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Original Article

Feeding ecology of the Red-and-green Macaw (*Ara chloropterus*; Gray 1859) in a habitat mosaic from Cerrado

Ecologia alimentar da arara vermelha (*Ara chloropterus*; Gray 1859) em um mosaico de habitas no Cerrado

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Abstract

In the Brazilian Cerrado, the Red-and-green Macaw (*Ara chloropterus*) populations are facing an accelerated rate of habitat loss. Despite this, their feeding areas and primary food sources remain poorly understood. In this study, I assessed the relationship between the diet of the Red-and-green Macaw and available food resources in a habitat mosaic from the fragmented Cerrado in Mato Grosso do Sul State, Brazil. Red-and-green Macaws fed on 20 native and five exotic species, mainly in dry habitats (Cerrado, dry forest, and an urban area along the Maracaju Cliffs) during the dry season, while year-round foraging in the riparian vegetation (Aquidauana River and streams). Then, the number of feeding macaws paralleled variations in food abundance and diversity, besides the number of food species. On the other hand, by using a wide variety of abundant foods, macaws' diet breadth presented high values throughout the year. The seasonal consumption of large-seeded fruits across the habitat mosaic displayed a gradient ranging from the urban area to dry habitats, along which macaws ate from exotic to Cerrado species. In this respect, *Terminalia catappa* seeds and *Mangifera indica* fruit pulp were important for Red-and-green Macaws in the urban area during the wet season, while *Caryocar brasiliense* seeds comprised the same in the Cerrado. At this site, both *Dipteryx alata* and *Buchenavia tomentosa* seeds composed much of the Red-and-green Macaws' diet during the dry season. Between those habitats, in the watercourse vegetation, macaws frequently foraged on palm fruits across seasons. Therefore, throughout the year, the abundance and variety of food resources strongly influenced the number of foraging Red-and-green Macaws across the habitat mosaic. Understanding the effect of varying seed availability on the spatial and temporal abundance patterns of Red-and-green Macaws, which primarily feed on large-seeded species, is central to developing effective conservation strategies. Due to the accelerated habitat loss, the Maracaju Cliffs emerge as crucial for the Red-and-green Macaw among the Cerrado remnants of Mato Grosso do Sul.

Keywords: Psittacidae, phenology, seed predation, frugivory, animal-plant interaction.

Resumo

No Cerrado brasileiro, as populações de arara-vermelha (*Ara chloropterus*) estão sob forte pressão de perda de habitat, ao mesmo tempo em que suas áreas de alimentação e importantes itens alimentares permanecem praticamente desconhecidos. Neste estudo, avaliei a relação entre a dieta e oferta de recursos alimentares para a arara-vermelha, em um mosaico de habitats, no fragmentado Cerrado do estado de Mato Grosso do Sul. Registrei o consumo de 20 espécies nativas e 5 exóticas, sendo que os hábitats secos (Cerrado, mata estacional e área urbana em meio a Serra de Maracaju) serviram como principais áreas de alimentação no decorrer da estação seca. Por outro lado, a vegetação ripária (Rio Aquidauana e riachos) foi explorada em proporções semelhantes em ambas estações. O uso sazonal de espécies com grandes sementes, ao longo do mosaico de habitats, exibiu um gradiente da área urbana aos habitats secos ao longo do qual as araras consumiram desde espécies exóticas até as do Cerrado. As sementes de *Terminalia catappa* e polpa de *Mangifera indica* foram responsáveis por grande parte da alimentação delas na área urbana durante a estação chuvosa, enquanto as sementes de *Cariocar brasiliense* correspondeu ao mesmo no Cerrado. As sementes de *Dipteryx alata* e *Buchenavia tomentosa*, também no Cerrado, ficaram no extremo oposto do gradiente, sendo consumidos durante a estação seca. Em meio ao gradiente, ficaram os frutos de palmeiras, explorados na vegetação dos cursos d`água, tanto nas chuvas quanto na seca. O número de araras-vermelhas se alimentando foi paralelo a abundância de alimentos, bem como ao número e diversidade de espécies de alimentares. Já a amplitude de nicho alimentar exibiu valores elevados durante o ano todo, refletindo o consumo de uma variedade de frutos abundantes. Portanto, não apenas a abundância, mas também a variedade de recursos alimentares influenciou fortemente o número de araras-vermelhas alimentando-se ao longo do mosaico de habitats durante todo o ano. Como as araras-vermelhas dependem extensamente de espécies com sementes grandes, entender como a oferta diversificada desses recursos pode afetar suas variações temporais e espaciais de abundância são fundamentais

