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A meeting of opportunists: birds and other visitors to *Mabea fistulifera* (Euphorbiaceae) inflorescences

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RESUMO. **Um Encontro de Oportunistas: As Aves Visitantes das Inflorescências de *Mabea fistulifera* (Euphorbiaceae).** Aves visitantes das inflorescências de *Mabea fistulifera*, uma árvore de pequeno porte das florestas semi-decíduas e cerradões do sudeste brasileiro, dependente de fertilização cruzada e adaptada à polinização por morcegos, foram observados em um fragmento isolado na Estação Experimental de Assis, estado de São Paulo, em maio-junho de 1996. Aves pertencendo a 17 espécies, principalmente traupídeos e beija-flores, visitaram as inflorescências, traupídeos sendo o grupo mais comum. *Thraupis sayaca, Tangara cayana* e *Dacnis cayana* foram responsáveis por 65% das visitas por aves, sendo considerados polinizadores efetivos prováveis, embora também pilhassem néctar. Além disso, quatro espécies de morcegos, incluindo os frugívoros *Artibeus lituratus, Sturnira lilium* e *Chiroderma doriae* foram capturadas apresentando o corpo coberto de pólen de *Mabea*. Estes morcegos podem visitar as inflorescências de maneira intensa, sendo considerados os polinizadores primários de *Mabea*. Um registro de quatis *Nasua nasua* possivelmente polinizando inflorescências também foi feito. *Mabea fistulifera* é uma espécies oportunista capaz de utilizar uma grande diversidade de nectarívoros não especializados (oportunistas) como polinizadores, permitindo sua reprodução mesmo em áreas faunisticamente pobres. Esta arvoreta pode constituir um recurso-chave para algumas espécies de frugívoros, especialmente pássaros *Thraupinae*, durante a estação seca em habitats isolados e empobrecidos.

PALAVRAS-CHAVE: cerrado, *Mabea fistulifera*, morcegos, ornitofilia, polinização, quatis, quiropterofilia, sudeste do Brasil, Thraupinae.

ABSTRACT. Bird visitors to the nectar-producing inflorescences of *Mabea fistulifera* (Euphorbiaceae) were recorded in an isolated habitat fragment at Assis Experimental Station, São Paulo state, in May-June 1996. *Mabea fistulifera* is a small tree of the semi-deciduous forest and *cerradão* of south-eastern Brazil presumed to be dependent on outcrossing fertilization by bat pollinators. Birds belonging to 17 species, mostly tanagers, followed by hummingbirds, visited the inflorescences. *Thraupis sayaca, Tangara cayana* and *Dacnis cayana* accounted for 65% of the bird visits. These species are considered to be effective pollinators; they also robbed nectar. Bats of four species were captured around the flowering *Mabea*: the mainly frugivorous *Artibeus lituratus, Sturnira lilium* and *Chiroderma doriae* were found with *Mabea* pollen. Bat visits may be very frequent, and bats are considered to be the primary pollinators of *Mabea*. An instance of coatis *Nasua nasua* possibly pollinating the flowers was also recorded. *Mabea fistulifera* is an opportunistic species able to use many species of non-specialized nectarivores, also opportunists, as pollinators. These pollinators therefore allow the plant to breed even in impoverished faunal assemblages. This tree may be a keystone resource for some frugivorous species during the dry season in isolated habitat patches.

KEY WORDS: cerrado, *Mabea fistulifera*, bats, ornithophily, pollination, coatis, chiropterophily, Southeast Brazil, Thraupinae.

Mabea fistulifera Mart. (Euphorbiaceae) is a medium-sized tree 4-8 m tall (sometimes up to 15 m) common in the south-eastern Brazilian mesophytic forests, especially at forest-cerrado ecotones or edge habitats (Lorenzi 1992). This species blooms from March to June, with a flowering peak in April-May (Vieira and Carvalho-Okano 1996) at the begining of the local dry, cool season. Each individual bears tens of reddish to ferruginous pendulous inflorescences at the ends of the branches, which produce abundant nectar (Torres de Assumpção 1981, Vieira and Carvalho-Okano 1996).

