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Flowering phenology and pollination of ornithophilous species in two habitats of Serra da Bodoquena, Mato Grosso do Sul, Brazil

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ABSTRACT

The aim of this study is to describe interactions between hummingbirds and ornithophilous species at Serra da Bodoquena in midwest Brazil, with focus on flowering phenology and pollination of these plant species. In two habitats, gallery forest and semi-deciduous forest, data on flowering phenology of ornithophilous species were collected monthly over 14 months. In addition, data on morphology and floral biology, as well as visitor frequency and hummingbird behavior, were recorded. The studied community contained eight ornithophilous plant species and six hummingbird species. The ornithophilous species flowered throughout the year, and the greatest abundance of flowers was at the end of the rainy season and the beginning of the dry one. The hermit hummingbird *Phaethornis pretrei* and females of *Thalurania furcata*, were the most similar in floral resource use. Acanthaceae is the most representative family of ornithophilous plant species in Serra da Bodoquena and, thus, represents the main food source for hummingbirds. *Ruellia angustiflora* is especially important because it flowers continuously throughout the year and is a significant food resource for *P. pretrei*, which is the main visitor for this plant guild.

Key words: flowering, floral resources, hummingbirds, ornithophily, Acanthaceae, circular statistics.

INTRODUCTION

Phenology and pollination are two major factors in the reproductive biology of plant species (Rathcke and Lacey 1985). Phenology studies provide data on annual cycles and seasonal rhythms of individual plants, availability of community resources, and interactions between plants and animals that depend on these resources such as herbivores, pollinators and seed dispersers (Sarmiento and Monasterio 1983, Talora and Morellato 2000). Pollination studies have contributed with useful information regarding the degree of mutual dependence among species, reproductive ecology of plant communities, and resource supply for pollen vectors (Smith-Ramírez et al. 2005).

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Bird-pollinated or ornithophilous plants are usually characterized by having brightly colored (e.g. red or yellow) odorless flowers, tubular and evenly curved corollas, diurnal anthesis and sucrose-rich nectar (Faegri and Van der Pijl 1980). A common feature in ornithophilous communities is the occurrence of species that flower throughout the year, with little seasonal variation and reproductive asynchrony within a species (Wolf et al. 1976, Sazima et al. 1996). This phenological pattern is associated with long-lived pollinators that set fixed daily foraging routes (Gentry 1974).

Hummingbirds (Trochilidae) depend on nectar over most of their life cycles (Wolf 1970), and visit flowers to sustain their daily energy balance. The family Trochilidae comprises about 118 genera and 330 species, with 82 species currently identified in Brazil (Grantsau 1988). Extant hummingbirds are restricted to the Americas and represent 10% of the South American avifauna (Grantsau 1988). In the neotropics, hummingbirds are the main vertebrate pollinators (Bawa 1990) and may account for the pollination of two to 15% of angiosperms in a given community (Feinsinger 1983).

The interactions between hummingbirds and flowers in the state of Mato Grosso do Sul, midwest Brazil, are poorly known. Only one study, in the south Pantanal wetlands on naturally vegetated fragments ("capões"), has been conducted in this area (Araújo and Sazima 2003). Serra da Bodoquena is situated near south Pantanal and might function as a species source for the lowlands (Brown-Junior 1984). Therefore knowledge on hummingbird-flower interactions in the surroundings could add useful information in the wetlands as well. Thus, the goals of the present study were:

1. to identify the ornithophilous species in Serra da Bodoquena and to obtain data on their floral biology in two habitats: a riparian area and a semi-deciduous forest;
2. to record the flowering phenology and mean flowering date of the ornithophilous plant species;
3. to document which hummingbird species visit ornithophilous plants and to record visitation frequency;
4. to assess the similarity among hummingbird species regarding their use of ornithophilous species.

MATERIALS AND METHODS

Serra da Bodoquena is located in the mid-south region of the state of Mato Grosso do Sul, Brazil. This area is bordered by the Paraguay River Depression (Pantanal plain) to the north and west, the Miranda River basin to the east, and the Apa River basin to the south. Elevation ranges from 400 to 650 m (Boggiani and Coimbra 1995). The climate is tropical and warm – Aw (Köppen 1948), with average annual temperatures between 20 and 22°C. The rainy season extends from November to March, and total annual rainfall is roughly 1500 mm. The main physiognomies are cerrado (savanna), stationary deciduous forest, stationary semi-deciduous forest, and riparian forest.

Data were collected between July 2005 and August 2006 in the surrounding of Rancho Branco Farm, in the municipality of Bodoquena. Ornithophilous species (*sensu* Faegri and van der Pijl 1980) were sampled every month during four to five day excursions to two studied habitats: a riparian forest (RF) along the Salobrinha stream (20°41′03″S–56°47′11″W) and a semi-deciduous forest (SDF) (20°39′58″S–56°45′52″W). A 6000 m^2 belt transect (1000 m long × 6 m wide) was established in each of the habitats. Phenological data (number of flower buds and open flowers) were recorded monthly at predetermined individuals.

For half of the documented ornithophilous plant species (*Ruellia brevifolia*, *Ruellia angustiflora*, *Seemannia sylvatica* and *Lophostachys floribunda*), flowering phenology was observed in 20 individuals. Fewer individuals of the remaining plant species were observed (*Manettia rojasiana* and *Justicia ramulosa*: N = 5; *Ananas ananassoides*: N = 8; *Geissomeria tetragona*: N = 10) because these were the only individuals that were present in the sampling area.