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para o desenvolvimento de planos de conservação. Dessa forma, face ao acelerado desmatamento do Cerrado no Mato Grosso do Sul, a Serra de Maracaju, em meio aos remanescentes do Cerrado, emerge como crucial para as populações persistentes de araras-vermelhas.

Palavras-chave: Psittacidae, fenologia, predação de sementes, frugivoria, interação animal-planta.

1. Introduction

The Red-and-green Macaw (*Ara chloropterus*; Gray, 1859) mainly occurs in forests and savannas across northern and central South America (Collar et al., 2020). In Brazil, it currently inhabits the Amazon, Pantanal, and Cerrado, besides some fragments of the Atlantic Forest with isolated populations (Sick, 1997; Collar et al., 2020). Despite being considered Least Concerning by the IUCN (2023), many of its populations are declining due to ongoing habitat destruction and the pet trade (Olah et al., 2016; Collar et al., 2020). Particularly, in the Brazilian Cerrado, Red-and-green Macaw populations have experienced an intense process of habitat loss. In fact, 50% of the Cerrado's former range has been cleared, resulting mainly in fragments within a matrix of pastures, besides agricultural and urban areas (Carvalho et al., 2009; Beuchle et al., 2015). Due to similar pressures, a third of all parrots are declining, at risk of at least becoming locally extinct (Olah et al., 2016; Collar et al., 2020). This threatened bird group remains poorly investigated with respect to their natural history, lacking specific data on their feeding areas and major foods (Berg et al., 2007; Rivera et al., 2019; Collar et al., 2020). This scarcity of information on the feeding ecology is a challenge to be overcome by those concerned with endangered parrot conservation (Rivera et al., 2019).

Ara (Lacépède, 1799) macaws are generalist feeders (Collar et al., 2020), although they often feed on some abundant seed types for extended periods (Matuzak et al.; 2008; Santos and Ragusa-Netto, 2014; de la Parra-Martinez et al., 2019). Regardless, these large parrots typically have diets dominated by large seeds (Matuzak et al., 2008; Lee et al., 2014, de la Parra-Martinez et al., 2019; Ragusa-Netto, 2022). Indeed, macaws generally have a moderate diet breadth, consisting of a limited set of prolonged available foods while consuming small amounts of other items (Matuzak et al., 2008; Contreras-González et al., 2009; Lee et al., 2014). Due to spatiotemporal fluctuations in resource availability, *Ara* macaws regularly move over large areas, searching for suitable food patches (Haugaasen and Peres, 2007; Ragusa-Netto, 2006, 2022). Despite this, many macaw species have declined due to the increasing rarity of their main foods (Berg et al., 2007). In this respect, the Red-and-green Macaws' diet data are scattered across its current range (Roth, 1984; Santos, 2001; Lee et al., 2014; Volpe et al., 2022), remaining unknown for populations in Central Brazil, as well as their responses to fluctuations in food availability over time and space (Haugaasen and Peres, 2007). Knowledge of this dynamic is central, in addition to assessments of the diets of threatened macaws, to planning conservation efforts (Berg et al., 2007; Volpe et al., 2022).

