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TOCO TOUCAN FEEDING ECOLOGY AND LOCAL ABUNDANCE IN A HABITAT MOSAIC IN THE BRAZILIAN CERRADO

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Resumo. – Ecologia alimentar e abundância local do Tucano Toco, em um mosaico de habitats do cerrado. – Os tucanos são frugívoros do dossel que exploram áreas amplas e heterogêneas. O Tucano Toco (*Ramphastos toco*) é comum no Brasil Central, principalmente no cerrado. Nesse estudo avaliei a produção de frutos, a abundância do Tucano Toco e seus hábitos alimentares em um mosaico de habitats do cerrado. Tanto as variações espaciais quanto temporais de abundância dos tucanos coincidiram com o período de frutificação das espécies consumidas extensivamente. Essas espécies, principalmente *Virola sebifera* na mata ciliar e *Schefflera macrocarpa* no cerrado, exibiram períodos prolongados de frutificação, além de serem conhecidas por produzirem diásporos com elevado teor de lipídeos. Por outro lado, com exceção de *Eugenia punicifolia* e *Miconia albicans*, os tucanos consumiram moderadamente muitos tipos de frutos ricos em açúcares, que estiveram disponíveis por breves períodos. Portanto, em razão do Tucano Toco explorar, durante a maior parte do tempo, proporções elevadas de poucas espécies de frutos e oportunamente alternar para uma dieta mais variada, ele exibiu variações acentuadas de amplitude de nicho alimentar. As profundas variações espaciais e temporais de abundância, ao longo do ano, sugerem que os tucanos exploram áreas amplas e heterogênas em resposta à disponibilidade de frutos que são importantes em sua dieta. Potencialmente, toda essa flexibilidade, pelo menos em parte, está relacionada com a abundância do tucano toco no altamente heterogêneo e fortemente sazonal cerrado, onde nenhuma outra espécie de *Ramphastos* é comum.

Abstract. – Toucans are canopy frugivores which forage over large and diverse areas. Toco Toucan (*Ramphastos toco*) is common in the dry interior of Brazil, mainly in the 'cerrado' areas, dominated by savanna like habitats. In this study, I evaluated fruit production, Toco Toucan abundance and their feeding activity within a habitat mosaic in the Brazilian cerrado. Toco Toucan exhibited substantial temporal and spatial variations of abundance, which coincided with the availability of specific fruits. These food resources, mainly *Virola sebifera* in gallery forests and *Schefflera macrocarpa* in the cerrado, presented such traits as prolonged availability and lipid-rich diaspores. Conversely, with the exception of both *Eugenia punicifolia* and *Miconia albicans* fruits, toucans foraged moderately on a variety of briefly available sugar-rich fruits. As a result, due to an extensive use of few fruit types alternated with periods of an opportunistic broad diet, Toco Toucan exhibited substantial variations of niche breadth. The enhanced spatial and temporal variations of Toco Toucan abundance suggest a year-round use of wide and diverse areas mainly in response to fruiting species, which comprise the bulk of their diet. Potentially, all those flexibility, at least partly, may explain Toco Toucan abundance in the highly diverse and marked seasonal cerrado, in which no other *Ramphastos* species is common. *Accepted 15 April 2008*.

Key words: Ramphastidae, *Ramphastos toco*, Toco Toucan, toucans, cerrado, abundance, frugivory, feeding ecology, canopy phenology, central Brazil.

INTRODUCTION

Toucans (Ramphastidae) inhabit a wide range of Neotropical areas occurring from dry to tall rain forests (Short & Horne 2002). These prominent birds use large home ranges in which they forage mostly for canopy fruits (Terborgh *et al.* 1990). In this respect, toucans recurrently may experience food shortage due to the seasonality of fruit production in this vegetation layer (Frankie *et al.* 1974, Bullock & Solis-Magallanes 1990). Therefore, toucans often move from one to another habitat type in response to fruit availability (Graham 2001, Ragusa-Netto 2006). In fact, food resources are among the major causal factors influencing both the movements and local abundance of canopy frugivorous birds (Kinnaird *et al.* 1996, Anggraini *et al.* 2000, Solorzano *et al.* 2000). Despite relying mostly on fleshy fruits, toucans also prey upon large arthropods and small vertebrates and depredate nests (Skutch 1971, Sick 1997, Remsen *et al.* 1993, Short & Horne 2002). In the rain forests, toucans often forage on large and oily fruits (Galetti *et al.* 2000; but see Chaves-Campos 2004), which they disperse efficiently (Howe 1981, 1993). Nevertheless, in dry areas, species such as the Toco Toucan (*Ramphastos toco*) tend to exploit extensively less rewarding diaspores such as figs and *Cecropia* catkins (Ragusa-Netto 2002, 2006).

The Toco Toucan, the largest toucan species (over 500 g), mostly occurs in the dry interior of Brazil (Sick 1997, Short & Horne 2002). It is particularly common in the Brazilian "cerrado" (Neotropical savanna), which vegetation ranges from open fields to dense deciduous wood (cerradão), besides the evergreen gallery forests and palm stands (Ribeiro & Walter 1998). In this respect, the Toco Toucan is singular in its use of both savanna like and dense habitats, instead of only using continuous forests (Sick 1997, Short & Horne 2002). The typical habitat types of cerrado differ both in soil quality and moisture (Oliveira-Filho *et al.* 1990), besides tree species composition (Ribeiro & Walter 1998). Consequently, variable fruiting patterns are expected within this habitat mosaic (van Schaik *et al.* 1993, Oliveira 1998), which can potentially affect the feeding ecology and local patterns of abundance of Toco Toucans. Detailed knowledge on the relationships between Toco Toucans and food resources may allow the identification of important fruit species, habitats, and critical areas for conservation. This issue is of special concern because, despite Toco Toucans persisted in fragmented areas (Short & Horne 2002, pers. observ.), it is under a severe process of habitat loss due to the accelerated clearing of cerrado areas (Ratter *et al.* 1997). Hence, studies on their ecology could contribute to conservation plans, which may be important to prevent pronounced population declines. To improve our knowledge on the dynamics of both Toco Toucan use of foraging areas and diet, in this study I evaluated fruit production as well as Toco Toucan abundance in a habitat mosaic of the cerrado. In addition, I examined Toco Toucan feeding activity and analyzed the relationships between this parameter and both fruit and Toco Toucan abundance in each habitat type.

