

# Overlap and resource sharing in coterie of fruit-eating birds

Adriano Marcos da Silva<sup>1</sup> and Celine de Melo

Instituto de Biologia, Universidade Federal de Uberlândia, Campus Umuarama, Bloco 2D, sala 28, Uberlândia, MG, Brazil  
(Received 18 June 2013; revised 31 July 2013; accepted 31 July 2013)

**Abstract:** A range of species eating the same fruit suggests that niche overlap can occur, along with potential competition among them. To test if the overlap in the coterie of fruit-eating birds is larger than would be expected by chance, we performed a comparison with coterie generated from the use of null models. The study was carried out in an area of savanna woodland of 127 ha in Uberlândia city, Brazil. Four individuals of five zoochorous plant species were selected and 60 h of focal observation was performed on each species. We recorded species of birds that consumed fruits and the quantity of fruit removed. We used an index of Proportional Similarity (PS) between each pair of plant species, using the relative proportion of fruit taken by each bird species of each plant. The mean value of observed PS was compared with the mean PS generated from randomizations. Thirty-six bird species were recorded eating fruits in the selected plant species. The mean overlap observed (PS = 0.183) was significantly higher ( $P = 0.032$ ) than the mean overlap generated by the null models (PS = 0.123). This pattern suggests that competition is not an important factor in the formation of the coterie and there is sharing of resources. The abundance of fruits offered, especially in the rainy season, and the relatively low number of frugivorous species may be factors explaining the low influence of interactions and therefore the overlap between coterie.

**Key Words:** Brazil, competition, frugivorous birds, frugivory, niche overlap

## INTRODUCTION

Fruit consumption by birds occurs in practically all terrestrial environments, but is prevalent in tropical regions (Fleming *et al.* 1987, Kissling *et al.* 2009), where most species of angiosperm develop zoochorous fruits (Howe & Smallwood 1982). Birds are the most important vectors in seed dispersal due to their species diversity, abundance, range of sizes (Fleming & Kress 2011) and the fact that, in several cases, they eliminate the seeds undamaged (Traveset 1998, Traveset *et al.* 2007).

In spite of being easily digested, fruits are irregularly distributed, both spatially and temporally, and tend to be a nutritionally inferior class of food (Fleming *et al.* 1987). Because of this, fruit-eating birds usually consume fruits of various species (Muller-Landau & Hardesty 2005, Pizo & Galetti 2010), not specializing in a specific species or families (Githiru *et al.* 2002), and consuming other resources such as insects to supplement their diet (Corlett 2011, Izhaki & Safriel 1989). In the Brazilian savanna, for example, most fruit-eating birds are omnivorous, with

only part of their diet being composed of fruits (Gottsberger & Silberbauer-Gottsberger 2006, Macedo 2002).

In general, a coterie of frugivores (set of species that eats the fruit of a specific species; Fleming *et al.* 1993) includes a broad taxonomic, trophic and morphological diversity (Foster 1987, Melo & Oliveira 2009, Pizo 1997). Such variety of species eating the same resource suggests niche overlap and potential competition between them (Terborgh & Diamond 1970). The competition between animals for nutritional resources (Fleming 1979, Guix *et al.* 2001) and among plant species for seed dispersers (Herrera 1981, Howe & Estabrook 1977) may influence fruit selection and the proportion in which they are consumed by different fruit-eating species.

This study tested whether the overlap in coterie of fruit-eating birds is different than would be expected at random. For this, we conducted a comparison with randomizations generated through a null model. This method allows us to test whether a pattern is similar to that observed in the absence of some mechanism (Gotelli & Graves 1996), by generating a control treatment for observational data (Connor & Simberloff 1986).

Through the null model, three hypotheses were formulated about the occurrence of overlap between the

<sup>1</sup> Corresponding author. Email: adriano.biologia@yahoo.com.br

**Table 1.** Fruit morphological traits (length, width and mass) and number of seeds per fruit of the five savanna plant species chosen for focal-plant observation, Uberlândia city, Brazil.