For ornithophilous species with open flowers, their place of occurrence, habit, height, number of open flowers per day, corolla orifice diameter and length, and main color of calyx, corolla and bracts were recorded. The concentration of nectar solutes was measured using a pocket refractometer, and nectar volume was measured using micropipettes, both in previously bagged flowers (Dafni et al. 2005). Vouchers of all plant species were collected for identification and, then, housed in the herbaria of Campo Grande (CGMS/UFMS) and EMBRAPA – Embrapa Beef Cattle (CPAP).

Hummingbird visits to the flowers were generally recorded between 0800 h to 1100 h, and 1400 h to 1700 h. Hummingbirds were identified through direct observations, photographs, taken during the visits, and illustrated guides (Ruschi 1982, Grantsau 1988). For species with evident sexual dimorphism, males and females were treated separately. Time and frequency of visits (number of visits per number of observed flowers per hour) were recorded. Visits were also recorded as pollination (legitimate visitation, i.e., the hummingbirds made contact with the anthers and stigma) or nectar robbing (illegitimate visitation, i.e., no contact with anthers and stigma). Hummingbird behavior was also assessed during visitation. We sub-divide hummingbird visitors into the following categories: major visitor was designated for the hummingbird species with the highest visitation frequency that performed only legitimate visits; secondary visitor for those that visited flowers less frequently than the major visitor and performed both legitimate and illegitimate visits; and occasional visitor for those that performed sporadic legitimate and illegitimate visits, which were less frequent than those performed by major and secondary visitors.

Frequency of flowering throughout the year was plotted on a circular histogram. A Rayleigh test (Z) for circular distribution (software: Oriana 2.0, Kovach 2004) was used to calculate the mean flowering date for the guild of ornithophilous species and the concentration (r) of individuals around this mean (Morellato et al. 1989). The vector length in the graph is related to the concentration value that ranges from 0 to 1, and the mean angle of frequency distribution (mean date) is indicated by the arrow. The potential overlap of different hummingbird species in their use of floral resources was assessed by an analysis of clustered matched-pair data and a Jaccard's similarity index (Harmer et al. 2001).

RESULTS

Ornitophilous Species

Eight ornithophilous species were found in the study area; five of these belonged to the family Acanthaceae and three belonged to Gesneriaceae, Rubiaceae and Bromeliaceae. *Manettia rojasiana* (Rubiaceae) is a liana, whereas the other seven species are herbaceous (Table I). All ornithophilous species occurred in the understory and have a mean height that ranged from 0.2 to 1.2 m.

Ruellia angustiflora and *Seemannia sylvatica* were found exclusively in RF, and *Justicia ramulosa*, *Lophostachys floribunda* and *Ananas ananassoides* occurred only in SDF. *Ruellia brevifolia*, *Manettia rojasiana* and *Geissomeria tetragona* were present in both habitats.

The mean number of flowers opening daily ranged from 1.6 to 23.4 per individual. *Seemannia sylvatica* and *G. tetragona* produced the lowest means, in contrast to *M. rojasiana* that had the greatest number of flowers opened daily (Table I).

Phenology of Ornithophilous Species

Lophostachys floribunda, *A. ananassoides*, *G. tetragona* and *J. ramulosa* flowered within a specific period and, thus, can be considered annual (Fig. 1). Even though *S. sylvatica* and *M. rojasiana* had two flowering events during the study period (one in 2005 and another in 2006), these cycles did not occur in the same annual cycle and, hence, these species were also considered to be "annual" regarding the frequency of flowering episodes. *Ruellia angustiflora* was the only species flowering throughout the year, and *Ruellia brevifolia* was the sole species exhibiting a "sub-annual" flowering pattern (*sensu* Newstrom et al. 1994) (Fig. 1). Flowering was "brief" in *A. ananassoides*, "intermediate" in *L. floribunda*, *G. tetragona*, *S. sylvatica*, *J. ramulosa* and *M. rojasiana*, and "extended" in both Ruellia species (*sensu* Newstrom et al. 1994).

Guild Phenology

Circular analysis revealed that the mean flowering date of the ornithophilous species in the studied habitats is June 2nd (Fig. 2) ($Z = 30.94$; $p<0.001$), with moderate synchrony ($r = 0.44$). The greatest flowering frequency was recorded in July 2005 (28.91%) and in April and May 2006 (31.25% and 26.56%, respectively). The lowest frequencies were recorded in November (1%), December (3.13%) and January (3.13%) of 2005, and in July 2006 (4.69%) (Fig. 2).

Flower Density

The highest density of ornithophilous flowers (240 flowers per hectare) occurred in April in the SDF. No ornithophilous flowers were found in the SDF in September, November and December 2005, or in January and June 2006 (Fig. 3). The flowering peak in the RF was not pronounced, and the highest flower densities occurred in July (65 flowers per hectare), September (48 flowers per hectare) and December of 2005 (38 flowers per hectare), as well as in April (five flowers per hectare), May (58 flowers per hectare) and July of 2006 (45 flowers per hectare) (Fig. 3). No ornithophilous flowers were recorded in the RF area in October.