METHODS

Study area. This study was carried out in the Emas National Park (hereafter ENP), which is in the cerrado core region. The total area is 133 000 ha, located in the Brazilian Central Plateau, in the southwest of the State of Goiás (17°19'–18°28'S and 52°39'–53°10'W, altitude 900–1100 m). The climate is seasonal and marked with wet (October to March) and prolonged dry (April to September) seasons. Annual rainfall is approximately 1500 mm (70% in the wet season), and mean annual

temperature lies around 24.6°C (Batalha & Martins 2002).

The vegetation in the area is a mosaic of gallery forest, palm (*Mauritia flexuosa*) stands, and the dominant cerrado (93% of the area), which exhibit a gradient from open fields to dense wood vegetation. However, 70% of the cerrado is semi-open (savanna like habitat) in which trees are interspersed with open grassy areas (Batalha & Martins 2002). During the dry season, tree species drop their leaves, mainly in the late dry season (August and September). The richest plant families are Asteraceae, Fabaceae, Poaceae, and Myrtaceae (for details see Batalha & Martins 2002). Data collection was conducted in the southern part of ENP (18º15'S and 52º53'W, altitude 900 m). This area is dominated by semi-open cerrado (hereafter cerrado vegetation) cut by the Formoso river (west-east direction) and by the Buriti torto stream (north-south direction). The dominant vegetation in the Buriti torto (hereafter palm swamp) consists of *Mauritia flexuosa* palms besides scattered trees of species such as *Xylopia emarginata*, and *Virola sebifera*. The soil alongside this stream is wet or even flooded. The evergreen riparian vegetation of Formoso river (hereafter gallery forest) is very dense and dominated by *Xylopia emarginata*. The canopy is around 12–17 m in height, but emergent trees may reach 25 m. The deciduous cerrado vegetation consists mainly of small trees (2–6 m in height) spaced by 3–15 m within a matrix of native grasses. Common tree species are *Pouteria torta*, *P. ramiflora*, *Stryphnodendron adstringens*, *Anadenathera falcata*, *Kielmyera coriaceae*, and *Piptocarpha rotundifolia* (pers. observ.).

Fruit production. As mentioned above, the cerrado vegetation area was dominant and not uniform, including a gradient ranging from open to dense tracts of tree community. Hence, both tree species density and composition highly vary across this gradient (Ribeiro & Walter 1998). Due to the implications of this heterogeneity in the spatial and temporal patterns of fruit availability, to sample the wide cerrado vegetation, as well as both the slender gallery forest and palm swamp, I adopted a stratified sampling design within which a system of points was positioned. The number of sample points to assess fruit production was defined according to the proportion of each habitat type in the sampled area (rectangle of 9 x 30 km, determined using a map, scale 1 : 50 000), in the southern part of ENP. Also, the distance between points was inversely related to tree density in each habitat type, which crudely was at least twice higher in the gallery forest. In the cerrado vegetation, I sampled fruit production using 36 points (1000 m apart from each other) along three 11–km permanent access trail (12 points/trail). In the gallery forest, I positioned 12 points (500 m apart from each other; total 120 trees) along 6-km permanent access trail while, in the palm swamp, eight points were used (1000 m from each other). At each point in the cerrado vegetation, the 10 nearest trees with diameters at base equal to or greater than 10 cm were numbered with aluminum tags (n = 360 trees). This procedure assures the inclusion of mature trees. On the other hand, in the gallery forest, I marked the 10 nearest trees with diameters at breast height equal to or greater than 30 cm to sample only canopy and emergent trees (n = 120 trees), because Toco Toucans forage mostly in the canopy (Sick 1997, Short & Horne 2002, Ragusa-Netto 2006). Also, due to the closed canopy in this habitat a tree was selected only if at least 80% of the crown could be observed from the forest floor. At every point in the palm swamp I marked the four nearest palms (*Mauritia flexuosa*; n = 32 trees). This sample of 512 trees was unknown with respect to their importance for Toco Toucans. Monthly, from January 2004 to December 2005 I monitored, at each habitat type, individual crowns

for the presence of fruits with 8 x 40 binoculars. The abundance of fruits was ranked on a relative scale, ranging from total absence (0) to a plentiful fruit crop (4) (Fournier 1974). Thus, for each habitat type, the sum of scores resulted in a monthly index of fruit abundance. Tree species were identified by comparison with samples in the herbarium at the Universidade Federal do Mato Grosso do Sul (Campus Três Lagoas); nomenclature followed Lorenzi (1994, 1998).

