Foraging suggests high behavioral flexibility in the blue-winged parrotlet (Forpus xanthopterygius, Psittacidae) in response to fleshy fruit availability

Forrageamento sugere alta flexibilidade comportamental no tuim-de-casa-azul (Forpus xanthopterygius, Psittacidae) em resposta à disponibilidade de frutos carnosos

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Abstract

Parrots primarily consume seeds and pulp and sometimes flowers, nectar and leaves. Plants usually offer these items seasonally, forcing flexible consumption behavior in parrots, mostly when food is scarce. However, seasonal changes in behavior in the Forpus genus (the small Neotropical parrots) guided by the food supply have still not been identified. Here, we investigate the foraging patterns of *Forpus xanthopterygius* (the blue-winged parrotlet) and identify the plants and items it consumes. This information, together with data on its occurrence, flock size and dietary niche breadth, were used to elucidate whether the behavioral flexibility of this bird is related to shifts in fleshy fruit availability from the wet to the dry season. The data were obtained during two years of systematic sampling (n = 432) along nine roadside transects located in an anthropogenic landscape. Forpus xanthopterygius consumed the seeds, flowers/nectar and fruit pulp (in this order of preference) of 24 plant species (10 exotics) belonging to 18 families. The dietary niche breadth was narrow, likely because fleshy fruits of Cecropia pachystachya, Maclura tinctoria, and especially Trema micrantha predominated in their diet. Forpus xanthopterygius was shown to be seasonal, being more common in the wet season, when the availability of fleshy fruits was greater. This parrot proved to be flexible in some behaviors, perhaps to minimize the negative impacts of the decline in fleshy fruit availability during the driest period. Evidence of this flexibility is the increase in flock size and the number of food plant species, as well as the use of dry fruits, nectar and exotic plants as alternative food sources.

Key words: Exotic Plants; Feeding Ecology; Fruiting Phenology; Fleshy and Dry Fruits; Nectar.

Resumo

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Psitacídeos consomem principalmente sementes e polpa, as vezes flores, néctar e folhas. As plantas geralmente oferecem esses itens sazonalmente, forçando o comportamento alimentar flexível nos psitacídeos, principalmente quando o alimento é escassa. No entanto, mudanças sazonais no comportamento do gênero Forpus (os menores psitacídeos Neotropicais) guiadas pelo suprimento de alimentos ainda não foram identificados. Aqui, investigamos os padrões de forrageamento de Forpus xanthopterygius (tuim-de-asa-azul) e identificamos as plantas e itens que ele consome. Essas informações, juntamente com os dados sobre sua ocorrência, tamanho do bando e amplitude do nicho alimentar, foram utilizadas para elucidar se a flexibilidade comportamental desta ave está relacionada a mudanças na disponibilidade de frutos carnosos da estação úmida para a seca. Os dados foram obtidos durante dois anos de amostragem sistemática (n = 432) ao longo de nove transecções localizados em uma paisagem antropogênica. Forpus xanthopterygius consumiu sementes, flores/néctar e polpa de frutas (nesta ordem de preferência) de 24 espécies de plantas (10 exóticas) pertencentes a 18 famílias. A amplitude do nicho alimentar foi estreita, provavelmente porque os frutos carnosos de Cecropia pachystachya, Maclura tinctoria e especialmente de Trema micrantha predominaram em sua dieta. Forpus xanthopterygius mostrou ser sazonal, sendo mais comum na estação chuvosa, quando a disponibilidade de frutos carnosos foi maior. Este psitacídeo mostrou-se flexível em alguns comportamentos, talvez para minimizar os impactos negativos do declínio na disponibilidade de frutos carnosos durante o período mais seco. A evidência dessa flexibilidade é o aumento no tamanho do bando e o número de espécies de plantas alimentícias, bem como o uso de frutos secos, néctar e plantas exóticas como fontes alternativas de alimento.

Palavras-chave: Ecologia Trófica; Fenologia de frutificação; Frutos Carnosos e Secos; Néctar; Plantas exóticas.

Introduction

Parrots are primary consumers, ingesting mostly seeds and fruit pulp and sometimes flowers, nectar, and leaves (ROTH, 1984; DESENNE, 1994; GILLARDI; TOFT, 2012). The supply of these plant food items is usually seasonal (VAN SCHAIK et al., 1993), forcing parrots to have flexible behavior in order to adjust to plant phenology (RENTON et al., 2015). In fact, variation in abundance, flock size and alternative food use by parrots are often related to shifts in primary productivity (CANNON, 1984; WERMUNDESEN, 1997; 1999; RENTON, 2001). However, seasonal behavioral changes driven by the supply of plant food items have not been identified in the *Forpus* genus, the small Neotropical parrots (12-14.5 cm long) recognized as parrotlets (FORSHAW, 1989).

The genus *Forpus* comprises eight species (IUCN, 2018), of which *Forpus xanthopterygius* (Taczanowski, 1883), or the blue-winged parrotlet, stands out. It is the most widespread parrotlet, occurring in Argentina, Bolivia, Ecuador, Paraguay, Peru and several states of Brazil (IUCN, 2018). Some information about the feeding habits and abundance of this species have been obtained in forested environments (PIZO et al., 1995; GALETTI, 1997). These data, however, seem fortuitous: *F. xanthopterygius* is a forest-independent bird (SILVA, 1995), mostly inhabiting open vegetation, including anthropogenic landscapes (FORSHAW, 1989). Other studies have shown interactions with some plant species, such as seed and flower predation (FIGUEIREDO, 1996; MELO et al., 2009; ATHIE; DIAS, 2012). There have also been reports of this parrotlet

occupying a nest of the rufous hornero (Furnarius rufus, Furnariidae) and ingesting soil and the seeds of some plants (SAZIMA, 2008). The most comprehensive ecological study on F. xanthopterygius was conducted by Barros (1995) but remains unpublished. We note that this investigation was based on inadequate field procedures. Feeding records, for example, were obtained during repeated inspections around nesting sites (BARROS, 1995). In addition, there is no report of how environmental factors, such as the seasonal supply of fruits, affect the behavior of this parrotlet. Considering the paucity of ecological data, which are often casual or biased the knowledge of the ecology of F. xanthopterygius remains based on inconsistent information.

