# Chaco Chachalaca (*Ortalis canicollis*, Wagler, 1830) feeding ecology in a gallery forest in the South Pantanal (Brazil)

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## Abstract

Cracids are generalist frugivores, which often exploit plant food resources such as flowers and leaves, mainly when fruit production declines. The Chaco chachalaca (*Ortalis canicollis*) is the most abundant cracid in the Pantanal (Brazil), and particularly common in the gallery forests. However, the factors related to their occurrence in this habitat type are unclear. In this study I describe the feeding habits and feeding niche breadth fluctuations of the Chaco chachalaca in relation to food resources abundance and diversity at the Miranda river gallery forest (Southern Pantanal). I also analyzed the relationships between Chaco chachalacas feeding activity and food resources abundance. This parameter (flowers and fruits) exhibited significant seasonal differences of abundance in which flowers were plentiful at the end of the dry, while fruits were abundant during the early wet season. However, food resources diversity to Chaco chachalacas exhibited no seasonal difference. Their feeding activity paralleled the availability of food resources, so that when some items were massively available an enhanced number of Chaco chachalacas foraged in the gallery forest, particularly during the prolonged dry season when they extensively used flowers and *Genipa americana* fruits. In fact, the Chaco chachalaca feeding niche breadth value presented low values in this period, while high values were common in the rest of the year. The flexible diet of this cracid, potentially favors their year round presence in the gallery forest, mainly during the prolonged dry season when the propensity for famine might be high. Since the Chaco chachalaca is among the largest and most abundant canopy frugivores in the gallery forest, it may contribute to forest regeneration, an underscored role due to the impact of annual floods and meandering dynamics on tree loss.

*Keywords:* Cracidae, canopy phenology, Pantanal, *Ortalis canicollis*, frugivory.

## Ecologia alimentar do aracuã-do-pantanal (*Ortalis canicollis*) em uma floresta ripária no Pantanal Sul

## Resumo

Cracídeos são frugívoros generalistas que, também, exploram flores e folhas, sobretudo quando frutos são escassos. No Pantanal (Brasil), o aracuã-do-pantanal (*Ortalis canicollis*) é o cracídeo mais abundante, sendo particularmente comum em matas ciliares. No entanto, os fatores relacionados com sua ocorrência nesse habitat são desconhecidos. Nesse estudo eu descrevo tanto os hábitos alimentares quanto as variações de amplitude de nicho alimentar do aracuã-do-pantanal em relação à abundância e diversidade de recursos alimentares na mata ciliar do rio Miranda (Pantanal-Sul, Brasil). Também, analisei a relação entre atividade alimentar e oferta de recursos alimentares. Esse parâmetro (flores e frutos) exibiu variações significativas de abundância em que a produção de flores foi pronunciada de meados para o final da estação seca, enquanto a oferta de frutos foi elevada do início para meados da estação chuvosa. No entanto, a diversidade de recursos alimentares disponíveis para o aracuã-do-pantanal não diferiu entre as estações. A atividade alimentar do aracuã-do-pantanal foi paralela a oferta de recursos alimentares, tal que quando alguns itens eram abundantes um grande número de Aracuãs forrageava na mata ciliar, sobretudo durante a severa estação seca em que consumiram extensivamente flores e frutos de *Genipa americana*. De fato, a amplitude do nicho alimentar do aracuã-do-pantanal foi baixa nesse período, enquanto valores elevados foram comuns no restante do ano. A dieta flexível do aracuã-do-pantanal, potencialmente, favorece sua permanência continua na mata ciliar, principalmente durante a severa estação seca, quando a propensão a escassez de alimento se acentua. O aracuã-do-pantanal está entre os maiores frugívoros da mata ciliar, portanto, sua importância para regeneração desse habitat deve ser elevada em razão da constante perda de árvores causada pelas cheias anuais e a dinâmica de formação de meandros.

*Palavras-chave:* Cracidae, fenologia, Pantanal, *Ortalis canicollis*, frugivoria.