In Mato Grosso do Sul state (Brazil), where the Red-and-green Macaw persists, the Cerrado declines abruptly, remaining only 23.9% of its original area (Beuchle et al., 2015). Due to habitat loss, pet trade, and potential hunting pressures, this macaw is nearly extinct in neighboring Paraná and São Paulo states (Collar et al., 2020; Oliveira et al., 2023). Its decline, among other reasons, is not surprising due to a diet dominated by large seeds, often present in pristine areas (Lee et al., 2014; Collar et al., 2020). Because large-seeded species have become increasingly rare in fragmented areas (Tabarelli et al., 2008), evaluations of feeding area use dynamics are central to developing conservation plans for declining species such as the Red-and-green Macaw (Berg et al., 2007; Contreras-González et al., 2009; Rivera et al., 2019). Given the threats and scarcity of studies, basic data is needed on the Red-and-green Macaw. Then, in this study, I assessed the dietary responses of Red-and-green Macaws to available food across a habitat mosaic from the fragmented Cerrado in Mato Grosso do Sul State, Brazil. Specifically, I analyzed the relationship between the number of feeding macaws and the local food availability, besides examining the association of food species used with the macaws' feeding areas.

2. Methods

2.1. Study site

Data collection was carried out near the city of Rochedo (19° 54' S, 55° 01' W; central Brazil) in the Maracaju Cliffs, Mato Grosso do Sul State (Brazil). The study site has a dry tropical climate with a marked seasonality in precipitation, with 75% of the 1400 mm average annual rainfall occurring from October to March and a prolonged drought from April to late September. The area has a hilly topography, varying in elevation from 400 to 900 m asl. The dominant vegetation type is dense Cerrado (Brazilian savanna) on flat areas, deciduous forests on slopes, semi-deciduous forests alongside the major watercourse (Aquidauna River), and permanent green gallery forest along streams, besides the urban area of Rochedo. Rochedo City has a population of 5,000 inhabitants and street tree planting reaches 94%, in an urban area of around 2 km^2 (IBGE, 2010).

2.2. Food resource production

To sample fruit production through habitat types, I established 15 phenology transects of 300 m x 4 m, with three transects in each of five habitat types: (1) deciduous forest, (2) dense Cerrado, (3) one large (Aquidauna River; hereafter River), and (4) small watercourses, in addition to (5) Rochedo urban area. Transects in deciduous forest were positioned in three foothill areas of the Maracaju cliffs (mountain chain: 19° 53' S, 55° 00' W; 19° 54' S, 54° 59' W; 19° 54' S, 55° 05' W). The same was done in the dense Cerrado (19° 55' S, 54° 56' W; 19° 56' S, 55° 01' W; 19° 57' S, 54° 54' W), so that transects were at least 2000 m apart from each other. Transects along the Aquidauna River were in three segments of riparian forest (at least 1000 m apart; 20° 00' S, 54° 53' W; 20° 01' S, 54° 55' W; 20° 03' S, 54° 55' W). I positioned one transect in the gallery forest of each stream (at least 2000 m apart from each other: Carrapato: 19° 56' S, 54° 56' W; Onça: 19° 51' S, 54° 57' W; and Lageado, 19° 58' S, 54° 52' W, streams). The placement of transects along these habitat types was determined using a map of the region (scale 1:50,000) within an imaginary square of 120 km^2. Finally, I also positioned three parallel (E - W direction) transects within the Rochedo urban area, one at the center (19° 57' S, 54° 53' W), another at the north, and another at the south, both in the peri-urban area, at least 400 m apart from each other. I attempted to include, as much as possible, the flora heterogeneity present in the region. Then, transects were dispersed within the study area to obtain a representative sample of resource availability.

Transects were monitored during the third week of each month, from January to December 2008. I checked individual crowns for the presence of food resources (leaves, flowers, and fruits) with 8 x 40 binoculars. I recorded fruit-bearing trees (> 15 cm in diameter at breast height [dbh]) whether detected within a 2-m band on either side of the transect line. Where a tree occurred on the boundary of the 2-m transect, the tree was included if the midpoint of the trunk was rooted within the transect area. I ranked the abundance of resources at a given crown on a relative scale, ranging from total absence (0) to a plentiful resource crop (4). Thus, for each habitat type, the sum of scores resulted in a monthly index of fruit abundance (Fournier, 1974). 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).