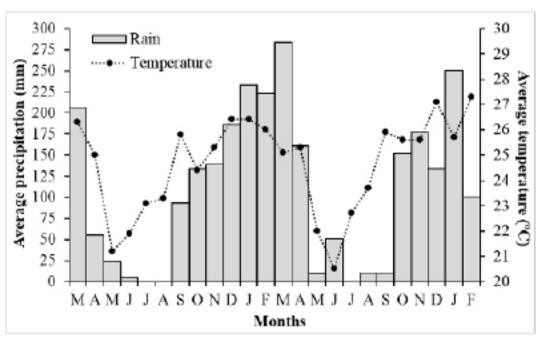
In this study, we assess the ecology of *F. xanthopterygius* based on data systematically obtained in an anthropogenic landscape. Ecological studies of parrots inhabiting anthropic environments are fundamental since the human alteration of natural habitats has been the trademark of the current world (ELLIS et al., 2010). As a result, parrots will be increasingly threatened with extinction (BERKUNSKY et al., 2017), and many of them are forced to live in highly human-modified areas (SILVA; MELO, 2013; RENTON et al., 2015). Therefore, the future of many parrot species may depend on anthropogenic landscape management actions, but this will only be possible by obtaining basic and consistent ecological data from the species (GARDNER et al., 2009). The ecological study performed here consists of describing the foraging behavior of *F. xanthopterygius* by identifying the food plants and plant parts that it consumes. We also verified whether their local pattern of occurrence, flock size, dietary niche breadth, food plant composition and inclusion of alternative food items are related to shifts in fleshy fruit availability from the wet to the dry season. We used these seasonality data to infer the behavioral flexibility of *F. xanthopterygius*.

Materials and Methods

Study area

We performed this study in Ilha Solteira in northwestern São Paulo state, SE Brazil (20°25'S, 51°20'W, 380 m a.s.l), a confluence region of the São José dos Dourados and Tietê Rivers with the Paraná River. Only 2% of the 63,900 ha of the area has natural vegetation cover, consisting of riparian forest and small fragments of semideciduous and dry forest, savanna, unidentified vegetation (KRONKA et al., 2005), possibly secondary mixed forests of exotic and native plants, and pure forest of the exotic tree *Leucaena leucocephala* (Fabaceae). The main recent human impacts on the landscape come from sugarcane crops, pastureland, small farm expansion, and urbanization. The area is rich in pioneer tree species of prominent abundance, particularly in riparian forest edges, such as *Cecropia pachystachya* (Urticaceae), and in savanna and unidentified vegetation, such as *Trema micrantha* (Cannabaceae). According to the Köppen classification, the regional climate is Aw, with an average temperature of 25.6°C and two well-defined seasons: a wet season from October to March and a dry season from April to September (Figure 1).

Figure 1 - Average rainfall and temperature in Ilha Solteira between March 2010 and February 2012.



Source: http://www.agr.feis.unesp.br/clima.php

General procedures

We collected ecological data for *F. xanthopterygius* during systematic sampling along nine 5-km-long roadside transects (PIZO et al., 1995; MATUZAK et al., 2008); sampling was conducted from March 2010 to February 2012. All transects crossed a variety of environments, such as cultivated areas, pastures, primary and secondary forests, reforested areas, riparian forest, orchards in the rural area and gardens in the urban area. Each transect was sampled twice a month, once in the morning (07:30-10:30 h) and again in the afternoon (15:30-18:30), at intervals of 11 to 15 days. Two transects were usually sampled each day.

Foraging observations

A foraging observation consisted of a parrotlet or group of *F. xanthopterygius* detected feeding on plants located up to 20 m perpendicular from a transect. During each observation, we recorded the food item, i.e., flower, nectar, pulp or seed. We identified food plants as being exotic or native species using the specialized literature (LORENZI, 2008; 2009a; 2009b; SOUZA; LORENZI, 2008; LORENZI et al., 2003). We considered seed predation the behavioral act in which parrotlets discarded the exocarp and/or mesocarp of the fruit to ingest the seeds (JORDANO, 1992).

Occurrence data

The occurrence data consisted of a parrotlet or flock of *F. xanthopterygius* detected up to 20 m perpendicular from a transect. We recorded whether the parrotlets were perched, feeding or flying. We used the number of parrotlets and flight direction to avoid the repeated recording of occurrences in the same sample (GILLARD; MUNN, 1998).

Phenological evaluation

Simultaneous to the occurrence sampling, we evaluated the reproductive phenology (flower and fruit availability) of plants located up to 20 m perpendicular from each transect (BENCKE; MORELATTO, 2002). The presence or absence of phenophases was recorded in order to determine the absolute duration of the phenological episode (FRANKIE et al., 1974; MORELLATO et al., 1989; BENCKE; MORELATTO, 2002). Thus, if at least one individual of a plant species was found with flowers or fruits in a given month, we considered this species as being in its flowering or fruiting period (BATALHA; MANTOVANI, 2000).

