day, showing a peculiar behavior: they crawled around the upper and lower surface of the petals and perforated the epidermis or even the entire petal every 1–1.2 mm with their proboscis (Fig. 5). This caused dehydration and premature wilting of the petals. There was no evidence that the beetles fed on petal sap. The beetles then succeeded in closing the now flaccid petals actively with their claws and front tibial spines (Figs. 6, 7, 8). Ten flower closing beetles were collected to determine their sex. All of them were females. At 8:00 h, about two hours after beginning of anthesis, 50% of individually marked *Pavonia*-flowers had already been closed by the beetles (Fig. 9). Only few flowers remained open until 12:00 h to 13:00 h (the normal closing time).



Fig. 5. *Pristimerus calcaratus* in a flower of *Pavonia cancellata*. The curculionid beetle perforates the petals (dark shining points) and thereby causes premature wilting of the flowers



Fig. 6. *Pristimerus calcaratus* closing the flower of *Pavonia cancellata*

Discussion

Synchronous pollen presentation in Pavonia cancellata

All flowers of a *P. cancellata* population that bloom on the same day open synchronously with their anthers already dehisced. This means that all the pollen of these flowers is presented at the same time to flower visitors. This synchronous pollen presentation should favor species of bees whose females show rapid pollen foraging behavior.



Fig. 7. Flower of *Pavonia cancellata* prematurely closed by *Pristimerus calcaratus*