## 1. Introduction

Several Neotropical vertebrate species rely on plant food resources. In fact, frugivorous vertebrates are the dominant group in the neotropical forests and, in some areas, comprised much of the mammalian and avian biomass (Fleming et al., 1987, Terborgh et al., 1990). However, in most habitats such resources are seasonally produced, mainly in areas subjected to a prolonged dry season. As responses to spatial and temporal variation in fruit availability many frugivorous periodically resort to other plant resources such as flowers, leaves, and petioles, or they move around within a local habitat mosaic according with staggered fruiting peaks in a series of habitats (van Schaik et al., 1993; Renton, 2001, Ragusa-Netto, 2008a, 2010, 2013). While in markedly seasonal areas fleshy fruit production declines during the dry season, flowering is often pronounced, so that flowers may turn an important food resource both for sedentary (Ferrari and Strier, 1992), and mobile frugivores (Galetti, 1993; Ragusa-Netto, 2004, 2005, 2007, 2008b).

Cracids, conspicuous medium to large-sized birds, rely mostly on plant food resources; hence they are exposed to the seasonality of Neotropical areas (Bullock and Solis-Magallanes, 1990; van Schaik et al., 1993). Fruits form most of their diet, so that the most exploited plant families are Moraceae, Arecaceae, Rubiaceae, Fabaceae, Cecropiaceae and Lauraceae, although a total of 113 families have been reported (Muñoz and Kattan, 2007). However, they often forage on flowers, leaves, seeds, and arthropods (Caziani and Protomastro, 1994; Galetti et al., 1997; Sick, 1997). In fact, due to their generalist feeding habits, they often resort to feeding on those items when fruits are scarce (Muñoz and Kattan, 2007).

The Chaco chachalaca (*Ortalis canicollis*, Wagler, 1830) is a conspicuous cracid from Southwestern of South America, locally abundant in the Pantanal (Sick, 1997), which vegetation is a mosaic of patches of deciduous forest, gallery forest, palm swamps, savannas, and grassy open areas accordingly to soil quality and effect of annual floods (Pott and Pott, 1994). Chaco chachalacas are common in the gallery forests (Sick, 1997). Nevertheless, the factors related to their occurrence along watercourses remain unclear. Taking into account the effect of food resources on patterns of habitat use by animals, an important factor influencing foraging activity is the variation in temporal and spatial availability of plant food resources (van Schaik et al., 1993). Flood plains systems, as the Pantanal, are characterized by different environmental conditions compared to most tropical areas, in particular higher seasonality, which is expressed by periods of rains and floods followed by a prolonged dry season (Pott and Pott, 1994). Seasonal differences in food resources availability are thought to cause diet shifts of frugivores, as observed for instance by Ragusa-Netto and Fecchio (2006). As cracids mostly rely on plant food resources, the direct examination of their responses to flowering and fruiting patterns, may explain the importance of such parameters on their local occurrence, yet almost unstudied for most cracids (but see Galetti et al., 1997). In this study I describe both the feeding habits and feeding niche breadth fluctuations of the Chaco chachalaca in relation to food resources abundance and diversity at the Miranda river gallery forest (Southern Pantanal). I also analyzed the relationships between Chaco chachalacas feeding activity and food resources abundance. I focused on the composition and temporal variability of Chaco chachalaca's feeding habits and asked whether the diet of this cracid is mostly formed by fruits as in the case of other cracid species from Neotropical areas (Pacagnella et al., 1994; Galetti et al., 1997; Mikich, 2002; Zaca et al., 2006; Muñoz and Kattan, 2007; Muñoz et al., 2007). I expected temporal variation in the diet and feeding activity of Chaco chachalacas because of strong seasonality in the study area, mainly caused by annual floods and a prolonged dry season, which could affect fruit availability for this species.

## 2. Material and Methods

### *2.1. Study area*

This study was developed in the Southern Pantanal flood plain at the gallery forest of the Miranda river (Municipality of Corumbá, State of Mato Grosso do Sul-Brazil, 19° 35'S, 57° 2'W, altitude ±100 m). The vegetation in the area is a mosaic of palm savanna (*Copernicia alba* Morong), tecoma savanna (*Tabebuia aurea* (Manso) B. et H.), patches of deciduous forest interspersed with open grassy areas and the dense Miranda river gallery forest. This forest is 50-200 m wide, with an 8-13 m canopy, but emergent trees may reach 17 m (*e.g. Tabebuia heptaphylla* (Vell.) Tol.). From July to September many tree species drop their leaves, although evergreen species contribute to an evident semi-deciduous pattern. Annual rainfall is around 1000 mm, most of which occurs from November to March (wet season). In this period average temperature is 27 °C, while in the dry season (April to October) average temperature is 20 °C, and in coldest months (June-July) frosts may occur. In this area of Pantanal, inundation pulses typically occur from January to March. During floods, the water level in the gallery forest is up to 1.5 m (pers. obs.; Miranda river water level enhances 3-6 m, source Base de Estudos do Pantanal/UFMS administration).