Species	Family	Fruits			Seeds per fruit
		Length (mm)	Width (mm)	Mass (g)	
<i>Cecropia pachystachya</i> Trécul	Urticaceae	113	12.8	6.5	> 5000
<i>Ouratea hexasperma</i> (A. St.-Hil.) Baill.	Ochnaceae	13.2	7.9	0.55	1
<i>Eugenia punicifolia</i> (H. B. & K.) DC.	Myrtaceae	7.8	6.7	0.25	1
<i>Schefflera macrocarpa</i> (Seem.) D. C.	Araliaceae	12.9	8.4	0.5	1–2
<i>Byrsonima intermedia</i> A. Juss.	Malpighiaceae	9.1	7.8	0.3	1–3

coterics of fruit-eating birds. The null hypothesis ( $H_0$ ) is that the overlap between the coterics does not differ from that expected by the model. The first alternative hypothesis ( $H_{A1}$ ) suggests a scenario where interspecific competition influences the composition of the coterics, generating niche partitioning and overlap smaller than that generated by the model. The second alternative hypothesis ( $H_{A2}$ ) expresses a scenario with a lack of competition in the formation of the coterics and shared resource utilization, generating an overlap index larger than predicted by the null model.

## METHODS

### Study site

The study was carried out in an area of 127 ha (18°55'S, 48°17'W) in Uberlândia city, central Brazil. Brazilian savanna (cerrado) is the dominant phytophysognomy in the area where the data collection occurred. This vegetation is dominated by 3–8m-tall trees and shrubs with more than 30% crown cover, but with a fair amount of herbaceous vegetation between them (Oliveira & Marquis 2002). The climate in the region, according to Köppen (Kottek *et al.* 2006), is characterized as *Aw*, the annual rainfall is around 1500 mm and the average temperature is 22 °C (Silva & Assunção 2004).

### Observations and characterization of birds

Between June 2011 and February 2012, four individuals of five sympatric plant species producing fruits dispersed by birds were selected (Table 1): *Cecropia pachystachya*, *Ouratea hexasperma*, *Eugenia punicifolia*, *Schefflera macrocarpa* and *Byrsonima intermedia*. These species were selected because they were among the ones with the most abundant fruiting in the area and offered fruits that were potentially consumed by most birds, due to their size and softness. This choice was with the aim of ensuring that differences in the coterics of fruit-eating birds were not influenced by morphological limitations.

To minimize non-independence of samples, each plant included in the observations was at least 50 m away from any other, regardless of species.

Focal-plant observation sessions were conducted between 06h30 and 11h30, totalling 300 h of observation, with 60 h spent on each plant species. At each visit by birds including fruit consumption, the following data were recorded: (1) bird species that made the visit followed by consumption; (2) number of fruits consumed during the visit (in cases of large infructescences, such as *C. pachystachya*, each piece plucked was recorded as a fruit); and (3) fruit handling behaviour, differentiated as: swallow, when the whole fruit is ingested without seed breakage; bite, where bits of pulp are removed by biting or pecking a fruit, and can or cannot swallow the seed; and mash, where the fruit is manipulated by damaging or dropping the seed (adapted from Schupp 1993). When there was more than one individual of the same species visiting the plant simultaneously, only one was chosen randomly.

The bird visitors were identified and classified in relation to their trophic guild (Motta-Junior 1990, Sick 1997) to determine which ones are most representative as fruit-eaters in the plant species included in the study.

### Coterie overlap

To obtain the overlap between the coterics of fruit-eating birds from each plant species, we used the Proportional Similarity index (PS) between each pair of coterics of fruit eaters of the plants species (Fuentes 1995, Githiru *et al.* 2002, Jordano 1994):

$$PS = \sum_{i=1}^n \min(p_{ai}, p_{bi})$$

where  $n$  is the number of bird species in the largest coterie, and  $p_{ai}$  and  $p_{bi}$  the relative proportion of fruits removed by the bird species  $i$  on plant species  $a$  and  $b$ , respectively. The PS is calculated by determining the smallest relative abundance of eating of each bird species over each pair of plant species ( $p_{ai}, p_{bi}$ ), ranging from 0 (no overlap between coterics) to 1 (complete overlap). The term 'overlap' was

used in reference to the proportion of bird species in common between each pairs of plant species (Githiru *et al.* 2002). This similarity index has advantages over those using only binary data because it takes into regard the relative abundance (Balmer 2002) in the proportion of fruits removed.

A matrix with values of relative frequency of fruit removed by all bird species on each plant species was generated, from which 10 000 randomized matrices were generated. In each of these matrices, a proportional similarity index was applied. The mean of all values of PS was compared with the observed distribution of values of average PS generated from randomizations to verify the difference between the observed results and those expected by chance.

We used the Randomization Algorithms 3 (RA3; Winemiller & Pianka 1990), which is the most suitable for the detection of non-random patterns of overlap. This algorithm retains the niche breadth of each species, but randomizes particular resource states, which are the zero states reshuffled. To generate this model we used the software EcoSim 7.

