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Floral traits as potential indicators of pollination *vs.* theft

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Abstract

Floral visitation does not necessarily mean pollination, as several animals utilize floral resources without transferring pollen. Since pollinators and thieves can affect the reproduction, morphology and diversification of flowering plants, we here investigated if attributes of flowers and flowering of plant species collected in the central Brazilian *vereda* would predict the pollination (pollen seeking) or theft (pollen/nectar theft) during the visits. It was hypothesized that non specialized flowers would have a higher incidence of thievery, where as specialization, for example, the presence of large and medium flowers with long corolla, making it difficult to access nectar, would lead to increased pollination. As a result, four attributes were mainly associated with illegitimate visits, and in order of importance, they are size (small), quantity of flowers per plant (large), flowering time (< 10 months) and floral type (inconspicuous). The richest and most abundant visitor groups, including bees, flies and wasps, acted mainly as potential pollinators, while cockroaches, butterflies, beetles, ants and hemipterans acted as thieves. However, further studies are required to confirm that this pattern is repeated in other larger and more diverse communities, thus confirming the possible preference for floral thieves.

Key words: *vereda*, bees, anthophilous fauna, flowering, generalist flower.

Resumo

Tipos florais de plantas como potenciais indicadores da ocorrência de polinização *vs.* pilhagem. A visitação floral não é sinônimo de polinização, vários animais utilizam recursos florais sem transferir pólen. Essas visitas podem ser consideradas pilhagem. Polinizadores e pilhadores podem afetar a diversificação morfológica, taxonômica e reprodutiva das espécies de plantas, e nós investigamos se os atributos florais e de floração das espécies de plantas amostradas em vegetação de *vereda* nos dariam evidência de visitas de polinização (transporte de pólen) ou de pilhagem (roubo de néctar/pólen). Esperamos que as flores não especializadas tenham uma maior incidência de pilhagem, enquanto flores especializadas, por exemplo com tamanho grande e médio e corolas longas, com néctar menos acessível, tenderiam a ser polinizadas e menos pilhadas. Quatro atributos foram associados principalmente com visitas ilegítimas, tamanho da flor (pequeno), quantidade de flores por planta (muitas flores), tempo de floração (<10 meses) e tipo floral (inconspícuo). Os grupos mais ricos e mais abundantes de visitantes, incluindo abelhas, moscas e vespas, atuaram principalmente como potenciais polinizadores, enquanto baratas, borboletas, besouros, formigas e hemípteros atuaram como pilhadores. No entanto, mais estudos são necessários para confirmar se esse padrão se repete em outras comunidades maiores e mais diversificadas, confirmando assim a eventual preferência dos pilhadores.

Palavras-chave: *vereda*, abelhas, fauna antófila, floração, flor generalista.

Introduction

Mutualistic relationships occur in all ecosystems and contribute to the generation and maintenance of diversity in different habitats or communities (Rech & Brito 2012). These interactions can be categorized as trophic, defensive or dispersive, as well as obligate or facultative (Ricklefs 2001; Thompson 2005). Interactions between flowers and the animals that visit them are an example of dispersive

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mutualism. In this case, animals obtain floral resources, *e.g.*, nectar, resins, or oils, and, in return, transport and disperse pollen between flowers and plants, thus performing pollination (Rech & Brito 2012).

Pollination units, such as flower blossoms or inflorescences (sensu Faegri & van der Pijl 1979), are visited by a large variety of floral visitors (Faegri & van der Pijl 1979; Corlett 2004). Importantly, however, flower visitation does not necessarily mean pollination (Waser *et al*. 1996; Waser *et al*. 2015). Thus, in some cases, only floral visitors reap benefits since they are not all effective pollinators (Inouye 1980; Strauss & Whittall 2006; Irwin *et al*. 2010). In this sense, floral visitors can either act as pollinators or thieves, indicating that these mutualistic and antagonistic interactions are part of a continuum and that visitor species can have multiple behaviors within their respective repertories (Rech & Brito 2012). Within such continuum, flower morphology is fundamental because floral traits can restrict access to floral resources and thus prevent visits from the antagonists visits (Olesen *et al*. 2007; Vázquez *et al*. 2009).