2.3. Food resources of the Red-and-green Macaw

I used the permanent access trails, along which I positioned the phenology transects in order to sample foraging Red-and-green Macaws. Every month, in the dry season, I walked those trails for 40 h (8 h per habitat type), from 06:00 to 11:00, and again from 15:00 to 18:00 h. In the wet season, from 05:00 to 10:00 h and from 16:00 to 19:00 h (real-time). These periods correspond to parrots' peak activity time (Marsden, 1999). Whenever I detected, within a 30 m ray of each side of a given transect, at least one Red-and-green Macaw eating a resource, I recorded: a) tree species, b) resource consumed (leaf, flower, or fruit), c) part eaten (petiole, blade, peduncle, petal, nectar, pulp, seed), and d) number of feeding macaws. In the case of seed consumption, I assigned as large seeds those ≥ 1.0 cm (Brewer, 2001), according to scales presented in Lorenzi (1994, 1998). Red-and-green Macaws were not individually marked. Then, to avoid pseudoreplication, I walked the trails only in one direction and recorded the first ingestion of a specific food item eaten by each observed Red-and-green Macaw. Additionally, I used initial rather than sequential observations of macaw feeding to ensure independence among samples (Hejl et al., 1990). Indeed, I counted feeding macaws according to the transect sampling bird technique (Bibby et al., 2000) because of the focus on the relationship between macaw numbers and food resources. Additionally, I assumed that the conspicuous Red-and-green Macaws were equally likely to be spotted at short-to-medium distances within the arboreal vegetation of every habitat type (20-50 m; Marsden 1999; Bibby et al., 2000).

2.4. Data analysis

Phenology patterns often exhibit short periods of plant resource increases followed by abrupt declines (Ragusa-Netto, 2007, 2022, and references therein). Then, I grouped resource production into four periods of the year: 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). For each period, the accumulated monthly index of resource abundance (= sum of scores) was taken as a variable for analyses, in addition to the following parameters: a) the number of feeding Red-and-green Macaws, b) the number of food species, c) the food diversity, and d) the niche breadth value. I correlated those food parameters with the number of feeding Red-and-green Macaws using generalized linear models (GLM) with a Poisson error and log-link function. I evaluated the range of their diet using the standardized Hurlbert's niche breadth 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 resources in trees exploited by Red-and-green Macaws, besides the number of them eating a given food item. A value close to 0 indicates dietary specialization, while a value close to 1 indicates a broad diet (Hurlbert, 1978). I used the Simpson index (D; Simpson 1949) to describe the resource diversity available to Red-and-green Macaws. The Simpson index is sensitive to changes in common species. Because Red-and-green Macaws are generalist frugivores (Lee et al., 2014; Collar et al., 2020), I chose the Simpson index to minimize the influence of the rarely used species and to emphasize changes in the commonly consumed plant species because macaws often use abundant resources (Ragusa-Netto, 2007, 2022). To compare variations in food parameters (abundance, the number, and diversity of food species) in the four periods of the year, I used a Chi-square test. I assessed the temporal use of feeding areas by Red-and-green Macaws, using Chi-square contingency analysis, to test for differences in the number of feeding macaws in each of the five habitat types in the four periods of the year. To further explore the variation in the use of feeding areas associated with particular consumed species (> 2.5% feeding macaws, Table 1), I ran a correspondence analysis (CA). Correspondence analysis is an ordination method that attempts to place similar samples in similar positions in the ordination plot. The measure of the distance between samples is proportional to the Chi-square statistic. Samples for this ordination procedure consisted of the number of Red-and-green Macaws in each habitat type (rows), feeding on each food species (columns).

3. Results

3.1. Fruit production

In the phenology transects, I recorded 25 (20 native and five exotic) species belonging to 13 families bearing

Table 1. Plant species and respective plant parts eaten by the Red-and-green Macaw (*Ara chloroptera*) at a habitat mosaic of Cerrado in the Maracaju Cliffs (Rochedo, State of Mato Grosso do Sul, Brazil, 2008).

