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Seasonal abundance and feeding ecology of parrots and parakeets in a lowland Atlantic forest of Brazil

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RESUMO: **Abundância sazonal e ecologia alimentar de papagaios e periquitos em uma floresta de baixada no Brasil.** A sazonalidade e dieta de seis psitacídeos simpátricos foi estudada em uma floresta de baixada na Mata Atlântica no Brasil. O objetivo desse estudo foi investigar como essas espécies partilham os recursos e elucidar os principais fatores que determinam a abundância sazonal dos psitacídeos. A comunidade de psitacídeos foi observada consumindo 31 espécies de plantas na área, sendo Myrtaceae e Euphorbiaceae as famílias de plantas mais utilizadas. As principais diferenças entre as espécies de psitacídeos foram dieta e uso de hábitat. Houve uma correlação positiva entre massa corpórea e dureza do fruto, sugerindo que espécies maiores podem usar frutos mais duros enquanto espécies menores são forçadas a usar apenas frutos moles. Ambos periquitos, (*Brotogeris tirica* e *Pyrrhura frontalis*), com tamanho semelhante mostraram dieta similar quanto à dureza do fruto, mas diferiram quanto às plantas consumidas. Exeto *Forpus crassirostris*, nenhuma espécie mostrou marcada variação em abundância. Essa espécie é possivelmente uma espécie que migra altitudinalmente na Serra do Mar, aumentando sua abundância nas matas de baixada durante o inverno e primavera. Nenhuma espécie de psitacídeo mostrou especialização quanto a dieta, mas *Triclaria malachitacea* consumiu várias espécies de Myrtaceae. Fortes evidências sugerem que esse papagaio não é dependente dos frutos do palmito, *Euterpe edulis*, como sugerido previamente.
PALAVRA-CHAVE: dieta, Mata Atlântica, papagaio, predação de sementes, Psittacidae.

ABSTRACT. The seasonality and diet of six sympatric psittacids were studied in a lowland Atlantic forest in Brazil. The aim of this study was to investigate how these species partition resources and to elucidate the main factors that determine the seasonal abundance of psittacids. The parrot community was observed eating 31 plant species in the area, being Myrtaceae and Euphorbiaceae the most commonly consumed plant families. Psittacid species differed principally in diet composition and habitat use. Body mass and fruit hardness were found to be correlated, suggesting that large parrots can use both soft and hard fruits, while smaller species are forced to use only soft fruits. Parakeets with similar body size, (*Brotogeris tirica* and *Pyrrhura frontalis*), used fruits of similar hardness, but they differed in the plant species eaten. Except for *Forpus crassirostris* no species showed marked seasonal changes in abundance. This species is possibly an altitudinal migrant, increasing its abundance in the lowlands during winter and spring. No species showed diet specialization, but *Triclaria malachitacea* consumed several species of Myrtaceae. Strong evidence suggests that this parrot is not dependent on *Euterpe edulis* fruits, as suggested previously.
KEY WORS: Atlantic forest, diet, parrot, Psittacidae, seed predation.

Tropical frugivorous birds are known to have large seasonal population fluctuations following changes in food resources (e.g. Wheelwright 1982, Leighton and Leighton 1983, Loiselle and Blake 1993), rainfall (Poulin *et al.* 1992, 1993) and breeding season (Poulin *et al.* 1993). Granivorous birds are particularly sensitive to seed availability and marked fluctuations of abundance have been frequently observed (Grant and Grant 1980, Olmos 1996). Although several studies have focused on seasonal fluctuation of "legitimate" frugivores (sensu Snow 1981) or passerine granivores (mainly finches), very little is known about the seasonality and diet of one of the most diverse and abundant bird family in the Neotropics, the Psittacidae (Chapman *et al.* 1989, Pizo *et al.* 1995, 1997).

Although morphologically very uniform, feeding habits among psittacids varied from frugivore-granivores (e. g. Amazons, Martuscelli 1995) to frugivore-nectarivores (e. g. Lorikeets, Cannon 1984), frugivore-herbivores (Kakapo, Best 1984) and even frugivore-carnivores (Keas, Jackson 1963).

In general, Neotropical parrots are mainly seed predators (Janzen 1981, Galetti and Rodrigues 1992), but

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they also include flowers, nectar, leaves and invertebrates in their diet (Forshaw 1989). In this region most year-round studies on psittacid ecology have concentrated on highly-endangered taxa (e. g. Munn 1988, Varty *et al.* 1994, Martuscelli 1995) and the common species are usually ignored (Roth 1984, Galetti 1993, Pizo *et al.* 1995, Galetti and Pedroni 1996).

The seasonal abundance and feeding ecology of six sympatric psittacids in a lowland Atlantic forest of Brazil are discussed in this paper. The main aim of this study was to answer the following questions: What are the possible roles of abiotic factors (temperature, rainfall) and biotic (food abundance, food selection and habitat use) for allowing sympatric parrots to coexist? How does fruit availability influence parrot abundance? Does fruit hardness determine fruit choices by each parrot species?