Toco Toucan abundance. I used point counts to sample toucan abundance because this technique is adequate to assess populations of large frugivorous birds (Marsden 1999). In fact, I counted toucans to evaluate variations in their occurrence in each habitat type and to compare with food resources production, instead of assessing Toco Toucan actual density at those areas. The points established to sample fruit production were also used as survey stations. Every month, three mornings without rain or heavy mist were selected to count toucans (12 points/morning) in cerrado vegetation, two in the gallery forest (6 points/morning), and one in palm swamp (8 points/morning). All survey work was carried out from 06:30 h to approximately 08:30 h in the dry, and from 06:00 to 08:00 h in the wet season. As other conspicuous canopy frugivorous birds, Toco Toucans are, potentially, evenly detected from short–medium distances (~100 m), mainly due to their large body size, prominent colors, unambiguous loud contact calls and wing beat sound (Marsden 1999). Therefore, at each point, I counted all Toco Toucans seen or heard within a radius of 100 m during 10 min. The use of a fixed radius avoids bias towards visual or auditory detections, potentially, caused by the increase of the distance from the observer (Bibby *et al.* 1992). Toucans typically do not defend all purpose territories, are highly monogamous, and often give loud contact calls. Hence, intense seasonal nuptial/territorial vocalizations are unusual (Sick 1997, Short & Horne 2002, and see results below). So, I assumed that they were equally likely to be detected during both seasons. The toucans observed and/or heard flying over the canopy were not recorded.

Toco Toucan food resources use. To sample Toco Toucan food resources consumption, I used the 33 km of trails in the cerrado vegetation, as well as the 14 km including both the gallery forest and palm swamp. Every month, I walked these trails for 30 h, from 06:00 to 11:00 h, and from 15:00 to 18:00 h, the period of toucans peak activity (Marsden 1999). Hence, around 70% (21 h) of this time was spent searching for feeding toucans in the cerrado vegetation (3 days every month, 7 h/transect), and the rest in the wet habitats (2 days every month, 5 h/gallery forest, and 4h/palm swamp). Whenever at least one feeding toucan was detected, I recorded: a) tree species, b) food resources (flower, fruit, or arthropod), c) part eaten (petal, nectar, pulp), and d) number of toucans eating. If toucans capture arthropods I recorded the size (cm, visually estimated) and taxa (usually the order). Toucans may spent prolonged periods (up to 10 min, Howe 1981) foraging at a given crown. To avoid resampling toucans feeding on a specific food source during an observation period, I walked the trails only in one direction. The diet of *Ramphastos* species consists mostly of canopy fruits (Sick 1997, Galetti *et al.* 2000, Short & Horne 2002, Ragusa-Netto 2006). Then, I recorded only the first ingestion of a specific food item eaten by Toco Toucans. Each observation of a toucan ingesting a given food item was taken as replicate on food resources exploited by them. I used only the initial, instead of sequential observations of feeding toucans to assure the independence among feeding samples, and also because it can be assumed that

TABLE 1. Items eaten by Toco Toucans (*Ramphastos toco*), number (percentage) of feeding records, and number of Toco Toucans recorded foraging on each food item in a habitat mosaic in the Brazilian cerrado of Emas National Park (State of Goiás, Brazil, 2004–2005; data from palm swamp and gallery forest are grouped).

Plant taxa	Items	Numbers		Months	Habitat types
		Feeding records (%)	Toucans		
Annonaceae					
Xylopia emarginata	Aril	4 (2.3)	7	Jun, Jul	Gallery Forest
Araliaceae					
Schefflera macrocarpa	Pulp	47 (28.0)	88	Mar, Apr, May, Jun	Cerrado
Schefflera vinosa		9 (5.2)	19	Jul, Ago, Sept	Cerrado
Burceraceae					
Protium heptaphillum	Aril	2 (1.2)	2	Oct, Nov	Gallery Forest
Cecropiaceae					
Cecropia pachystachya	Pulp	3 (1.7)	6	May	Gallery Forest
Erythroxilaceae					
Erythroxylum suberosum	Pulp	2 (3.4)	11	Oct, Nov, Dec	Cerrado
Lauraceae					
Ocotea diospyrifolia	Pulp	2 (1.2)	4	Jan	
Leguminosae					
Inga sp	Aril	6 (3.4)	9	Mar, Apr, May	Gallery Forest
Melastomataceae					
Miconia albicans	Pulp	22 (13.0)	38	Nov, Dec, Jan	Cerrado
Meliaceae					
Guarea guidonea	Aril	2 (1.2)	2	Nov, Dec	Gallery Forest
Miristicaceae					
Virola sebifera	Aril	25 (15.0)	47	Nov, Dec, Jan, Feb	Gallery Forest
Myrtaceae					
Eugenia punicifolia	Pulp	12 (7.0)	19	Jan, Feb	Cerrado
Nyctaginaceae					
Guapira noxia	Pulp	9 (5.2)	17	Oct, Nov	Cerrado
Ochnaceae					
Ouratea spectabilis	Pulp	6 (3.4)	16	Nov, Dec	Cerrado
Sapindaceae					
Cupania sp	Aril	2 (1.2)	2	Oct	Cerrado
Styracaceae					
Styrax ferrugineus	Pulp	5 (3.0)	8	Sept	Cerrado
Arthopods		6 (3.4)	14	Feb, Dec	Cerrado
Eggs		2 (1.2)	2	Sept	Cerrado/G Forest
Total		170	311		

the birds are equally likely to be seen feeding on any conspicuous food source (Hejl *et al.* 1990). At each habitat type, the total number of Toco Toucans recorded monthly ingesting food resources was taken as an index of Toco Toucan feeding activity. Food resources, potentially, highly differ in distribution, abundance, nutritional content, and gut passage time, which may influence the consumption rate (van Schaik *et al.* 1993, Levey & Martinez

del Rio 2001). Then, to calculate a conservative frequency of food species consumed by Toco Toucans (Table 1), I used the feeding records, which consisted only of the number of times a given food item was consumed, regardless of the number of feeding toucans, time they spent feeding and amount of food ingested. However, to improve the analysis on the extent of food source use, I provided the number of feeding toucans together with the proportion of every food item used by them (Table 1). Taking into account the potential intra-seasonal changes in fruit production, to analyse Toco Toucan temporal use of feeding areas, I calculated the proportion of individuals recoded feeding at a given habitat type in four periods of the year. The periods were the followings: the late wet season (January–March), the early dry season (April–June), the late dry season (July–September), and the early wet season (October–December).