Very little or no self-pollination occurs in *Mabea fistulifera*, which depends on its pollinators for reproduction (Vieira and Carvalho-Okano 1996). The tree has large and strong reddish and yellow inflorescences at the end of the branches, offering well-defined landing perches. Nectar and pollen production begins in late afternoon and peaks during the night. This timing along with a strong odor suggest adaptations to pollination by bats and other nocturnal mammals (Faegri and van der Pijl 1980, Vieira and Carvalho-Okano 1996). Nevertheless, pollination by birds, diurnal arboreal mammals and some insects is also possible (Vieira and Carvalho-Okano 1996). *Mabea fistulifera* reportedly is able to attract and use most of the pollen vectors available in its habitat, including non-specialized nectarivores like primates (Torres de Assumpção 1981, Ferrari and Strier 1992), opossums (Vieira *et al.* 1991), birds like tanagers, caciques and macaws (Ferrari and Strier 1992, Vieira *et al.* 1992), long-nosed bats and fruit-bats (Vieira and Carvalho-Okano 1996).

Vieira *et al.* (1992) and Vieira and Carvalho-Okano (1996), in a 3-year study of the pollination biology of *Mabea fistulifera* in southern Minas Gerais, recorded 31 bird species feeding on nectar. Fourteen were tanagers (Thraupinae and Coerebinae) and six were hummingbirds. *Coereba flaveola* (Coerebinae), *Thraupis sayaca* (Thraupinae) and *Eupetomena macroura* (Trochilidae)

were reported as the commonest visitors, but no quantitative analysis was made to assess the relative importance of species or their feeding techniques.

Here we identify the bird visitors to *Mabea fistulifera* inflorescences in an isolated cerradão and introduced tree plantation mosaic, describe and quantify their feeding behavior and discuss their effectiveness as pollinators. We consider implications for the breeding success of this tree in human-disturbed habitats, seeking to broaden the existing knowledge on the species. We also present our observations on other vertebrate visitors pertinent to an understanding of the ecology of *Mabea fistulifera*.

STUDY AREA AND METHODS

Observations were conducted at the 3,167 ha Assis Experimental Station, São Paulo state, south-eastern Brazil (22°37'S 50°24' W) from late May to late June 1996. Annual precipitation in the area averages 1,450 mm and is seasonal, July and August being the driest months with less than 50 mm of rain. The station presently is covered by introduced *Pinus* (most of the area) and *Eucalyptus* plantations interspersed by a few small remnant patches of native "cerradão" forest (see Eiten 1970 for a description). The local cerrradão was subject to selective cutting and cattle grazing decades ago, but such practices have long stopped (M. Garrido, pers. com.). A vigorous undergrowth of native trees, herbaceous plants and bushes also occurs in the areas planted with *Pinus*. These may serve as corridors connecting the native vegetation patches, which are only a few ha in size. A larger (1,312 ha) protected, continuous area of cerradão, the Assis Ecological Station, is adjacent to the experimental area. Both stations are isolated from other native vegetation patches by roads and agriculture, mostly sugarcane and pasture, effectively turning them into habitat islands.

Observations were made on a *Mabea* patch with 12 individual trees, 5-9 m tall, growing in a cerradão patch by the side of an unpaved road and adjacent to a *Pinus* grove. This edge situation allowed optimum observation conditions. All trees were in full blossom, some already bearing immature fruits. *Mabea fistulifera* was the only bat-pollinated tree we found flowering during our study. Records were made mostly during the morning, usually between 07:00 and 09:00, or 1.5 hours after sunrise, and during late afternoon, between 15:00 and 18:00; sunset was by 18:30. A few nocturnal observations, totaling 90 minutes, were carried out during the night to assess bat behavior and visitation rates. Diurnal visitors (birds and mammals) were observed with the aid of binoculars. Bats were observed with the aid of flashlights or a car's lights, which they quickly habituated to, and captured with mist-nets located beside the flowering trees. Netted bats were checked for the presence of *Mabea* pollen, identified and released.

We defined each time a visitor touched an inflorescence with its mouth or bill as a visit. Visits by birds were sorted into three categories: 1) flying, when a hovering bird drank nectar or captured insects from an inflorescence; 2) perching, when a bird perched by the side of, and not on, an inflorescence to drink its nectar; and 3) hanging, when a bird perched on the peduncle of an inflorescence to drink its nectar, in which situation it always adopted a head-down posture, touching both male and female flowers with its belly, neck and head. We assumed that hanging was the only one in which pollen transfer to the female flowers was likely, a view supported by the observations of Vieira and Carvalho-Okano (1996). Bat visits were classified similarly for comparisons with birds.