Therefore, within a community, plant species compete for pollination services (Waser 1983), but also present barriers against would be thieves (Gonzálvez *et al*. 2013). In this sense, the floral or flowering traits of a given species derive from a set of distinct selective pressures when pollinators and thieves may share the same preferences. Althought we have clues on selection pressure exerted by thieves (Strauss & Whittall 2006), few studies have explored the relative selection pressure of this group or its floral preferences (*e.g.*, Maruyama *et al*. 2015). Furthermore, while robbers may negatively influence plant reproduction by reducing floral attractiveness to pollinators, they may also have a positive influence by either increasing the number of flowers the pollinators must visit or by increasing travel distances to obtain their daily energy requirements (Irwin *et al*. 2010; Maruyama *et al*. 2015).

Since pollinators and thieves can affect the morphology and diversification of plants (Strauss & Whittall 2006), as well as reproduction, we herein investigated whether attributes of flowers and flowering of plant species collected in the central Brazilian *vereda* would be useful to predict pollinating or antagonistic visits. To accomplish this, we conducted a survey of floral visitors and verified their pollination performance on the sampled species. We considered some floral attributes as less specialized, *e.g.*, small nectariferous flowers, with resources accessible to all visitors, assembled in collective or congested pollination units, and produced in large quantity. We hypothesized that such attributes would tend to be less restrictive and thus allow the indiscriminate visitation of several groups of visitors, or generalists, to the floral resources, thereby increasing the chance of antagonistic visits.

Material and Methods

Study area

This study was carried out from September 2012 to August 2013 in a *vereda* wetland of the Área de Proteção Ambiental (APA) Guariroba (20º32’39’’S, 54º23’54’’W), which supplies water to the urban area of Campo Grande, Mato Grosso do Sul, Brazil, and is located 35 km to the north (Dias 2005) (Fig. 1a). The study area consists of approximately 1.44 ha and is surrounded by pasture, cerrado stricto sensu, cerrado woodland and eucalyptus. Typical of *vereda* vegetation, the palm *Mauritia flexuosa* is the most abundant tree in the area (Fig. 1b).

The study area consists of three distinct stages: an outer part with an open grassland, an intermediate shrubland, and an innermost part with tree species. In the innermost part, the water table is lower, and running water is found, as well as humid soil (Fig. 1b).

The climate of the region is tropical Aw (Köppen 1948), with a warm and rainy season from October to March, a warm and dry period from April to September, and a transitional season in July. Annual rainfall is approximately 1400 mm, with mean temperatures ranging from 21 and 26ºC (Vilas Boas *et al*. 2013).

Sampling

Fieldwork was conducted monthly in eight fixed plots of 50 m × 3 m (10 m apart), crossing the *vereda* in a westerly direction (Fig. 1c). Sampling of the diurnal floral visitors was conducted on all flowered plants between 07h30 and 17h30. Each flowering plant found in the transect was sampled for ten minutes; however, sampling time depended on species occurrence and abundance, resulting in an observation time for each individual ranging from 10 to 9900 minutes (565.66 ± 846.26) (Tab. 1).