### *2.2. Flower and fruit production*

To sample flower and fruit abundance, phenology transects (a total of 5 km) were established in four tracts (400-800 m apart) of the gallery forest. At this habitat the topography and drainage are not uniform neither is the effect of floods. Consequently, due to the patchy occurrence and/or distribution of tree species (Oliveira-Filho et al., 1990, Oliveira-Filho et al., 1994), I randomly positioned (parallel to the water course) continuous 300 m transect segments with regular distances from the river up to the proximity of the forest edge (5 m, 35 m, 65 m, and 95 m). Along these trails, a total of 370 trees were numbered with aluminum tags. Trees were selected both if they were

located within a 2.0 m band on either sides of the trails and if their diameter at breast height (DBH) was equal to or greater than 20 cm. This criterion was adopted to assure the inclusion of canopy trees in this sample, since in the forests the Chaco chachalaca typically forages in the canopy (Caziani and Protomastro, 1994; pers. obs.). Also, a tree was selected only if at least 80 percent of the crown could be observed from the forest floor. Individual crowns were monthly monitored (between day 5 and 10, from April 2000 to March 2002) for the presence of flowers and fruits with the aid of 8 x 40 binoculars. The abundance of flowers, unripe and ripe fruits was noted and ranked on a relative scale ranging from total absence to the full crown capacity of a given phenophase (0 to 4, Fournier, 1974). Thus, the monthly index of resource abundance of a given phenophase resulted from the sum of all abundance scores. Tree species were identified by comparison with samples in the herbarium at the Universidade Federal do Mato Grosso do Sul (Campus Corumbá) and following Pott and Pott (1994). The analysis of dispersal syndromes was out of the scope of this study; hence the fruits were classified only according to the presence of fleshy edible parts, instead of dispersal features (zoochory, autochory, and anemochory). Thus, tree species whose diaspores had a pulp or aril were assigned as species with fleshy fruit, whereas those with dry mesocarp as species with dry fruits.

*2.3. Chaco chachalacas food resources use*

To sample the feeding habits of Chaco chachalacas, I used the permanent access trails in which I positioned the phenology transects. Every month, I walked those trails for 30 h, from 06:00 to 11:00 h, and from 15:00 to 18:00 h, dry season; 05:00 to 10:00 h, and from 16:00 to 19:00 h (real time, summer time unconsidered), wet season. These periods corresponded to the Chaco chachalaca peak activity (Marsden, 1999). Chaco chachalacas may spent prolonged periods (up to 10 min, Howe, 1981) foraging at a given crown. To avoid resampling birds feeding on a specific food source during an observation period, I walked the trails only in one direction. Whenever I spotted at least one feeding Chaco chachalaca I recorded: a) tree species, b) food resource (flower or fruit), c) part eaten (petal, pulp, or aril), d) the number of Chaco chachalacas foraging, and e) the time and date. The diet of Chaco chachalacas consists mostly of canopy items (Caziani and Protomastro, 1994), which were conspicuously foraged by these birds. Then, I recorded only the first ingestion of a specific food item eaten by Chaco chachalacas. I used only the initial, instead of sequential observations of feeding Chaco chachalacas to assure the independence among feeding samples. In fact, cracids are opportunistic feeders and will include in their diet food items that make up relatively large, but only seasonally available, portions of biomass that serves as potential food. Hence, it is valid to use the initial observation of birds feeding on such resources, because it can be assumed that the birds are equally likely to be seen feeding on any abundantly available resource (Hejl et al., 1990).

