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FEEDING ECOLOGY OF A PARROT ASSEMBLAGE IN THE BRAZILIAN *CERRADO*

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Abstract · For two years, I documented the feeding habits of a parrot assemblage in relation to food resources offer (abundance, number, and diversity of food species) across a habitat mosaic in the Brazilian *cerrado*. In addition, for each parrot species, I compared variations in those parameters across seasons, as well as in feeding niche breadth. The number of feeding individuals of every parrot species paralleled both, food abundance and the number of food species available. In fact, despite fluctuations, the food abundance and the number and diversity of food species exhibited similar values through seasons, suggesting a trend of adequate food supply across the three major habitat types (palm swamp, gallery forest, and the dominant *cerrado* vegetation). Except for *Orthopsittaca manilata* (that foraged only on *Mauritia flexuosa* fruit pulp), all other five species (*Ara ararauna*, *Amazona aestiva*, *Alipiopsitta xanthops*, *Eupsittula aurea*, and *Diopsittaca nobilis*) showed broad feeding niche breadth. Their broad diets resulted from the opportunistic use of a rich collection of seasonal food species. Moreover, parrot species highly diverged in terms of the eaten plant part, and the parrots' diet displayed a gradient that had an increasingly greater dominance of seeds (*A. ararauna*, *A. aestiva*, and *A. aurea*) to a diet composed mainly by fruit pulp and flowers (*A. xanthops*, and *D. nobilis*). The accelerated fragmentation process of the Brazilian *cerrado* has been suppressing the feeding areas available to parrots; nonetheless, the present study showed that the availability of food resources strongly affected the number of feeding parrots in a given area. This highlights the importance of a rich pool of scattered food patches for parrot abundance. Thus, conservation plans should prioritize the inclusion of habitat mosaics, at least as diverse as documented in the present study. As a concern, food resources available may be scarce in the smaller *cerrado* remnants, mainly in terms of the variety and year-round abundance required by parrots.

Resumo · Ecologia alimentar de uma assembleia de psitacídeos no Cerrado brasileiro
Neste estudo, durante dois anos, documentei os hábitos alimentares de uma assembléia de psitacídeos em resposta a oferta de recursos alimentares (abundância, nº e diversidade de espécies alimentares), em um mosaico de habitats do Cerrado. Também, para cada espécie, comparei as variações estacionais quanto aos parâmetros acima, bem como em relação a amplitude do nicho alimentar. A quantidade de indivíduos de cada espécie de papagaio foi paralela à oferta de recursos alimentares e ao número de espécies de vegetais disponíveis. De fato, apesar de flutuações, o número de espécies alimentares, a abundância e diversidade de alimentos exibiram valores semelhantes ao longo das estações, sugerindo ofertada adequada de alimentos disponíveis nos três principais tipos de habitat (savana de palmeiras, mata ciliar e a vegetação do Cerrado). Com exceção de *Orthopsittaca manilata* (consumidora de polpa de frutos de Buriti), todas as outras cinco espécies (*Ara ararauna*, *Amazona aestiva*, *Alipiopsitta xanthops*, *Eupsittula aurea* e *Diopsittaca nobilis*) exibiram amplos valores de nicho alimentar. A rica dieta dessas espécies resultou da exploração oportunista de uma variedade de espécies estacionais. Além disso, cada espécie apresentou uma dieta associada a itens particulares das plantas consumidas. Neste sentido, ficou claro um gradiente no qual houve predomínio de sementes (*A. ararauna*, *A. aestiva* e *A. aurea*), a dietas compostas principalmente por polpa de frutas e flores (*A. xanthops* e *D. nobilis*). O acelerado processo de fragmentação do Cerrado brasileiro tem suprimido as áreas de alimentação disponíveis para os papagaios. Em contraste, o presente estudo mostrou que a variedade de recursos alimentares disponíveis afetou fortemente o número de papagaios alimentando-se em uma determinada área. Isso enfatiza o quanto uma rica coleção de manchas de alimento favorece a abundância de papagaios. Dessa forma, os planos de conservação envolvendo psitacídeos deveriam priorizar a inclusão de mosaicos de habitat, pelo menos, como documentado nesse estudo. É preocupante o fato de que recursos alimentares disponíveis em remanescentes menores sejam insuficientes, principalmente, quanto a abundância e variedade de alimento necessários à essas aves ao longo do ano.

Key words: Brazil · Diet · Frugivory · Granivory · Phenology · Psittacidae

INTRODUCTION

Neotropical parrots heavily rely on fluctuating plant food resources whose use often requires a combination of strategies, including mesoscale movements leading to habitat shifts and diet switching, to withstand pronounced changes in food offer (Renton 2001, Ragusa-Netto 2006, 2007, Haugaasen & Peres 2007, Renton et al. 2015, Silva 2018). Evaluations of the foraging

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behavior of parrots in response to such erratic food offer should be carried out over areas composed by habitat mosaics as diverse as possible (Haugaasen & Peres 2007). In fact, important feeding areas and the resources exploited by parrots should be identified and assessed because such basic data are central to be employed as a tool for their long-term conservation (Renton 2001, Berkunsky et al. 2017, Rivera et al. 2019). Notwithstanding, the scarcity of basic knowledge for many species continues to be one of the major gaps in parrot ecology (Renton et al. 2015), which is a concern as they are among the most threatened group of birds (Olah et al. 2016).

The Emas National Park in central Brazil presents an adequate opportunity to assess the feeding ecology of a parrot assemblage in a Neotropical savanna. The park is among the largest protected areas of the Brazilian *cerrado*, including a complete habitat collection typical of *cerrado* vegetation (Batalha & Martins 2002). Six parrot species are common in the area, ranging from the small *Eupsittula aurea* to the large *Ara ararauna*, in addition to *Alipiopsitta xanthops, Amazona aestiva*, *Diopsittaca nobilis*, and *Ortopsittaca manilata*. Although none of them are critically endangered, all are vulnerable due to pet trade (Berkunsky et al. 2017) and the accelerated clearing of the *cerrado*, as approximately 50% of the original area is under agricultural use (Carvalho et al. 2009, Beuchle et al. 2015).

In the *cerrado*, the dynamics of the relationship between the spatio-temporal variability of food availability and parrot diet is poorly known (see Ragusa-Netto 2006, Bianchi 2009, de Araújo & Marcondes-Machado 2011). Since the Brazilian *cerrado* includes marked seasonal habitat types (Batalha & Martins 2002), parrots may exhibit an opportunistic response to a variable food offer, as expected for frugivorous/granivorous birds with reduced or no dependence on a particular food source (Walker 2007). Thus, to improve our knowledge about the dynamic use of foraging areas by parrots and their diet, I documented in this study the feeding habits of a parrot assemblage in response to the availability of food resources in a habitat mosaic of the *cerrado*. Specifically, I analyzed the relationships between the use of food resources and feeding niche breadth by each parrot species, as well as variables related to food availability (abundance, and number and diversity of food species).