Analyses. At each habitat type, the total number of toucans recorded every month from the survey stations was taken as a monthly index of toucan abundance. To evaluate the relationship between both Toco Toucan and fruit abundance, as well as between these parameters and Toco Toucan feeding activity, Spearman correlation was used. The monthly index of feeding activity and the indices of both resources and Toco Toucan abundance were taken as variables. Only Toco Toucan food–plant species (Table 1), and respective fruit abundance (= sum of scores), were included in the analyses mentioned above. Also, I crudely grouped plant species according to lipid content: species with fruits composed of more than 10% dry weight lipid were classed lipid-rich, whereas species with lower values were classed as sugar-rich fruits (adapted from Stiles 1993). I used data on fruit pulp nutrient content from Snow (1981), Howe & Smallwood (1982), Wheelwright *et al.* (1984), Moermond & Denslow (1985), Stiles (1993), and Silva *et al.* (2001). If no information was available for a given species, I classed it according to a congener. As Toco Toucan is highly frugivorous (Ragusa-Netto 2002, 2006), and inhabits marked seasonal areas (Sick 1997, Short & Horne 2002), I evaluated the flexibility of their diet by analysing niche breath, also, in four periods of the year, using the standardized Hulrbert's niche-breath index, because it incorporates a measure of the proportional abundance of resources used (Hulrbert 1978). To calculate this parameter, I used the sum of scores of fruiting trees exploited by Toco Toucans, as well as the proportion of individuals observed feeding on a particular food item. As every habitat type was sampled according to its proportional area and potential heterogeneity, in principle, the chance that Toco Toucans feed on a given food item conforms to the stratified sample design. Hence, to calculate niche breadth value, I used the actual sample size of trees at every habitat type. Therefore, a value close to 0 indicates dietary specialization, and a value close to 1 indicates a broad diet (Hulrbert 1978).

RESULTS

Fruit production. The tree species exploited by Toco Toucans (Table 1) in the cerrado vegetation exhibited a fruiting pattern with two annual peaks (Fig. 1). A smaller peak (more clear in 2004) occurred in the dry season, arising in March due to the fruiting of *Schefflera macrocarpa*, and *S. vinosa* (Table 1). Then, from June to August (dry season), fruit production declined up to the lowest values (Fig. 1). On the other hand, from September to November (transition from the dry to the wet season), fruit production increased abruptly due to fruiting of *Erytroxilum suberosum*, *Guapira noxia*, *Ouratea spectabilis*, and *Styrax ferrugineus.*