*2.4. Analyses*

In seasonal forests fruiting pattern fluctuates exhibiting short periods of pronounced fruit enhancement followed by abrupt declines (Funch et al., 2002; Ragusa-Netto and Silva, 2007). Hence, in the course of a season, variations in fruit production have implications for frugivores (van Schaik et al., 1993). Then, taking into account the potential intra-seasonal changes in fruit production at a given habitat type (Renton, 2001; Ragusa-Netto, 2007, 2008a, 2010, 2013), I grouped fruit production in four periods of the year. The periods were the following: 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). I made the same with the following parameters: a) fruit diversity, and b) niche breadth value. For every period the accumulated monthly index of resource abundance (= sum of scores) was taken as variable for the analyses. I compared food resources production across seasons with a repeated measures analysis of variance (ANOVA). The score data were log transformed both to achieve normality and reduce heteroscedasticity (Shapiro-Wilk test, $W = 0.94$, $P = 0.200$). 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 and Martinez del Rio, 2001). Thus, as Chaco chachalacas were not individually marked, I used the feeding records to avoid pseudoreplication. This conservative data for the analyses consisted only of the number of times a given food item was consumed, regardless of the number of feeding Chaco chachalacas, time they spent feeding and amount of food ingested. I also used the feeding records to calculate the frequency of food species consumed by Chaco chachalacas (Table 1). However, to improve the analysis on the extent of food source use, I provided the number of feeding Chaco chachalacas together with the proportion of every food item used by them (Table 1). As the Chaco chachalaca is highly frugivorous (Caziani and Protomastro, 1994), and inhabits marked seasonal areas (Sick, 1997), I evaluated the range of their diet by analysing niche breath, using the standardized Hurlbert's niche-breath index, because it incorporates a measure of the proportional abundance of resources used (Hurlbert, 1978). To calculate this parameter, I used the sum of scores of flowering and fruiting trees exploited by Chaco chachalacas, as well as the proportion of feeding records on a particular food item. Therefore, a value close to 0 indicates dietary specialization, and a value close to 1 indicates a broad diet (Hurlbert, 1978). I used the Simpson index (D), the reciprocal of Simpson's original formula (Simpson, 1949), to describe the fruit diversity available to Chaco chachalacas. The Simpson index (and its derivatives) is sensitive to changes in the common species, whereas the more widely used Shannon index is more sensitive to changes in the rare ones (Peet, 1974). As the Chaco chachalaca is a generalist frugivore (Caziani and Protomastro, 1994), I chose the Simpson index to minimize the influence on fruit diversity indices of the rarely available fruits and to emphasize changes in

**Table 1.** Plant species used, feeding records ($n$ = 478 feedings records), and number of feeding Chaco chachalacas ($n$ = 1033 *Ortalis canicollis*), in the Miranda river gallery forest (South Pantanal, Brazil).

| Plant taxa | Item* | Month | Feeding records (%) | N° feeding Chaco chachalacas |
|---|---|---|---|---|
| APOCYNACEAE | | | | |
| *Aspidosperma australe* M. Arg. | f | Sept | 0.3 | 3 |
| ARECACEAE | | | | |
| *Copernicia alba* Morong | p | May | 1.0 | 10 |
| BIGNONIACEAE | | | | |
| *Tabebuia aurea* (Manso) B. et H. | f | Sept | 0.3 | 3 |
| *T. heptaphylla* (Vell.) Tol. | f | Jul, Aug | 26.0 | 271 |
| CAPPARIDACEAE | | | | |
| *Crataeva tapia* L. | f | Sept | 0.6 | 6 |
| | p | Feb | 0.3 | 3 |
| CECROPIACEAE | | | | |
| *Cecropia pachystachya* Trec. | p | Jan, Feb, May, Sept | 12.0 | 123 |
| ERYTROXILACEAE | | | | |
| *Erytroxilum anguifungum* Mart. | p | Nov | 0.5 | 5 |
| FLACOURTIACEAE | | | | |
| *Banara arguta* Briq. | f | Jan, March | 1.4 | 14 |
| | p | March, Apr, May | 7.3 | 75 |
| LAURACEAE | | | | |
| *Ocotea diospyrifolia* Hassl. | p | Jan | 5.4 | 56 |
| LEGUMINOSAE | | | | |
| *Andira inermis* H. B. K. | p | Jan | 1.2 | 12 |
| *Inga vera* H. et A. | f | Sept, Oct, Nov | 10.3 | 107 |
| MALPIGHIACEAE | | | | |
| *Birsonima orbignyana* A. Juss. | p | Feb, March | 1.2 | 12 |
| MORACEAE | | | | |
| *Ficus luschnathiana* (Miq.) Miq. | p | Jul, Sept, Oct | 5.9 | 61 |
| MYRTACEAE | | | | |
| *Eugenia pseudoverticilata* DC. | p | Nov | 1.2 | 12 |
| *Myrcia egences* DC. | p | Nov | 0.3 | 3 |
| POLYGONACEAE | | | | |
| *Coccoloba cujabensis* Wedd. | p | Oct | 0.3 | 3 |
| RUBIACEAE | | | | |
| *Genipa americana* L. | f | Jan | 0.4 | 4 |
| | p | Jun, Jul, Aug, Sept, Oct | 12.6 | 131 |
| SMILACACEAE | | | | |
| *Smilax fluminensis* Steud. | p | May | 0.8 | 8 |
| VERBENACEAE | | | | |
| *Vitex cymosa* Bert. | f | Sept, Oct | 5.6 | 58 |
| | p | Dec, Jan | 3.3 | 34 |
| Others** | | | 1.8 | 19 |