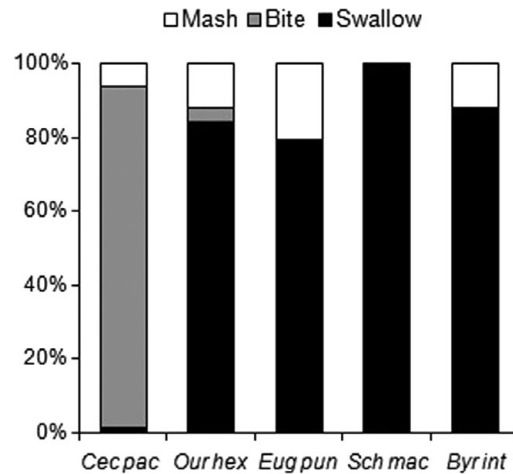
**RESULTS**

Thirty-six bird species were recorded (distributed in four orders and 13 families) eating fruits in the selected plant species (Appendix 1). Thraupidae were the family with the greatest number of species (n = 10; 27%), followed by Tyrannidae (n = 8; 22%). About 56% (n = 20) were omnivorous species, with 25% (n = 9) being predominantly frugivorous, 8% (n = 3) granivorous and 8% (n = 3) insectivorous.

However, frugivores of the Psittacidae (n = 4) were predominantly predatory, either damaging or dropping the seeds during fruit handling. For *Cecropia pachystachya*, except *Ramphastos toco*, which consumed the whole fruit, all consumptions was partial (biter; 92%) or predatory (masher; 6%). Consumption of the whole fruit was prevalent for all of the other fruit species (swallower; 79–100%; Figure 1). The visitation rate ranged from 0.33 visits h<sup>-1</sup> in *Byrsonima intermedia* to 2.95 visits h<sup>-1</sup> in *C. pachystachya*.

*Tangara palmarum* and *Turdus leucomelas* were the only bird species to consume all fruit species. Over 80% of the birds consumed only one (n = 19) or two (n = 11) species. *Tangara palmarum* accounted for most fruit removal in four of the five species: *C. pachystachya* (n = 547; 33% of total) *Ouratea hexasperma* (n = 25; 20%), *Eugenia punicifolia* (n = 29; 38%) and *Schefflera macrocarpa* (n = 25; 29%).

*Cecropia pachystachya* had the largest coterie of fruit-eating birds, with 25 species, and *S. macrocarpa* had the smallest, with eight species. Coterie of *S. macrocarpa* and



**Figure 1.** Relative proportion of the fruit handling behaviour (mash, bite and swallow) by bird species that ate some of the five savanna plant species included in the study. *Cec pac* = *Cecropia pachystachya*, *Our hex* = *Ouratea hexasperma*, *Eug pun* = *Eugenia punicifolia*, *Sch mac* = *Schefflera macrocarpa* and *Byr int* = *Byrsonima intermedia*.

**Table 2.** Proportional similarity between the relative amount of each fruit taken by birds in coterie of five plant species in a savanna woodland in Uberlândia, Brazil. *Cec pac* = *Cecropia pachystachya*, *Our hex* = *Ouratea hexasperma*, *Eug pun* = *Eugenia punicifolia*, *Sch mac* = *Schefflera macrocarpa* and *Byr int* = *Byrsonima intermedia*.

Plant species	Similarity			
	Our hex	Eug pun	Sch mac	Byr int
Cec pac	0.112	0.0581	0.329	0.216
Our hex	–	0.0975	0.126	0.178
Eug pun		–	0.366	0.220
Sch mac			–	0.122

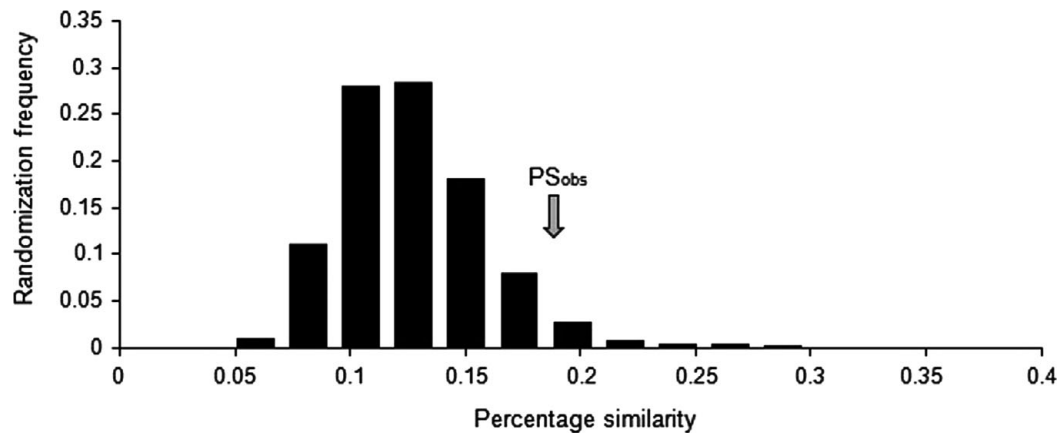
*E. punicifolia* (Table 2) had the highest similarity (PS = 0.366) and *E. punicifolia* and *C. pachystachya* the lowest similarity (PS = 0.058).