Before all diurnal and nocturnal observation bouts we randomly selected a minimum of 80 mature inflorescences and checked them for the presence of nectar droplets. We estimated the volume of available nectar in inflorescences with 10 ml hypodermical syringes during morning and afternoon observations. While providing only an approximate value, this method allowed us to extract nectar in a way similar to some of the visitors, like hovering and hanging birds and bats, providing a measure of resource size and availability. In addition, 22 inflorescences were monitored daily for nectar production throughout their anthesis period in order to assess how long they were able to attract visitors.

RESULTS

Nectar Production. More flowers had available nectar during the morning (21.24 ± 9.54 %, n = 723 inflorescences) than during the afternoon (6.83 ± 4.67 %, n = 442 inflorescences) in 13 countings (7 morning, 5 afternoon). This difference is probably due to the fact that nectar production peaks during the night (Vieira and Carvalho-Okano 1996) and the resource is still available during the morning, drying from the flowers by noon. Nectar production then begins again in the late afternoon. Another important factor leading to the non-availability of nectar after noon is its intensive harvesting by bees and wasps, especially *Apis melifera, Trigona* spp., *Polybia* spp. and *Polistes* spp, which became very active only after air temperatures rose.

Measurable nectar volume in 38 inflorescences was 0.37 ± 0.67 ml (pooled night and day records), with a maximum record of 1.4 ml taken at night. This is less than the maximum production (3 ml) recorded by Vieira and Carvalho-Okano (1996), but as our method often resulted in nectar being spilled or dropped, comparisons are not fair. Nevertheless, our wastage was probably more similar to one caused by landing birds and bats, which often caused nectar to drop.

Twelve out of 22 inflorescences (54.5%) produced nectar for three consecutive days, while eight (32%) had nectar

available during four days. Only one each (4.5%) produced nectar for five and six days. First-producing inflorescences had their first nectar droplets either by late afternoon or after nightfall, anthers opening in the base to apex pattern described by Vieira and Carvalho-Okano (1996).

Bird Visitors. We recorded 323 visits by 17 species of birds (table 1), belonging to such diverse groups as tanagers, hummingbirds, tyrant flycatchers and thrushes, all of which were observed feeding on nectar. Outside the observation periods we once observed a group of five Coatis *Nasua nasua* and, in another instance, a Plush-crested Jay *Cyanocorax chrysops* feeding on *Mabea* nectar. The jay was one of a flock that was resting and preening by the *Mabea* grove and spent a few minutes drinking the nectar from inflorescences overhanging the branch where it was perched, adopting an erect, facing upwards, posture that allowed contact with the open anthers.

Among the regular visitors, most records belong to non-obligate nectarivorous birds (table 1), with three tanagers (Thraupinae), *Tangara cayana*, *Thraupis sayaca* and *Dacnis cayana*, accounting for 65% of the recorded visits. Overall, eight species of tanagers accounted for 70% of the visits. In comparison, the five species of hummingbirds accounted for 25% of the visits.

Most visits were made by birds in the hanging posture (50%), meaning that half of the visits had a chance of providing pollen transfer to the inflorescences. All birds adopting this feeding posture were tanagers, except for one visit by the tyrannid *Elaenia flavogaster* (table 1). The observed tanagers, except for *Dacnis* and *Cyanerpes cyaneus*, have no special adaptations to feed on nectar, and are known to feed mainly on fruits and insects (Schubart *et al.* 1965, Isler and Isler 1987, Rodrigues 1995, Sick 1997). Even *Dacnis* and *Cyanerpes*, despite their long, slender bills pointing to an adaptation to nectar feeding, are known to include many insects and fruits in their diet (Schubart *et al.* 1965, Snow and Snow 1971, Sick 1997).

Tanagers visited the *Mabea* patch in mixed-species flocks of 10-20 birds, that arrived and departed together. *Dacnis cayana, Tangara cayana* and *Thraupis sayaca* were the most common species. These flocks sometimes fed on the flowers for more than an hour, activity on the patch being almost continuous as long as nectar was available. But the usual behavior was for the flock to come and go to the patch, alternating feeding periods with resting or foraging for other items in the nearby cerradão.

Although hummingbirds visits accounted for one-fourth of the visits, the fact they always fed while hovering, hardly contacting the female flowers (although sometimes touching the anthers), means they were robbing nectar rather than acting as pollinators (see also Vieira and Carvalho-Okano, 1996). In contrast to the tanagers, hummingbirds visited the patch as lone individuals, with rarely more than one bird on sight and usually only as passing individuals, a fact reflected in the few records of some species (table 1). The commonest species, *Hylocharis chrysura*, showed intra and inter-specific territorial behavior, which may have prevented access by other individuals. A similar pattern of visitation by hummingbirds and perching birds was reported for the inflorescences of *Norantea brasiliensis* (Marcgraviaceae) by Sazima *et al.* (1993).