*Item eaten: a = aril, n = nectar, f = flower, p = pulp, s = seed. **Ten species ate by Chaco chachalacas few times. They consumed leaves from three of them, flowers from four, and fruit pulp from the rest).

the commonly available ones. To compare fruit diversity (Simpson index (D)) available to Chaco chachalacas in the four periods of the year, I used the Wilcoxon match test. In this respect, I made paired comparisons of semi-wet *versus* semi-dry season periods values of this parameter in the four periods of the year (see above). The relationship between Chaco chachalacas feeding activity (monthly sum of feeding records), and food resources availability was evaluated through correlation analysis. Then, the Log of monthly percentage of feeding records was correlated (Pearson correlation) with Log of food resources (sum of scores of flowers + fruits). The relationship between food resource abundance and feeding niche breadth was also evaluated through correlation analysis. Only Chaco

chachalacas food-plant species (Table 1), and respective fruit abundance (= sum of scores), were included in the above analyses.

## 3. Results

### *3.1. Flower and fruit production*

I recorded 29 tree species in the phenology transects, which belong to 18 families (see those ones foraged by Chaco chachalacas in Table 1). Both species and trees with fleshy fruits predominated in the phenology sample (66%, and 80%, respectively, $n$ = 370 trees), while the occurrence of species with dry fruits was smaller (10 species, and 76 trees). The most common species were *Inga vera* (66 trees), *Ocotea diospyrifolia* (62), *Vitex cymosa* (43), *Tabebuia heptaphylla* (36), *Cecropia pachystachya*, and *Genipa americana* (both 24 trees). Annually flowering was conspicuous twice, firstly in the middle of the dry season resulting mainly from flowering of *Tabebuia heptaphylla* and *Ocotea diospyrifolia*, and later a very pronounced flowering peak aroused during the transition from the dry to the wet season (Figure 1b). Such massive flower production resulted mainly from flowering of *Vitex cymosa*, *Cecropia pachystachya*, *Genipa americana*, besides the highly abundant *Inga vera*, whose massive flowering yearly lasted two months (Figure 1b).

Fruiting was seasonal and exhibited three annual peaks. In the middle of the wet season a very prominent fruiting peak aroused, other occurred in the transition from the wet to the dry season (March-May, flood period). From the middle to end of the dry season another fruiting peak arouse (July-September, Figure 1c). The major fruiting peak in the middle of the wet season (December 2000 to February 2001) mostly resulted from fruiting of *Vitex cymosa*, *Ocotea diospyrifolia*, and *Cecropia pachystachya*. All such species bore large fruit crop (Figure 1c), however, in the following wet season *Ocotea diospyrifolia* produced no fruits, and *Cecropia pachystachya* bore fruits later. Thus, in this period the large fruit crop of *Vitex cymosa* comprised most of this fruiting peak (Figure 1). The peak of fruit production in the transition from the wet to the dry season resulted from fruiting of *Banara arguta*, *Sapium obovatum*, *Crataeva tapia*, *Copernicia alba*, and *Inga vera*. The later, despite of the massive flowering, generally bore small fruit crops, while the abundant *Banara arguta* and *Sapium obovatum* comprised most of this fruiting peak. Fruits of all such species matured during floods. From the middle to the end of the dry season much of the fruit production was comprised by fruiting in *Cecropia pachystachya*, *Genipa americana*, and *Ficus luschnathiana* (Figure 1). As food resources production exhibited peaks followed by valleys, their abundance differed significantly according to year period ($F$ = 3.78, $P$ = 0.013; Figure 2). However, food diversity available to Chaco chachalacas exhibited moderate fluctuations so that no seasonal difference emerged ($z$ = 1.10, $P$ = 0.380, Figure 3a).