METHODS

Study area. This study was carried out at Emas National Park (hereafter ENP), in the *cerrado* core region. It is located in the Brazilian Central Plateau, southwest of the state of Goiás (17°19'–18°28'S and 52°39'–53°10'W, 900–1100 m a.s.l.), and it has a total area of 134,000 ha. The climate is seasonal. with wet (October to March) and prolonged dry (April to September) seasons. Annual rainfall is approximately 1,500 mm (70% in the wet season), and the 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 exhibits a gradient from open fields to dense wood vegetation. However, 70% of the *cerrado* is a semi-open savanna-like habitat in which trees are interspersed with open grassy areas (Batalha & Martins 2002). During the dry season, tree species shed 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 carried out in the southern part of ENP (18°15'S 52°53'W, 900 m a.s.l.). This area is dominated by semi-open *cerrado* (hereafter *cerrado* vegetation), cut by the Formoso river (direction west-east) and by the Buriti Torto stream (direction north-south). The dominant vegetation in the Buriti Torto (hereafter palm swamp) consists of *M. flexuosa* palms beside scattered tree species such as *Xylopia emarginata* and *Virola sebifera*. The soil alongside this stream is wet or even flooded. The evergreen riparian vegetation of the Formoso river (hereafter gallery forest) is dense, with a canopy of around 12–17 m in height, although 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* (Batalha & Martins 2002).

Production of food resources. As previously mentioned, the *cerrado* vegetation area was dominant and not uniform, including a gradient ranging from open to dense tracts of trees. Hence, tree species density and composition vary highly across this gradient (Batalha & Martins 2002). To sample the dominant *cerrado* vegetation, as well as the slender gallery forest and palm swamp, I used a stratified sampling design. A system of sampling points was positioned in each habitat type. Because this system encompassed the flora gradient in terms of tree density and composition, samples represented the heterogeneity of the spatial and temporal patterns of the availability of food resources (leaves, flowers, and fruits). The number of sampling points was determined according to the proportion of each habitat type in the sampled area (a rectangle of 9 x 30 km set in the southern part of ENP using a map to the scale 1:50,000). The distance between points was inversely related to the tree density in each habitat type, which was at least twice as high in the gallery forest.

I sampled fruit production in the *cerrado* vegetation using 36 points (1,000 m apart from each other) along three 11 km permanent access trails (12 points/trail). In the gallery forest, I placed 12 points (500 m apart from each other) along 6 km of a permanent access trail, and eight points in the palm swamp (1,000 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 ensured the inclusion of mature trees. In the gallery forest, I marked the 10 nearest trees with diameters at breast height equal to or greater than 20 cm, in order to sample only canopy and emergent trees (N = 120 trees), because Neotropical parrots forage mostly in the canopy (Ragusa-Netto 2006, Lee et al. 2014, Renton et al. 2015). 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. I marked the four largest and nearest palms (*M. flexuosa*; N = 32) at every point in the palm swamp. The importance of these 512 trees for parrots was unknown. I monitored individual crowns for the presence of leaves, flowers, and fruits monthly, from January 2004 to December 2005, using 8 x 40 binoculars. The abundance of each resource was ranked on a relative scale, ranging from total absence (0) to a plentiful crop (4) (Fournier 1974). Thus, for each habitat type the sum of scores resulted in a monthly index of resource abundance. Tree species were identified by comparison with samples in the herbarium at the Universidade Federal do Mato Grosso do Sul (Campus Três Lagoas). Plant nomenclature followed Lorenzi (1994, 1998).

Food resources use. To sample parrot diet, I used the 33 km of trails in the *cerrado* vegetation, as well as the 14 km including the gallery forest and the 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 (GTM - 04:00), the periods of parrot peak activity (Marsden 1999). Hence, around 70% (21 h) of this time was spent searching for parrots feeding in the *cerrado* vegetation (3 days every month, 7 h/transect), and the remaining time in the wet habitats (2 days every month, 5 h/ gallery forest, and 4 h/palm swamp). Whenever at least one feeding parrot was detected, I recorded: a) tree species; b) food resources available (leaf, flower, fruit, or arthropod); c) eaten plant part (petiole, blade, peduncle, petal, nectar, pulp, and seed); and d) species and number of parrots feeding. If parrots captured arthropods, I recorded the size (cm, visually estimated) and taxa (usually the order). Due to differences in food resources with respect to distribution, abundance, nutritional content, and gut passage time of parrots, which may influence the rate of their consumption (van Schaik et al. 1993, Levey & Martinez del Rio 2001), parrots may spend prolonged periods foraging at a given crown (up to 20 min, Ragusa-Netto 2005). Assuming that parrots are equally likely to be seen feeding on any conspicuous food source, to avoid resampling during an observation period I walked the trails only in one direction. In addition, I used only the initial, instead of sequential, observations of parrots eating to ensure independence among feeding samples (Hejl et al. 1990). Then, I recorded only the first ingestion of a specific food item by a parrot species at a given plant species, which I assumed as a feeding record. This was done to improve the independence of samples, as parrots were not individually marked. The conservative data used for the analyses resulted from the records on parrots ingesting food items, regardless of the number of feeding birds, the time they spent feeding, and the amount of food ingested. I also used the feeding records to calculate the frequency of food species consumed by parrots (Table 1). However, to improve evaluations on the extent of food source use, I provided the number of feeding parrots according to every food item used by them (Table 1). I did the same for each habitat type each year (see below).