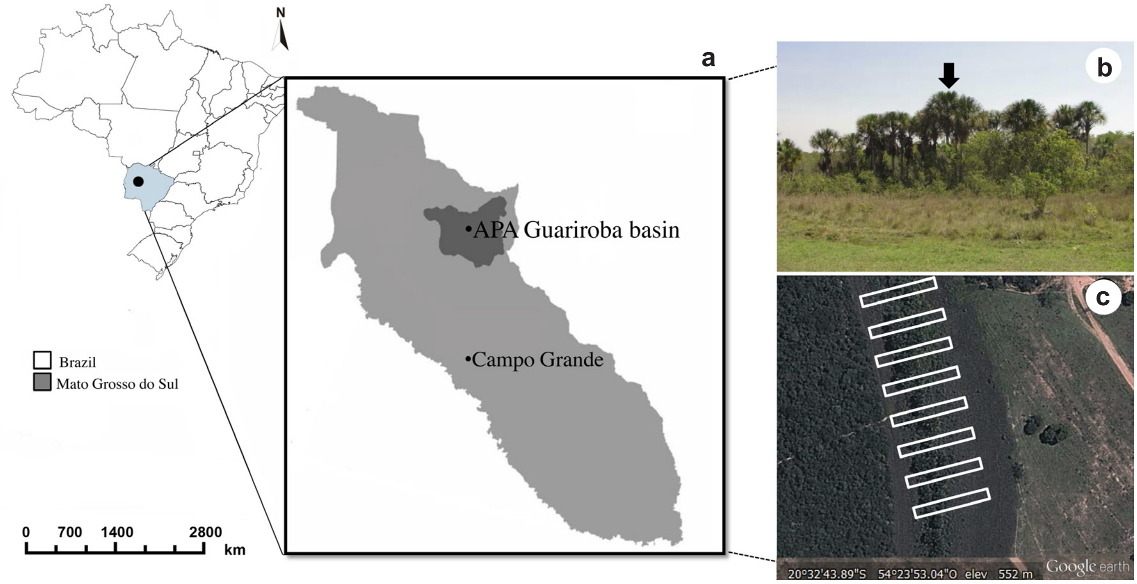

Figure 1 – a. Map of the Área de Proteção Ambiental (APA) Guariroba, Campo Grande, Mato Grosso do Sul, Brazil. b. front view of vegetation of the studied *vereda* wetland, showing the "buriti" palm *Mauritia flexuosa* (arrow), a typical vegetation type of this area, in the background. c. aerial view showing the approximate distribution of plots in the study area (source: Google Earth).

We excluded Poaceae spp., which are generally anemophilous (sensu Faegri & van der Pijl 1979; Proctor *et al*. 1996). Most sampled species have herbaceous habit (47%), followed by sub-shrubs (19%), shrubs (16%), trees (12%) and climbers (7%) (sensu Guedes-Bruni *et al*. 2002). Vouchers of the sampled plant species were collected, dried, identified and deposited in the Herbarium CGMS of the Universidade Federal de Mato Grosso do Sul, Campo Grande (Tab. 1). Botanical identification was achieved after consulting a specialized bibliography, the herbarium CGMS, and specialists. Plant names followed APGIII (2009) and Mobot (2011).

For all species, the following attributes were verified: number of flowering months, number of flowers per individual, organization (solitary flowers or assembled in inflorescences) and dimension (large: >10 mm; medium: >5 mm and <10 mm; small: <5 mm) of the pollination units (visited flower or inflorescence), main color (yellow, blue, white, brown, pink, purple, green), symmetry (actinomorphic, zygomorphic). Following this analysis, the flowers were classified into floral types as described in Machado & Lopes (2004) (Tab. 1).

During the study period, we recorded only insects in pollination units. These insects were collected with entomological nets and kept in glass jars with ethyl acetate or alcohol 70%. Later, they were pinned or stored in alcohol, morphotyped and sent to specialists for identification. Classification of insect groups followed Corlett (2004). Performance of the floral visitor as a pollinator was determined through observations of intrafloral behavior, analysis of photographic records, floral morphology and/or the size relationship between flower and visitor. The visitor was considered a potential pollinator when it touched anthers to receive pollen and stigma to deposit it. The visitor was considered a thief of pollen or nectar (sensu Inouye 1980; adapted as described in Irwin *et al*. 2010) if it did not show such behavior while collecting floral resource. Specimens of floral visitors were deposited in the Zoological Collection of the Universidade Federal de Mato Grosso do Sul (ZUFMS), Museu de Zoologia of Universidade de São Paulo (MZUSP), Museu de História Natural/Zoologia of Universidade Federal da Bahia (MHNBA/MZUFBA) and private collections of some taxonomists (*e.g*., Ayr de Moura Bello).

Table 1 – Plant species, habit, flowering time, floral traits, size of flowers, pollination unit, symmetry, color, resource, observation time and CGMS number recorded in a *vereda* vegetation, Campo Grande, Mato Grosso do Sul, Brazil, from September 2012 to August 2013. Habit: A = arboreal, S = shrub, H = herb, Sb = sub-shrub, C = climbing; Floral traits: D = dish; T = tube, G = gullet, In = inconspicuous, F = flag; Size of flower: S = small, B = big, M = medium; Pollination unit: F = flower, Inf = inflorescence; Symmetry: Ac = actinomorphic, Z = zigomorphous; Resource: N = nectar, P = pollen; CGMS = Herbarium CGMS. * = plant species with nocturnal anthesis.