TABLE I
Habit, mean height, number of open flowers/individual/day, occurrence habitat, flower morphometric data, nectar concentration and nectar volume in the ornithophilous species sampled in two habitats of Serra da Bodoquena.

Family	Species	Habit	Height x ± sd (n)	Flowers x ± sd (n)	Habitat	Corolla color	Corolla shape x ± sd (n)	Corolla length x ± sd (n)	Corolla opening x ± sd (n)	Nectar concentration x ± sd (n)	Nectar volume x ± sd (n)
Acanthaceae	*Ruellia brevifolia* (Pohl) C. Ezcurra	Herbaceous	1.1 ± 0.49 (n=10)	3 ± 1.8 (n=10)	SDF/RF	Red	Tubular	28 ± 4.6 (n=8)	5.6 ± 2.2 (n=8)	10.8 ± 7.29 (n=8)	1.4 ± 1.3 (n=8)
	Ruellia angustiflora (Nees) Lindau ex Rambo	Herbaceous	1.2 ± 0.52 (n=9)	3 ± 2.18 (n=9)	RF	Red	Tubular	51.1 ± 3.8 (n=8)	4.8 ± 1.17 (n=8)	20.1 ± 2.25 (n=8)	8.3 ± 4.92 (n=8)
	Lophostachys floribunda Pohl	Herbaceous	1 ± 0.48 (n=6)	5.8 ± 5.35 (n=6)	SDF	Pink	Tubular	36.1 ± 8.07 (n=16)	3.8 ± 0.78 (n=16)	25.3 ± 2.91 (n=16)	11.88 ± 3.91 (n=16)
	Geissomeria tetragona Lindau	Herbaceous	0.6 ± 0.29 (n=5)	1.6 ± 0.89 (n=5)	SDF/RF	Red	Tubular	30 ± 5.35 (n=8)	3.8 ± 1.65 (n=8)	20.1 ± 2.81 (n=8)	11.3 ± 5.8 (n=8)
	Justicia ramulosa (Morong) C. Ezcurra	Herbaceous	0.4 ± 0.12 (n=3)	2 ± 1 (n=3)	SDF	Purple	Tubular	8.5 ± 2.12 (n=2)	3.3 ± 0.35 (n=2)	16 ± 4.24 (n=2)	3 (n=2)
Gesneriaceae	*Seemannia sylvatica* (Kunth) Hanst.	Herbaceous	0.2 ± 0.09 (n=12)	1.6 ± 0.9 (n=12)	RF	Red	Tubular	20.9 ± 1.86 (n=6)	5.9 ± 0.79 (n=6)	14 ± 2.28 (n=6)	11.7 ± 7.63 (n=6)
Rubiaceae	*Manettia rojasiana* Chodat and Hassl.	Liana	1.5 ± 0.66 (n=5)	23.4 ± 32.53 (n=5)	SDF/RF	Red/Orange	Tubular	19.2 ± 5.88 (n=10)	5.2 ± 5.23 (n=10)	7.8 ± 10.14 (n=10)	2.4 ± 2.99 (n=10)
Bromeliaceae	*Ananas ananassoides* (Baker) L.B.Sm.	Herbaceous	0.2 ± 0.05 (n=6)	4 ± 1.67 (n=6)	SDF	Pink	Tubular	24.5 ± 1.52 (n=6)	4.3 ± 1.1 (n=6)	27.3 ± 0.55 (n=6)	114.8 ± 16.25 (n=6)

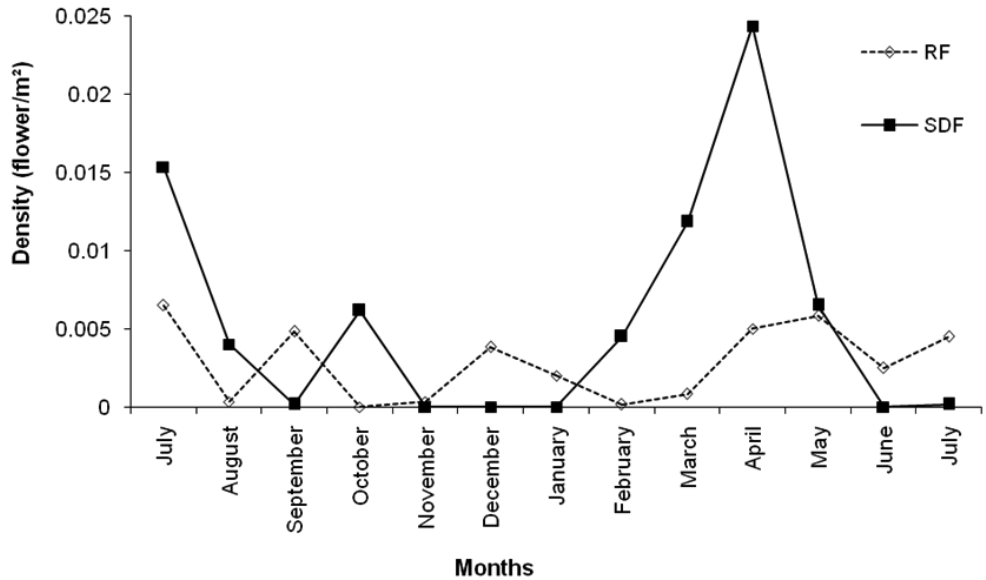

Fig. 1 – Flowering periods (■) of eight ornithophilous species from two habitats in Serra da Bodoquena from June 2005 to July 2006.