Analyses. Due to the pronounced seasonal variation in production of food resources (Justiniano & Fredericksen 2000, Ragusa-Netto & Silva 2007), I grouped monthly food availability data in four periods of the year: late wet season (January-March), early dry season (April-June), late dry season (July-September), and early wet season (October-December). I made the same grouping with the following data: a) number of parrots of a given species feeding; b) number of food tree species; c) food diversity; and d) niche breadth value. To analyze the possible relationship between the number of parrots of a given species feeding and a) food abundance, b) number of food tree species, c) food diversity, and d) niche breadth value, I used the Pearson correlation on log-transformed data to improve linearity. Only parrot food plant species (Table 1) and their respective food part abundance (sum of scores of leaves, flowers, and fruits) were included in the aforementioned analyses. I used Simpson's index (D), the reciprocal of Simpson's original formula (Simpson 1949), to describe the food diversity exploited by parrots. Simpson's index (and its derivatives) is sensitive to changes in common species, whereas the more widely used Shannon index is more sensitive to changes in rare ones (Peet 1974). I chose Simpson's index to minimize the influence of the rarely available resources and to emphasize changes in the commonly available ones because parrots often use abundant resources (Renton et al. 2015). I evaluated the range of parrot diets by niche breadth in every year period using the standardized Hurlbert's niche-breadth index because it incorporates a measure of the proportional abundance of resources used and the proportional use of that resource (Hurlbert 1978). To calculate this index, I used the sum of scores of food resources, as well as the feeding records of each parrot species on a particular source. A value close to 0 indicates dietary specialization, while a value close to 1 indicates a broad diet (Hulrbert 1978). As every habitat type was sampled according to its proportional area and potential variety of plant species, in principle the chance of parrots feeding on a given food item conforms to the stratified sample design. Hence, to calculate both food diversity and niche breadth value, I used the actual sample size of trees at every habitat type. To compare inter-seasonal variations in the production of food resources (by the sum of scores), the number of food species, food diversity, and niche breadth value, I used the Wilcoxon match test. For this, I made paired comparisons of wet vs dry period values of these parameters obtained for the aforementioned four periods of the year (i.e., January—March vs April—June, and July—September vs October—December values). I used a Detrended Correspondence Analysis (DCA) to compare associations between each parrot species and their consumption of different species' plant parts (number of feeding records, Table 1). DCA is an ordination method adequate for comparing associations containing counts of taxa or counted taxa accross associations. Like other ordination methods, DCA attempts to place similar samples in similar positions in the ordination plot. Detrending is a sort of normalization procedure in two steps. The first step involves an attempt to 'straighten out' points lying in an arch, which is a common occurrence. The second step involves 'spreading out' the points to avoid clustering of the points at the edges of the plot. Considered plant parts were leaves, flowers, fruit pulp or aril, and seeds. Here, parrot species was positioned in the graph in accordance with its diet dominance (plant parts) in relation to the diet dominance of other species. For two genera with very small seeds, *Miconia* and *Ficus*, I included the consumption of the whole fruit as fruit pulp. *Orthopsittaca manilata* was excluded from this analysis due to its exclusive consumption of *Mauritia flexuosa*'s fruit pulp (see Results below), which would clump all other species in the DCA scatter plot diagram.

Table 1. Plant species and respective items eaten by parrots at a *cerrado* habitat mosaic in Emas National Park, Brazil (January 2004 – December 2005). Total of feeding records and total of individuals ingesting food items: *Alipiopsitta xanthops* (N= 354, N= 1,319), *Amazona aestiva* (N= 242, N= 421), *Ara ararauna (*N= 312, N= 676), *Diopsittaca nobilis* (N = 111, N= 561), *Eupsittula aurea* (N= 56, N= 178), *Orthopsittaca manilata* (N= 54, N= 353). Habitat type: MS = *Mauritia* stand, C = *cerrado*, GF = gallery forest.

Plant taxa	Parrot species	Item	Feeding records	Feeding individuals	Month	Habitat
ANACARDIACEAE						
Anacardium humili	*A. xanthops*	seed	12 (3.4)	61	Sep, Oct	C
	A. aestiva	seed	24 (10.0)	52	Sep, Oct	C
	A. ararauna	seed	48 (15.4)	91	Sep, Oct, Nov	
	E. aurea	seed	20 (36.0)	73	Sep, Oct	C
ANNONACEAE						
Annona crassiflora	*A. xanthops*	leaf	3 (0.08)	12	May	C
Xylopia emarginata	*A. xanthops*	seed	4 (1.1)	13	Apr, Jun, Jul	GF
	A. aestiva	seed	28 (11.6)	59	Jun, Jul	GF
	D. nobilis	seed	5 (4.5)	17	Jun, Jul	GF
APOCYNACEAE						
Hancornia speciosa	*A. xanthops*	pulp	2 (0.6)	10	Oct, Nov	C
	A. aestiva	seed	3 (1.2)	6	Oct, Nov	C
ARECACEAE						
Acrocomia aculeata	*A. ararauna*	pulp	1 (0.3)	4	May	C
Attalea geraensis	*A. ararauna*	seed	4 (1.3)	8	Aug, Sep	C
Mauritia flexuosa	*A. ararauna*	pulp	12 (3.8)	40	Feb, Mar, Apr, Sep	MS
	O. manilata	pulp	54 (100.0)	353	Jan, Feb, Mar, Apr, Jul	MS
ASTERACEAE						
Calea cuneifolia	*E. aurea*	flower	4 (7.1)	10	Jul, Aug	C
		seed	7 (12.5)	40	Jun, Jul, Aug	C
Piptocarpha rotundifolia	*A. xanthops*	seed	7 (2.0)	31	Mar, Apr	C
	E. aurea	seed	5 (8.9)	15	Apr, May	C
BIGNONIACEAE						
Tabebuia ochracea	*A. xanthops*	flower	5 (1.4)	18	Aug	C
	A. aestiva	flower	4 (1.7)	8	Aug	C
		seed	1 (0.4)	8	Oct	C
Tabebuia sp.	*A. aestiva*	flower	1 (0.4)	2	Sep	GF
BOMBACACEAE						
Eriotheca gracilipes	*A. xanthops*	leaf	26 (7.3)	121	Apr-Jul, Sep, Oct	C
		flower	22 (6.2)	33	Jun, Jul	C
		bark	4 (1.1)	9	Oct	C
	A. aestiva	seed	55 (22.7)	76	Jul, Aug, Sep	C
		bark	4 (1.6)	4	March	C
Eriotheca pubescens	*A. aestiva*	seed	8 (2.3)	16	Aug, Sep	C
CARYOCARACEAE						
Caryocar brasiliense	*A. xanthops*	flower	12 (3.4)	19	Sep, Oct	C
	A. ararauna	seed	62 (20.0)	123	Jan, Oct, Nov, Dec	C
CHRYSOBALANACEAE						
Couepia grandiflora	*A. xanthops*	flower	2 (0.6)	9	Oct, Nov	C
DILLENEACEAE						
Davilla eliptica	*E. aurea*	aril	1 (1.8)	2	Sept	C
ERYTHROXIELACEAE						
Erythroxylum suberosum	*A. xanthops*	leaf	6 (1.6)	18	Apr, Oct	C
GUTTIFERAE						
Kielmeyera coreacea	*A. xanthops*	seed	15(5.1)	41	Mar, Apr, May, Jun	C
		bark	3 (0.8)	28	Mar, Apr	C
	A. aestiva	seed	3 (1.2)	6	Jul, Aug	C
	D. nobilis	flower	1 (0.9)	3	Nov	C
LEGUMINOSAE						
Anadenanthera falcata	*A. aestiva*	seed,	43 (17.8)	72	May, Jun, Jul, Aug	C
		bark	2 (0.8)	2	Sep	C
Bauhinia sp.	*E. aurea*	flower	7 (12.5)	20	Sep	C
Dimorphandra mollis	*A. xanthops*	leaf	2 (0.6)	8	Apr	C
	A. aestiva	seed	23 (9.5)	34	May, Jun, Jul, Aug	C
	A. ararauna	seed	21 (6.7)	44	Apr, Jun, Jul, Aug	C
	D. nobilis	leaf	1 (0.9)	8	Apr	C
Hymenaea stigonocarpa	*A. xanthops*	flower	37 (10.5)	114	Jan, Feb, Mar, Nov, Dec	C
	A. ararauna	seed	3 (1.0)	6	Jun	C
Inga sp.	*A. xanthops*	aril	3 (0.8)	10	Apr	GF