Plant taxa	Item	Number of individuals feeding and (%)	Habitat type	Month	Origin
ANACARDIACEAE					
Mangifera indica L.	p	14 (6.0)	UA	Oct, Nov, Dec	E
Spondias dulcilis Sol. ex Parkinson	p	4 (1.8)	UA	Apr, Jul	E
Tapirira guianensis Aubl.	p/s	2 (0.9)	GF	Jan	N
ARALICEAE					
Schfflera morototonii Aubl.	p/s	3 (1.3)	DF	Aug	N
ARECACEAE					
*Acrocomia aculeata**(Jacq.) Lodd. ex Mart.	s	23 (10.0)	R	Feb, Apr, May, Jun, Sep, Nov	N
*Attalea phalerata** Mart. ex Spreng.	s	12 (5.2)	R	Apr, Aug	N
*Mauritia flexuosa** L.f.	p	9 (3.9)	GF	Nov, Dec, Jan, Feb, Mar	N
*Syagrus oleraceae** (Mart.) Becc.	s	8 (3.5)	UA	Mar, Apr, May, Aug	N
BIGNONIACEAE					
*Jacaranda cuspidifolia** Mart.	s	5 (2.2)	UA	May, Sep	N
CARYOCAREACEAE					
*Cariocar brasiliense** Cambess.	s	19 (8.2)	C	Nov, Dec	N
COMBRETACEAE					
*Buchenava tomentosa** Eichler	s	16 (6.9)	C	May, Jun, Jul	N
*Terminalia catappa** L.	s	20 (8.6)	UA	Jan, Jul, Nov	E
LEGUMINOSAE					
*Dipteryx alata** Vogel	s	31 (13.4)	C	May, Jun, Jul	E
*Hymenaea coubari*l* L.	s	17 (7.4)	DF	Apr, Jun, Aug	N
Inga laurina (Sw.) Willd.	p	4 (1.7)	R	May, Sep	N
*Pterodon emarginatus** Vogel	s	2 (0.9)	C	Jun, Sep	N
LECYTIDACEAE					
*Eschiwerella nana** (O.Berg) Miers	s	7 (3.1)	C	Jun, Aug	N
*Cairiniana stellaris** Casar.	s	5 (2.2)	DF	Jun, Jul	N
MALVACEAE					
Eriotheca sp. Schott & Endl.	s	3 (1.3)	DF	May	N
*Sterculia striata** A.St.-Hil. & Naudin	s	8 (3.5)	DF	Aug	N
MELIACEAE					
*Guarea guidonea** (L.) Sleumer	s	2 (0.9)	R	Nov	N
*Melia azedarach** L.	s	4 (1.7)	UA	May, Jun	E
MORACEAE					
Ficus sp. L.	p/s	4 (1.7)	R	Aug, Nov	E
MYRTACEAE					
Pisidium guajava L.	p/s	5 (2.6)	UA	Dec, Feb, Mar	E
VOCHYSIACEAE					
*Qualea parviflora** Mart.	s	4 (1.7)	C	Jul, Sep	N
Total		231 (100)			

Food items: p - pulp, s - seed; Habitat types: DF - Dry Forest, C - Cerrado, R - Riparian forest, GF - gallery forest, UA - Urban Area; Origin: E - exotic, N - native. *Species with large seeds (≥ 1.0 cm).

fruits exploited by Red-and-green Macaws (Table 1). Both Leguminosae and Arecaceae included four species, whereas Anacardiaceae had three. The other families had only two or one species (Table 1). Leguminosae also had the most consumed species, *Dipteryx alata*, present in the Cerrado, followed by *Acrocomia aculeata* (Arecaceae), dispersed along the River vegetation (Table 1). Conversely, the exotic *Terminalia catappa*, the third most consumed, was only in the urban area. The food available to macaws fluctuated substantially during the year. Higher values occurred during the dry season, mainly due to fruiting in *Dipteryx alata*, *Terminalia catappa*, and *Buchenavia tomentosa*. On the other hand, minor values in the late wet season resulted from fruiting in *Mauritia flexuosa*, *Acrocomia aculeata*, and *Psidium guajava* (χ^2 = 24.92, *P* = 0.0001, df = 3, Figure 1). The number of species consumed fluctuated from a maximum in the late dry season (N = 17) to a minimum (N = 6) during the late wet season (χ^2 = 15.56, *P* = 0.001, df = 3, Table 2). The food diversity of macaws varied from D = 11.5 in the late dry season to D = 4.8 in the late wet season (χ^2 = 12.70, *P* = 0.009, df = 3, Table 2).