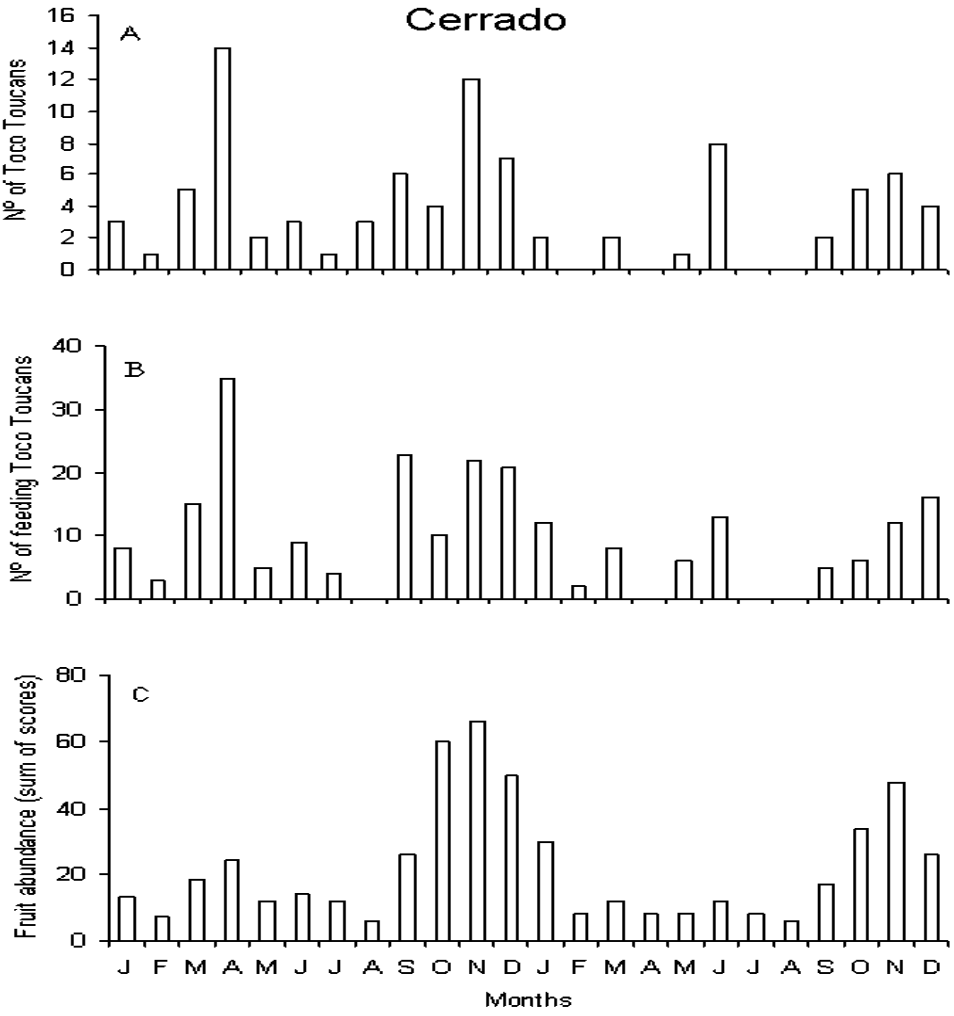

FIG. 1. Seasonal variations in the number of Toco Toucans (*Ramphastos toco*) (A), number of Toco Toucans recorded eating the available food items (B), and fruit production (values result from the sum of scores, see methods) (C), in the cerrado (Emas National Park, State of Goiás, Brazil, 2004 and 2005).

From December to February, fruit production declined substantially, although both *Miconia albicans*, and *Eugenia punnicifolia* usually bore large fruit crops in this period (Fig. 1, Table 1).

The food trees of Toco Toucans in the gallery forest also exhibited a fruiting pattern with two pronounced annual peaks (Fig. 2). The first and major peak arose in the transition from the dry to the wet season, declining from December up to May. Species such as *Virola sebifera*, *Ocotea diospyrifolia*, *Guarea guidonea*, and *Protium heptaphillum* comprised much of this peak (Table 1). The other pronounced, although brief peak, took place in the middle of the dry season and was dominated by fruit-

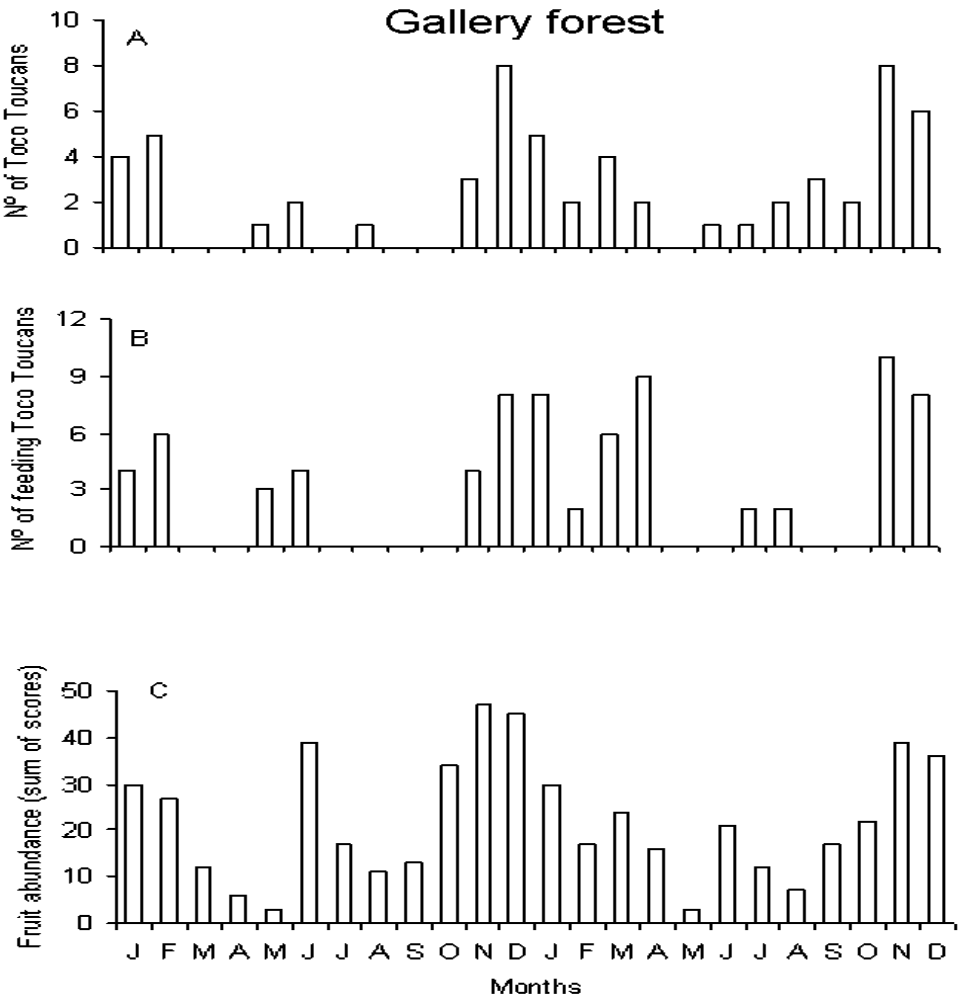

FIG. 2. Seasonal variations in the number of Toco Toucans (*Ramphastos toco*) (A), number of Toco Toucans recorded eating the available food items (B), and fruit production (values result from the sum of scores, see methods) (C), in the gallery forest (Emas National Park, State of Goiás, Brazil, 2004 and 2005)

ing of the highly abundant *Xylopia emarginata* (Fig. 2, Table 1).

Fruit production in *Mauritia flexuosa* in the palm swamp was seasonal, but extended. In the first year, palms bore fruits from January to June, and fruited again from November to May. However, toucans foraged in this habitat only for *Virola sebifera* fruits, making no use of the oily pulp of *M. flexuosa* nuts. Thus, feeding data recorded in the palm swamp were grouped together with data from the gallery forest.