Data analysis

We assessed the assumptions for the statistical tests by verifying the data normality using the Kolmogorov-Smirnov test (ZAR, 1999). We used a conservative method that considered only the first observation of *F. xanthopterygius* foraging within a plant (GILARDI; TOFT, 2012). Therefore, each observation of foraging within a plant species was unique and independent.

We used the number of parrotlets feeding to estimate the dietary niche breadth based on the standardized Levins' index calculated as $B_A = (Y^2/\Sigma N^2) - 1/n - 1$, where Y is the total number of parrotlets feeding, N is the number of parrotlets associated with each plant species, and n is the total number of food plant species. A value close to 0 indicates dietary specialization, i.e., among food plant species, some are disproportionately selected by parrotlets, and a value close to 1 indicates a broad diet with an equal spread of use across plants (COLWELL; FUTUYMA, 1971).

We used a paired t-test to examine the seasonal variation in the proportion of plant species bearing fruits. We used the Mann-Whitney U test to verify seasonal changes in the occurrence and flock size of parrotlets. We calculated the mean occurrence of F. x anthopterygius for 48 periods (two sampling events in each month). Then, we used a Spearman correlation analysis (r) to identify relationships between the occurrence of F. x anthopterygius and the proportion of plant species bearing fruits in each of the 48 sampling periods.

The type of fruit (dry or fleshy) as well as the item (seed, pulp, flower or nectar) preferred by *F. xanthopterygius* during feeding were determined based on the percentage of foraging parrotlets. We used the chi-square contingency test to verify seasonal shifts (from the wet to dry season) in the type of fruit consumed and the origin of the food plant species (native or exotic).

We used the standardized Levins' index and the number of food plant species to identify seasonal shifts in F. xanthopterygius foraging (RENTON, 2001; MATUZAK et al., 2008). We used the Morisita-Horn index (C_H) to explore similarity (values close to 1) and dissimilarity (values close to 0) in the composition of plant species foraged by parrotlets according to the seasons.

The values given below represent the mean ± 1 standard deviation.

Results

Foraging

During the systematic sampling (n = 432) along the transects, we obtained 45 foraging observations, which included 167 individuals of F. xanthopterygius. This parrotlet foraged among 24 plant species belonging to 18 families (Table 1). The overall dietary niche breadth was narrow (Levins'index; B_A = 0.14), indicating a specialized diet. Exotic plants (n = 10 species) accounted for 24.4% of the foraging observations (Table 1). One plant species, the native tree *Trema micrantha*, comprised almost a third of the observations, followed by *Cecropia pachystachya* and *Maclura tinctoria*, both composing 6.7% of the diet of F. xanthopterygius (Table 1).

Table 1 – Plant species and items eaten by Forpus xanthopterygius between March 2010 and February 2012 in the anthropogenic landscape of Ilha Solteira.

-				Parrotl		
Family	Species	Fruit type ^a	Item ^b	Wet season (n = 74)	Dry season (n = 93)	Observations (%) (n = 42)
Anacardiaceae	Astronium graveolens	D	se	-	1.1	2.2
	Myracrodruon urundeuva	D	se	-	8.6	2.2
Araliaceae	Schefflera actinophylla	F	se	-	2.2	2.2
Asteraceae	Unidentified	D	se	2.7	-	2.2
Bignoniaceae	Handroanthus impetiginosus		ne	-	2.2	2.2
Boraginaceae	Cordia abyssinica*	F	pu	-	3.2	2.2
Cannabaceae	Trema micrantha	F	se	58.1	36.6	31.1
Euphorbiaceae	Croton urucurana	D	se	8.1	-	4.4
	Mabea fistulifera		ne	-	2.2	2.2
Fabaceae	Leucaena leucocephala*	D	se	-	3.2	2.2
	Peltophorum dubium	D	se	2.7	-	2.2
Lamiaceae	Ocimum basilicum*	D	se	-	3.2	2.2
Malvaceae	Bombax ceiba*		ne	-	3.2	2.2
	Guazuma ulmifolia	D	fl, se	1.4	2.2	4.4

Meliaceae	Melia azedarach*	F	se	2.7	-	2.2
Moraceae	Ficus benjamina*	F	se	2.7	4.3	4.4
	Maclura tinctoria	F	se	8.1	-	6.7
Myrtaceae	Corymbia sp.*		fl	2.7	-	2.2
	Syzygium cumini*	F	pu	-	5.4	2.2
Rutaceae	Genipa americana	F	pu	2.7	3.2	4.4
Sapotaceae	Ligustrum lucidum*	F	se	-	2.2	2.2
Turneraceae	Unidentified	D	se	-	12.9	2.2
Urticaceae	Cecropia pachystachya	F	se	8.1	2.2	6.7
Verbenaceae	Tectona grandis*	D	se	-	2.2	2.2
ource: Authors (2018)						

Source: Authors (2018)

Notes: * Indicates exotic species. ${}^{a}F = fleshy fruit; D = dry fruit. {}^{b}fl = flower; ne = nectar; pu = pulp; se = seed.$

Fruits comprised 88.9% of the observations, and fleshy fruits were foraged more often than dry fruits: 74.8% vs. 25.2% of the parrotlets were detected feeding on fruits. Forpus xanthopterygius mainly ingested seeds (80% of the observations), followed by flowers and nectar (11.1%) and pulp (8.9%). Behavior during seed consumption was consistent. When exploiting the fruit, F. xanthopterygius opened the exocarp and mesocarp with its beak, removing and chewing the seeds before swallowing them, thus acting as a seed predator.