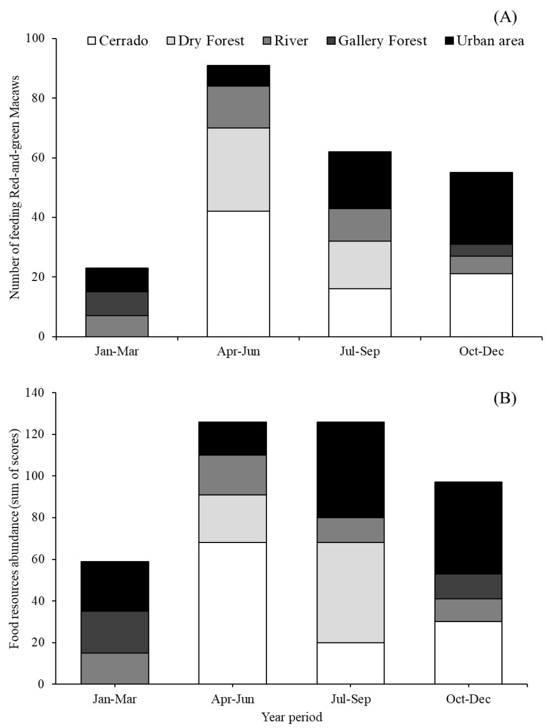

Figure 1. The number of Red-and-green Macaws recorded feeding (A) and the abundance of food resources consumed at each habitat type across seasons (B; Maracaju Cliffs, Municipality of Rochedo, State of Mato Grosso do Sul, Brazil, 2008).

3.2. Red-and-green Macaws use of food resources

I documented 231 macaws feeding on fruits in the five habitat types (Table 1, Figure 1). They foraged on six species in the Cerrado, five in the dry forests, other five in the River riparian forest, two along streams' gallery forests, and seven in the urban area (Table 1). Red-and-green Macaws consumed mainly large seeds (183 observed individuals), followed by fruit pulp (31), fruit pulp together of seeds (14), and only smaller seeds (3) (Table 1). In the Cerrado, I observed 58 feeding macaws during the drought, while only 21 foraged there in the rainy season. Macaws foraged in the dry forests only during the dry season (44 macaws), in the River in both seasons (13 wet, 25 dry), and in gallery forests only in the wet season (12). During the year (32 wet, 26 dry season), macaws often foraged on exotic species in the urban area (Figure 1, Table 1). Consequently, the number of foraging macaws differed between seasons and habitat types (Contingency analysis, χ^2 = 107.29, *P* = 0.0001, df = 12, Figure 1).

As mentioned above, during the year, food-related parameters vary (Figure 1, Table 2). As a result, the number of feeding Red-and-green Macaws paralleled food abundance (Generalized Linear Model, G = 23.99, P = 0.0001; Figure 1), the number of food species (G = 12.95, P = 0.003; Table 2), and food diversity (G = 4.05, P = 0.044; Table 2). Hurlbert's niche breadth showed year-round wide-values (minimum B' = 0.83, July-September, maximum B' = 0.92, January-March; Table 2). This trend reflected the consumption of a diverse array of abundant foods from different habitat types in the four periods of the year (Table 2, Figure 1). However, the low variation in diet breadth across the year was unrelated to food parameters.

During the dry season, Red-and-green Macaws often foraged on large-seeded species such as *Dipteryx alata* (31 macaws), *Buchenavia tomentosa* (16), *Hymenaea courbaril* (17), and *Attalea phalerata* (12). On the other hand, in the wet season, macaws ate seeds of *Caryocar brasiliense* (19) and *Terminalia catappa* (13), as well as pulps of *Mangifera indica* (14) and *Mauritia flexuosa* (9). Then, the gradient of seasonal food consumption across the habitat mosaic ranged from the urban area to dry forests and Cerrado, in which macaws foraged from exotic to native

Table 2. Parameters related to the Red-and-green Macaw (*Ara chloropterus*) feeding habits in the four periods of the year at a habitat mosaic of Cerrado in the Maracaju Cliffs (Rochedo, State of Mato Grosso do Sul, Brazil, 2008).