Despite tanagers adopting the hanging posture in most (70%) visits, the remainder were probably ineffective in transferring pollen, as other postures were adopted. Perching visits were clearly instances of nectar robbing, while flying visits were aimed either to drink nectar or to capture insects that gathered on the inflorescences, as were some visits by *Elaenia chiriquensis*.

Vieira *et al.* (1992) and Vieira and Carvalho-Okano (1996) recorded 31 bird species feeding on nectar, including fourteen tanagers (Thraupinae and Coerebinae) and six hummingbirds; *Coereba flaveola* (Coerebinae), *Thraupis sayaca* (Thraupinae) and *Campylopterus macrourus* (formerly *Eupetomena macroura,* Trochilidae) were reported as the commonest visitors. It is very interesting that some seed-eating emberizids (*Sicalis flaveola, Sporophila caerulescens, Zonotrichia capensis*) and the omnivorous tyrannid *Pitangus sulphuratus* were recorded feeding on nectar by these authors, something we did not record at Assis despite the presence of those birds there.

Mammal Visitors. A group of coati *Nasua nasua* was observed feeding on nectar before we started this study. The coatis were first detected at 07:50 already moving atop the trees and inspecting the inflorescences. Nectar producing ones were held with both forepaws and licked, the coatis moving to another inflorescence after finishing the nectar. This behavior continued for eight minutes before our presence frightened them away. Inspection revealed no fresh inflorescences on the ground that could have been torn out by the coatis, confirming the gentle handling we had observed.

Although observations during the night were very limited, we were able to record 89 visits (i.e. bats alighting on or touching the flowers while hovering) between 22:17 and 23:17 h on 21 June, and 213 visits between 18:32 and 19:02 on 23 June, showing that visit rates can be quite high (up to 7 visits/min). In most visits (85%) one individual bat alighted on the inflorescence, bending the branch under its weight, and departed after 1-2 seconds. Observed bats always hanged on the inflorescence in full contact with the open anthers and stigmata (see photograph in Vieira and Carvalho-Okano 1996). The bat's weight frequently caused the branches with the inflorescences to bend, causing much nectar spillage.

Seven bats were captured, four *Artibeus lituratus* individuals, one *Chiroderma doriae*, one *Sturnira lilium*

Table 1. Bird species observed feeding on *Mabea fistulifera* nectar at Assis Experimental Station, São Paulo, and their feeding position per species and taxonomic group. Percentages are relative to total number of observations.

Species	Feeding position (%)			n (% observations)
	Flying	Perching	Hanging	
Trochilidae				
Phaethornis pretrei	3 (0.93)	–	–	3 (0.93)
Anthracothorax nigricollis	1 (0.31)	–	–	1 (0.31)
Calliphlox amethistina	3 (0.93)	–	–	3 (0.93)
Campylopterus macrourus	3 (0.93)	–	–	3 (0.93)
Hylocharis chrysura	28 (8.67)	–	–	28 (8.67)
Leucochloris albicollis	24 (7.43)	–	–	24 (7.43)
Melanotrochilus fuscus	19 (5.88)	–	–	19 (5.88)
Total	81 (25.08)	–	–	81 (25.08)
Tyranninae				
Elaenia flavogasrer	8 (2.48)	2 (0.62)	1 (0.31)	11 (3.41)
Elaenia chiriquensis	3 (0.93)	1 (0.31)	–	4 (1.24)
Total	11 (3.41)	3 (0.93)	1 (0.31)	15 (4.64)
Turdinae				
Turdus leucomelas	–	2 (0.62)	–	2 (0.62)
Total	–	2 (0.62)	–	2 (0.62)
Thraupinae				
Dacnis cayana	4 (1.24)	4 (1.24)	31 (9.60)	39 (12.07)
Cyanerpes cyaneus	–	–	2 (0.62)	2 (0.62)
Conirostrum bicolor	1 (0.31)	–	2 (0.62)	3 (0.93)
Tangara cayana	10 (3.10)	16 (4.95%)	65 (20.12)	91 (28.17)
Thraupis sayaca	8 (2.48)	21 (6.50%)	58 (17.96)	87 (26.93)
Thraupis palmarum	2 (0.62)	–	–	2 (0.62)
Nemosia pileata	–	–	1 (0.31)	1(0.31)
Total	25 (7.74)	41 (12.69)	159 (49.23)	225 (69.66)
All families total	**117 (36.22)**	**46 (14.24)**	**160 (49.54)**	**323**