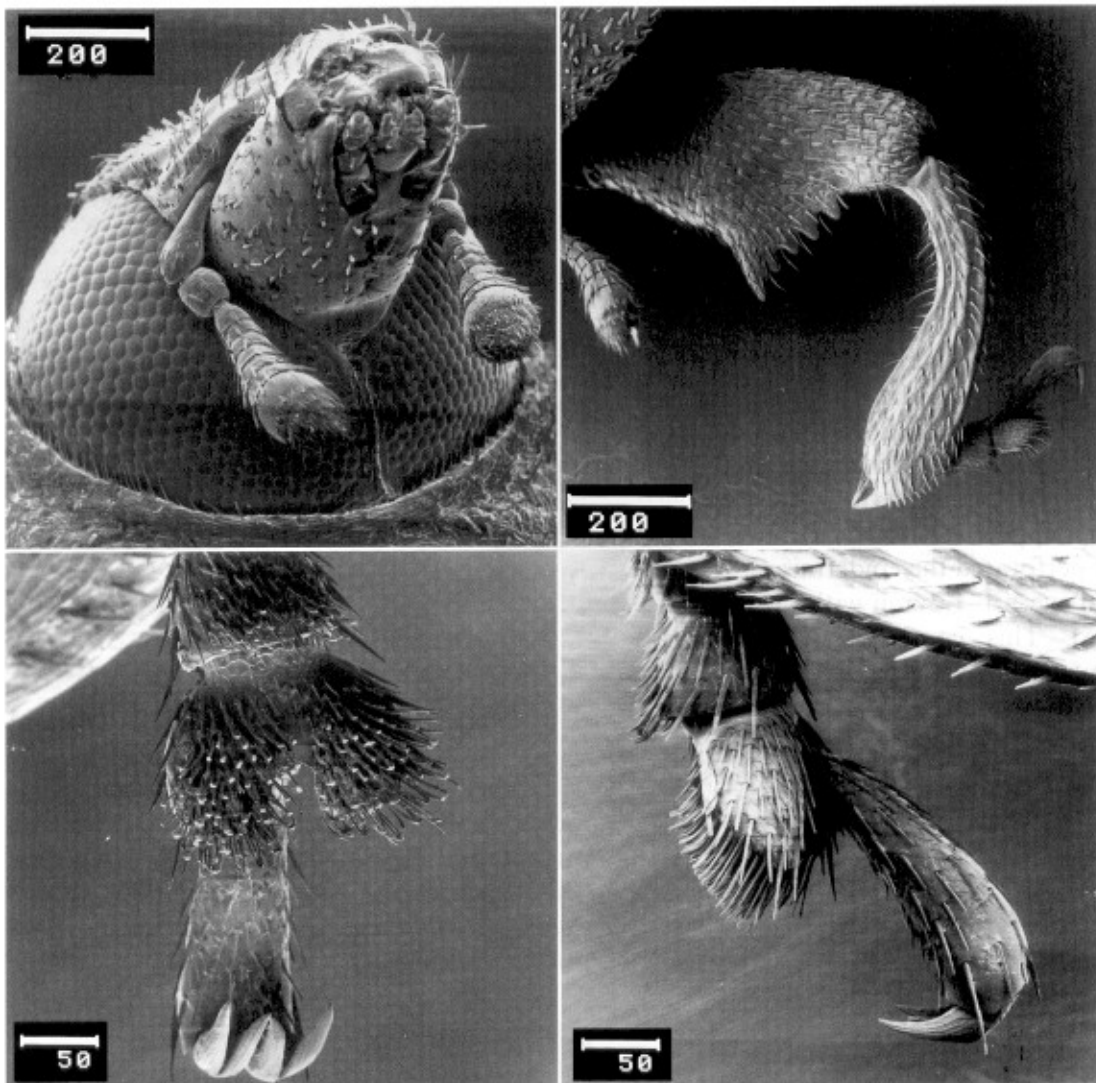


Fig. 8. *Pristimerus calcaratus*. Top left: ventral view of the head. The huge eyes contact each other below. The reduced mouthparts are used to perforate the petals. Top right: front leg, anterior view. The apical spines on tibia and coxa as well as tarsal claws facilitate flower closure. Bottom left and right: tarsal segments and claws of front legs. The sensorial pads on second and third tarsal segments are probably involved in floral tissue recognition (scale bar in μm)

Ptilothrix plumata as effective pollinator

Females of *P. plumata* are highly efficient pollen foragers, apparently adapted to the synchronous pollen presentation of the flowers of *Pavonia*. The pollen collection trips, in general, last for less than three minutes and are only interrupted for about one minute inside the nest to remove the *Pavonia*-pollen load from the scopae. Such rapid pollen collection

and handling may be possible due to the very large size of the *Pavonia* pollen grains.

In a single pollen foraging trip, a female *Ptilothrix plumata* collects about the amount of pollen presented in a single *Pavonia* flower. A female, therefore, can theoretically fill her pollen baskets in one fresh *Pavonia* flower and then return to her nest without visiting and pollinating a second flower. However, we did

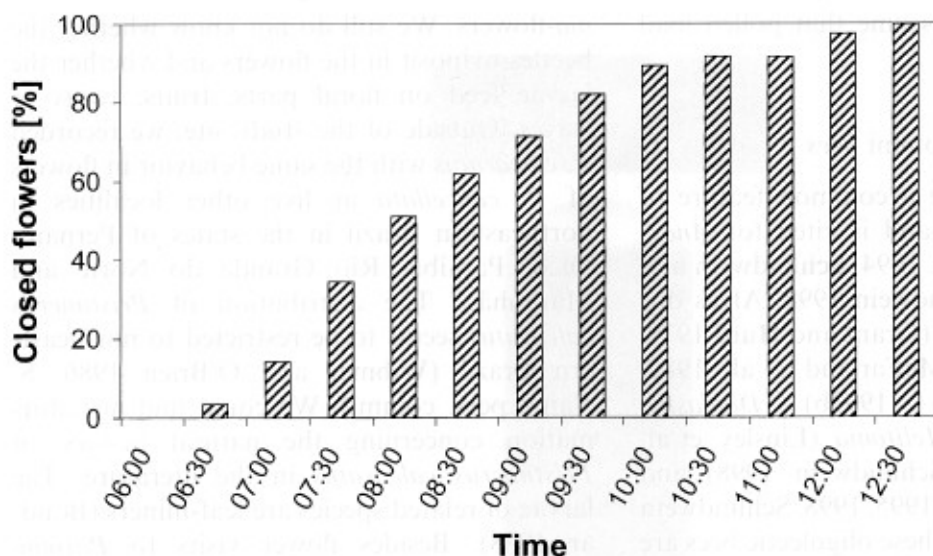


Fig. 9. Number of closed flowers of *Pavonia cancellata*, surveyed in 30-minute intervals after opening of the flowers ($n = 84$). Females of *Pristimerus calcaratus* actively closed the flowers of *Pavonia cancellata*. Fifty percent of the flowers have been already closed at 8:00 h. Only a few flowers remained open until the normal end of anthesis

not observe such single-flower foraging trips. Based on the pollen collection time per flower, we can estimate that a female visits 5 to 20 flowers during a pollen foraging trip to complete her pollen load. In general, only 1–3 flowers of a *P. cancellata* plant bloom on the same day; thus, females of *Ptilothrix* frequently cause cross-pollination, visiting flowers of several conspecific plant individuals.

After their last pollen foraging trip, females of *P. plumata* generally carried out a long-lasting nectar collection flight and returned to the nest without pollen. Apparently they first provision the brood cell exclusively with pollen and then add nectar to it.