	A.aestiva	aril	4 (1.7)	8	Apr	GF
Stryphnodendron adstringens	*A. xanthops*	seed	30 (8.5)	87	Jun, Jul, Aug, Sep	C
	A. aestiva	seed	11 (4.5)	20	May, Jun, Jul	C
	A. ararauna	seed	48 (15.4)	112	Apr, May	C
	D. nobilis	seed	1 (0.9)	12	Apr	C
Vignia peduncularis	*A. aestiva*	seed	3 (1.2)	6	Aug, Sep	C
MALPIGHIACEAE						
Byrsonima cocolobifolia	*A. xanthops*	pulp	4 (1.1)	16	Feb, Mar	C
Byrsonima verbacifolia	*D. nobilis*	seed	6 (5.4)	60	Dec, Jan	C
MELASTOMACEAE						
Miconia albicans	A. xanthops	pulp	6 (1.7)	29	Dec, Jan	C
	E. aurea	seed	3 (5.4)	6	Nov, Dec	C
Miconia ferruginata	*E. aurea*	seed	1 (1.8)	4	Nov	C
MIRISTICACEAE						
Virola sebifera	*A. xanthops*	flower	4 (1.3)	12	Sep	GF
MORACEAE						
Ficus gardineriana	*A. xanthops*	pulp	3 (0.8)	18	Oct	GF
MYRTACEAE						
Eugenia punicifolia	*A. xanthops*	pulp	10 (2.8)	42	Jan, Feb	C
Myrcia sp	*D. nobilis*	seed	2 (1.8)	21	Nov	C
Psidium firmum	A. xanthops	pulp	2 (0.5)	10	Jan	C
	A. aestiva	seed	4 (1.6)	8	Jan, Nov, Dec	C
	D. nobilis	seed	25 (22.5)	114	Jan, Nov, Dec	C
NYCTAGINACEAE						
Guapira noxia	*A. aestiva*	seed	2 (0.8)	2	Oct	C
OCHNACEAE						
Ouratea spectabilis	*A. xanthops*	leaf	2 (0.5)	10	May	C
		pulp	26 (7.3)	104	Oct, Nov	C
	A. ararauna	seed	15 (4.8)	32	Nov, Dec	C
	E. aurea	pulp	1 (1.8)	2	Dec	C
	D. nobilis	pulp	54 (48.6)	260	Nov, Dec	C
SAPINDACEAE						
Matayba elaegnoides	*A. ararauna*	seed	1 (0.3)	8	Jan	GF
SAPOTACEAE						
Pouteria ramiflora	*A. xanthops*	leaf	3 (0.8)	14	May	C
	A. ararauna	seed	8 (2.5)	16	Jan, Dec	C
Pouteria torta	*A. xanthops*	flower	18 (5.0)	77	Jul, Aug	C
		aril	40 (11.3)	176	Nov, Dec	C
		bark	2 (0.5)	8	Mar	C
	A. aestiva	flower	1 (0.4)	3	Jul	C
		aril	3 (1.2)	3	Dec	C
		bark	1 (0.4)	4	Jul	C
	A. ararauna	seed	53 (17.0)	138	Jan, Sep, Oct, Dec	C
	D. nobilis	aril	5 (4.5)	29	Nov, Dec	C
STYRACACEAE						
Styrax ferrugineus	*A. aestiva*	seed	3 (1.2)	14	Sep, Oct	C
VOCHYSIACEAE						
Qualea grandiflora	*A. xanthops*	bark	1 (0.3)	22	Apr	C
	A. aestiva	seed	1 (0.4)	2	Jul	C
	A. ararauna	seed	2 (0.6)	4	Sep	C
Qualea multiflora	*A. ararauna*	seed	2 (0.6)	8	Apr, Jun, Jul	C
Qualea parviflora	*A. xanthops*	bark	1 (0.3)	13	Apr	C
	A. aestiva	seed	1 (0.4)	8	Jul	C
	A. ararauna	seed	26 (8.3)	40	Apr, Jun, Jul, Sep, Oct	C
NOT IDENTIFIED	*A. xanthops*	flower	4 (1.1)	20	Feb, Mar, May	GF
	A. ararauna	seed	1 (0.3)	4	Aug	GF
	E. aurea	seed	1 (1.8)	4	Jun	C
ASH	*D. nobilis*		1 (0.9)	34	May	C
TERMITARIA SOIL	*S. xanthops*		6 (1.7)	16	May, Jun	C
	E. aurea		1 (1.8)	2	May	C

RESULTS

Production of food resources. Due to the dominance of fruit in the parrots' diets, I described only the fruiting pattern, which in the *cerrado* vegetation exhibited two annual peaks (Figure 1A). A smaller one (stronger in 2005) occurred in the dry season, beginning in April, due to fruiting of species such as *Stryphnodendron adstringens*, *Piptocarpha rotundifolia*, and *Gochnathia polymorpha*. It continued with *Anadenathera falcata*, *Dimorphandra mollis*, and *Eriotheca gracilipes*, all of which bore dry fruits (Figure 1A). From September to November, fleshy fruit production increased abruptly due to fruiting in *Anacardium humile*, *Pouteria torta*, *P. ramiflora*, *Caryocar brasiliense*, *Erytroxilum suberosum*, and *Ouratea spectabilis* (clearer in 2004). From December to February, those fruits declined, although both *Miconia albicans* and *Eugenia punnicifolia* usually bore large fruit crops this period (Figure 1A).

The gallery forest exhibited a fruiting pattern with two pronounced annual peaks (Figure 1B). The first and major