Species	Habit	Flowering time	Floral traits	Size of flower	Pollination unit	Symmetry	Color	Resource	Observation time (minutes)	CGMS number
Alismataceae										
Echinodorus longipetalus Micheli	H	1	D	B	F	Ac	white	P	10	38665
Sagittaria rhombifolia Cham.	H	7	D	B	F	Ac	white	P	180	38648
Alstroemeriaceae										
Alstroemeria longistyla Schenk	H	1	T	B	F	Ac	white	N	10	38658
Apiaceae										
Eryngium ebracteatum Lam.	H	4	In	Sm	Inf	Ac	purple	N	60	38659
Aquifoliaceae										
Ilex affinis Gardner	A	10	D	Sm	F	Ac	white	N	9900	38637
Araceae										
Urospatha sagittifolia (Rudge) Schott	H	1	In	Sm	Inf	Ac	brown	P	20	38663
Asteraceae										
Achyrocline alata (Kunth) DC.	H	3	T	M	Inf	Ac	yellow	P, N	60	38674
Chromolaena maximilianii (Schrad. *ex* DC.) R.M. King & H. Rob.	Sb	1	T	Sm	Inf	Ac	white	P, N	20	38686
Clibadium armanii (Balb.) Sch. Bip. *ex* O.E. Schulz	Sb	2	T	Sm	Inf	Ac	white	P, N	50	38670
Elephantopus palustris Gardner	H	3	T	M	Inf	Ac	white	P, N	90	38672
Erechtites hieraciifolius (L.) Raf. *ex* DC.	H	1	In	Sm	Inf	Ac	green	P, N	10	38684
Raulinoreitzia crenulata (Spreng.) R.M. King & H. Rob.	Sb	1	T	Sm	Inf	Ac	white	P, N	10	38682
Lessingianthus bardanoides (LeSb.) H.Rob.	S	4	T	Sm	Inf	Ac	purple	P, N	80	38671
Mikania psilostachya DC.	C	1	T	Sm	Inf	Ac	white	P, N	10	38679
Mikania stenophylla W.C. Holmes	C	1	T	Sm	Inf	Ac	white	P, N	20	38680
Vernonanthura sp.	S	1	T	Sm	Inf	Ac	white	P, N	20	38642

Species	Habit	Flowering time	Floral traits	Size of flower	Pollination unit	Symmetry	Color	Resource	Observation time (minutes)	CGMS number
Chloranthaceae										
Hedyosmum brasiliense Mart.	A	1	In	Sm	Inf	Ac	green	N	30	38645
Cyperaceae										
Ascolepis brasiliensis (Kunth) Benth. ex C.B. Clarke	H	5	In	Sm	Inf	Ac	white	P	90	38667
Rhynchospora globosa (Kunth) Roem. & Schult.	H	7	In	Sm	Inf	Ac	brown	P	410	38651
Rhynchospora nervosa (Vahl) Boeckeler	H	8	In	Sm	Inf	Ac	white	P	390	38639
Rhynchospora robusta (Kunth) Boeckeler	H	3	In	M	Inf	Ac	brown	P	190	38673
Eriocaulaceae										
Comanthera xeranthemoides (Bong.) L.R. Parra & A.M. Giuletti	H	12	In	Sm	Inf	Ac	white	N	980	38634
Eriocaulon cf. *magnum* Abbiatti	H	10	In	Sm	Inf	Ac	white	N	1150	38635
Syngonanthus caulescens (Poir.) Ruhland	H	7	In	Sm	Inf	Ac	white	N	210	38654
Syngonanthus gracilis (Bong.) Ruhland	H	6	In	Sm	Inf	Ac	white	N	90	38657
Gentianaceae										
Chelonanthus alatus (Aubl.) Pulle *	S	8	F	B	F	Z	green	N	330	38650
Gesneriaceae										
Sinningia elatior (Kunth) Chautems	H	1	G	B	F	Z	red	N	10	38676
Iridaceae										
Trimezia spathata (Klatt) Baker	H	1	D	B	F	Ac	yellow	O	10	38678
Lamiaceae										
Hyptis brevipes Poit.	Sb	1	F	Sm	F	Z	white	N	10	38677
Malpighiaceae										
Heteropterys coriacea A. JuSb.	S	2	D	M	F	Z	yellow	O	90	38647
Heteropterys eglandulosa A. Juss.	S	1	D	M	F	Z	yellow	O	10	38660
Melastomataceae										
Desmoscelis villosa (Aubl.) Naudin	Sb	1	D	B	F	Ac	purple	P	10	38675
Miconia albicans (Sw.) Steud.	A	1	D	M	F	Ac	white	P, N	10	38681
Miconia chamissois Naudin	S	6	D	M	F	Ac	white	P, N	7200	38644