Seasonality

We performed 216 samplings during each season, i.e., wet and dry. The occurrence of F. xanthopterygius was higher in the wet (n = 182 detections) than in the dry season (n = 111), and this difference was significant (Table 2). As the parrotlets fed mostly on fleshy fruits, we analyzed the seasonal variation in the fruiting of 78 plant species that bear this fruit type. The proportion of species bearing fleshy fruits was significantly higher in the wet than in the dry season (Table 2). Therefore, parrotlet occurrence paralleled the fleshy fruit availability (Figure 2).

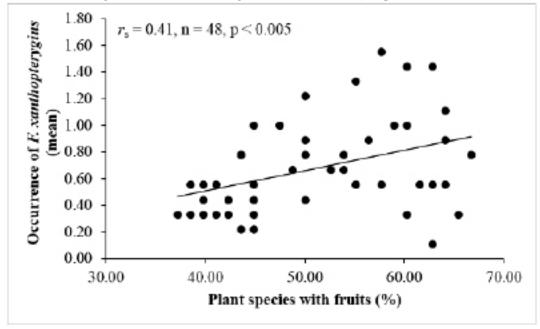
Table 2 – Seasonality in terms of the proportion of plant species producing fleshy fruits and the occurrence and flock size of F. xanthopterygius in the anthropogenic landscape of Ilha Solteira.

Season								
Variables	Wet		Dry	7	df	p values		
	Mean	SD	Mean	SD				
Plant species with fruits (%)	56.40	6.50	45.60	6.50	23	0.001ª		
Occurrence	0.83	1.10	0.52	0.93	430	0.001^{b}		
Flock size	2.09	3.68	1.40	2.75	430	0.004^{b}		

Source: Authors (2018)

Notes: ^a Based on paired t-test. ^b based on the U test.

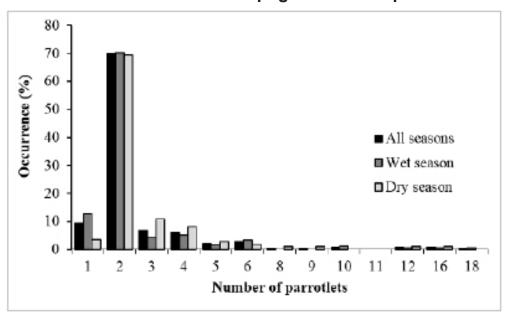
Figure 2 – Relationship between the occurrence of F. xanthopterygius and fleshy fruit availability in the anthropogenic landscape of Ilha



Source: Authors (2018).

The flock size of *F. xanthopterygius* also varied significantly according to the seasons (Table 2). Approximately 70% of the detected flocks contained two parrotlets (Figure 3). Only one parrotlet was more frequently recorded in the wet season, while flocks containing 3-5 parrotlets were observed especially often in the dry season (Figure 3). Flocks with more than six parrotlets were rare, and those with 8-9, 12 and 16 parrotlets were detected mainly in the dry season (Figure 3). The largest flock, with 18 parrotlets, was detected during the wet season (Figure 3).

Figure 3 – Variation in the flock size of Forpus xanthopterygius based on 293 occurrences in the anthropogenic landscape of Ilha Solteira



Source: Authors (2018).

Fleshy fruits were widely foraged by *F. xanthopterygius* in both the wet and dry seasons. However, a higher number of parrotlets was observed foraging dry fruits in the dry than in the wet season ($\chi^2 = 8.66$, df = 1, p < 0.001, Figure 4). Similarly, native plants were widely foraged in both seasons. However, a greater number of parrotlets was observed feeding on exotic plants in the dry than in the wet season ($\chi^2 = 8.77$, df = 1, p < 0.001, Figure 4). Floral resources were more commonly foraged in the dry (7.53% of parrotlets feeding) than in the wet season (4.05% of parrotlets) (Table 1).

■ Wet season (a) 100 (b) 100 □ Dry season 90 F. xanthopterygius feeding (%) 90 80 80 70 70 60 60 50 50 40 40 30 30 20 20 10 10 0 0 Native Fleshy Exotic Dry Fruit type Plant origin

Figure 4 – Seasonal variation in the foraging of Forpus xanthopterygius in the anthropogenic landscape of Ilha Solteira.

Source: Authors (2018).

There was also seasonal variation in the composition of food plant species and in dietary niche breadth. Forpus xanthopterygius foraged 11 plant species in the wet season (n = 20 foraging observations, 74 parrotlets) (Table 1), with a narrow dietary niche (Levins' index; B_A = 0.18). In the dry season, they foraged 18 plant species (n = 25 observations, 93 parrotlets) (Table 1), an increase of 38.9% in the plant species foraged, with a wider dietary niche (B_A = 0, 30). There was high seasonal similarity in the use of plant species (Morisita-Horn index; C_H = 0.80), with the fleshy fruits of T. micrantha being widely foraged in both the wet and dry seasons (Table 1).

Discussion

Foraging

Forpus xanthopterygius fed on a variety of plant species (n = 24) belonging to a broad phylogenetic spectrum (18 families). This number is remarkable, especially in comparison to previous studies. This parrotlet was observed foraging among five and four plant species in protected areas (PIZO et al., 1995; GALETTI, 1997, respectively). In an anthropogenic area, it fed on only six plant species (ATHIE; DIAS, 2012). Although F. xanthopterygius has been

observed feeding on 32 plant species in four distinct areas, an average of 15 species were foraged in each area, with a maximum of 22 in one area (BARROS, 1995). The variety of plant species in the diet of this parrotlet recorded here certainly correlates with the sampling method used. Roadside transects are advantageous since they allow sampling across a large area, with multiple environments, which increases the likelihood of parrot detection (DÉNES et al., 2018). As a result, a variety of plants tends to be recorded in the parrot diet (see BLANCO et al., 2015).