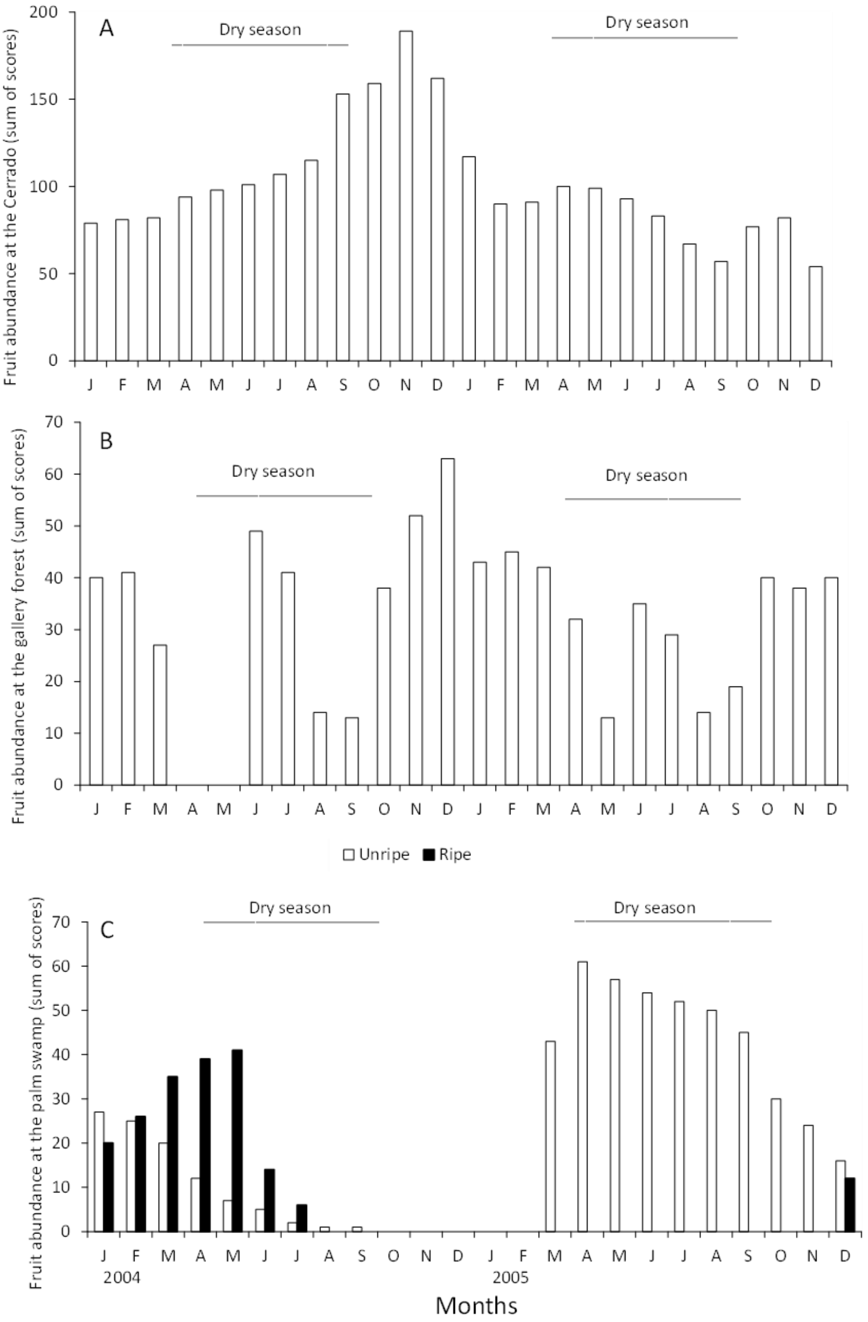

Figure 1. Fruiting pattern: (A) *Cerrado* vegetation. (B) Gallery forest. (C) Palm swamp (Emas National Park, State of Goiás, Brazil, 2004 and 2005). The values of abundance result from the sum of scores (see Methods).

one began on the early wet season, before decreasing, from December to May. Species such as *Virola sebifera*, *Ocotea diospyrifolia*, *Guarea guidonea*, and *Protium heptaphillum* comprised much of this peak (Figure 1B). The other pronounced peak, although brief, took place in the middle of the dry season and was dominated by the fruiting of *Xylopia emarginata* (Figure 1B). In the palm swamp, fruiting in *M. flexuosa* was seasonal, although extended. In the first year, palms bore fruits from January to June and fruited again from November to May (Figure 1C).

All habitats sampled exhibited substantial temporal fluctuations in the production of food resources. However, most parrot species experienced no seasonal change during both years, either in food resource abundance (Wilcoxon match test, *A. ararauna*: $z = 0.37$, $P = 0.88$, Figure 2A; *A. aestiva*: $z = 1.83$, $P = 0.13$; *A. xanthops*: $z = 0.00$, $P = 1.00$; *D. nobilis*: $z = 1.09$, $P = 0.38$; *E. aurea*: $z = 1.83$, $P = 0.13$) or in the number of available food species (Wilcoxon match test, *A. ararauna*: $z = 1.46$, $P = 0.25$, Figure 2B; *A. aestiva*: $z = 1.47$, $P = 0.25$; *A. xanthops*: $z = 1.07$, $P = 0.70$; *D. nobilis*: $z = 0.53$, $P = 0.75$; *E. aurea*: $z = 0.45$, $P = 1.00$). In the case of *O. manilata*, there was a seasonal discontinuity in *M. flexuosa* fruit availability (Figure 1C).

Food diversity available to each parrot species fluctuated across seasons. Peaks occurred during the late dry season, both for *A. ararauna* (2004, $D = 5.7$, Figure 2C), and *A. aestiva* (2005, $D = 6.9$), due to dry fruit production in 4 and 11 species, respectively. Minor values occurred for *A. ararauna* in the late wet season (2004, $D = 1.2$ Figure 2C), while for *A. aestiva* it occurred in the early wet season (2004, $D = 2.4$). *A. xanthops* experienced a peak of food diversity (2005, $D = 6.2$) in the late wet season due to the fruiting of six species.