To close the nest after nest provisioning as well as to build new nests, female *P. plumata* collect water to moisten and work the hard substrate. During nest closure and nest construction the fast water collection trips are interrupted by flights that last up to several minutes (see Fig. 4). In this period, we recorded females collecting nectar in the flowers of *P. cancellata* but no pollen. These flower visits may serve to cover the bees' energy demand during nest construction and

closure. Nectar foraging flights have a much longer duration than pollen collection trips, and the females visit a greater number of flowers. Therefore, nectar foraging flights should enhance cross pollination in the population of *P. cancellata*.

As a consequence of their brief, efficient pollen collection, females of *P. plumata* rapidly diminish the amount of pollen present in the *Pavonia* flowers. It is to be expected that as pollen availability decreased, the bees have to prolong the duration of their pollen collection flights to fill their scopae. It is unclear whether pollen loads of individual bees during early pollen collection flights are larger than those during later collection flights. Pollen grains of *Pavonia cancellata* are covered with pollenkitt, which forms sticky threads on the pollen loads, resembling viscin threads of Onagraceae pollen. As a result, pollen loads can not be removed completely from the living bee in the field. Moreover, females that are captured in order to sample pollen loads, subsequently abandon their nests. However, pollen loads of females captured after early pollen collection trips do not differ from those collected after

later ones. Thus, we assume that pollen load size remains stable.

Specialization of Melitomini bees

Oligolecty seems to be a common feature of species of Melitomini and is cited for *Ancylloscelis* (Michener et al. 1994, Schlindwein and Wittmann 1995, Schlindwein 1998, Alves dos Santos 1999); *Diadasia* (Grant and Hurd 1979, Osborn et al. 1988, McFarland et al. 1989, Neff and Simpson 1993b) *Diadasina* (Schlindwein 1998), *Melitoma* (Linsley et al. 1980, Pinheiro and Schlindwein 1998) and *Ptilothrix* (Schlindwein 1995, 1998; Schlindwein and Wittmann 1997). These oligolectic bees are morphologically and/or behaviorally adapted to collect pollen from specific food plants, and, in general, are effective pollinators of these plants.

It is noteworthy that in various cases of close relations between melitomine species and their food plants, the respective flowers produce extraordinarily large pollen grains, as for example in *Opuntia* (Cactaceae), *Ipomoea* (Convolvulaceae), *Ludwigia* (Onagraceae) and *Pavonia*. Females of melitomine species have long, unbranched bristles in their hind tibial scopae, adapted to transport large pollen grains. In Minas Gerais (southeastern Brazil), females of a population of *P. plumata* were found to frequently collect pollen in flowers of *Ludwigia* (Y. Antonini, pers. comm.). Another species of *Ptilothrix*, *P. relata*, visits flowers of Malvaceae (*Hibiscus*, *Pavonia*) and *Ludwigia* (Schlindwein not publ.; Schlindwein 1998, Alves dos Santos 1999). Bee specialization in these cases seems to be related to the size of the pollen grains.

Relation between Pristimerus calcaratus and Pavonia cancellata

Our studies indicate that the curculionid *Pristimerus calcaratus*, like *Ptilothrix plumata*, is specialized to use the floral resources of *Pavonia cancellata*. These beetles feed on *Pavonia*-pollen and sleep and mate in *Pavo-*

nia-flowers. We still do not know whether the beetles oviposit in the flowers and whether the larvae feed on floral parts, fruits, twigs or leaves. Outside of the study site, we recorded *P. calcaratus* with the same behavior in flowers of *P. cancellata* at five other localities in northeastern Brazil in the states of Pernambuco, Paraíba, Rio Grande do Norte and Maranhão. The distribution of *Pristimerus calcaratus* seems to be restricted to northeastern Brazil (Wibmer and O'Brien 1986, S. Vanin pers. comm.). We could find no information concerning the natural history of *Pristimerus calcaratus* in the literature. The larvae of related species are leaf-miners (Bondar 1938). Besides flower visits to *Pavonia cancellata*, we recorded sporadic flower visits to *Turnera ulmifolia* (Turneraceae) whose flowers are similar to those of *P. cancellata* in shape, size, color and period of anthesis. These flower visits were short and the beetles did not show the typical behavior to close the flowers. As the curculionid beetles did not move between conspecific flowers, they affected only self-pollination.