This variety of food plants, by itself, suggests high behavioral flexibility in *F. xanthopterygius* and therefore the ability to inhabit human-modified landscapes (SANTOS; RAGUSA-NETTO, 2014). However, the standardized Levins' index estimated from the foraging data approached zero. This means that *F. xanthopterygius* has a narrow dietary niche, i.e., among a variety of food plants, it chose few of them. In fact, only *T. micrantha* fruits accounted for a high proportion of the parrotlet foraging records (Table 1). Interestingly, this plant composed 16-33% of the diet of *F. xanthopterygius* at other sites (PIZO et al., 1995; GALETTI, 1997). *Trema micrantha* is a pioneer tree of prominent abundance in our study area, which likely influenced the extensive consumption of its fruits by *F. xanthopterygius*. A similar relationship was reported between the yellow-faced parrotlet (*Forpus xanthops*, Salvin 1895) and fleshy fruits of the family Cactaceae (BERGAZO, 1996). It is true that parrots frequently feed on fruits produced by locally abundant pioneer trees (PIZO et al., 1995), among them *Cecropia* spp., a genus also common in the diet of *F. xanthopterygius* at our study site and in other areas (cf. BARROS, 1995; PIZO et al., 1995; GALETTI, 1997; ATHIE; DIAS, 2012).

Approximately one quarter of the foraging records indicated parrotlets feeding on exotic plant species, which represented 41.66% of all food plants. The use of exotic plants as a food resource has been shown to be a typical foraging pattern of parrot species living in anthropic areas (MATUZAK et al., 2008). As examples, we mention the Pacific parakeet, *Psittacara strenuus* (WERMUNDSEN, 1997), the blue-winged macaw, *Primolius maracana* (NUNES; GALETTI, 2007), and the golden-capped parakeet, *Aratinga auricapillus* (SILVA; MELO, 2013), as well as other parrots (MATUZAK et al., 2008). It is apparent that the use of exotic species by parrots is a behavioral adjustment that promotes a high tolerance of the environmental changes inflicted by humans (NUNES; GALETTI, 2007). In this regard, *F. xanthopterygius* seems to tolerate anthropogenic environments by associating with exotic cultivated plants.

Forpus xanthopterygius acted mainly as a seed predator. Therefore, it potentially plays an important ecological role in diversifying the local plant community. It can, for example, control the dissemination and dominance of abundant plant species, among them *T. micrantha* and *C. pachystachya*. Similar functions have been attributed to a variety of Neotropical parrots (DESENNE, 1995; RENTON, 2001; GILARDI; TOFT, 2012). However, we note that mutualistic roles, such as the internal dispersal of tiny seeds (endozoochory), have been demonstrated in some parrots (BLANCO et al., 2016). Both *T. micrantha* and *C. pachystachya*, as well as other plants (e.g., *Ficus* spp.), produce fruits containing tiny seeds, and *F. xanthopterygius* can ingest some of these seeds without damaging them, enabling endozoochory (*sensu* BLANCO et al., 2016). However, the role of this parrotlet as a disperser of such seeds requires detailed investigations.

Seasonality

In this study, we found evidence of seasonality and therefore behavioral flexibility in *F. xanthopterygius* as a response to variation in fleshy fruit availability.

The first evidence was the variation in the local occurrence of this parrotlet. In general, parrots exhibit nomadic behavior, moving through the landscape according to fruit availability (LOISELLE, 1988; RENTON, 2001). Shifts in their local occurrence have been considered to be a seasonal response to the supply of fruits (TERBORGH et al., 1990; HAUGAASEN; PERES, 2007). The paired *t*-test showed a reduction in the number of plant species offering fleshy fruits during the dry season at the study site (Table 2). Concomitantly, and perhaps symptomatically, the occurrence of *F. xanthopterygius* decreased, as confirmed by the *t*-test. On the other hand, the number of plant species with fleshy fruits significantly increased during the wet season. As shown in the correlation analysis, the increase in the local occurrence of *F. xanthopterygius* was related to an increase in the proportion of plant species producing fleshy fruits (Figure 2). We emphasize that *F. xanthopterygius* breeds during the wet season (BARROS, 1995), which may have influenced the influx of parrotlets into the study area (Table 2). However, the breeding season of parrot species generally coincides with an increase in food availability (BRIGHTSMITH, 2005; RENTON et al., 2015), possibly of fleshy fruits.

The second evidence was the variation in flock size. The average flock size of *F. xanthopterygius* was slightly higher in the wet season. However, we generally detected larger flocks (8-16 parrotlets) during the dry season (Figure 3), when the proportion of plant species bearing fleshy fruits decreased in the study area. Shifts in food supply may influence gregariousness in parrots (CANON, 1984), which is advantageous because it promotes a higher rate of food gathering in the environment (POLLIAM; CARACO, 1984). For example, with a reduction in the food supply, an increase in flock size leads to an increase in the foraging area (CHAPMAN et al., 1989). It also leads to a decrease in the time necessary to locate food, which would likely not occur if the parrotlets were foraging alone (CANON, 1984). Presumably, an increase in the flock size in *F. xanthopterygius* is a behavior aimed toward minimizing the impacts of the reduction in the fleshy fruit supply during the driest period. In fact, an increase in flock size when fruits are scarce has been observed in a variety of Neotropical parrots (CHAPMAN et al., 1989; WERMUNDSEN, 1999), including those living in anthropogenic areas (SOUTH; PRUETT-JONES, 2000). This reflects a very clear behavioral flexibility pattern among Psittaciformes, i.e., adjustments to the limiting factors of environments, such as reductions in the food supply.