Toco Toucan food resources use. Toucans foraged on 16 plant species from 15 families, including 7 in the gallery forest, and the rest in the

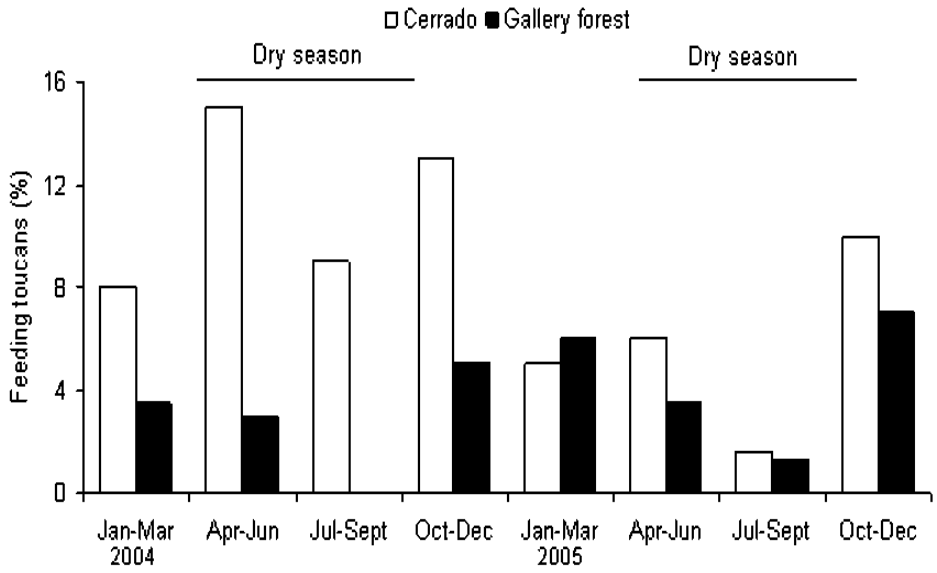

FIG. 3. Percentage of Toco Toucans (*Ramphastos toco*, n = 311 individuals) recorded foraging in the cerrado and gallery forest during four periods of the year in the Emas National Park (State of Goiás, Brazil, 2004 and 2005; data from palm swamp and gallery forest are grouped).

cerrado vegetation. They made no use of other 44 (10 in the gallery forest and the rest in the cerrado vegetation) tree species monitored for fruit production. In fact, 54% of them bore dry fruits. A total of 170 feeding records included 311 toucans eating food resources available (Table 1). The exploitation of food resources by Toco Toucans in the cerrado vegetation (74% of feeding records) reflected the proportion of time I devoted (70%, see above) to observe them feeding in this habitat type. In relation to the total of Toco Toucans recorded ingesting food resources (n = 311) in every habitat type during the two years, the proportion of individuals feeding in the cerrado vegetation was similar in both seasons in 2004 (21% in the wet and 24% in the dry season), although in 2005 toucans used this area more often (15% of individuals) in the wet than in the dry season (8%, Fig. 3). During much of the dry season they extensively exploited *Schefflera macrocarpa* fruits (28% of feeding records, n = 170). In the early rainy season, toucans ate in this habitat a variety of fruits, especially those from *Guapira noxia*, *Ouratea spectabilis*, and *Erytroxilum suberosum* (grouped = 11.8% of feeding records, Table 1). With the progress of the wet season, toucans often foraged on *Miconia albicans* and *Eugenia punnicifolia*, which together comprised 20.0% of feeding records (Table 1).

Toco toucans ate fruits in the gallery forest more often during the wet season (9% in the wet, and 3% in the dry season 2004; 13% in the wet, and 5% in the dry season 2005; n = 311 toucans, Fig. 3). In this period (October to March), they mostly fed on *Virola sebifera* fruits, which comprised 15.0% of feeding records (n = 170). Toco Toucans moderately ate other fruits, although *Inga* sp., and *Xylopia emarginata*, which were exploited during the dry season, comprised more than 6% of feeding records (Table 1).

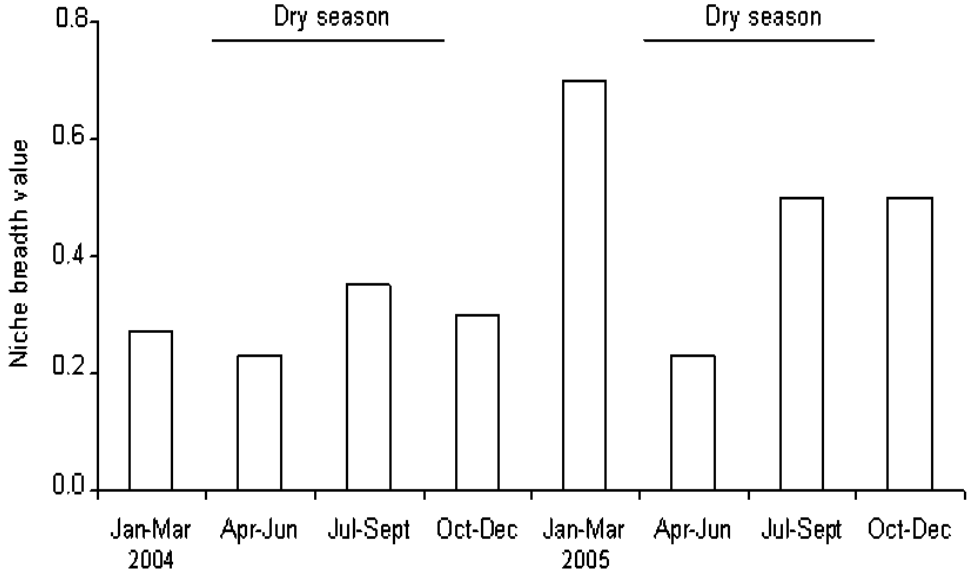

FIG. 4. Variations of Hurlbert's niche breadth values of Toco Toucan diet during four periods of the year in the Emas National Park (State of Goiás, Brazil, 2004 and 2005).