and one *Glossophaga soricina*. Of these, three of the *Artibeus* had their faces, wings and belly fully covered with *Mabea* pollen, the *Sturnira* and the *Chiroderma* less so, and the remaining *Artibeus* had no visible pollen on them. Only *Glossophaga* is a specialized nectarivore able to feed while hovering, the others feeding mostly on fruit and occasionally on pollen and nectar (Emmons and Feer 1990, Redford and Eisenberg 1999). However, Sazima (1976) suggested visits of *Chiroderma doriae* to flowers, while Esbérard *et al.* (1996) captured one individual with pollen on its head, suggesting it had visited flowers.

Due to its large size, *Artibeus lituratus* may be recognized while in flight and during visits. These bats came to the *Mabea* grove in groups of 3-4 that flew together around the trees for a while before starting to feed, a behavior similar to that reported for other stenodermatine bats when feeding on flowers (Sazima and Sazima 1975). Bats would probe some inflorescences, touching them with the snout while briefly hovering in front of them before perching to feed. Feeding occurred in bouts of several visits in rapid succession interspaced by periods with no bats around.

DISCUSSION

Most visits to *Mabea fistulifera* inflorescences in the study area were made by frugivorous perching birds and bats with no special adaptation to nectar feeding, presumably these species were taking advantage of a locally abundant resource, predictable both in time and space, and available during a period when fruits are scarce or non-existent (see also Sazima and Sazima 1975). It is remarkable the fact that the commonest bird (*Thraupis* and *Dacnis* tanagers) and mammal (*Artibeus* fruit bats) visitors behaved in very similar ways while visiting the inflorescences, using the hanging posture and showing flocking behavior.

The use of nectar by frugivores as an alternative resource during periods of fruit scarcity has been reported in Neotropical rain forests (Terborgh 1986, Carthew and Goldingway 1997; see Mills *et al.* 1993 for a review). In the southeastern Brazilian mesophytic forests and in the cerrado fleshy fruits normally are scarce in the dry season (e.g. Dietz 1984, Morellato and Leitão-Filho 1992, 1996, Morellato 1995), favoring the use of *Mabea* nectar by vertebrates that are mostly frugivorous.

Besides being fed on by birds and bats, *Mabea* nectar has been considered a valuable dry-season resource for primates like *Brachyteles arachnoides*, *Callithrix flaviceps* (Ferrari and Strier 1992), *Cebus apella* (Torres de Assumpção 1981) and for *Didelphis* opossums (Vieira *et al.* 1991).

The continuous presence of birds and bats attending nectar-producing flowers and the high visit rates suggest that nectar is an important resource during the dry season, and may account for the presence of some species. Willis (1979) relates the seasonal occurrence of some hummingbird species in the mesophytic forests of São Paulo to the flowering of *Mabea fistulifera*, whereas Gonzaga (1983) suggests the presence of the threatened tanager *Dacnis nigripes* in the coastal lowlands of Rio de Janeiro to be linked to the flowering of *Mabea brasiliensis*. Vieira *et al.* (1992) also suggests that the presence of some birds (including tanagers) in their study area could be due to the flowering of *Mabea fistulifera*. Our record of a female *Cyanerpes cyaneus* in Assis may be related to the presence of flowering *Mabea* and *Eucalyptus* in the area, as this bird is known only as a rare winter visitor in São Paulo state, where it is recorded feeding on introduced *Eucalyptus* nectar and apparently returning to the same trees year after year (Willis and Oniki 1993).

Establishing and keeping *Mabea fistulifera* groves could serve as a management tool aiming to conserve populations of frugivore and nectarivore birds and other vertebrates in the remnant south-eastern Brazilian cerradão and mesophytic forests now reduced to fragmented and isolated remnants that are quickly losing their faunal diversity (see Willis 1979, Aleixo and Vielliard 1995 for a discussion on bird faunas).

Perhaps the most interesting aspect of the pollination ecology of *Mabea fistulifera* is the ability of the tree to harness such a diverse array of visitors, making the best even from impoverished faunas like the one found at Assis. Its morphology and abundant nectar production both attract and allow access to nectar-searching animals from bees to the largest Neotropical monkey, while the presence of latex assures that larger animals will avoid damaging or eating the inflorescences. Such use of non-specialist nectarivores like Thraupinae tanagers is remarkable. The diversity of pollinators this tree can use finds few matches among the Neotropical flora.

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