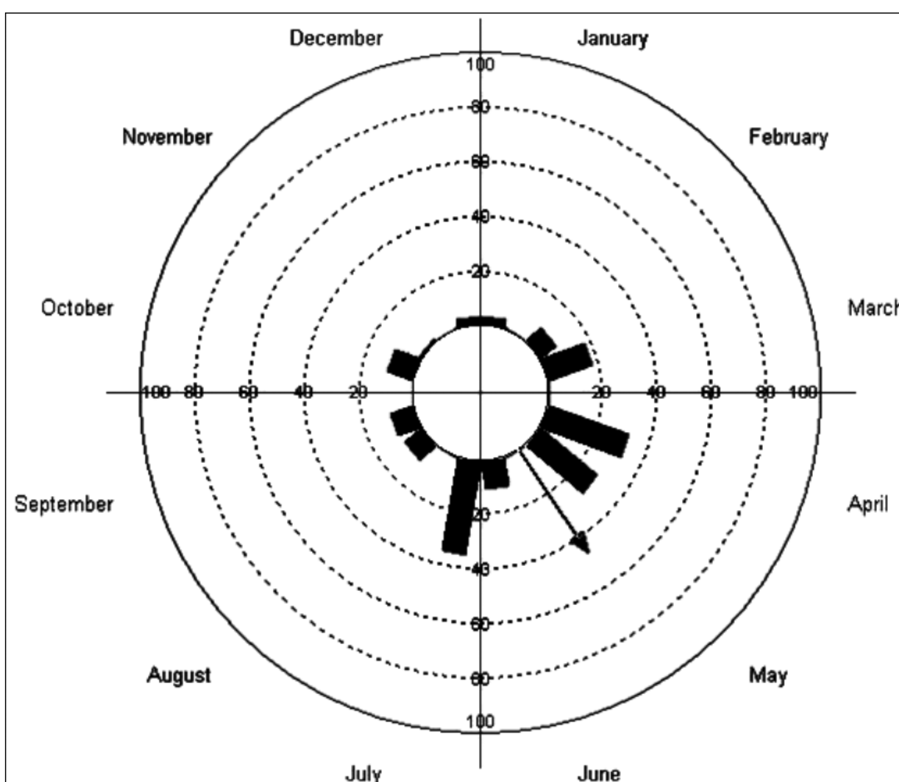

Fig. 2 – Cumulative circular histogram for flowering periods of ornithophilous species in two habitats of Serra da Bodoquena from June 2005 to July 2006. The axis indicates frequency scale, and the bars indicate the frequency of flowering individuals in the guild of ornithophilous species in every month. The arrow indicates mean flowering date.

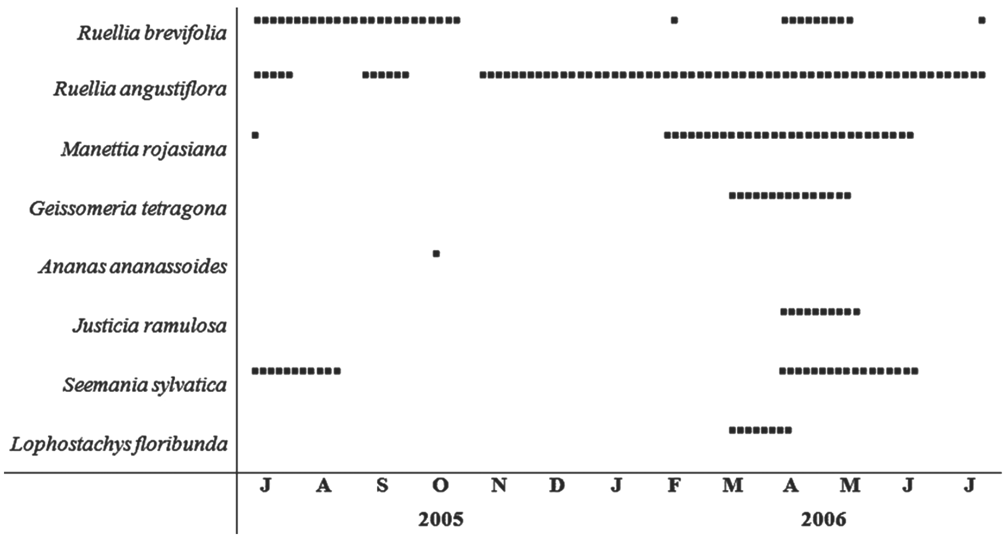

Fig. 3 – Flower density in riparian and semi-deciduous forests at Serra da Bodoquena from June 2005 to July 2006.

Flower Morphology and Nectar

The recorded species had tubular corollas, which were mostly red (*R. brevifolia*, *R. angustiflora*, *S. sylvatica* and *G. tetragona*) or red and orange (*M. rojasiana*). *Lophostachys floribunda* and *A. ananassoides* were pink, and *J. ramulosa* was purple. Mean corolla length ranged from 8.5 mm in *J. ramulosa* to 51.1 mm in *R. angustiflora* (Mean = 30.3 ± 11.66, N = 64). Mean corolla orifice diameter was 3.3 mm in *J. ramulosa* and 5.9 mm in *S. sylvatica* (Mean = 4.5 ± 2.39, n = 64). The highest nectar volume and concentration was recorded in *A. ananassoides*, whereas the lowest nectar volume was recorded in *R. brevifolia* and the lowest nectar concentration in *M. rojasiana* (Table I). Mean nectar concentration in the community was 20.9 ± 5.16% (N = 59), and mean nectar volume was 26.6 ± 53.84 μL (N = 59).