Species	Habit	Flowering time	Floral traits	Size of flower	Pollination unit	Symmetry	Color	Resource	Observation time (minutes)	CGMS number
Tibouchina gracilis (Bonpl.) Cogn.	H	3	D	B	F	Ac	purple	P	40	38666
Tococa guianensis Aubl.	Sb	2	D	M	F	Ac	purple	P	40	38649
Ochnaceae										
Ouratea floribunda (A.St.-Hil.) Engl.	S	1	D	B	F	Ac	yellow	P	10	38640
Sauvagesia racemosa A. St.-Hil.	Sb	9	D	B	F	Ac	pink	P	540	38643
Onagraceae										
Ludwigia nervosa (Poir.) H. Hara	Sb	7	D	G	F	Ac	yellow	P, N	5500	38638
Ludwigia octovalvis (Jacq.) P.H. Raven	Sb	2	D	G	F	Ac	yellow	P, N	40	38683
Rubiaceae										
Coccocypselum lanceolatum (Ruiz & Pav.) Pers.	Sb	4	T	P	F	Ac	blue	N	80	38668
Diodella radula (Willd. & Hoffmanns. ex Roem. & Schult.) Delprete	H	3	T	P	F	Ac	white	N	230	38661
Emmeorhiza umbellata (Spreng.) K. Schum.	C	4	T	P	F	Ac	white	N	230	38641
Ferdinandusa speciosa (Pohl) Pohl	A	4	T	G	F	Ac	red	N	40	38662
Psychotria tenerior (Cham.) Müll. Arg.*	S	2	T	M	F	Ac	white	N	40	38669
Sipanea pratensis Aubl.	H	2	T	M	F	Ac	pink	N	40	38664
Smilacaceae										
Smilax fluminensis Steud.	C	2	In	M	F	Ac	green	N	40	38653
Solanaceae										
Brunfelsia obovata Benth.	S	3	T	G	F	Ac	purple	N	80	38655
Cestrum axillare Vell.*	Sb	2	T	M	F	Ac	white	N	20	38685
Styracaceae										
Styrax camporum Pohl	A	2	D	M	F	Ac	white	N	40	38652
Urticaceae										
Cecropia pachystachya Trécul	A	1	In	P	Inf	Ac	green	N	10	38646
Xyridaceae										
Abolboda egleri L.B. Sm. & Downs	H	3	T	M	F	Ac	blue	P, N	100	38636
Xyris jupicai Rich.	H	8	T	M	F	Ac	yellow	P	1090	38656

Table 2 – Floral attributes, classification of variable type and characteristics used in the construction of the decision tree with the plant species of the *vereda* in Campo Grande, Mato Grosso do Sul, Brazil, from September 2012 to August 2013.

Attributes	Variable type	Characteristics and number of samples observed	Total of each partition to the decision tree
(1) Number of flowers per plant	Numerical	Minimum 1; Maximum 1900; Median 32; Average 156	38,43
(2) Flower color	Categorical	Yellow - 99; Blue - 1; White - 263; Brown - 21; Pink - 3; Purple - 4; Green - 10	10,71
(3) Floral symmetry	Categorical	Actinomorphic - 397; Zygomorphic - 4	0
(4) Floral type	Categorical	Inconspicuous - 98; Dish - 258; Tube - 42; Gullet - 1; Flag - 3	15,81
(5) Anthesis	Categorical	Diurnal - 396; Nocturnal - 5	0
(6) Resource pollen	Categorical	Absent - 204; Present - 197	8,14
(7) Resource nectar	Categorical	Absent - 95; Present - 306	1,86
(8) Flowering time (number of months)	Numerical	Minimum 1; Maximum 11; Median 8	20,96
(9) Flower size	Categorical	Big - 120; Medium - 66; Small - 215	6,54
(10) Inflorescence type	Categorical	Collective = 24; No collective = 29	2,96

Data Analysis

Classification trees are suited for the analysis of complex ecological data, which, in our case, involved a set of continuous and categorical predictors. This method can also treat nonlinear relationships and high-order interactions, which inflate the number of parameters needed for regression models commonly used (De'Ath Fabricius 2000). Therefore, we utilized this method of recursive partitioning to generate a classification decision tree, as suggested by Breiman *et al*. (1984). This method aims to ordinate, in a more parsimonious way, the behaviors of pollination and theft based on 10 attributes and 401 samples. The utilized attributes were (1) number of flowers per plant, (2) flower color, (3) floral symmetry, (4) floral type, (5) anthesis, (6) pollen as resource, (7) nectar as resource, (8) flowering time, (9) size of flower and (10) type of inflorescence (Tab. 2).