Parameters	Year period			
	Jan - Mar	Apr - Jun	Jul - Sep	Oct - Dec
Nº of food species	6	13	17	8
Food diversity	4.8	5.8	11.5	4.9
Niche breadth	0.92	0.91	0.83	0.90

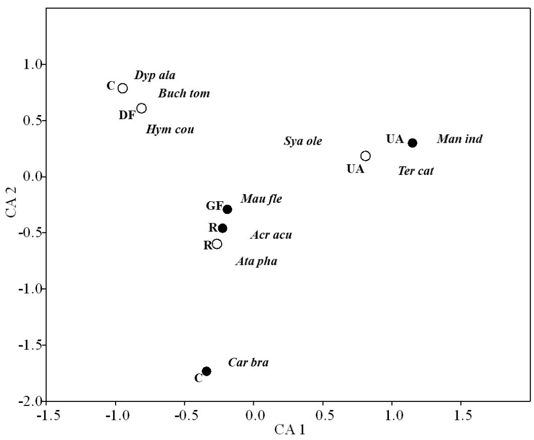

Figure 2. Correspondence analysis (CA) ordination plot with circles denoting habitat type (open: dry season; full: rainy season), overlapping food species consumed (>2.5% of diet) by Red-and-green Macaws. Species consumed are represented by the first three letters of their genera and species names (Maracaju Cliffs, Municipality of Rochedo, State of Mato Grosso do Sul, Brazil, 2008; see Table 1).

species (Correspondence Analysis, Axis 1 = 31.23%, and Axis 2 = 24.11% of the variance associated with feeding area and plant species across season, Figure 2). *Terminalia catappa* and *Mangifera indica* accounted for much of the macaw diet in the urban area during the wet season, while *Caryocar brasiliense* performed the same in the Cerrado. On the opposite extreme of the scatter plot, also in the Cerrado, were *Dipteryx alata* and *Buchenavia tomentosa*, used by macaws during the dry season. Between those extremes were palm species, which Red-and-green Macaws exploited at watercourse vegetation during both seasons (Figure 2).

4. Discussion

The present results pointed out the Red-and-green Macaw temporal variations in the use of feeding areas as a response to local food availability, coherent with the far-ranging use, by macaws, of habitat mosaics, including anthropized areas (Berg et al., 2007; Haugaasen and Peres, 2007; Silva, 2018; Ragusa-Netto, 2022). Furthermore, there was an increase in the number of foraging macaws in a given area during a season as a response to the simultaneous availability of a set of foods (Ragusa-Netto, 2007, 2022). This was pronounced in the Cerrado during the early dry season, mainly due to the availability of *Dipteryx alata* and *Buchenavia tomentosa*. To a lesser extent, the same occurred during the same or different periods in dry forests and the urban area in response to at least three food species available. Indeed, the number of feeding macaws reflected the abundance of food, as well as the number and diversity of food species present in the habitat mosaic at specific times of the year (Ragusa-Netto, 2022). It is worth noting that macaws foraged across seasons in both the River and urban area, conforming to the often-fruiting episodes in palms and *Terminalia catappa*. This foraging response to variable resource availability underscores the Red-and-green Macaw opportunism for the best feeding reward, in which the nutritional synergism taken from varied foods attracted increased numbers of individuals (Pyke, 1984). Therefore, Red-and-green Macaws tracked seasonal fruit patches across the habitat mosaic, resulting in variable local occurrence throughout the year, although presenting a consistent number of foraging individuals at the landscape scale (Gilardi and Toft, 2012; Lee et al., 2014).