STUDY AREA AND METHODS

The present study was carried out at the Parque Estadual Intervales, Base do Saibadela (hereafter Saibadela forest), municipality of Sete Barras in the state of São Paulo, Brazil (24°14'S, 48°04'W). The Parque Estadual Intervales is 380 Km² of protected forest, established in 1986. It was managed by the Fundação Florestal do Estado de São Paulo until 1995. In June 1995 the area was declared a "Parque Estadual" (State Park) and another 110 Km² were added to the reserve. This reserve is surrounded by three other reserves; Carlos Botelho, Petar and Xituê parks comprising more than 1.200 Km² of protected forests. Now, the area comprises one of the largest blocks of "typical" coastal Atlantic forest in Brazil.

In the Saibadela area there was a seasonal distribution of rain: the wettest months are January, February and March and the driest months, June, July and August (figure 1). The annual rainfall in 1994 and 1995 was 4,244 mm and 3,958 mm, respectively. A striking characteristic of Parque Intervales is that while rainfall reached more than 4,000 mm in the lowland (70 m a.s.l.), only 1,600 mm were recorded at higher elevations (900 m a.s.l). Moreover, the Saibadela region received much more rain than the nearest city, Sete Barras, 42 km distant (c. 2,500 mm annual rainfall).

Temperature was more variable throughout the year at Saibadela. The hotter and wetter season ran from October to March (mean of 26.8°C) and the colder and drier season from April to September (21.1°C). Minimum temperatures rarely drop below 5°C (winter 1994) (figure 1). The annual mean temperature was about 24°C with the maximum temperature of 42°C and the minimum of 3°C (figure 2).

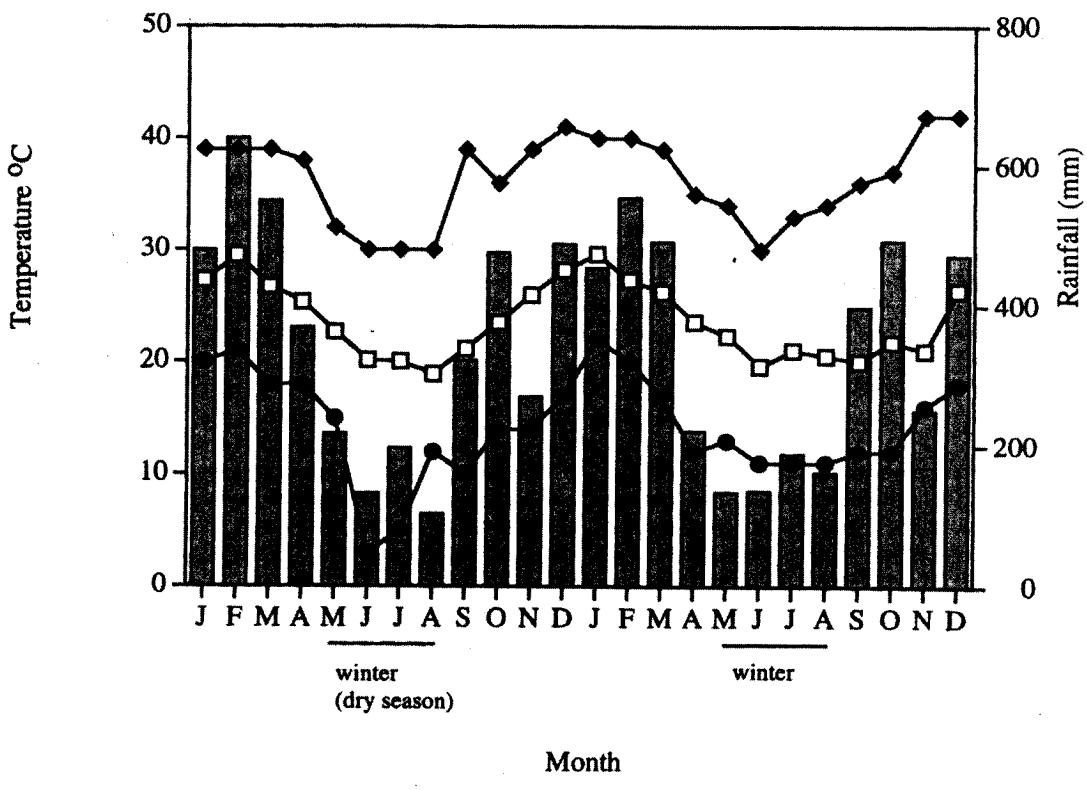

Figure 1. Climatic diagram of Saibadela site, Sete Barras, São Paulo (bars are rainfall and lines are maximim, mean and minimum temperature).