The overlap generated by the model ranged from 0.0695 to 0.306, with an average of 0.183. This value is significantly higher (P = 0.032) than the mean overlap between the coterie of fruit-eating birds generated by the null model (PS = 0.123), consistent with the second alternative hypothesis (Figure 2). The average observed variance (0.0102) did not differ (P = 0.585) from that expected by the models.

**DISCUSSION**

**Observations and characterization of birds**

*Tangara palmarum*, a common species in various types of natural and disturbed environments (Ridgely & Tudor 1989, Sick 1997), was the most important bird species in the removal of zoochoric fruits of plants included in



**Figure 2.** Distribution value of the observed Proportional Similarity ( $PS = 0.183$ ) between the coteries of frugivores in a savanna woodland in Uberlândia, Brazil, compared with the frequency of randomizations generated from the null model. The observed similarities were significantly higher than the values generated by the model ( $P = 0.032$ ).

the study. It is an omnivorous species that has the habit of foraging in small flocks (Gwynne *et al.* 2010) and has more than half of the diet consisting of insects (Collins & Watson 1983, Snow & Snow 1971). Although few fruits were taken per visit, *Tangara palmarum* is an abundant species (A. M. Silva pers. obs.) and compensates for the proportion of fruit in the diet by making numerous visits, resulting in a large quantity of seeds being taken from the parent plant. As the amount of fruit removed by a species is the product of the number of visits by the number of fruits taken per visit (Schupp 1993), a species can achieve a high rate of fruit removal with different combinations of numbers of visits and numbers of fruits per visit (Schupp *et al.* 2010).

In *Cecropia pachystachya*, the number of species and feeding records were much higher than the other species included in the study. It is a pioneer species with a prolonged fruiting period, the seeds are dispersed by a variety of animal vectors and it is one of the most abundant tree species in the Brazilian savanna (Bocchese *et al.* 2008). It can be considered a 'frugivory hub', which has a higher probability of visitation than the other species and captures a large share of frugivory and dispersal services (Carlo *et al.* 2007).

By being taller in relation to other savanna woodland species, this tree stands out in the landscape, which can facilitate the meeting and access to a greater number of disperser species (Toh *et al.* 1999). By presenting large infructescences that are more than 10 cm long, but do not have a thick coating, the smaller birds easily bite off pieces of the infructescences. Since most birds recorded in the study have a small body size, the fruits of *C. pachystachya* have been partially consumed. However, that does not mean that the seeds cannot be effectively dispersed, because, due to their small size, they can be ingested intact by birds of various sizes (Snow 1981).

### Coterie overlap

As competition influences the use of resources, the niche overlap in communities with the presence of competition should be lower than in communities with a lack of competition (Pleasants 1990, Schoener 1974). Studies that found niche overlap greater than expected by chance concluded that, at that time, the competition would not be important in structuring these communities (Griffiths 1987, Tokeshi 1986).

The high overlap between the coteries of the plant species included in the study suggests that there is sharing of resources, and that the competition among fruit-eaters is not a determining factor in interactions between frugivorous birds and fruits. The low influence of competition in the establishment of this interaction may be due to the combination of factors such as: (1) a greater availability of fruits in relation to demand of consumers; (2) a low specificity of the plant–frugivore interactions; and (3) a low dependence of birds for the fruits.

The strength of competition is related to resource availability (Tilman 1982), and in general, the fruit availability exceeds the demand of consumers (Carlo *et al.* 2007). This investment excess in seed production is typical of plants that produce generalized fruits (Howe & Estabrook 1977, Fleming *et al.* 1993), which produce a lot of seeds, but with a reduced chance of individual reproductive success (Howe 1993). The investment excess is a strategy that can reduce competition among consumers, generating coteries of more diverse dispersers (Howe & Smallwood 1982), which contribute to the seeds being dispersed into a wider variety of habitats, so the plants do not rely on a small range of seed dispersers (Howe & Estabrook 1977).