In the Cerrado, Red-and-green Macaws ate a variety of large-seeded species, a dietary habit also documented elsewhere (Gilardi and Toft, 2012; Lee et al., 2014). The nutritional quality of seeds is often superior to that of other plant organs, including the fruit pulp (Gilardi and Toft, 2012). Diets rich in large seeds fulfill the daily energy and nutritional requirements of macaws, given the typical large birds' demand for high-quality food to support their metabolic needs (Koutsos et al., 2001). Indeed, macaws often concentrate their diets on a few fruit types with prolonged availability (Berg et al., 2007; Matuzak et al., 2008; Lee et al., 2014; de la Parra-Martinez et al., 2019). However, in the present study, Red-and-green Macaws mainly explored seasonally available fruits, although much of their food was also large seeds (Agostini-Costa and Vieira, 2004; Reis and Schmiele, 2019). Additionally, in the urban area, they consumed the nonnative *T. catappa*, *M. indica*, and *P. guajava*, which have also been observed in macaws' diets in anthropized areas. In this respect, *T. catappa* composed much of the diet of Scarlet Macaws (*Ara macao* [Linnaeus, 1758], Matuzak et al., 2008) in an anthropized area of Costa Rica. *Terminalia catappa* is often present in urban afforestation and frequently produces large fruit crops enclosing nutritious seeds (Mbah et al., 2013). This makes it a valuable resource within anthropized areas (Matuzak et al., 2008).

The Red-and-green Macaw exhibited a broad feeding niche breadth throughout the year. Their diet had no item preponderance, even those consumed throughout the seasons, such as palm nuts and *T. catappa* seeds. In contrast, macaws from other plant species-rich sites often showed low diet breadth due to consuming a reduced set of items over extended periods while adding a moderate proportion of seasonal foods to their diets (Matuzak et al., 2008; Lee et al., 2014; de la Parra-Martinez et al., 2019). This pattern regularly occurs in less seasonal areas where some tree species bore large fruit crops exploited by macaws over prolonged periods (Gilardi and Toft, 2012; de la Parra-Martinez et al., 2019). It is worth noting that macaws commonly use a suit of food species smaller than those available throughout the year (Matuzak et al., 2008; de la Parra-Martinez et al., 2019). Indeed, large macaws frequently rely on fewer than 15 plant species, mainly consuming the seeds of some tree and palm species (Pitter and Christiansen, 1995; Matuzak et al., 2008; Lee et al., 2014). However, the macaws' diet can be influenced by the ecological context. For instance, the closely related Scarlet Macaw (*Ara macao*) consumed up to 15 plant species in Belize (Renton, 2006), whereas it fed on 43 species in Costa Rica (Vaughan et al., 2006). In western Amazonia, Red-and-green Macaws moderately exploited 33 species, including flowers and leaves, although they fed most frequently only on *Bertholletia excelsa* Bonpl. seeds, composing 14% of their diet (Lee et al., 2014). In the present study, Red-and-green Macaws ate 25 species, mainly their seeds, of which only eight achieved percentages ranging from 5 to 13.4% (*Dipteryx alata*) of their diet. On the other hand, in northeastern Argentina, direct observations detected 32 species in the diet of reintroduced Red-and-green Macaws, of which *Psidium guajava* consumed throughout the year, composed 60% of their diets (Volpe et al., 2022). This pronounced variability highlights the extent of dietary flexibility present in, at least part, *Ara* macaws.

To conclude, in terms of importance for conservation, diverse feeding areas with asynchronous fruit patches can provide food for Red-and-green Macaws on at least one site when resources decline elsewhere. Indeed, macaws' scarcity during a given period in one location while abundant in another, where they spent time foraging, suggests that they track fruit across the habitat mosaic. This heterogeneity plays a central role in their opportunistic foraging dynamics, although the extent to which each feeding area may be exploited likely varies over time and space (van Schaik et al., 1993; Haugaasen and Peres, 2007; Ragusa-Netto, 2022). Furthermore, not only the abundance but also the variety of food resources available influenced the local number of feeding macaws in the habitat mosaic throughout the year (Ragusa-Netto, 2007, 2022). This highlights the importance of understanding the peculiarities of each feeding area while supplying food to macaws throughout different seasons. Given that Red-and-green Macaws heavily depend on large-seeded species (Lee et al., 2014, this study), clarifying how food abundance and diversity may explain temporal changes in local macaws' abundance is crucial. With this, we may develop management plans to prevent their progressive decline in the Brazilian Cerrado. Therefore, Maracaju Cliffs include several habitat types with important food plants for the Red-and-green Macaw, emerging as a priority area of its conservation amid the fragmented Cerrado.

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