The third evidence was the shifts in the number and composition of food plant species and food items. The fleshy fruit supply was lowest during the dry season. As a result, *F. xanthopterygius* increased its number of food plant species. In addition, although it was less common during this season, there is evidence that this parrotlet remains in the area by exploiting alternative food sources, such as flowers and dry fruits. These resources are usually abundant during the dry season (MORELATTO et al., 1989), as verified in the study area (SILVA; MELO, 2013). In fact, parrotlets foraged nectar exclusively during this season; e.g., from *Handroanthus impetiginosus*, *Bombax ceiba* and *Mabea fistulifera* (see Table 1). The parrotlets also exploited dry fruits mostly during this period; e.g., those of *Myracrodruon urundeuva* and Turneraceae (see Table 1). We note that most exotic plant species were foraged during the dry season (Table 1). This suggests that exotic plants are also alternative foods, particularly in view of the low supply of fleshy

fruits during this period (*sensu* FORSHAW, 1989). *Forpus xanthopterygius* thus behaved as an opportunistic and therefore flexible consumer, exploiting other abundant foods when the supply of fleshy fruits (its major resource) decreased. Regarding the composition of food plant species, the Morisita-Horn index showed low seasonality in the diet of this parrotlet, apparently because it substantially consumed *T. micrantha* fruits in both seasons (see Table 1).

Finally, the fourth evidence was the variation in dietary niche breadth. The dietary niche tends to widen with an increase in resource abundance and food item diversity (WERMUNDSEN, 1997; RENTON, 2001). However, *F. xanthopterygius* had a narrow dietary niche during the wet season, when the number of plant species bearing fleshy fruits increased. This pattern is the inverse of that found for the lilac-crowned parrot (*Amazona finschi*, Sclater 1864), which demonstrates a narrow dietary niche during fruit scarcity (RENTON, 2001). The preference for a particular plant species seems to be one of the causes of a narrower dietary niche in parrots. For example, the narrow dietary niche exhibited by the scarlet macaw (*Ara macao*, Linnaeus 1758) likely resulted from its widespread preference for fruits of *Terminalia catappa* L. (MATUZAK et al., 2008). Therefore, it is likely that the narrower dietary niche during the wet season resulted from the focus of *F. xanthopterygius* on *T. micrantha* fruits, which represented 58.1% of foraging records in this period.

Conclusion

This study showed that *F. xanthopterygius* feeds on a wide spectrum of plant species in the anthropogenic landscape, some of them exotic. It also showed that this species prefers fleshy fruits, especially for seed consumption. However, few plant species (particularly *T. micrantha* and *C. pachystachya*, as well as *M. tinctoria*) were represented in the diet of this parrotlet, perhaps due to their prominent abundance in the study area. This study also provided evidence that seasonal changes, i.e., behavioral flexibility in *F. xanthopterygius* foraging, correspond to the fleshy fruit supply, which was lower during the dry season and higher in the wet season. *Forpus xanthopterygius* seems to adopt behavioral strategies aimed toward minimizing the negative impacts of the reduced fleshy fruit availability in the driest period. Among these strategies, we highlight the increase in flock size and number of food plant species, as well as the use of dry fruits, nectar and exotic species as alternative food sources.

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References

ATHIE, S.; DIAS, M. M. Frugivoria por aves em um mosaico de floresta estacional semidecidual e reflorestamento misto em Rio Claro, São Paulo, Brasil. **Acta Botânica Brasillica**, São Paulo, v.26, n.1, p.84-93, 2012. Doi: 10.1590/S0102-33062012000100010

BARROS, Y. M. 1995. **Biologia comportamental de** *Forpus xanthopterygius xanthopterygius* Spix (1824) - (Aves - Psittacidae): alimentação e reprodução. 1995. 131 f. Dissertação (Mestrado em Ciências Biológicas, Área de Zoologia) – Universidade Estadual Paulista Júlio Mesquita Filho, Instituto de Biociências, Rio Claro, 1995.

BATALHA, M. A.; MANTOVANI, W. Reproductive phenological patterns of cerrado plant species at the Pe-de-Gigante reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and woody floras. **Revista Brasileira de Biologia**, Rio Claro, v.60, n.1, p.129-145, 2000. Doi: 10.1590/S0034-71082000000100016

BENCKE, C. S. A.; MORELLATO, L. P. C. Comparação de dois métodos de avaliação da fenologia de plantas, sua interpretação e representação. Revista Brasileira de Botânica, São Paulo, v.25, n.3, p.269-275, 2002. Doi: 10.1590/S0100-84042002000300003

BERGAZO, A. J. Ecology and conservation of Yellow-faced Parrotlet. **Cotinga**, Sandy, v.6, n.1, p.20-23, 1996.