Flower Visitors

Six hummingbird species were recorded in the study area, one being the hermit (Phaethornithinae) *Phaethornis pretrei* (Lesson and Delattre 1839) and the five remaining being the trochilids (Trochilinae) *Hylocharis chrysura* (Shaw 1812), *Aphantochroa cirrochloris* (Vieillot 1818), *Amazilia versicolor* (Vieillot 1818), *Thalurania furcata* (Gmelin 1788) and *Chlorostilbon lucidus* (Shaw 1812).

The hermit *P. pretrei* was the main visitor of flowers in the community. It visited seven of the eight ornithophilous species recorded (i.e., all except *L. floribunda*) and always performed legitimate visits. *Phaethornis pretrei* was the major visitor of *R. angustiflora*, *R. brevifolia*, *S. sylvatica* and *G. tetragona*, and the secondary visitor of *A. ananassoides*, *M. rojasiana* and *J. ramulosa* (Table II).

Females of *T. furcata* were frequent visitors to five ornithophilous species (Table II). They were the major visitors of *A. ananassoides* and *M. rojasiana*, and the secondary visitors of *R. angustiflora*, *S. sylvatica* and *G. tetragona*.

The Trochilinae *H. chrysura*, which visited three ornithophilous species, was the only hummingbird that visited *L. floribunda* and was a sporadic visitor to *R. angustiflora* and *G. tetragona* (Table II). It behaved as a nectar robber of *R. angustiflora* flowers and as a legitimate visitor to the other two species.

Amazilia versicolor and males of *T. furcata* visited flowers of two species each (Table II). *Amazilia versicolor* was the major visitor to *J. ramulosa* and a sporadic visitor to *M. rojasiana*; it always performed legitimate visits. Males of *T. furcata* were sporadic visitors to *R. angustiflora* (as nectar robbers or legitimate visitors) and to *M. rojasiana* (as legitimate visitors). *Aphantochroa cirrochloris* performed legitimate and sporadic visits to *R. angustiflora* flowers (Table II).

The hummingbird *P. pretrei* visited grouped and sparse flowers in foraging bouts at regular 40-60 min

TABLE II
Frequency of hummingbird visitation to the ornithophilous species (number of visits/number of observed flowers/hour) during 8166 min of observation in two habitats (Riparian and semi deciduous forests) of Serra da Bodoquena. (l = legitimate visitation, i = illegitimate visitation).

	Phaethornis pretrei	*Thalurania furcata* male	*Thalurania furcata* female	*Hylocharis chrysura*	*Aphantochroa cirrochloris*	*Amazilia versicolor*	Duration (min)
Ruellia brevifolia	5.82 (l)	/	/	/	/	/	550
Ananas ananassoides	1.68 (l)	/	9.18 (l)	/	/	/	205
Ruellia angustiflora	1.62 (l)	0.006 (i)	0.42 (l/i)	0.006 (i)	0.06 (l)	/	2826
Seemannia sylvatica	1.56 (l)	/	0.36 (l/i)	/	/	/	1775
Manettia rojasiana	0.6 (l)	0.12 (l)	3.42 (l)	/	/	0.12 (l)	1162
Geissomeria tetragona	4.08 (l)	/	2.94 (l)	0.36 (l)	/	/	536
Lophostachys floribunda	/	/	/	7.26 (l)	/	/	1067
Justicia ramulosa	11.4 (l)	/	/	/	/	17.16 (l)	45

intervals. Females of *Thalurania furcata* defended territories around *M. rojasiana* and *R. angustiflora* flowers, but also visited *G. tetragona*, *A. ananassoides* and *S. sylvatica* flowers in regular 40-50 min intervals. *Hylocharis chrysura* defended territories around *L. floribunda* flowers, and occasionally visited *G. tetragona* and *R. angustiflora*. The hummingbirds *Ap. cirrochloris* and *Am. versicolor* were observed sporadically in the study area defending territories around *R. angustiflora* and *M. rojasiana*. Males of *T. furcata* were recorded sporadically visiting *M. rojasiana* and *R. angustiflora* flowers.

Hummingbirds exhibiting high similarity in the use of the ornithophilous flowers were *P. pretrei* and females of *T. furcata*, followed by *Am. versicolor* and males of *T. furcata* (Fig. 4).

DISCUSSION

Ornithophilous Species

The predominance of ornithophilous species from Acanthaceae at Serra da Bodoquena was similar to that found in communities of ornithophilous species in Mexico (Toledo 1975) and in a forest fragment in southeastern Brazil (Abreu and Vieira 2004), where most ornithophilous species were from Acanthaceae and Rubiaceae. In Atlantic and Amazonian rainforest areas, the most representative ornithophilous families are Rubiaceae, Gesneriaceae and Bromeliaceae (e.g. Snow and Snow 1980, Sazima et al. 1996, Lasprilla and Sazima 2004). However, in the south Pantanal, there is no predominance of any botanical family (Araújo and Sazima 2003).