With the exception of *Cecropia pachystachya*, the rate of fruit removal was low (about  $1 \text{ h}^{-1}$ ). This indicates that

the quantity of fruit was not a limiting factor, as evidenced by the large number of fruits that are not removed (Foster 1977), and agonistic interactions were not motivated by the consumption of fruits, signalling a lack of interference competition (Gherardi & Cioni 2004).

The Brazilian savanna has a pronounced seasonality, having a higher concentration of zoochoric species fruiting during the rainy season (Oliveira & Gibbs 2002), however, during the peak months of drought, June and July, there is a shortage of zoochoric plant species offering fruits (Batalha & Martins 2004). During these periods, the reduced fruit availability may not be greater than consumer demand, but most bird species adopt alternative diets. Irregular availability may be one factor that precludes the occurrence of exclusively frugivorous diets in open areas, having a domain of omnivorous in the composition of the coteries of fruit eaters.

About 14% of land-bird species consume fruits, but only 4% have a diet that is predominantly frugivorous (Kissling *et al.* 2009), so omnivorous birds can be important in seed dispersal in many environments (Howe 1993). In studies of frugivory by birds in savanna woodlands, the omnivorous bird species were quantitatively most important in seed removal (Francisco & Galetti 2001, Francisco *et al.* 2007, Motta-Junior & Lombardi 1990, Oliveira 2009) and that even the non-specialist frugivorous species can provide effective seed dispersal (Carlo *et al.* 2007, Moermond & Denslow 1985).

About half of the bird species recorded consumed only one plant species and 12 species made only one visit during the sampling. This demonstrates that the number of species that perform regular consumption is small, while 12 species were responsible for more than 75% of the fruits removed. Important species in the removal of fruits such as *Tangara palmarum*, *T. cayana* and *Turdus leucomelas* do not rely exclusively on fruit, also making use of invertebrates (Lopes *et al.* 2005).

The overlap between the coteries of frugivores and the resource sharing are related to the low specificity of plant–frugivore interactions. Most fruit–frugivore interactions involve the sharing of many frugivorous species and frugivores consuming multiple plants (Carlo *et al.* 2007), generating a functional redundancy, reducing the impact of an individual species in seed removal and increasing the weight of the interactions within the group (Loiselle *et al.* 2007). Even with species that are more important than others, the absence of some of them can be compensated by other species that exert an equivalent function, increasing the resilience of the community against species loss (Rosenfeld 2002).

It was concluded that plant–frugivore interactions in the savanna woodlands are not regulated by the interaction between consumers. The overlap between coteries is a sign that there was no selective pressure to generate niche partitioning among consumers, indicating

a sharing of resources. This may be because of the low specificity of interactions and low degree of dependence on fruits by bird species, which means that the fruit resources do not limit this interaction.

## ACKNOWLEDGEMENTS

We thank CAPES for the scholarship offer to AMS, to Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais of Universidade Federal de Uberlândia, to Paulo Eugênio Oliveira and Marco Aurélio Melo for the criticism of the thesis that resulted in this paper and to the team of the Laboratório de Ornitologia e Bioacústica.

## LITERATURE CITED

- BALMER, O. 2002. Species lists in ecology and conservation. Abundances matter. *Conservation Biology* 16:1160–1161.
- BATALHA, M. A. & MARTINS, F. R. 2004. Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). *Australian Journal of Botany* 52:149–161.
- BOCCHESI, R. A., OLIVEIRA, A. K. M. & LAURA, V. A. 2008. Germinação de sementes de *Cecropia pachystachya* Trécul (Cecropiaceae) em padrões anteriores e posteriores à passagem pelo trato digestório de aves dispersoras de sementes. *Revista de Biologia e Ciências da Terra* 8:19–26.
- CARLO, T. A., AUKEMA, J. E. & MORALES, J. M. 2007. Plant–frugivore interactions as spatially explicit networks: integrating frugivore foraging with fruiting plant spatial patterns. Pp. 369–390 in Dennis, A. J., Schupp, E. W., Green, R. J. & Westcott, D. A. (eds.). *Seed dispersal: theory and its application in a changing world*. CABI, Wallingford.
- COLLINS, C. T. & WATSON, A. 1983. Field observations of bird predation on neotropical moths. *Biotropica* 15:53–60.
- CONNOR, E. F. & SIMBERLOFF, D. 1986. Competition, scientific methods, and null models in ecology. *American Scientist* 74:155–162.
- CORLETT, R. T. 2011. How to be a frugivore (in a changing world). *Acta Oecologica* 37:674–681.
- FLEMING, T. H. 1979. Do tropical frugivores compete for food? *American Zoologist* 19:1157–1172.
- FLEMING, T. H. & KRESS, W. J. 2011. A brief history of fruits and frugivores. *Acta Oecologica* 37:521–530.
- FLEMING, T. H., BREITWISCH, R. & WHITESIDES, G. H. 1987. Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics* 18:91–109.
- FLEMING, T. H., VENABLE, D. L. & HERRERA, L. G. M. 1993. Opportunism vs. specialization: the evolution of dispersal strategies in fleshy-fruited plants. *Plant Ecology* 107/108:107–120.
- FOSTER, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58:73–85.
- FOSTER, M. S. 1987. Feeding methods and efficiencies of selected frugivorous birds. *Condor* 89:566–580.