Toco Toucans seldom consumed arthropods, which formed part of their diet only during the rainy season. In the early rains, they captured flying termites (± 1 cm), which swarmed close to the crown of cerrado trees. In the late wet season, toucans captured fitofagous coleopterans and large-bodied social spiders (both = 2 cm, Table 1). In the late dry season, Toco Toucans ate the eggs from two nests. One of them was a cavity nest in a mound termitaria in the cerrado vegetation, presumably used by the Yellow-Faced Parrot (*Alipiopsitta xanthops*), while the other, also a cavity nest, was in a dead *Mauritia flexuosa*, apparently, used by the Blue-Fronted Parrot (*Amazona aestiva*).

Hurlbert's niche breadth for Toco Toucan feeding activity fluctuated from low (B' = 0.23, April–June 2004) to high (B' = 0.70, January–March 2005), although variations between B' = 0.25 and B' = 0.50 were common (Fig. 4). In both years the lowest values took place in the early dry season when *Schefflera macrocarpa* fruits comprised most of Toco toucan diet (77%, n = 56 individuals recorded eating fruits in 2004, and 63%, n = 30 in 2005). On the other hand, the highest value corresponded to the late wet season 2005 when four important species were massively available (*Virola sebifera*, *Inga* sp., *Miconia albicans*, and *Eugenia punicifolia*, Table 1). Variations in Hurlbert's niche breadth for Toco Toucan diet exhibited both low and insignificant relationship with either the number of food species available (r_s = 0.45, P = 0.26), or fruit abundance (sum of scores; r_s = 0.24, P = 0.57) over each three month periods.

Toco Toucan local abundance. The occurrence of toucans at each habitat type varied substantially. In the cerrado vegetation, toucans were abundant during both the middle of the dry and the middle of the wet season. Toco Toucan peaks of abundance coincided with the

peaks of fruit production (r_s = 0.74, P < 0.001, Fig. 1). The fluctuations of this parameter was also significantly correlated with Toco Toucan feeding activity (r_s = 0.79, P < 0.001, Fig. 1). Finally, Toco Toucan abundance highly paralleled their feeding activity (r_s = 0.86, P = 000, Fig. 1). It is important to note the coincidence between the pronounced peaks of Toco Tocans abundance during the early–mid dry season, when they mostly foraged on *Schefflera macrocarpa* fruits. Hence, the frequency of the contact calls by which toucans were often detected was not high only during rains, when potentially both nuptial/territorial purposes and the exploitation of a variety of fruit types in the cerrado vegetation might be related to their frequent vocalizations (Fig. 1, Table 1).

The variations of Toco Toucan abundance in the gallery forest was significantly correlated with fruiting pattern (r_s = 0.68, P < 0.001, Fig. 2), which was also correlated with their feeding activity (r_s = 0.55, P < 0.005, Fig. 2). Moreover, as toucans often moved to the gallery forest when extensively exploited fruits were available, Toco Toucan abundance and their feeding activity were highly correlated (r_s = 0.82, P < 0.001, Fig. 2). In the palm swamp, toucans consumed only few fruit types, which were common in the gallery forest. Then, I analyzed only the relationship between toucan abundance and their feeding activity, which was significant (r_s = 0.53, P < 0.007).

DICUSSION

Food resource production. Few studies simultaneously evaluated fruit production within habitat mosaics in the cerrado. However, the available data point out a marked seasonal fruit production either in deciduous or evergreen habitats (Funch *et al.* 2002). As in the dry forests, both the gallery forest and the deciduous cerrado vegetation exhibited seasonal fruiting patterns, apparently conformed by rainfall (Frankie *et al.* 1974, Bullock & Solis-Magallanes 1990, McLaren & McDonald 2005). The cerrado vegetation and the gallery forest fruited massively during the wet season, although in the gallery forest other pronounced fruiting peaks occurred in the middle of the dry season, due to the highly abundant *Xylopia emarginata*.

These two habitat types also exhibited temporal differences related to the availability of the fruits often exploited by Toco Toucans. In the cerrado vegetation, lipid-rich fruits of *Schefflera* were produced and highly exploited during the dry season when no other fleshy fruit was available to them in this habitat. In the gallery forest, during the wet season, fruiting included lipid-rich diaspores, especially those of *Virola sebifera*, which comprised a substantial proportion of the fruiting pattern. Also, *V. sebifera* bore fruits during the entire wet season whereas, in the cerrado vegetation, species with sugar-rich fruits of *Miconia*, *Ouratea*, *Eugenia*, *Erytroxilum*, and *Guapira* bore large, but ephemeral fruit crops. Therefore, in this period, due to the combination of both lipid and sugar-rich fruits from the gallery forest and the cerrado vegetation, respectively, the diet of Toco Toucans was richest.