The high proportion of herbaceous species in the studied community is influenced by Acanthaceae, which are all herbaceous and account for 63% of the sampled plants. Other studies on ornithophilous communities report a marked predominance of epiphytes and shrubs (Arizmendi and Ornelas 1990, Sazima et al. 1996), which may be affected by the habits of the plant families that are most frequent at those sites.

The richness of six ornithophilous species recorded in Serra da Bodoquena was comparable to that recorded in the "capões" of Pantanal (Araújo and Sazima 2003). However, richness in other localities ranged from 15 (Arizmendi and Ornelas 1990) to 50 species (Stiles 1978). Comparisons with neighboring communities could explain the differences of predominance in habits and families, as well as the richness patterns here found. However, hummingbird-flower interactions have been insufficiently studied in and around the research area.

Phenology of the Ornithophilous Species

Most ornithophilous species had annual flowering patterns of intermediate duration. This suggests that these plants may have some degree of seasonality regarding flowering phenology. Given that the sampled plants are, in general, herbaceous, their response to environmental changes may be rapid and highly dependent upon water availability (Sarmiento and Monasterio 1983, but see Borchert 1983). Because climatic data for the studied area are non-existent, it was not possible to assess whether water availability triggers flowering in the recorded species. Moreover, this study was performed

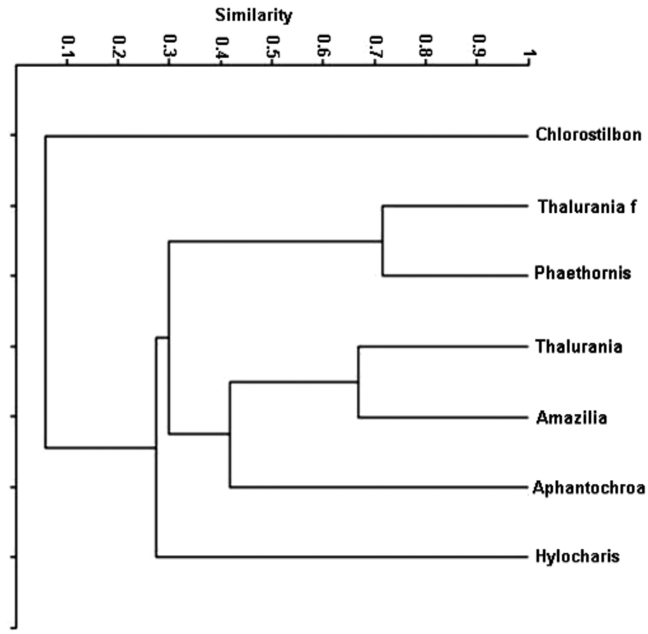

Fig. 4 – Cluster analysis representing the similarity (Jaccard's index) among the hummingbird species (*Chlorostilbon lucidus*, male and female of *Thalurania furcata*, *Phaethornis pretrei*, *Amazilia versicolor*, *Aphantochroa cirrochloris* and *Hylocharis chrysura*) concerning their use of floral resources in two habitats of Serra da Bodoquena.

over the course of a single year, yet good knowledge of phenological patterns necessarily requires study over several years (D'Eça-Neves and Morellato 2004).

Guild Phenology

The concentration value (r) determined by circular analyses indicates moderate synchrony among the individuals in the community, i.e., resources are regularly available for hummingbirds throughout the entire year. In addition, according to the classification of Newstrom et al. (1994) that is based on the frequency of flowering events in a guild, the flowering of ornithophilous species is deemed continuous in the studied community. This continuous flowering is characterized by flowering throughout the year with short, sporadic absences of flower availability. Despite the low richness of ornithophilous species, flowers were available throughout the year, thereby ensuring the availability of resources for hummingbirds at the study site. This is critical to the hummingbirds because they have a long life cycle and, thus, require resources throughout the year in order to supply their daily energy demands (Wolf 1970, Gentry 1974, Stiles 1975). However, differences in flower availability between habitats occurred, and in months of flower absence in a given habitat (e.g. October in RF), hummingbirds must make local migrations searching for flowers in other habitats.

Flower Density

The production of flowers and buds was more pronounced at the end of the rainy season and at the beginning of the dry season than at other times, as shown by the Rayleigh test (Z). Flowering events of ornithophilous plants in the dry season may be especially attractive to hummingbirds because such events are generally fewer than those in the rainy season, when more floral resources are expected to be found in the community (Sarmiento and Monasterio 1983) and when hummingbirds may use non-ornithophilous species more often than ornithophilous ones. In fact, hummingbirds can visit both flower types, despite their particular pollination adaptations (Araújo and Sazima 2003). For instance, six non-ornithophilous species in SDF and one in RF are known to be visited by hummingbirds (L.C. Rodrigues, personal communication). Another advantage that dry season flowers may have is the lack of heavy rains that harm or cause flowers and buds to fall, as observed in *Ruellia angustiflora* in the study area. In addition, leaf