We also ran a 10 k-fold cross-validation to evaluate the fitness of the model compared with other possible models and determine if the model improved our predictability of the behaviors of pollination and theft. We computed the accuracy and cross-tabulated the observed and predicted classes, calculating their probabilities for the model we present here. To calculate the importance of each attribute for the decision tree, the reduction in the mean square error contributed by each attribute to each partition was calculated, and the sum is presented in Table 2. The attributes which were candidates for partition, but not utilized, were also considered for each partition, as proposed by Quinlan (1992). All analyses were performed utilizing R language (R Core Team 2015) with the rpart package (Therneau *et al*. 2015) to generate the classification tree and caret packages (Kuhn 2015) for cross-validation and importance attribute calculations.

Results

In the 53 sampled plant species, flowering time varied from one to eleven months, with most plants typically flowering between one and four months (73.1%). The number of pollination

Table 3 – Group, richness, abundance and behavior of floral visitors sampled in plant species of *vereda* vegetation, in Campo Grande, Mato Grosso do Sul, Brazil, from September 2012 to August 2013. The last two columns are the percentage of the species in the group that perform with thieves or pollinators of the plant species visited.

Group	Richness (n)	Abundance (n)	Number of plant species visited (n)	Pollination (%)	Thief (%)
Bees	37	131	19	100	0
Spiders[a]	3	3	3	-	-
Cockroaches	1	1	1	0	100
Beetles	6	17	7	58,8	41,2
Butterflies	4	20	9	35	65
Ants	6	60	13	0	100
Crickets[b]	6	8	4	-	-
Hemipterans	5	13	3	0	100
Flies	46	77	12	93,5	6,5
Wasps	20	75	12	100	0

[a] predation; [b] feeding on floral parts

units per plant varied from 1 to 1900, most plants having 1–10 flowers (60%) or 200–500 (38%) (Tab. 1). Solitary flowers predominated (54%) over those assembled in inflorescences (45%). With respect to size, small flowers (43.3%) were the most representative, followed by large (32%) and medium flowers (24.5%). Most species displayed white (45.3%), yellow (15.1%) or lilac/violet/purple pollination units (13.2%); the others were brown, pink, red, blue or green (26.4%). Five floral types were recorded: tube (37.7%), dish (30.1%), flag (3.77%), inconspicuous (26.4%) and gullet (1.88%). Flowers with nectar (65%) were more frequent than those with only pollen (29.3%) or oil (5.7%). Actinomorphic flowers (96.2%) with diurnal anthesis (90%) predominated. Visits to individual flowers (54.7%) were slightly higher than visits to inflorescence (45.2%) (Tab. 1).

The pollination units of thirty plant species were visited by 138 species of insects, herein categorized into ten groups in decreasing order of richness: flies, bees, wasps, crickets, beetles, ants, hemipterans, butterflies, spiders and cockroaches. Bees, flies and wasps were the most abundant groups and visited the largest number of plant species, together with ants (Tab. 3). Most studied groups behaves as thieves, including a high percentage of butterflies, all species of ants, hemipterans and cockroaches. In this study, all floral thieves were observed collecting nectar or pollen and exhibited one morphological mismatch between flower and the thieves body, thus preventing pollination from taking place. Spiders probably predated other floral visitors, and crickets ate floral parts, including stamens (Tab. 3); therefore they are not proper flower visitors and so they were not included in the analyzes (Tab. 3). Bees, flies and wasps acted as potential pollinators.

Based on our hypothesis, which holds that decreasing specialization correlates with theft, while increasing specialization correlates with pollination, species with small, inconspicuous flowers, plants with a high number of flowers (>500) and flowering time shorter than 10 months would have a greater chance of illegitimate visits to the pollination units. In contrast, large or medium-sized flowers with tube or dish floral type, long flowering period (>10 months) and plants with a variable number of flowers (but < 500) would stand a greater chance of becoming pollinated (Tab. 2; Fig. 2). The classification tree had an accuracy of 82%, and the cross-validation results are as follows: 10% for true theft, 72.1% true pollination, 4.2% false theft and 13.7% for false pollination.