- FRANCISCO, M. R. & GALETTI, M. 2001. Frugivoria e dispersão de sementes de *Rapanea lacifolia* (Myrsinaceae) por aves numa área de cerrado do Estado de São Paulo, sudeste do Brasil. *Ararajuba* 9:13–19.
- FRANCISCO, M. R., LUNARDI, V. O. & GALETTI, M. 2007. Bird attributes, plant characteristics, and seed dispersal of *Pera glabrata* (Schott, 1858), (Euphorbiaceae) in a disturbed cerrado area. *Brazilian Journal of Biology* 67:627–634.
- FUENTES, M. 1995. How specialized are fruit–bird interactions? Overlap of frugivore assemblages within and between plant species. *Oikos* 74:324–330.
- GHERARDI, F. & CIONI, A. 2004. Agonism and interference competition in freshwater decapods. *Behavior* 141:1297–1324.
- GITHIRU, M., LENS, L., BENNUN, L. A. & OGOL, C. P. K. O. 2002. Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. *Oikos* 96:320–330.
- GOTELLI, N. J. & GRAVES, G. R. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, DC. 368 pp.
- GOTTSBERGER, G. & SILBERBAUER-GOTTSBERGER, I. 2006. *Life in the Cerrado: pollination and seed dispersal*. NHBS, Totnes. 383 pp.
- GRIFFITHS, R. A. 1987. Microhabitat and seasonal niche dynamics of smooth and palmate newts, *Triturus vulgaris* and *T. helveticus*, at a pond in mid-Wales. *Journal of Animal Ecology* 56:441–451.
- GUIX, J. C., RUIZ, X. & JOVER, L. 2001. Resource partitioning and interspecific competition among coexisting species of guans and toucans in SE Brazil. *Netherlands Journal of Zoology* 51:285–297.
- GWYNNE, J. A., RIDGELY, R. S., ARGEL, M. & TUDOR, G. 2010. *Guia Aves do Brasil: Pantanal & Cerrado*. Editora Horizonte, São Paulo. 336 pp.
- HERRERA, C. M. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos* 36:51–58.
- HOWE, H. F. 1993. Specialized and generalized dispersal systems: where does ‘the paradigm’ stand? *Vegetatio* 107/108:3–13.
- HOWE, H. F. & ESTABROOK, G. F. 1977. On intraspecific competition for avian dispersers in tropical tree. *American Naturalist* 111:817–832.
- HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology, Evolution, and Systematics* 13:201–228.
- IZHAKI, I. & SAFRIEL, U. N. 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54:23–32.
- JORDANO, P. 1994. Spatial and temporal variation in the avian–frugivore assemblage of *Prunus mahaleb*: patterns and consequences. *Oikos* 71:479–491.
- KISSLING, W. D., BÖHNING-GAESE, K. & JETZ, W. 2009. The global distribution of frugivory in birds. *Global Ecology and Biogeography* 18:150–162.
- KOTTEK, M., GRIESER, J., BECK, C., RUDOLF, B. & RUBEL, F. 2006. World map of the Köppen–Geiger climate classification updated. *Meteorologische Zeitschrift* 15:259–263.
- LOISELLE, B. A., BLENDINGER, P. G., BLAKE, J. G. & RYDER, T. B. 2007. Ecological redundancy in seed dispersal systems: a comparison between manakins (Aves: Pipridae) in two tropical forests. Pp. 178–195 in Dennis, A. J., Schupp, E. W., Green, R. J. & Westcott, D. A. (eds.). *Seed dispersal: theory and its application in a changing world*. CABI, Wallingford.
- LOPES, L. E., FERNANDES, A. M. & MARINI, M. A. 2005. Diet of some Atlantic Forest birds. *Ararajuba* 13:95–103.
- MACEDO, R. H. F. 2002. The avifauna: ecology, biogeography, and behavior. Pp. 242–265 in Oliveira, P. S. & Marquis, R. J. (eds.). *The Cerrados of Brazil – ecology and natural history of a neotropical savanna*. Columbia University Press, New York.
- MELO, C. & OLIVEIRA, P. E. 2009. Frugivory in *Lacistema hasslerianum* Chodat (Lacistemaceae), a gallery forest understory treelet in Central Brazil. *Brazilian Journal of Biology* 63:75–82.
- MOERMOND, T. C. & DENSLLOW, J. S. 1985. Neotropical avian frugivores: patterns of behavior, morphology and nutrition, with consequences for fruit selection. *Ornithological Monographs* 36:865–897.
- MOTTA-JUNIOR, J. C. 1990. Estrutura trófica e composição das avifaunas de três habitats terrestres na região central do estado de São Paulo. *Ararajuba* 1:65–71.
- MOTTA-JUNIOR, J. C. & LOMBARDI, J. A. 1990. Aves como agentes dispersores da copaíba (*Copaifera langsdorffii*, Caesalpiniaaceae) em São Carlos, estado de São Paulo. *Ararajuba* 1:105–106.
- MULLER-LANDAU, H. C. & HARDESTY, B. D. 2005. Seed dispersal of woody plants in tropical forests: concepts, examples and future directions. Pp. 267–309 in Burslem, D., Pinard, M. & Hartley, S. (eds.). *Biotic interactions in the tropics: their role in the maintenance of species diversity*. Cambridge University Press, Cambridge.
- OLIVEIRA, A. P. 2009. *Frutificação e frugivoria por aves em remanescente de cerrado Mato Grosso do Sul, Brasil*. M.Sc. dissertation, Universidade Federal de Mato Grosso do Sul.
- OLIVEIRA, P. E. & GIBBS, P. E. 2002. Pollination and reproductive biology in cerrado plant communities. Pp. 329–347 in Oliveira, P. S. & Marquis, R. J. (eds.). *The Cerrados of Brazil: ecology and natural history of a neotropical savanna*. Columbia University Press, New York.
- OLIVEIRA, P. S. & MARQUIS, R. J. 2002. Introduction: development of research in the Cerrados. Pp. 1–10 in Oliveira, P. S. & Marquis, R. J. (eds.). *The Cerrados of Brazil – ecology and natural history of a neotropical savanna*. Columbia University Press, New York.
- PIZO, M. A. 1997. Seed dispersal and predation in two populations of *Cabralea canjerana* (Meliaceae) in the Atlantic Forest of Southeastern Brazil. *Journal of Tropical Ecology* 13:559–577.
- PIZO, M. A. & GALETTI, M. 2010. Métodos e perspectivas da frugivoria e dispersão de sementes por aves. Pp. 493–506 in Von Matter, S., Straube, F. C., Accordi, I., Piacentini, V. & Cândido, J. F. (eds.). *Ornitologia e conservação: ciência aplicada, técnicas de pesquisa e levantamento*. Technical Books, Rio de Janeiro.
- PLEASANTS, J. M. 1990. Null-model tests for competitive displacement: the fallacy of not focusing on the whole community. *Ecology* 71:1078–1084.
- RIDGELY, R. S. & TUDOR, G. 1989. *The birds of South America: the oscine passerines, Vol 1: The oscine passerines*. Texas University Press, Austin. 516 pp.
- ROSENFELD, J. S. 2002. Functional redundancy in ecology and conservation. *Oikos* 98:156–162.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- SCHUPP, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108:15–29.