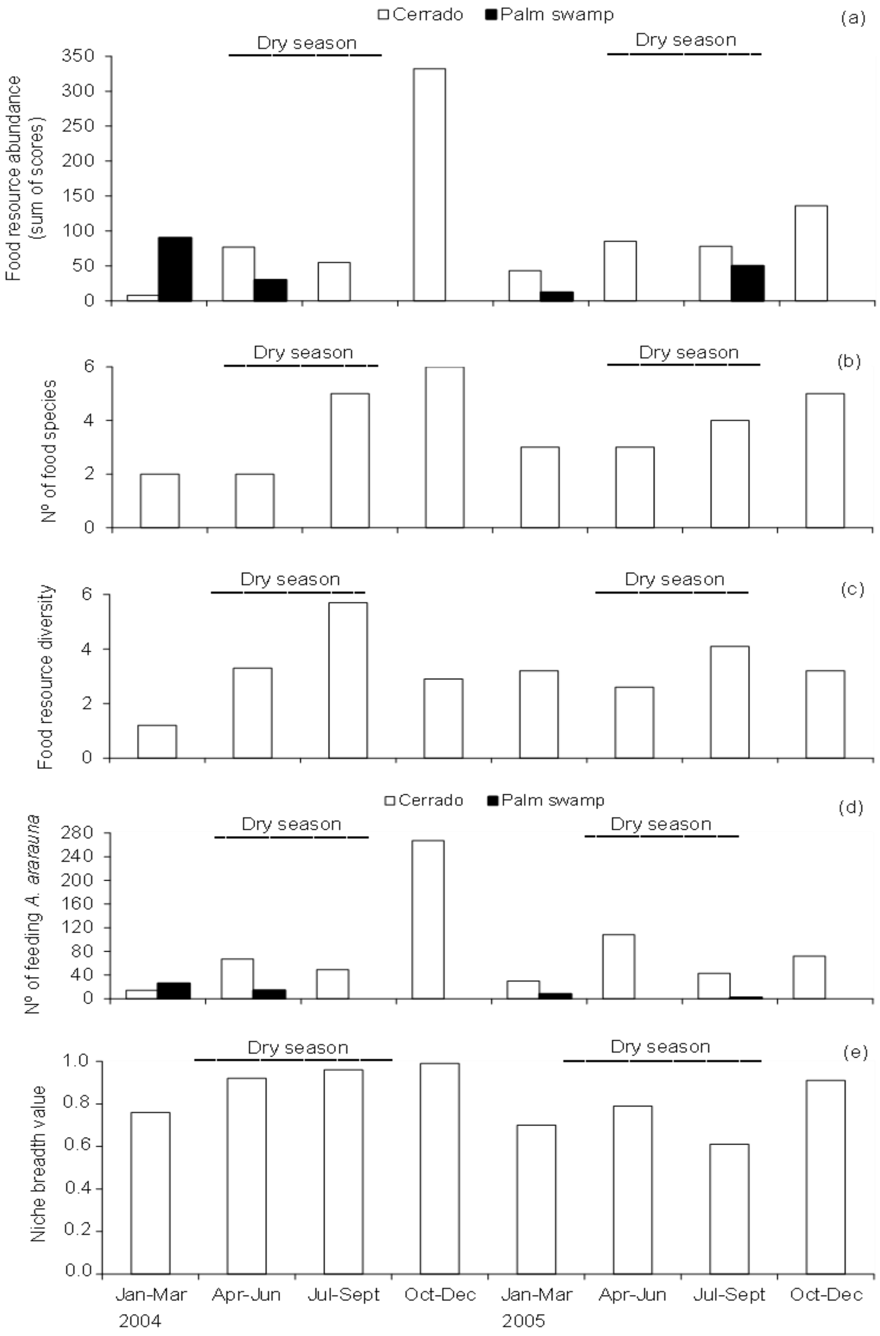

Figure 2. Parrot species assessed in relation to feeding ecology exemplified by *Ara ararauna*. From top to bottom: (A) food resources abundance, (B) number of plant species consumed, (C) diversity of food resources, (D) number of *A. ararauna* recorded feeding, and (E) niche breadth value across seasons at Emas National Park (State of Goiás, Brazil; 2004 and 2005).

Smaller values occurred at the end of the dry season (2005, *D* = 3.2), when only three species bore food items. During the early rains, fruit diversity for *D. nobilis* was the highest (2004, *D* = 4.4) due to the fruiting of four species, while in some periods less values of fruit diversity (*D* = 1) resulted from the fruiting of only one species. *E. aurea* experienced major food diversity in the early wet season (2004, *D* = 3.0), while smaller values (*D* = 1.0) occurred both in the late wet 2004 and 2005 early dry season due to the fruiting of *P. rotundifolia* only. For *O. manilata*, food diversity was always low (*D* = 1.0) due to its restricted consumption of *M. flexuosa*'s fruit pulp. Despite temporal fluctuations, parrot food diversity exhibited no significant differences between seasons in both studied years (Wilcoxon match test, *A. ararauna*: *z* = 1.46, *P* = 0.25, Figure 2C; *A. aestiva*: *z* = 0.73, *P* = 0.62; *A. xanthops*: *z* = 1.83, *P* = 0.13; *D. nobilis*: *z* = 0.53, *P* = 0.75; *E. aurea*: *z* = 0.55, *P* = 0.75; *O. manilata*: *z* = 1.00, *P* = 0.100).

Food resource use. Parrots foraged on 45 plant species from at least 23 families (three unidentified species, Table 1). The *cerrado* vegetation had 36 species, eight occurring in the gallery forest and only one in the palm swamp. From April to the end of September (dry season), dry fruits comprised much of the diet of *A. aestiva* (59% of individuals recorded feeding, N = 421). On the other hand, *A. ararauna*, *E. aurea*, *A. xanthops,* and *D. nobilis* consumed moderate amounts of dry fruit (32%, N = 676; 31%, N = 178; 19%, N = 1310; and 2%, N = 561, respectively; Table 1). During this period, *A. xanthops*, the parrot more often detected feeding, mostly ate flowers and leaves, which comprised 43% of its general diet, and totaled 72% of its food items during this period (N =

Table 2. Correlation between parrot feeding and food resources parameters (r = Pearson correlation coeficient, P = significance value).

Parrot species	No. feeding parrots x food abundance	No. feeding parrots x No. of food species	No. feeding parrots x food diversity
Ara ararauna	r = 0.94, P = 0.020	r = 0.73, P = 0.05	r = 0.10, P = 0.847
Amazona aestiva	r = 0.98, P = 0.001	r = 0.92, P = 0.007	r = 0.77, P = 0.026
Alipiopsitta xanthops	r = 0.76, P = 0.021	r = 0.87, P = 0.006	r = 0.33, P = 0.431
Diopsittaca nobilis	r = 0.89, P = 0.006	r = 0.89, P = 0.016	r = 0.85, P = 0.033
Eupsittula aurea	r = 0.76, P = 0.025	r = 0.92, P = 0.003	r = 0.80, P = 0.016
Ortopsittaca manilata	r = 0.99, P = 0.004	-	-

779 *A. xanthops* detected feeding across the dry season, Table 1). *E. aurea* consumed flowers moderately (17% of their diet, N = 178 *E. aurea* detected feeding), but this item was important in the dry season (34%, N = 89 individuals recorded ingesting food, Table 1).

During the wet season (October to March), fleshy fruits were plentiful and dominated the diet of parrots (Table 1). The large seeds of four species (*A. humile*, *O. spectabilis*, *P. torta*, and *C. brasiliense*), made up much of *A. ararauna*'s diet (57%, N = 676 macaws detected feeding, Table 1). On the other hand, both pulps and arils dominated the diet of *D. nobilis* (59%, N = 487 individuals detected feeding during the wet season) and *A. xanthops* (57%, N = 531, Table 1). *O. manilata* exploited only *M. flexuosa* fruit pulps both in the wet and dry seasons (Table 1). As previously mentioned, parrots foraged on food species/items whose offer fluctuated during seasons. The number of feeding individuals for each parrot species varied, paralleling either food abundance (Figure 2A, D; Table 2) or the number of food species (Figure 2B,D; Table 2). However, two species presented no significant relationship between the number of feeding parrots and food diversity (Figure 2C,D; Table 2).