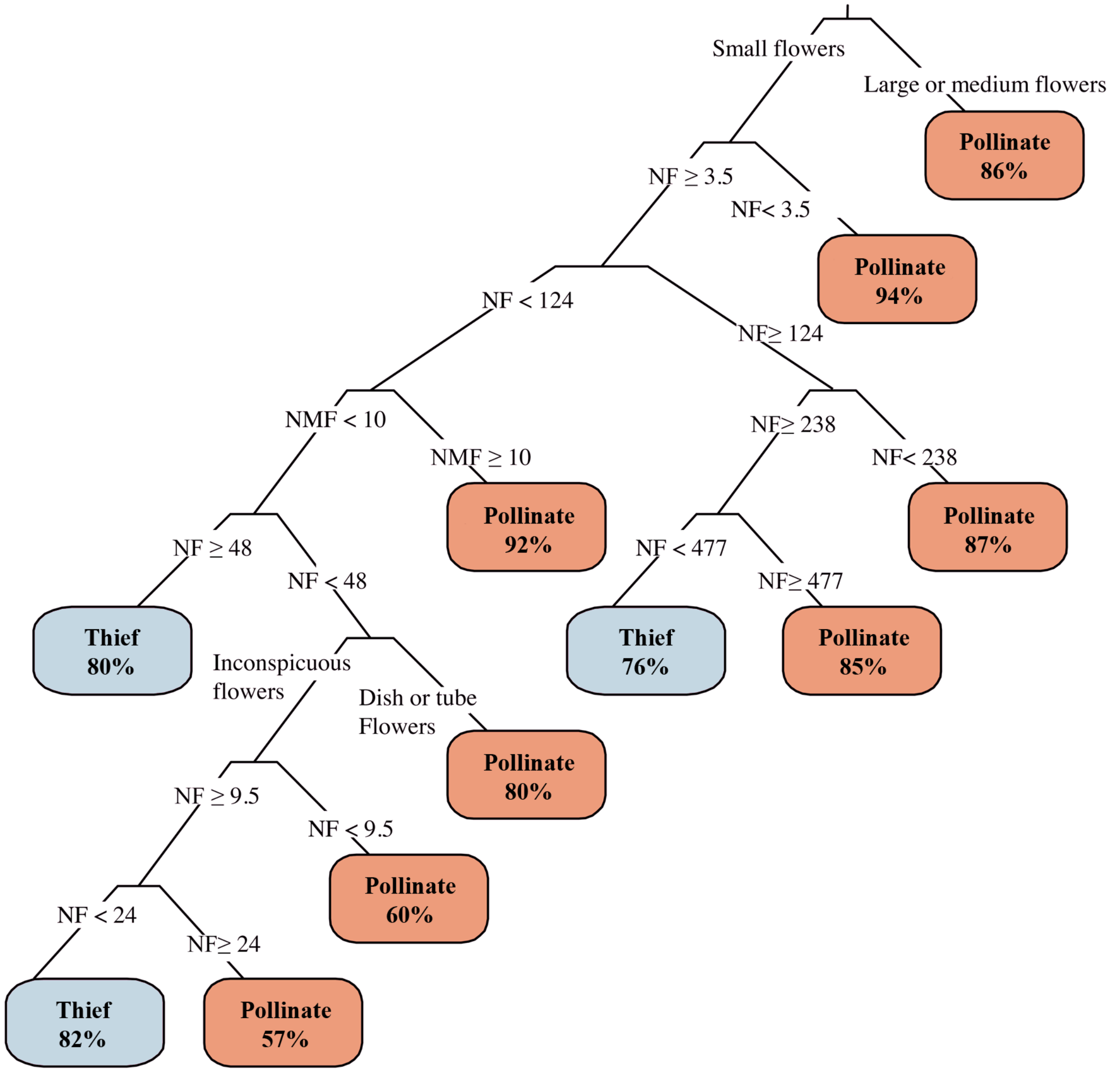

Figure 2 – Decision tree with the floral attributes and the probability of pollination or theft in a *vereda* community, Campo Grande, Mato Grosso do Sul, Brazil. Percentage indicates the probability of occurrence of theft or pollination. NF = number of flowers; NMF = number of months in flowering.

Discussion

Composition

Data obtained from floral and flowering characteristics in the studied *vereda* community are in accordance with results observed in other savanna communities (Freitas & Sazima 2006) and other physiognomies of the cerrado biome, i.e, predominance of diurnal, nectariferous, actinomorphic and light-colored flowers (*e.g.*, Silberbauer-Gottsberger & Gottsberger 1988; Barbosa 1997; Oliveira & Gibbs 2000).