BERKUNSKY, I.; QUILLFELDT, P.; BRIGHTSMITH, D. J./ et al. Current threats faced by Neotropical parrot populations. **Biological Conservation**, Amsterdam, v.214, p.278-287, 2017. Doi: 10.1016/j.biocon.2017.08.016

BLANCO, G.; HIRALDO, F.; ROJAS, A.; DÉNES, F. V.; TELLA, J. L. Parrots as key multilinkers in ecosystem structure and functioning. **Ecology and Evolution**, London, v.5, n.18, p.4141-4160, 2015. Doi: 10.1002/ece3.1663

BLANCO, G.; BRAVO, C.; PACIFICO, E. C.; CHAMORRO, D.; SPEZIALE, K. L.; LAMBERTUCCI, S. A.; HIRALDO, F.; TELLA, J. L. Internal seed dispersal by parrots: an overview of a neglected mutualism. **Peer J**, v. 4, p. e1688, 2016. Doi: 10.7717/peerj.1688

BRIGHTSMITH, D. J. 2005. Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. **The Condor**, Albuquerque, v.117, n.3, p.296-305, 2005. Doi: 10.1676/03-087A.1

CANNON, C. E. Flock size of feeding Eastern and Pale-headed Rosellas (Aves: Psittaciformes). **Australian Wildlife Research**, Melbourne, v.11, n.2, p.349-355, 1984. Doi: 10.1071/WR9840349

CHAPMAN, C. A.; CHAPMAN, L. J.; LEFEBVRE, L. Variability in parrot flock size: possible functions of communal roosts. **The Condor**, Albuquerque, v.91, n.4, p.842-847, 1989.

COLWELL, R. K.; FUTUYAMA, D. J. On the measurement of niche breadth and overlap. **Ecology**, Washington, v.52, n.4, p.567-576, 1971. Doi: 10.2307/1934144

DÉNES, F. V.; TELLA, J. L.; BEISSINGER, S. R. Revisiting methods for estimating parrot abundance and population size. **Emu - Austral Ornithology**, Collingwood, v.118, n.1, p.67-79, 2018. Doi: 10.1080/01584197.2017.1401903

DESENNE, P. Estudio preliminar de la dieta de 15 especies de psitacidos en un bosque siempreverde, cuenca del Rio Tawadu, Reserva Forestal El Caura, Edo. Bolivar. In: MORALES G.; NOVO, I.; BIGIO, D.; LUY, A.; ROJAS-SUAREZ, F. (Ed.). **Biología y conservación de los psitácidos de Venezuela**. Caracas: Graficas Giavimar, 1994. p. 25-42.

ELLIS, E. C.; GOLDEWIJK, K. K.; SIEBERT, S.; LIGHTMAN, D.; RAMANKUTTY, N. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography, Malden, v.19, n.5, p.589-606, 2010. Doi: 10.1111/j.1466-8238.2010.00540.x

FIGUEIREDO, R. A. Complex interactions in nature: Parrotlet feeding on fig lessen seed dispersal and pollen flow. **Ciência & Cultura**, São Paulo, v.48, n.4, p.282-283, 1996.

FORSHAW, J. M. Parrots of the world. Melbourne: Lansdowne Editions. 1989.

FRANKIE, G. W.; BAKER, H. G.; OPLER, P. A. Comparative phenological studies of trees in tropical lowland wet and dry forest sites of Costa Rica. **Journal of Ecology**, London, v.62, n.3, p.881-919, 1974.

GALETTI, M. Seasonal abundance and feeding ecology of parrots and parakeets in a lowland Atlantic forest of Brazil. **Ararajuba**, Rio de Janeiro, v.5, n.2, p.115-126, 1997.

GARDNER, T. A.; BARLOW, J.; CHAZDON, R.; EWERS, R. M.; HARVEY, C. A.; PERES, C. A.; SODHI, N. S. Prospects for tropical forest biodiversity in a human-modified world. **Ecology Letters**, Ontario, v.12, n.6, p.561-582, 2009. Doi:10.1111/j.1461-0248.2009.01294.x

GILARDI, J. D.; MUNN, C. A. Patterns of activity, flocking, and habitat use in parrots of the Peruvian Amazon. **The Condor**, Albuquerque, v.100, n.4. p.641-653,1998.

GILARDI, J. D.; TOFT, C. A. Parrots eat nutritious foods despite toxins. **PLoS ONE**, São Francisco, v.7, n.6, e38293, 2012. Doi: 10.1371/journal.pone.0038293

HAUGAASEN, T.; PERES, C. A. Vertebrate responses to fruit production in Amazonian flooded and unflooded forests. **Biodiversity and Conservation**, New York, v.16, n.14, p.4165-4190, 2007. Doi: 10.1007/s10531-007-9217-z

IUCN. Red List of Threatened Species: version 2017-3. Disponível em: www.iucnredlist. org. Acesso em: 16/03/2018.

JORDANO, P. Fruits and frugivory. In: FENNER, M. (Ed.). Seeds: the ecology of regeneration in plant communities. Wallingford: CAB International. p. 105-155. 1992.

KRONKA, F. J. N.; NALON, M. A.; MATSUKUMA, C. K.; KANASHIRO, M. M.; IWANE, M. S. S. I.; PAVÃO, M.; DURIGAN, G.; LIMA, L. M. P. R.; GUILLAUMON, J. R.; BAITELLO, J. B.; BORGO, S. C.; MANETTI, L. A.; BARRADAS, A. M. F.; FUKUDA, J. C; SHIDA, C. N.; MONTEIRO, C. H. B.; PONTINHA, A. A. S.; ANDRADE, G. G.; BARBOSA, O.; SOARES, A. P.; JOLY, C. A.; COUTO, H. T. Z. Inventário florestal da vegetação natural do estado de São Paulo. São Paulo: Secretaria do Meio Ambiente/Instituto Florestal. 2005.

LOISELLE, B. A. Bird abundance and seasonality in a Costa Rican lowland forest canopy. **The Condor**, Albuquerque, v.90, n.4, p.761-772,1988. Doi: 10.2307/1368833

LORENZI, H. Árvores Brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil. vol. 1, 5ª Edição. Nova Odessa: Instituto Plantarum, 2008.

LORENZI, H. Árvores Brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil. vol. 2, 3ª Edição. Nova Odessa: Instituto Plantarum, 2009a.