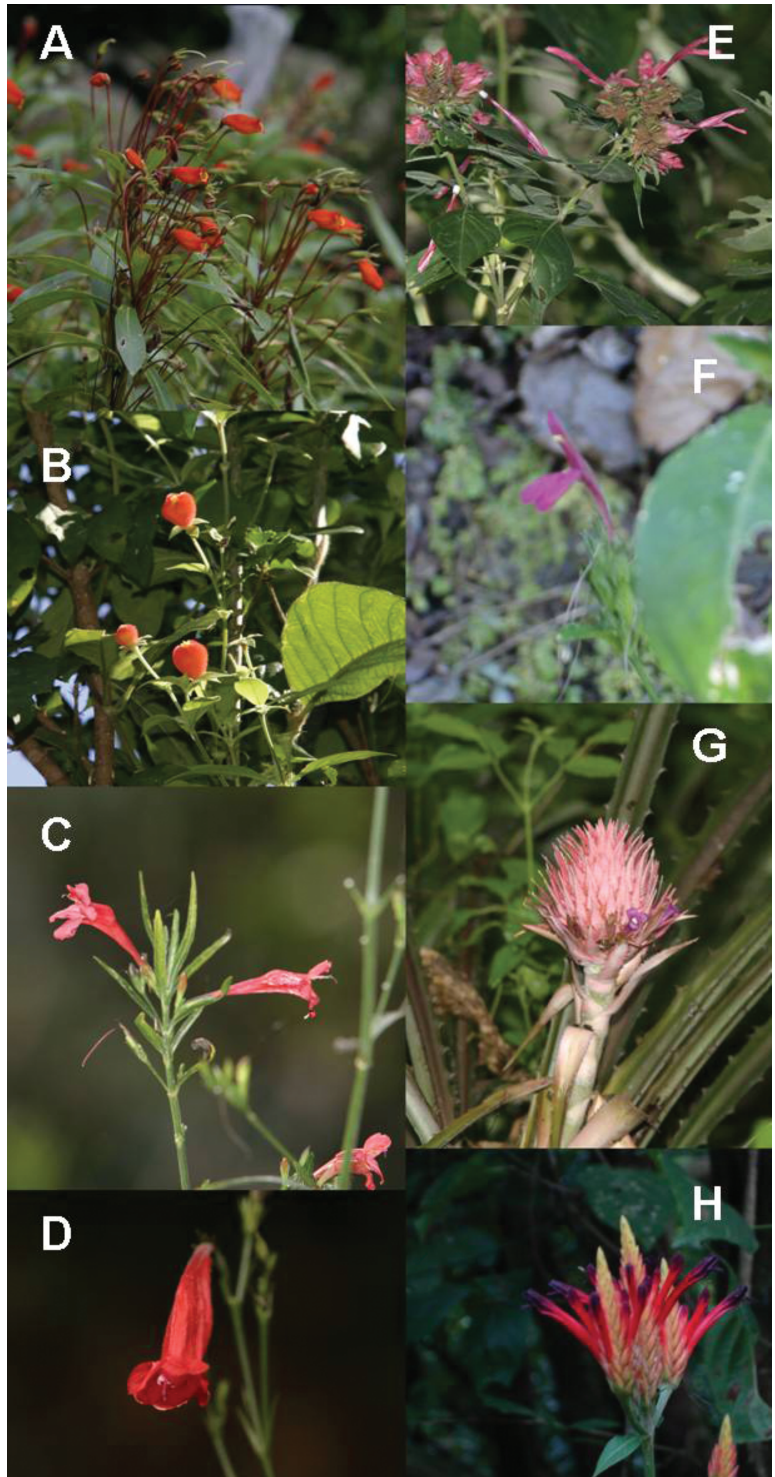

Fig. 5 – Ornithophilous species recorded at Serra da Bodoquena: A) *Seemannia sylvatica*, B) *Manettia rojasiana*, C) *Ruellia angustiflora*, D) *Ruellia brevifolia*, E) *Lophostachys floribunda*, F) *Justicia ramulosa*, G) *Ananas ananassoides*, and H) *Geissomeria tetragona*. Pictures by Eduardo Camargo (A, B, C, D, E, G) and Rogério Rodrigues Faria (F, H).

fall in the dry season increases flower visualization and favors the pollinator activity (Janzen 1967). In contrast to these results, other Brazilian neotropical communities with weak (e.g. Sazima et al. 1996, Buzato et al. 2000) or marked seasonality (Araújo and Sazima 2003) have higher flower density at the beginning of and throughout the rainy season.

Flower Morphology and Nectar

Characteristics of corolla coloration and shape, nectar volume and concentration, and floral morphometry in the ornithophilous species from Serra da Bodoquena are similar to those described in other neotropical areas. In these areas, the mean corolla length of ornithophilous species varied from 6.7 mm (e.g., Vasconcelos and Lombardi 2001) to 100-115 mm (e.g. Araújo and Sazima 2003) and corolla orifice diameter from 1.8 mm (e.g. Smith et al. 1996) to 20 mm (e.g. Temeles et al. 2002). Thus, species from the studied community had flowers with short to moderate corolla lengths and narrow widths, compared to these previously reported values. Nectar amount in neotropical ornithophilous species is commonly high (ranging on average from 15 to 123 μl), with diluted concentration (22-26% of sugar; Howe and Westley 1997, McDade and Weeks 2004). In contrast, ornithophilous species in Serra da Bodoquena have low nectar volumes and reduced nectar concentrations.