### *3.2. Chaco chachalacas food resources use*

Chaco chachalacas foraged on 25 plant species from 16 families, totaling 478 feeding records. They used several food items few times, while extensively foraged for fleshy

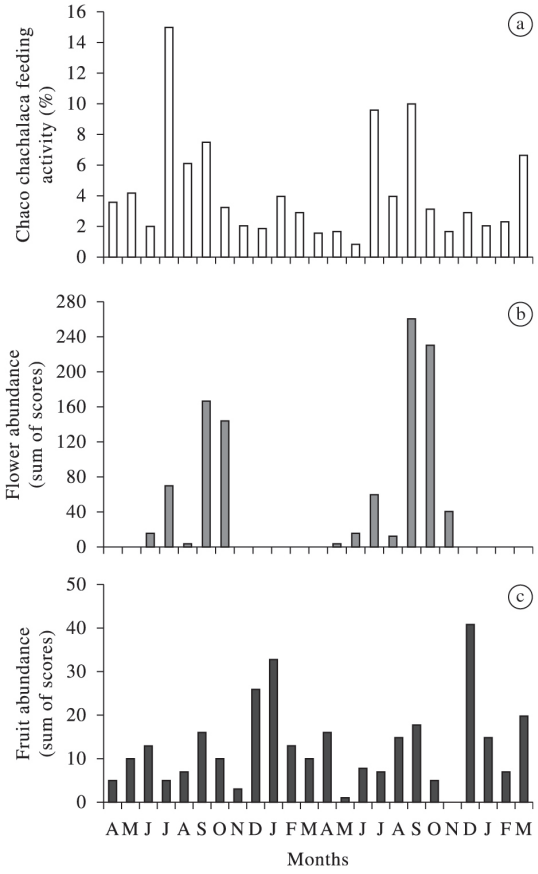


**Figure 1.** From top to bottom: (a) monthly percentage of *Ortalis canicollis* foraging activity ($n$ = 478 feeding records), and (b) the abundance of flowers, and (c) fleshy fruits (for both = sum of scores) in the Miranda river gallery forest (State of Mato Grosso do Sul, Brazil, 2000-2002).

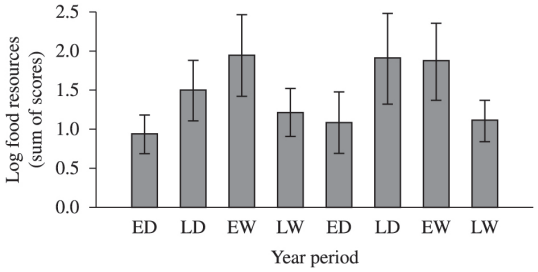


**Figure 2.** Mean food resources abundance (± SD of sum of scores) during four periods of the year in the Miranda river gallery forest (State of Mato Grosso do Sul, Brazil, 2000-2002). (ED: the early dry season [April-June], LD: the late dry season [July-September], EW: the early wet season [October-December], LW: the late wet season [January-March]).

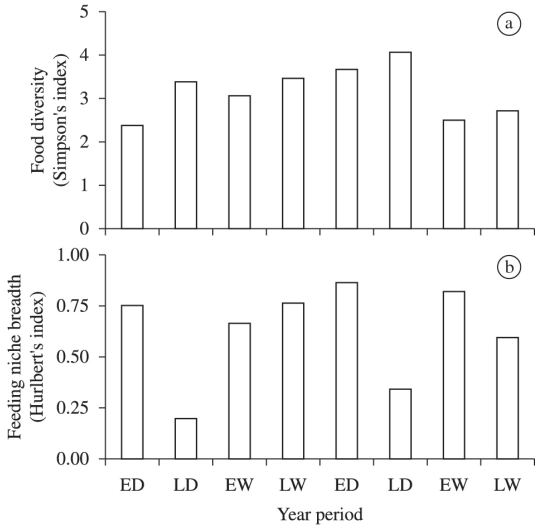


**Figure 3.** Variations of Sympson's diversity index of available fruits (a), and Hurlbert's niche breadth values (b), of *Ortalis canicollis* diet during four periods of the year in the Miranda river gallery forest (State of Mato Grosso do Sul, Brazil, 2000-2002; legend for year periods as in Figure 2).

fruits and flowers from few species (Table 1). Flowers comprised 44.6% of feeding records, mainly those from *Tabebuia heptaphylla*, *Inga vera*, and *Vitex cymosa*. During the dry season flowers comprised 55% ($n$ = 358 feeding records) of the foraging activity, and from the middle to the latter part of this period, such resource was even more important forming 68% ($n$ = 265) of Chaco chachalacas diet. The emergent *Tabebuia heptaphylla*, besides common in the gallery forest yearly bore extraordinary flower crops during the middle of the dry season. Groups of two to four Chaco chachalacas intensely foraged on these flowers, usually lasting 30-60 min in a foraging bout (pers. obs.). Flowering in both *Inga vera* and *Vitex cymosa* occurred in the late dry season, and were among the most important food resources in this period (Table 1).