Except for *O. manilata*, Hurlbert's niche breadth for parrot diet fluctuated abruptly for both *E. aurea* and *D. nobilis*, while *A. ararauna*, *A. xanthops*, and mainly *A. aestiva* exhibited moderate fluctuations across seasons. Besides that, despite variations, all five species had increased niche breadth values either in the early wet season, when several tree species bore fleshy fruits, or in the late dry season, when dry fruits were plentiful. *Ara ararauna* presented the highest values in the early wet seasons (2004 $B' = 0.99$, and 2005 $B' = 0.91$, Figure 2E), while *A. aestiva* had $B' = 0.83$ (2004), and $B' = 0.97$ (2005). In addition, *A. xanthops* exhibited $B' = 0.89$ (2004) and *E. aurea* $B' = 0.97$ (2005), whereas only *D. nobilis* exhibited the highest value in the early dry season ($B' = 0.71$, 2004). Except for *A. ararauna*, for which the lowest niche breadth value occurred in the late dry season ($B' = 0.61$, 2005, Figure 2E), the other parrots exhibited smaller values in the early dry season of 2005. Despite fluctuations, feeding niche breadth values for each species exhibited no significant differences between seasons in both study years (Wilcoxon match test, *A. ararauna*: $z = 0.21$, $P = 0.930$, Figure 2E; *A. aestiva*: $z = 0.37$, $P = 0.87$; *A. xanthops*: $z = 0.42$, $P = 0.73$; *D. nobilis*: $z = 0.12$, $P = 0.938$; *E. aurea*, $z = 0.01$, $P = 0.097$). Also, variations in niche breadth value of no parrot species paralleled food abundance (Figure 2A,E), the number of food species (Figure 2B,E), nor food diversity (Figure 2C,E).

Excluding *O. manilata*, which only ate *M. flexuosa*'s fruit pulp, the other species exhibited diet association according to the eaten part of the plant species. Axis 1 of the Detrended Correspondence Analysis (eigenvalue = 0.77) described a gradient of species in which the presence of seeds in the diet decreased progressively from *A. ararauna* to parrots that had a diet composed by a mix of plant parts, mainly fruit pulps and flowers (*D. nobilis* and *A. xanthops*; Figure 3, Table 1). In one extreme of the DCA 1, there were *C. brasiliense*, *P. torta*, and *O. spectabilis* seeds, in addition to *M. flexuosa*'s pulp, which was exclusively eaten by *A. ararauna*. On the opposite side, *Byrsonima verbacifolia* and *Myrcia* sp. seeds were found, used only by *D. nobilis*. On the other hand, axis 2 (eigenvalue = 0.48) separated a gradient of herbaceous/shrub seed species (*Calea cuneifolia* and *Bauhinia* sp.) consumed by *E. aurea* from two arboreal seed species exploited only by *A. aestiva* (*A. falcata* and *E. pubescens*). Within these extremes were the seeds of *A. humile* and *S. adstringens*, both foraged on by all parrot species, except for *D. nobilis* (Figure 3, Table 1).

DISCUSSION

Fruiting phenology. Habitat types exhibited seasonal fruiting patterns with moderate overlapping peaks. Particularly during the rainy season, all sites presented prominent fruit production, mainly in the *cerrado* vegetation, like that observed in seasonal forests (Justiniano & Fredericksen 2000). Most importantly, the intensity of fruiting patterns varied between years due to inter-annual variations in fruit production of some common species. For example, *P. torta* and *O. spectabilis* bore large fruit crops during one year, although fruiting declined the next. The same occurred with dry fruit production, mainly in *A. falcata*, *E. gracilipes*, and *D. mollis*, all of which are important for parrots. Moreover, despite inter-annual variations, Sapotaceae, Anacardiaceae, Leguminosae, Caryocariaceae, Ochnaceae, Myrtaceae, and Bombacaceae dominated the *cerrado* fruiting pattern and were important in terms of food supply, so that parrots mostly foraged on the most abundant food resources in the *cerrado* vegetation.

In the mid dry season, the gallery forest also exhibited a fruiting peak, which partially overlapped that of the *cerrado* vegetation. This pattern was mostly caused by the abundant *Xylopia emarginata*, while fruit availability in the palm swamp predominated from the late wet to the middle of the dry season, when other habitat types exhibited no fruiting peak. With regards to this, during the year there was a trend for staggered fruit production across all three-habitat types. Then, despite fluctuations, no substantial differences emerged in the general food offer due to the inter-habitat combined resource availability. Particularly, the number of fruiting trees, as well as both fruit abundance and diversity, exhibited similar values between seasons, which reinforce the assumption of an adequate year-round food supply. Importantly, the phenology sample encompassed a substantial proportion of a large *cerrado* reserve, in which both the abundance and diversity of food resources offered is not comparable to that of smaller *cerrado* remnants (Ragusa-Netto 2006).

Feeding ecology. In this study, the feeding habits of parrots

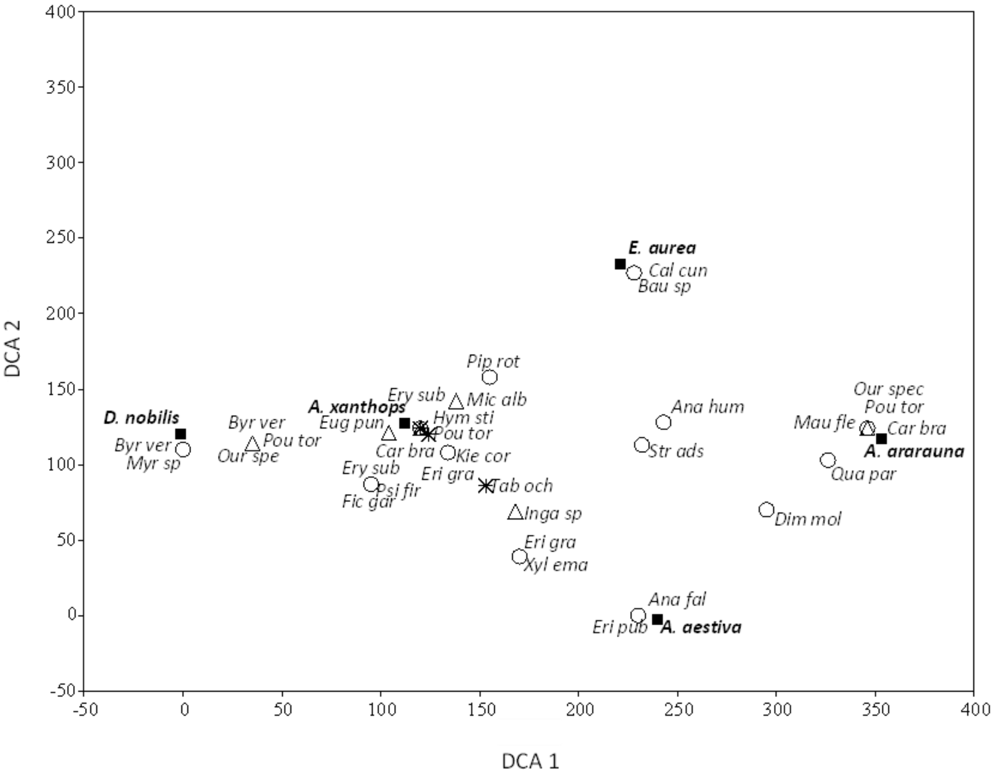

Figure 3. Association between each parrot species (black square) and the part of the plant species consumed (open circles: seed, open triangle: pulp, star: flower products) on DCA's axis 1 (eigenvalue = 0.77) and axis 2 (eigenvalue = 0.48). Both generic and species name represented by the first three letters.