Considering anthophilous fauna, the groups of insects recorded in the community were similar to those found in other vegetation types of cerrado (Aoki & Sigrist 2006), grasslands (Freitas & Sazima 2006; Pinheiro *et al*. 2008) or anthropic habitats, such as eucalyptus plantations (Lopes *et al*. 2007). In our study, the richest and most abundant groups, including bees, flies and wasps, were mainly potential pollinators of the sampled plant species. Bees are known as the main and most efficient pollinators in tropical vegetation types (Oliveira & Gibbs 2000; Freitas & Sazima 2006; Silva *et al*. 2012). Nectar and pollen constitute the main source of carbohydrates and proteins for bees, respectively, for nourishment of brood and adults (Faegri & van der Pijl 1979; Barbola *et al*. 2000). Flies are one of the most important groups of floral visitors (Kevan & Baker 1999; Larson *et al*. 2001), as adults can consume large amounts of pollen and nectar (Larson *et al*. 2001; Morales & Köhler 2008), and some groups of diptera are highly specialized flower visitors and important pollinators of several plant species (*e.g.*, Endara *et al*. 2010; Kearnes 2001). Furthermore, appropriate behavior and morphological adjustment on these groups in the flower visitation, causes them to be important pollinators of plant species.

In contrast, it was surprising that a high percentage of theft was recorded for butterflies, particularly because this group depends on floral nectar and has historically been considered as pollinators (Faegri & van der Pijl 1979; Proctor *et al*. 1996). The other studied insects, are commonly sampled on flowers and are generally not considered as "habitual" pollinators, except beetles (Proctor *et al*. 1996). Hence ants were the main thieves recorded in our study, tending to visit flowers with exposed nectar (Herrera *et al*. 1984; Ballantyne & Willmer 2012).

Floral traits and thieves

In this study, nonspecialized flowers were those having a higher frequency of thieves. The traits more related to thieving were: plants with small and inconspicuous flowers, high number of flowers, and flowering time under 10 months. These results confirm our hypothesis that nonspecialized flowers have a higher incidence of thievery, whereas specialization, for example, the presence of large and medium flowers with long corolla, making it difficult to access nectar, leads to increased pollination (Stang *et al*. 2006). Thus, theft correlates with the incompatible morphology between plant and animal visitor that gains access to the resource without offering pollen transfer (Irwin *et al*. 2001). In small and inconspicuous pollination units, including flowers and inflorescences, the floral resource is generally more accessible to the visiting fauna, in particular those with short mouthparts, such as ants, beetles, cockroaches and hemipterans, all groups with a high percentage of theft in this study.

The number of flowers per plant and flowering time were more important features than flower shape as indicators of frequent illegitimate visits. For example, while a larger number of flowers could help to increase floral display, acting to attract a wider range of visitors, legitimate or illegitimate, such displays could also indirectly represent higher amounts of available resources, a situation which seems to increase the chances of theft in this *vereda* community. In contrast, a smaller quantity of flowers may be more efficient in reducing geitonogamous pollination and promote cross pollination, in addition to reducing stigma obstruction with unsuitable pollen in self-incompatible species (Wyatt 1982).

Flowering time can promote the temporal variation of the resources, and in this study, most species flowered for up to four months (> 70%), although some flowered for up to 11 months, which is favorable for maintenance of floral visitors. In an assessment of impact of floral theft at different levels, Irwin *et al*. (2001) reported that theft could be related to flowering season of the plant species. Irwin & Maloof (2002) suggest that the direction and magnitude of theft could depend on the relative temporal and spatial abundance of thieves and pollinators and their synchrony with the flowering period of the visited species.

Thus, the net effects of cheating for plant reproduction can be negative, positive, or neutral. Thieves (morphological uncoupling) may have more subtle indirect effects on plant fitness, for example by altering the interaction between plants and pollinators. The result may be to decrease plant fitness if larceny reduces floral rewards sufficiently for pollinators to avoid a plant or to desert it after a brief visit (Inouye 1983; Wootton 1993; Maloof and Inouye 2000; Irwin *et al*. 2001).

According to Irwin *et al*. (2001), the evolution of floral traits surely must be understood, in part, with reference to pollinators. However for the plant, the selection environment includes larcenists, and other plant enemies, as well as mutualists. The net direction and magnitude of selection will likely depend on the relative abundances in space and time of robbers and pollinators.

In conclusion, other researches including color measurement, functional characteristics of nectar, quantitative measurement of odor and the corolla tubes are encouraged to better understand the floral traits that can predict the cheating in pollination. Also, efficiency measures for each visitor should be performed in the future. Furthermore, the pollinators in *vereda* community and other formations are part of a bigger network of interactions where plants, pollinators and larcenists are embedded. Plants with robbed flowers grow sympatrically with other plant species that share larcenists and/or pollinators

(Irwin *et al.* 2001). Thus, future studies investigating the role of these thieves in community interactions network should be encouraged in order to better understand the pressures and effects of thieves in the *vereda* community.

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