Competition between Ptilothrix plumata and Pristimerus calcaratus

At the study site, the two specialized insect species compete for floral resources of *Pavonia cancellata*. One, the bee, is an effective pollinator and the other, the curculionid beetle, probably shifts the ratio of self-pollination to cross-pollination towards more self-pollination. Both competitors start foraging at about the same time, soon after anthesis begins. Flower opening thus initiates a race for the floral resources of *P. cancellata*. Females of *Ptilothrix plumata* carry out pollen foraging trips without interruption until the brood cell, which has been prepared the day before, is provisioned with pollen. The pollen collection strategy of *Ptilothrix plumata* thus appears adapted to synchronized pollen presentation. The rapid, efficient pollen collection, on the other hand, also may result from competition with the flower-closing beetle. The distribution

of *Ptilothrix plumata* reaches from northern Brazil (Pará) to northern Argentina (Misiones) (Alves-dos-Santos 2000). In northeastern Brazil it overlaps with that of *Pristimerus calcaratus*. In those regions or populations in which the beetle does not occur, competition for floral resources of *Pavonia cancellata* might be just intraspecific, and the foraging strategy of the bee females may differ from the behavior described here.

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References

- Alves-dos-Santos I. (1999) Abelhas e plantas melíferas da mata atlântica, restinga e dunas do litoral norte do estado do Rio Grande do Sul, Brasil. *Revista Brasileira de Entomologia*, São Paulo 43 (3/4): 191–223.
- Alves-dos-Santos I. (2000) Notes on bees of the tribe Emphorini (Apidae). *Anais do Encontro sobre Abelhas 4* (in print).
- Barth O. M. (1975) Catálogo sistemático dos pólenes das plantas arbóreas do Brasil meridional XVIII – Malvaceae. *Mem. Inst. Oswaldo Cruz* 73 (1/2): 1–29.
- Bondar G. (1938) Notas entomológicas da Bahia (II). *Revta. de Entomologia* 8(1–2): 1–24.
- Cronquist A. (1981) An integrated system of classification of flowering plants. Columbia Univ. Press, New York, 1262p.
- Cruden R. W. (1977) Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32–46.
- Gimenes M. (1991) Some morphological adaptations in bees (Hymenoptera, Apoidea) for collecting pollen from *Ludwigia elegans* (Onagraceae). *Revta. bras. Ent.* 35(2): 413–422.
- Gottsberger G. (1972) Blütenbiologische Beobachtungen an brasilianischen Malvaceen. II. *Österr. Bot. Z.* 120: 439–509.
- Grant V., Hurd P. D. Jr. (1979) Pollination of the southwestern *Opuntias*. *Plant Syst. Evol.* 133: 15–28.
- Krapovickas A., Cristóbal C. L. (1962) Notas sobre la sección *Lebretonia*, *Pavonia*, (Malvaceae) y revisión de las especies Argentinas. *Lilloa* 31: 5–74.
- Linsley E. G., MacSwain J. W., Michener C. D. (1980) Nesting biology and associates of *Melitoma* (Hymenoptera, Anthophoridae). University of California Publications in Entomology 90: 1–39.
- McFarland J. D., Kevan P. G., Lane M. A. (1989) Pollination biology of *Opuntia imbricata* (Cactaceae) in southern Colorado. *Can. J. Bot.* 67: 24–28.
- Michener C. D., McGinley R. J., Danforth B. N. (1994) The bee genera of North and Central America (Hymenoptera: Apoidea). Smithsonian Institution, Washington, 209p.
- Neff J. L., Simpson B. B. (1993a) Bees, pollination systems and plant diversity. In: LaSalle J., Gauld I. D. (eds.) *Hymenoptera and Biodiversity*. CAB International, Wallingfor, UK.
- Neff J. L., Simpson B. B. (1993b) Partial bivoltinism in a ground-nesting bee: the biology of *Diadasia rinconis* in Texas (Hymenoptera, Anthophoridae). *J. Kansas Entomol. Soc.* 65(4): 377–392.
- Osborn M. M., Kevan P. G., Lane M. A. (1988) Pollination biology of *Opuntia polyacantha* and *Opuntia phaeacantha* (Cactaceae) in southern Colorado. *Plant Syst. Evol.* 159: 85–94.
- Paraíba, Governo do Estado. Universidade Federal da Paraíba (1985) Atlas geográfico do Estado da Paraíba Grafset, João Pessoa, 100p.
- Pinheiro M., Schlindwein C. (1998) A câmara nectarífera de *Ipomoea cairica* (L.) Sweet (Convolvulaceae) e abelhas de glossa longa como polinizadores eficientes. *Iheringia Sér. Bot.* 51(1): 3–16.
- Porsch O. (1929) Vogelblumenstudien II. *Jahrb. wiss. Bot.* 70: 181–277.
- Roubik D. W. (1989) Ecology and natural history of tropical bees. Cambridge University Press, New York, 514 pp.
- Roubik D. W., Moreno J. E. (1991) Pollen and spores of Barro Colorado Island. *Monographs in Systematic Botany, Missouri Bot. Grds.* 36: 1–270p.
- Schlindwein C. (1995) Melittophilous plants, their pollen and flower visiting bees in Southern Brazil. 2. Cactaceae. *Biociências* 3(2): 35–71.