were thoroughly documented in a broad *cerrado* area. My sample of 1,129 feeding records spread over 24 months — which encompasses 3,508 observations of parrots ingesting food—, accurately depicts the diet of parrots often present in ENP. Thus, the rich diet documented here resembled that noted elsewhere, either in seasonal or rain forest areas for most species (Renton 2001, Lee et al. 2014). Importantly, the diet composition of most species exhibited strong seasonality; during the dry season, the combination of dry fruits, flowers, and even suitable leaves accounted for the variety of food items, while a wide sort of fleshy fruits dominated the parrots' diet during the rains. Moreover, across the years, parrots unequally used a given plant species due to variations in resource production, which influenced the proportional consumption of other species (Ragusa-Netto 2007). There was pronounced variation in the offer and respective use of food resources, except for *S. adstringens*, which bore large fruit crops during 5–7 months in both years, perhaps contributing to its importance as a food source for the local parrot assemblage.

Parrots made a diffuse use of plant groups. For example, *A. ararauna* ate a variety of large seeds, while *A. aestiva* mostly foraged on Leguminosae seeds. *A. xanthops* and *D. nobilis* used a wide range of soft plant parts, mainly fruit pulps, and in the case of *A. xanthops*, also leaves and flowers. In fact, except for *O. manilata*, only a few food items comprised more than 20% of the diet of some parrot species. In general, each parrot species exploited a wide range of seasonal food resources —and therefore a rich collection of items predominated—, instead of only certain dominant foods. On the contrary, parrots from less seasonal areas often relied on certain food items produced during prolonged periods and complemented their diets with other seasonal resources (Matuzak et al. 2008, Lee et al. 2014). The diet spectrum documented here was coherent with previous studies on the diversity of parrot feeding habits and their affinity to particular food items due to the high variation in body and bill size of the members of a parrot assemblage (Roth 1984, Benavidez et al. 2018). At ENP, the use of a given food species by two or more parrot species often involved the use of different items. For example, in the same year, *P. torta* seeds were consumed by *A. ararauna*, while its flowers were previously eaten by *A. xanthops* and, subsequently, the fruit pulp. Thus, although eventually some parrot species exploited the same plant species, there was a trend for the use of diverse organs, which minimized diet overlap.

In marked seasonal areas, parrots forage on flowers mainly during the dry season (Galetti 1993, Ragusa-Netto 2005, 2007, Ragusa-Netto & Fecchio 2006). Although previous studies revealed that *A. xanthops* used flowers to a lesser extent (Bianchi 2009, de Araújo & Marcondes-Machado 2011), the present data showed that, according to the ecological context, flowers are an important food item during the harshest period of the year. In fact, the blossoms of common tree species accounted for a substantial proportion of *A. xanthops*'s diet during the dry season. The use of flowers by *A. xanthops* was similar to that of parakeets, for which flowers are among some of the main food items (Ragusa-Netto 2005, 2007, Lee et al. 2014). In contrast, flowers often comprise less than 20% of the diet of larger parrots (Pizo et al. 1995, Matuzak et al. 2008, Lee et al. 2014). The extensive use of flowers is well known as a dietary shift experienced by frugivores during periods of famine (van Schaik et al. 1993). However, in the *cerrado*, both flowers and dry fruits eaten by parrots were simultaneously available. Thus, flowers might not only be an alternative resource for periods when fruits decline, which happens to frugivores that heavy rely on fleshy fruits (van Schaik et al. 1993). Instead, the presence of blossoms at ENP potentially made flowers profitable to certain parrot species (Renton et al. 2015). In fact, the nutritional content of nectar, in addition to other floral parts, is similar to that of sweet fruit pulp (Ferrari & Strier 1992).

With the exception of *O. manilata*, already assumed (Roth 1984) and confirmed in this study as a feeding specialist, parrots often presented high feeding niche breadth values at ENP. For generalist parrots, the niche breadth often mirrors the variations in abundance and diversity of food items available to them (Renton 2001, Ragusa-Netto 2006, Santos & Ragusa-Netto 2014). Regarding this, some studies on parrot diet reported narrow seasonal values for feeding niche due to the extensive consumption of a few abundant resources (Renton 2001, 2006, de la Parra-Martinez et al. 2019). Although *D. nobilis* and *E. aurea* conformed to this pattern, diet breadth in *A. aestiva*, *A. ararauna*, and *A. xanthops* presented wide values all year. On the contrary, parrots from other rich floras have shown comparatively narrow diet breadths. The Lilac-crowned Parrot (*Amazona finschi*), found in Mexico's dry forests, presented values ranging from 0.22 in the dry season to 0.55 in the wet season, when the number of food species available peaked (Renton 2001). Also, both in Curú (western Costa Rica) and in the rich flora of western Amazonia, despite varied diets, members of parrot assemblages showed moderate niche breadth values due to the use of some preferred foods available in prolonged periods throughout the year (Matuzak et al. 2008, Lee et al. 2014). It is noteworthy that, depending on the food offer context, *Ara militaris* may incur in a specialized diet of large and nutritious seeds, which emphasizes the extent of diet flexibility in some parrot species (de la Parra-Martinez et al. 2019). In the *cerrado*, despite the variable resource offer, general food abundance and diversity varied moderately across seasons. Thus, parrots often experienced a rich collection of seasonally available food items, which in turn explains the predominance of broad diets.

In conclusion, there is an interesting diet diversity in the studied parrot assemblage, with one specialist species and the others displaying more generalist diets in which soft items or large seeds appeared to be preferred. Such diversity of feeding habits is coherent with the wide distribution of those species over seasonal areas, where a variable spectrum of food types may be available. Moreover, the flexible use of a given food plant emphasizes the feeding dynamics of opportunistic consumers prone to respond to the erratic spatial and temporal availability of food resources. There was a high variation from year to year in the availability of important seasonal foods, and thus the amount of a given resource influenced the use of simultaneously available foods. Moreover, the variety of food resources available strongly affected the number of feeding parrots in each area. This highlights the importance of a rich collection of scattered food patches for parrot abundance. Thus, conservation of parrots in the *cerrado* depends on preserving habitats in which food resources could be available in the dynamic form documented here. Deforestation has been reducing habitat types and the density of the main plants that provide the nutritional components required by parrots throughout the year (Renton et al. 2015). Subsequently, a serious concern emerges in relation to resource offer in small *cerrado* remnants, which include an impoverished abundance and diversity of food plants (Ragusa-Netto 2006). Indeed, the intense fragmentation of pristine areas, among other reasons, has been causing a severe decline in parrot populations worldwide (Olah et al. 2016). Management plans for parrots in the *cerrado* should focus on preserving wide areas, including as much habitat mosaics and plant species used as possible throughout the year.

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