Although Chaco chachalacas extensively used flowers from few species, they exploited a wide range of fruit types, produced in different periods. In the transition from the wet to the dry season (flood period), Chaco chachalacas foraged on *Banara arguta*, *Crataeva tapia*, and *Copernicia alba* fruits. Particularly, every year *B. arguta* produced very large fruit crops, on which this cracid often forged (Table 1). From the middle to the end of the dry season Chaco chachalacas mainly used three fruit types (Table 1). The few, but large *Ficus luschnathiana* trees, fruited asynchronously (pers. obs.), and produced very large fig crops on which up to ten individuals were recorded simultaneously foraging. *Cecropia pachystachya* also fruited in this period, as well as *Genipa americana*, the most used fruit species by Chaco chachalacas (Table 1). Trees of this common species yearly bore large fruit crops, which asynchronous maturation lasted by up three months (often from July to September-October). Hence, within a fruit crop often some fruits were available and avidly consumed. Usually, while foraging Chaco chachalacas ingested piecemeal one or more *G. americana* fruits (pers. obs.).

During the rains many fruit types were produced, however Chaco chachalacas often foraged on *C. pachystachya* catkins, especially in the latter part of this period when many trees bore large fruit crops (Figure 1a). Chaco chachalacas also foraged on *Ocotea diospyrifolia* and *Vitex cymosa* fruits. On the other hand, Chaco chachalacas seldom used most other fruit types available during the early rains. Chaco chachalacas consumed leaves from only three tree species (*Banara arguta*, *Crataeva tapia*, and *Genipa americana*), but this food item comprised less than 1% of the feeding records (Table 1).

The Chaco chachalaca foraging activity intensely fluctuated, as well as flower and fruit production. The peaks of foraging activity coincided with the availability of important food resources such as *T. heptaphylla* flowers (August 2000, July 2001), *Inga vera* flowers (October 2000, September 2001), *Genipa americana* fruits (September and October 2000, September 2001), and *Cecropia pachystachya* catkins (March 2002). Therefore, the Chaco chachalaca foraging activity paralleled the availability of food resources ($r$ = 0.53, $P$ < 0.008, Figure 1). Hurlbert's niche breadth for Chaco chachalacas exhibited during the year from moderate to wide values (minimum $B'$ = 0.20, July-September 2000, maximum $B'$ = 0.86, April-June 2001; Figure 3b). This differences resulted mostly from the extensive consumption of a reduced set of food items in the late dry season (mainly flowers), and a diverse array of abundant fruit species in the other periods of the year (Table 1, Figure 3b). Variations in Hurlbert's niche breadth for Chaco chachalacas diet exhibited both an inverse and insignificant relationship with food resources abundance ($r$ = –0.29, $P$ = 0.499) over each three month periods.

## 4. Discussion

### *4.1. Food resources production*

The Miranda river gallery forest included a large number of species and trees with fleshy fruits. Besides that, the massive flowering of some tree species pointed out this forest as an extraordinary source of nectar during the most severe period of the year. In Neotropical dry forests massive flowering usually occurs between the late dry and the early wet season, followed closely by fruit production (Bullock and Solis-Magallanes, 1990). At the Miranda river gallery forest, the major annual flowering peak matches this pattern, and aroused mainly from species that produced fleshy fruits during the rainy season. Annually, such pronounced flowering occurred when the river level was lowest (pers. obs.), therefore the dry conditions could contribute to trigger this phenophase, as in a gallery forest studied elsewhere (Kinnaird, 1992).

The predominance of fleshy fruit production during rains has been found in seasonal habitats such as dry

forests (Renton, 2001; Ragusa-Netto and Silva, 2007), and apparently is usual for gallery forests within dry areas (Funch et al., 2002; this study). It is important to emphasize the fruit production in the transition from the wet to the dry season (March-April, Figure 1), which aroused from species exposed to floods for longer periods (pers. obs.). Such species bore ripe fruits simultaneously to floods, dropping a large number of diaspores into the water (Kubitzki and Ziburski, 1994). Thus, the dynamic of flower and fruit production at Miranda river gallery forest confirmed the peculiarities of a flood plain, whose cycles are under the strong influence of water level. An important consequence of this phenology pattern for Chaco chachalacas was a similar diversity of food resources across seasons.