- Schlindwein C. (1998) Frequent oligolecty characterizing a diverse bee-plant community in a xerophytic bushland of subtropical Brazil. *Stud. Neotrop. Fauna & Environm.* 33: 46–59.
- Schlindwein C., Wittmann D. (1995) Specialized solitary bees as effective pollinators of South Brazilian species of *Notocactus* and *Gymnocalycium*. *Bradleya* 13: 25–34.
- Schlindwein C., Wittmann D. (1997) Stamen movements in flowers of *Opuntia* (Cactaceae) favour oligolectic bee pollinators. *Plant Syst. Evol.* 204: 179–193.
- Wibmer G. J., O'Brien C. W. (1986) Annotated checklist of the weevils (Curculionidae sensu lato) of South America (Coleoptera: Curculionidae). *Memoirs of the American Entomological Institute* 39: 1–563.
- Addresses of the authors: Clemens Schlindwein, Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. Moraes Rêgo s/n, Cidade Universitária, 50670-901 Recife, PE, Brazil. Celso Feitosa Martins, Departamento de Sistemática e Ecologia – CCEN, Universidade Federal da Paraíba, 58059-900 João Pessoa, PB, Brazil.
- Alves-de-Saunes J. (1999) *Zebrina* e plantas melíferas de uma mata atlântica: resenha e observações sobre o estado do estado do Rio Grande do Sul. *Brasil: Actas do Instituto de Entomologia São Paulo* 43: 191–222.
- Alves-de-Saunes J. (2000) *Zebrina* em borda de mata: uma espécie invasora? *Actas do Instituto de Entomologia São Paulo* 44: 109–110.
- Barbottin O. M. (1979) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 23: 1–24.
- Barbottin O. M. (1981) An integrated system of classification of flowering plants. *Columbianiana* 1: 1–120.
- Barbottin O. M. (1987) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 31: 1–24.
- Barbottin O. M. (1991) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 35: 1–24.
- Barbottin O. M. (1995) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 39: 1–24.
- Barbottin O. M. (1999) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 43: 1–24.
- Barbottin O. M. (2000) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 44: 1–24.
- Barbottin O. M. (2001) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 45: 1–24.
- Barbottin O. M. (2002) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 46: 1–24.
- Barbottin O. M. (2003) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 47: 1–24.
- Barbottin O. M. (2004) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 48: 1–24.
- Barbottin O. M. (2005) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 49: 1–24.
- Barbottin O. M. (2006) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 50: 1–24.
- Barbottin O. M. (2007) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 51: 1–24.
- Barbottin O. M. (2008) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 52: 1–24.
- Barbottin O. M. (2009) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 53: 1–24.
- Barbottin O. M. (2010) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 54: 1–24.
- Barbottin O. M. (2011) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 55: 1–24.
- Barbottin O. M. (2012) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 56: 1–24.
- Barbottin O. M. (2013) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 57: 1–24.
- Barbottin O. M. (2014) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 58: 1–24.
- Barbottin O. M. (2015) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 59: 1–24.
- Barbottin O. M. (2016) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 60: 1–24.
- Barbottin O. M. (2017) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 61: 1–24.
- Barbottin O. M. (2018) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 62: 1–24.
- Barbottin O. M. (2019) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 63: 1–24.
- Barbottin O. M. (2020) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 64: 1–24.
- Barbottin O. M. (2021) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 65: 1–24.
- Barbottin O. M. (2022) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 66: 1–24.
- Barbottin O. M. (2023) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 67: 1–24.
- Barbottin O. M. (2024) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 68: 1–24.
- Barbottin O. M. (2025) *Curculio* *zebrinus* (L.) (Coleoptera: Curculionidae) em borda de mata atlântica: observações sobre o comportamento de alimentação e sobre a distribuição. *Revista de Entomologia São Paulo* 69: 1–24.