Fruits and Toco Toucan local abundance. As Channel-billed (*Ramphastos vitellinus*) and Red-breasted (*R. dicolorus*) toucans, in the wet Atlantic forest (Galetti *et al.* 2000), Toco Toucans seldom consumed arthropods. These preys were present in the diet of Toco Toucans mainly in the wet, instead of in the dry season, when arthropods might be a substitute for the declining fleshy fruits (van Schaik *et al.* 1993, Kinnaird *et al.* 1996). However, in marked seasonal areas, arthropod abundance is also likely to decline during the dry season, so that, in place of experience diet shifts, frugivorous birds tend to move for favorable areas (van Schaik *et al.* 1993). Although

arthropod abundance was not sampled in this study, Toco Toucans fed on items, apparently, abundant because it boomed during brief periods during the wet season. Therefore, the consumption of both massive and brief available items suggests an opportunistic use of animal matter by Toco Toucans. Furthermore, during the wet season Toco Toucans, presumably, may require more protein for breeding. In fact, low amounts of animal matter comprised the diet of many species in the Ramphastidae whose stomach contents were analyzed (Remsen *et al*. 1993). Despite of that, due to the use of initial observation feeding data may be biased towards the consumption of conspicuous food items such as fruits (Hejl *et al*. 1990). Hence, at this time the reduced percentage of animal matter in the diet of Toco Toucans needs to be interpreted with caution.

Most *Ramphastos* species live in the richest forest of the Neotropics (Short & Horne 2002) and, as Toco Toucans, in the diverse, although dry, cerrado (Batalha & Martins 2002), they exploited a similar variety of fruit types. In the wet Atlantic forest, Channel-billed and Red-breasted toucans fed on 16 and 11 species, respectively (Galetti *et al*. 2000), while Toco Toucans ate 16. Other diet trait shared by most *Ramphastos* species is the use of palms, *Inga*, *Cecropia*, and Lauraceae fruits, besides figs (Sick 1997, Galetti *et al*. 2000, Ragusa-Netto 2002, 2006; Short & Horne 2002). Toco Toucans seldom foraged on these fruits, apparently scarce in the cerrado. With the exception of *Virola* fruits, Toco Toucans mostly exploited the fruits of Araliaceae, Myrtaceae, and Melastomataceae which, conversely, were rarely consumed by toucans in the rain forests (Galetti *et al*. 2000, Short & Horne 2002). Perhaps the abundance of plant taxa, at least partly, mirrors their proportion in the diet of toucans which, in fact, extensively foraged on only few fruit types (Galetti *et al*. 2000, this study). However, only further studies focusing on tree community structure may clarify the relationship between tree species densities and their importance in the diet of toucans.

Some tree species often exploited by toucans exhibit prolonged fruiting season, and produce lipid-rich diaspores (Galetti *et al*. 2000). Toco Toucans widely exploited *Schefflera macrocarpa* and *Virola sebifera*, which also bore lipid-rich fruits for prolonged periods. However, they also ate variable proportions of diverse sugar-rich fruits, usually massively produced, although briefly available (Howe & Smallwood 1982). As a consequence Toco Toucans exhibited fluctuations of niche breadth value, mainly due to the unbalanced consumption of some fruit species at every period of the year. This pattern of fruit exploitation may explain the absence of relationship between niche breadth value and either fruit richness or abundance. Only during a fruiting episode, in the late wet season, Toco Toucans consumed more similar proportions of a variety of fruit types, resulting in a comparatively wider niche breadth value. Perhaps, both the synchronous and massive availability of a variety of sugar-rich fruits caused a balanced consumption by Toco Toucans. Therefore, apparently, Toco Toucans opportunistically switched from a narrow to a broad diet according to the variations in fruiting patterns. In addition, a potential factor related to the frequent declines of niche breadth value would be the moderate use of most fruit species in the gallery forest. Perhaps, this reflected the structure of the gallery forest of Formoso river, which is small, slender, and dominated by *Xylopia emarginata*. At a larger gallery forest in the Pantanal Toco Toucans exploited 11 fruit species, 4 of which extensively (Ragusa-Netto 2006).

Toco Toucans foraged simultaneously in the cerrado vegetation and in the gallery forest, making clear their versatility to use both semi-open and dense habitats. In fact, their

flexibility to use diverse areas is not limited to the cerrado, because Toco Toucans are also common in the dry forest of the interior of Brazil and in the Pantanal (Sick 1997, Short & Horne 2002, Ragusa-Netto, 2002, 2006). In the ENP, the occurrence of Toco Toucans in both habitat types coincided with the availability of fruits on which they extensively foraged. Therefore, potentially, particular food resources mostly caused the fluctuations of Toco Toucan abundance at each habitat type. Indeed, the significant correlations between fruit production and Toco Toucan feeding activity emphasize the importance of food resources on their local abundance, as for other large canopy frugivorous birds (van Schaik *et al.* 1993, Kinnaird *et al.* 1996, Anggraini *et al.* 2000). Taking into account fruit availability as an important causal factor for the occurrence of toucans in a given habitat type (Graham 2001), presumably when general fruit availability declined abruptly, Toco Toucans moved to more distant, albeit favorable areas. This generalist use of contrasting habitat types performing meso or even large scale movements, besides an opportunistic diet (Short & Horne 2002, this study) may, at least partly, explain the wide occurrence of Toco Toucans in the highly diverse and marked seasonal cerrado, where no other *Ramphastos* species is common (Sick 1997, Short & Horne 2002).

Some toucan species are well known for their importance as seed dispersers (Howe 1981, Howe & Vande Kerckhove 1981). Although Toco Toucan behavior at fruiting trees was out of the scope of this study, in many instances I observed them at a given crown removing fruits (usually 1-5 min), and then moving over distances of dozens or hundred meters. Also, during these visits, toucans did not regurgitate or defecate seeds. Thus, by carrying away a large number of seeds, Toco Toucans are, potentially, important seed dispersers in the cerrado. As this wide and highly diverse biome has been heavily reduced to a collection of small remnants (Ratter *et al.* 1997), we urgently need to continue improving our knowledge on the ecology of these fantastic birds, because the conservation of large populations requires not only wide, but as diverse as possible areas of cerrado, within which Toco Toucans might search for their major fruits and contribute for tree regeneration.

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