Floral Visitors

In the present study, four of the 11 hummingbird species reported at Serra da Bodoquena during an avian survey (Pivatto et al. 2006) were recorded during the present study. This survey included 24 sites in the counties of Bonito, Jardim, Bodoquena and Porto Murtinho, and involved over 500 h of sampling effort and literature data. The other two hummingbird species recorded here, *Aphanthocroa cirrochloris* and *Chlorostilbon lucidus*, had not previously been recorded at Serra da Bodoquena. Following a list of Pantanal birds (Tubelis and Tomas 2003), *Ap. cirrochloris* was the only species not observed in the lowlands as well. The other species were recorded in both the north and south Pantanal.

The hermit *P. pretrei* is the major visitor of the studied community in terms of number of visited species, frequency and mode of visitation (mainly legitimate). This result differs from that recorded in natural fragments of the Pantanal (Araújo and Sazima 2003), where *Hylocharis chrysura* was the major visitor.

The community roles of "high-reward trapliner", "low-reward trapliner", "territorial", and "generalist" (*sensu* Feinsinger and Colwell 1978) were fulfilled by the hummingbirds visiting the ornithophilous flowers in the studied community. The hummingbird *P. pretrei* was both a high- and low-reward trapliner because of the corolla lengths and nectar offer in the visited flowers; and it visited flowers in foraging bouts at regular intervals. This visiting behavior, as already described for these species in other sites (Sazima 1981, Machado and Sazima 1987, Piratelli 1997, Vasconcelos and Lombardi 2001), promotes cross-pollination. However, intra and interspecific antagonistic interactions of *P. pretrei* were also observed, especially when it visited patches of *R. angustiflora*. These patches occasionally contained a large number of flowers (around 100 flowers/patch) that attracted many hummingbirds. Records of antagonistic behavior in the Phaethornithinae family are uncommon and have been described in only a few studies (e.g. Sazima et al. 1995).

Hylocharis chrysura and females of *T. furcata* behaved either as territorial or low-reward trapliners. *Aphantochroa cirrochloris*, *Am. versicolor*, and males of *T. furcata* were considered generalists because they visited sparse flowers sporadically and used flower patches that were unguarded by other hummingbirds. The community roles described here were not fixed for a given hummingbird species. This indicates that the visiting behavior of these birds is closely related to resource availability rather than morphological characteristics, as wing disc loading (ratio of body weight to a circle whose diameter is wing span; Feinsinger and Colwell 1978), body size, bill morphology and feet size. This situation was suggested by Feinsinger and Colwell (1978) and is often described in other communities (Sazima et al. 1996, Buzato et al. 2000). Moreover, the hummingbirds reported in the present study are nomadic, have a generalist use of floral resources, and are broadly distributed (Ruschi 1982, Grantsau 1988).

Phaethornis pretrei and females of *T. furcata* displayed the greatest similarity in species of plant(s) they visited. This high degree of overlap in resource use involving one Phaethornithinae and one Trochilinae has been observed in other Brazilian communities. Piacentini and Varassin (2007) described the pair *Ramphodon naevius* and *Thalurania glaucopis* in a study on bromeliad-hummingbird interaction in southern Brazil. Sazima et al. (1996) and Buzato et al. (2000) recorded the pair *Phaethornis eurynome* and *Leucochloris albicollis* in an area of Atlantic forest in southeastern Brazil. This indicates that morphology alone does not account for hummingbird organization in a given community. Instead, organizational patterns are better explained by morphological-behavioral attributes together with resource availability and hummingbird vagility, i.e., permanence time, in a given environment (Feinsinger and Colwell 1978).

In conclusion, Acanthaceae is the most representative ornithophilous family in Serra da Bodoquena. It includes the greatest number of species that provide resources to the hummingbirds and, along with other ornithophilous families, flowers throughout the year. The period of the highest abundance of floral resources is at the end of the rainy and beginning of the dry season. For this plant guild, the hermit *P. pretrei* is the major visitor, and *R. angustiflora* is an important food source because it flowers continuously throughout the year.

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RESUMO

O objetivo deste estudo é descrever as interações entre beija-flores e espécies ornitófilas na Serra da Bodoquena na região Centro-Oeste do Brasil, com foco na fenologia de floração e polinização destas espécies vegetais. Em dois habitats, mata ciliar e floresta semi-decídua, dados de fenologia de floração de espécies ornitófilas foram coletados mensalmente ao longo de 14 meses. Além disso, dados de morfologia e biologia floral bem como a frequência dos visitantes e o comportamento dos beija-flores foram registrados. A comunidade estudada contém oito espécies de plantas ornitófilas e seis espécies de beija-flores. As espécies ornitófilas floresceram todo o ano, e a maior abundância de flores foi no final da estação chuvosa e início da seca. O beija-flor eremita *Phaethornis pretrei* e a fêmea de *Thalurania furcata* foram os mais similares no uso dos recursos florais. Acanthaceae é a família mais representativa das espécies vegetais ornitófilas na Serra da Bodoquena e representa a principal fonte de recurso para os beija-flores. *Ruellia angustiflora* é especialmente importante porque floresce continuamente ao longo do ano e é uma importante fonte de recurso para *P. pretrei*, que é o principal visitante floral para esta guilda de plantas

Palavras-chave: floração, recurso floral, beija-flores, ornitofilia, Acanthaceae, estatística circular.

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