*4.2. Ortalis canicollis feeding habits*

Despite of fluctuation in Chaco chachalacas foraging activity, they exploited food resources all year-round in the gallery forest. Their occurrence was very distinct from those of toucans and parrots, which periodically moved in large numbers to the gallery forest in order to deplete massive food resource (Ragusa-Netto, 2004, 2006, 2007, 2008b), a pattern of habitat use typical of frugivorous birds in which their abundance often switch from absence to enhanced numbers according to the fruit pattern (van Schaik et al., 1993). Therefore, the Miranda river gallery forest, potentially, is a permanent habitat for the Chaco chachalaca. Furthermore, during the rainy season Chaco chachalacas bred and roused chicks in the gallery forest (pers. obs.)

The feeding ecology of cracids continues poorly known (but see: Muñoz and Kattan, 2007). They have been assumed as generalists feeders so that the most common plant families in their diets correspond to the most common and diverse plant families in Neotropical forests they inhabit (Muñoz and Kattan, 2007). Chaco chachalacas extensively foraged on massive flower and fruit crops from the most abundant tree species in the gallery forest. In the Argentinean Chaco, besides fruits, Chaco chachalacas often consumed leaves from herbaceous plants, especially during the dry season (Caziani and Protomastro, 1994). On the other hand, in the gallery forest they seldom consumed tree leaves, presumably due to the toxic secondary compounds (Caziani and Protomastro, 1994). Foliage and flowers usually represent less than 20% of items, but may be over 30%. In the case of Chaco chachalacas the pronounced flower consumption (> 44%) might result from the abundance of this item during the dry season. The presence of massive blossoms in the gallery forest, presumably, made flowers a profitable item (Ferrari and Strier, 1992), since individuals consumed large amounts of flowers when visiting a tree during prolonged time (dozens minutes, pers. obs.). Among dietary shifts experienced by frugivores during periods of famine, the use of flowers is well documented (van Schaik et al., 1993). In the gallery forest the abundant tree species, which comprised most of the flowering pattern, formed a substantial proportion of the Chaco chachalaca diet, especially from the middle to the late dry season. In this period of the year, figs are also a usual food resource for several frugivores (Lambert and Marshall, 1991; van Schaik et al., 1993). Fig trees produce fruits asynchronously, so that figs are often available (Lambert and Marshall, 1991; Ragusa-Netto, 2002). However, only few fig trees were present in the gallery forest. Perhaps this may explain the moderate presence of figs in the Chaco chachalaca's diet. Conversely, *Genipa americana* trees were common and yearly produced much of the fleshy fruits available during a substantial part of the dry season. For such an opportunistic feeder this abundant resource, potentially, contributes for their persistence in the gallery forest during the most severe period of the year in the Southern Pantanal.

Chaco chachalacas exhibited wide niche-breadth values almost year-round. The major fluctuations resulted from the extensive consumption of flowers from the middle to the end of the dry season in both years. In the other months this parameter fluctuated moderately due to the consumption of balanced proportions of different fruit types at every period of the year. In marked seasonal areas frugivores often exhibit fluctuations of niche-breadth values according to the seasonality of food resources (Renton 2001; Ragusa-Netto, 2008a, 2013). However, in the course of the studied years the simultaneous availability of diverse food types might explain the low frequency of major fluctuations in niche breadth. Chaco chachalacas exhibited low niche breadth value, mainly due to the unbalanced consumption of food resources at some periods of the year. This pattern of food consumption might explain the absence of relationship between niche breadth value and food resources abundance. Apparently, this resulted from their opportunist feeding habits.

The Chaco chachalaca is among the largest canopy frugivores in the Miranda river gallery forest, as well as in the Southern Pantanal (Sick, 1997). This cracid often ingested a substantial amount of fruits during a foraging bout (pers. obs.). In many instances I found intact seeds regurgitated or defecated by them. In fact many cracid species usually pass seeds intact through their digestive tracts and may act as seed dispersers (Galetti et al., 1997; Mikich; 2002; Muñoz and Kattan, 2007). Therefore, the Chaco chachalaca may be an important seed disperser, similarly to other cracids (Gonçales-Garcia, 1994; Peres and van Roosmalen, 1996; Galetti et al., 1997). The Miranda river gallery forest often loose trees (pers. obs.), at least in part, due to the severity of annual floods and meandering dynamics. Therefore, Chaco chachalacas may play an underscored role on forest regeneration, which emphasize the importance of its conservation.

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