LORENZI, H. Árvores Brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil. vol. 3, 1ª Edição. Nova Odessa: Instituto Plantarum, 2009b.

LORENZI, H.; SOUZA, H. M.; TORRES, M. A. V. Árvores exóticas no Brasil: Madeiras, ornamentais e aromáticas. Nova Odessa: Instituto Plantarum. 2003.

MATUZAK, G. D.; BEZY, M. B.; BRIGHTSMITH, D. J. Foraging ecology of parrots in a modified landscape: Seasonal trends and introduced species. **The Wilson Journal of Ornithology**, Villanova, v.120, n2, p.353-365, 2008. Doi: 10.1676/07-038.1

MELO, C.; OLIVEIRA, A. D.; BORGES, C. A.; RIBEIRO, G.; TAVARES, J. Impacts of *Forpus xanthopterygius* (Spix, 1824) (Aves, Psittacidae) in flowers of *Handroanthus serratifolius* (Vahl.) S. O. Grose (Bignoniaceae). **Brazilian Journal of Biology**, Rio Claro, v.69, n.4, p.1149-1151, 2009. Doi: 10.1590/S1519-69842009000500020

MORELLATO, L. P.C.; RODRIGUES, R. R.; LEITAO-FILHO, H. F.; JOLY, C. A. Estudo comparativo da fenologia de espécies arbóreas de floresta de altitude e floresta mesofila semidecídua na Serra do Japi, Jundiaí, São Paulo. Revista Brasileira de Botânica, São Paulo, v.12, n.2, p.85-98, 1989. Doi: 10.1590/S0100-84042002000200012

NUNES, M. F. C.; GALETTI, M. Use of forest fragments by Blue-winged Macaws (*Primolius maracana*) within a fragmented landscape. **Biodiversity and Conservation**, New York, v.16, n.4, p.953-967. 2007. Doi: 10.1007/s10531-006-9034-9

PIZO, M. A.; SIMÃO, I.; GALETTI, M. Diet and flock size of sympatric parrots in the Atlantic forest in Brazil. **Ornitologia Neotropical**, Bonn, v.6, n.1, p.87-95, 1995.

PULLIAM, H. R.; CARACO, T. Living in groups: Is there an optimal size? In: KREBS, J. R.; DAVIES, N. B. (Ed.). **Behavioral ecology: an evolutionary approach**. Oxford: Blackwell Scientific, 1984. p. 122-147.

RENTON, K. Lilac-crowned Parrot diet and food resource availability: Resource tracking by a parrot seed predator. **The Condor**, Albuquerque, v.103, n.1, p.62-69, 2001. Doi: 10.1650/0010-5422(2001)103[0062:LCPDAF]2.0.CO;2

RENTON, K.; SALINAS-MELGOZA, A.; DE LABRA-HERNÁNDEZ, M. A.; PARRA-MARTÍNEZ, S. M. Resource requeriments of parrots: nest site selectivity and dietary plasticity of Psittaciformes. **Journal of Ornithology**, Heidelberg, v.156, supl.1, p.73-90, 2015. **DOI** https://doi.org/10.1007/s10336-015-1255-9

ROTH, P. Repartição do habitat entre psitacídeos simpátricos no sul da Amazônia. **Acta Amazonica**, Manaus, v.14, n.1-2, p.175-221, 1984

SAZIMA, I. The parrotlet *Forpus xanthopterygius* scrapes at clay nests of the ovenbird *Furnarius rufus*: tasting or testing a new home? **Revista Brasileira de Ornitologia**, Rio Claro, v.16, n.3, p.256-259. 2008.

SILVA, J. M. C. Birds of the Cerrado region, South America. **Steenstrupia**, Copenhagen v.21, n.1, p.69-92, 1995.

SILVA, P. A.; MELO, C. Foraging of the Golden-capped Parakeet (*Aratinga auricapillus*) in an anthropogenic landscape in Brazil. **Ornitologia Neotropical**, Bonn, v.24, n.1, p.55-66, 2013.

SOUTH, J. M.; PRUETT-JONES, S. Patterns of flock size, diet, and vigilance of naturalized Monk Parakeets in Hyde Park, Chicago. **The Condor**, Albuquerque, v.102, n.4, p.848-854. 2000. Doi: 10.1650/0010-5422(2000)102[0848:POFSDA]2.0.CO;2

SOUZA, V. C.; LORENZI, H. Botânica sistemática: guia ilustrado para identificação das famílias de angiospermas da flora brasileira, baseado em APG II. 2ª Ed. Nova Odessa: Instituto Plantarum. 2008.

TERBORGH, J.; ROBINSON, S. K.; PARKER, T. A.; MUNN, C. A.; PIERPONT, N. Structure and organization of an Amazonian forest bird community. **Ecological Monographs**, Ithaca, v.60, n.2, p.213-238, 1990.

VAN SCHAIK, C. P.; TERBORGH J. W.; WRIGHT, S. J. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. **Annual Review of Ecology and Systematics**, Palo Alto, v24, p.353-377, 1993. Doi: 10.1146/annurev. es.24.110193.002033

WERMUNDESEN, T. Seasonal change in the diet of the Pacific Parakeet *Aratinga strenua* in Nicaragua. **Ibis**, Oxford, v.139, n.3, p.566-568, 1997. Doi: 10.1111/j.1474-919X.1997.tb04674.x

WERMUNDESEN, T. Seasonal and diurnal variation in Pacific Parakeet *Aratinga strenua* flocks sizes in Nicaragua. **Ardeola**, Madrid, v.46, n.1, p.39-43. 1999.

ZAR, J. H. Biostatistical analysis. 4^a Ed. New Jersey: Prentice Hall. 1999.