- SCHUPP, E. W., JORDANO, P. & GÓMEZ, J. M. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* 188:333–353.
- SICK, H. 1997. *Ornitologia Brasileira*. Nova Fronteira, Rio de Janeiro. 912 pp.
- SILVA, E. M. & ASSUNÇÃO, W. L. 2004. O clima na cidade de Uberlândia – MG. *Sociedade & Natureza* 16:91–107.
- SNOW, B. K. & SNOW, D. W. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. *The Auk* 88:291–322.
- SNOW, D. W. 1981. Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13:1–14.
- TERBORGH, J. W. & DIAMOND, J. M. 1970. Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bulletin* 82:29–52.
- TILMAN, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ. 297 pp.
- TOH, I., GILLESPIE, M. & LAMB, D. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. *Restoration Ecology* 7:288–297.
- TOKESHI, M. 1986. Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. *Journal of Animal Ecology* 55:491–506.
- TRAVESET, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics* 1/2:151–190.
- TRAVESET, A., ROBERTSON, A. W. & RODRÍGUEZ-PÉREZ, J. 2007. A review on the role of endozoochory in seed germination. Pp. 78–103 in Dennis, A. J., Schupp, E. W., Green, R. J. & Westcott, D. A. (eds.). *Seed dispersal: theory and its application in a changing world*. CABI, Wallingford.
- WINEMILLER, K. O. & PIANKA, E. R. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60:27–55.

**Appendix 1.** Characteristics of the bird species that ate some of the five plant species in a savanna woodland in Uberlândia, Brazil. C = *Cecropia pachystachya*, O = *Ouratea hexasperma*, E = *Eugenia punicifolia*, S = *Schefflera macrocarpa* and B = *Byrsonima intermedia*. Fru = frugivorous, Omn = omnivorous, Ins = insectivorous, Nec = nectarivorous and Gra = granivorous.

Family	Species	Number of visits					Trophic Guild	
		C	O	E	S	B		
Columbidae	<i>Patagioenas picazuro</i> (Temminck, 1813)		1			1	Fru	
Psittacidae	<i>Diopsittaca nobilis</i> (Linnaeus, 1758)			2			Fru	
	<i>Aratinga aurea</i> (Gmelin, 1788)		3				Fru	
	<i>Forpus xanthopterygius</i> (Spix, 1824)	2					Fru	
	<i>Brotogeris chiriri</i> (Vieillot, 1818)	1					Fru	
Ramphastidae	<i>Ramphastos toco</i> Statius Muller, 1776	3					Omn	
Picidae	<i>Colaptes melanochloros</i> (Gmelin, 1788)	1					Ins	
Thamnophilidae	<i>Thamnophilus doliatus</i> (Linnaeus, 1764)	1					Ins	
Tyrannidae	<i>Elaenia flavogaster</i> (Thunberg, 1822)	9	5				Fru	
	<i>Elaenia cristata</i> Pelzeln, 1868	3		8		3	Fru	
	<i>Elaenia chiriquensis</i> Lawrence, 1865		8		1		Fru	
	<i>Myiarchus tyrannulus</i> (Statius Muller, 1776)	1	1				Omn	
	<i>Pitangus sulphuratus</i> (Linnaeus, 1766)	3				2	Omn	
	<i>Tyrannus albogularis</i> Burmeister, 1856	1	1				Omn	
	<i>Tyrannus melancholicus</i> Vieillot, 1819	2	1	1	1		Omn	
	<i>Xolmis cinereus</i> (Vieillot, 1816)		1				Ins	
	Turdidae	<i>Turdus rufiventris</i> Vieillot, 1818	1					Omn
		<i>Turdus leucomelas</i> Vieillot, 1818	11	7	1	2	4	Omn
<i>Turdus amaurochalinus</i> Cabanis, 1850		1	2				Omn	
Mimidae	<i>Mimus saturninus</i> (Lichtenstein, 1823)	2	2				Omn	
Coerebidae	<i>Coereba flaveola</i> (Linnaeus, 1758)	1					Nec	
Thraupidae	<i>Saltator maximus</i> (Statius Muller, 1776)			1			Omn	
	<i>Saltator similis</i> d'Orbigny & Lafresnaye, 1837		3	1		2	Omn	
	<i>Nemosia pileata</i> (Boddaert, 1783)		3				Omn	
	<i>Tangara sayaca</i> (Linnaeus, 1766)	14		1			Omn	
	<i>Tangara palmarum</i> (Wied, 1823)	61	8	9	9	5	Omn	
	<i>Tangara cayana</i> (Linnaeus, 1766)	18	1		6		Omn	
	<i>Neothraupis fasciata</i> (Lichtenstein, 1823)					1	Omn	
	<i>Schistochlamys ruficapillus</i> (Vieillot, 1817)		1				Omn	
	<i>Tersina viridis</i> (Illiger, 1811)	1					Omn	
	<i>Dacnis cayana</i> (Linnaeus, 1766)	18					Omn	
Emberizidae	<i>Sporophila nigracollis</i> (Vieillot, 1823)	11					Gra	
	<i>Sporophila caerulescens</i> (Vieillot, 1823)	1					Gra	
	<i>Sporophila leucoptera</i> (Vieillot, 1817)	1					Gra	
Icteridae	<i>Icterus pyrrhopterus</i> (Vieillot, 1819)	1				2	Oni	
Fringillidae	<i>Euphonia chlorotica</i> (Linnaeus, 1766)	8			2		Fru	
	Total	177	47	24	27	19		