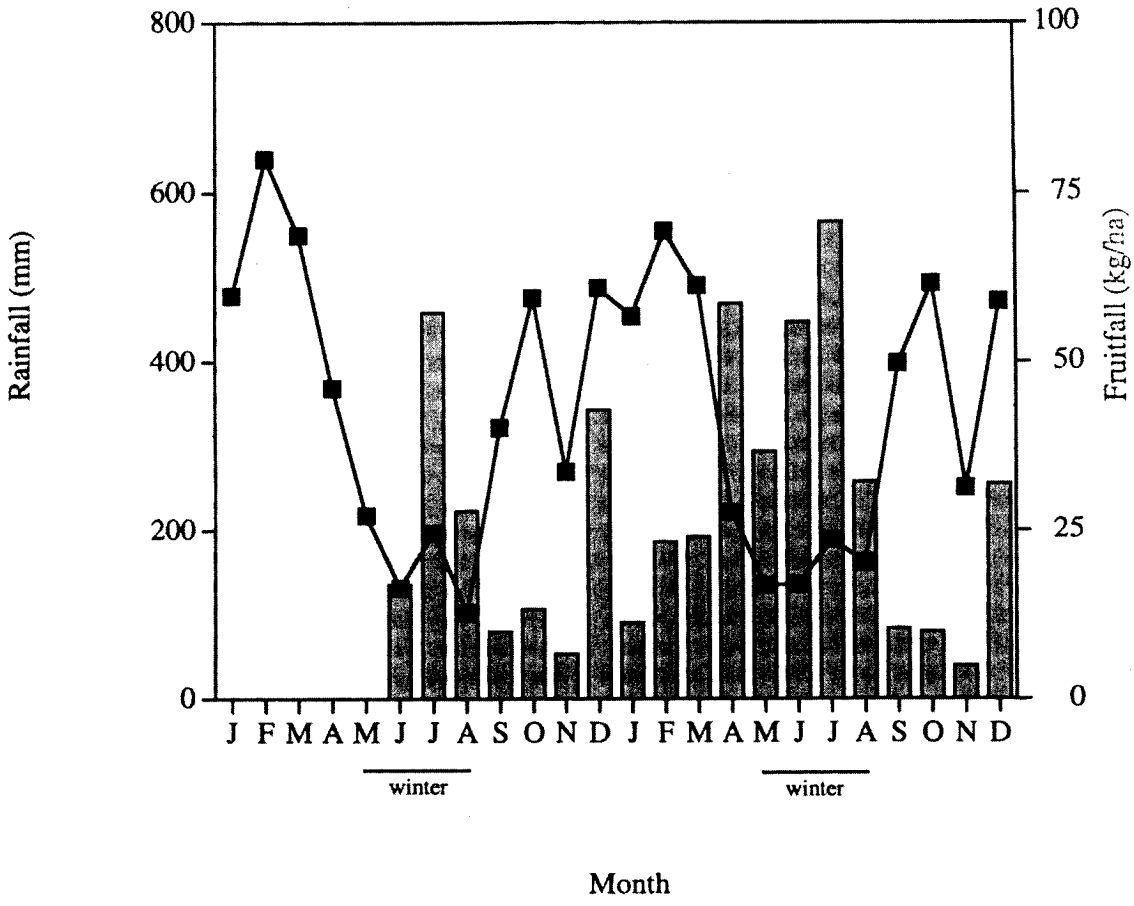

Figure 2. Seasonal fruitfall (lines) and rainfall (lines) during the study period at Saibadela site. There are no data on fruitfall from January to May 1994.

Temperatures below freezing, also known as "geadas" (frost) occur every four-five years in the state of São Paulo (Guix 1995). In the higher elevations of Intervales (Carmo and Sede stations), temperatures can drop below 0°C (e. g., July 1994).

Species studied. Eight parrot species occur in the lowlands at the Saibadela site: the Blue-winged Parrotlet *Forpus crassirostris*, Plain Parakeet *Brotogeris tirica*, Reddish-bellied Parakeet *Pyrrhura frontalis*, Red-capped Parrot *Pionopsitta pileata*, Blue-bellied Parrot *Triclaria malachitacea*, Scaly-headed Parrot *Pionus maximiliani*, Black-eared Parrotlet *Touit melanonota*, and Vinacea Amazon *Amazona vinacea* (Aleixo and Galetti 1997). *Touit melanonota* and *A. vinacea*, however, were rarely observed in the study site and they were excluded from the analysis presented here.

Forpus crassirostris (Blue-winged Parrotlet, Tuim) - The Blue-winged Parrotlet is one of the smallest Psittacidae known (26 g, 12 cm) (Sick 1993). It occurs north-eastern, eastern and south-eastern Brazil to Paraguay, Bolivia and also in the Peruvian Amazon (Sick 1993). Although extremely common in captivity and in the wild, the biology of this genus is poorly known (Waltman and Beissinger 1992, Pizo *et al.* 1995).

Brotogeris tirica (Plain Parakeet, Periquito). The Plain Parakeet is one of the commonest psittacids in the Atlantic forest (Pizo *et al.* 1995) occurring in both primary and secondary vegetation and also in urban areas (pers. obs.). This parakeet weighs 70 g, and is about 16 cm in length. It is endemic to the Brazilian Atlantic forest, occurring from Bahia to Santa Catarina (Sick 1993). Previous studies of this species showed that its population declines in the summer (wet season) in the highlands of the Atlantic forest (Pizo *et al.* 1995).

Pyrrhura frontalis (Reddish-bellied Parakeet, Tiriva) - This parakeet (also known as Reddish-bellied Conure) is the second most abundant psittacid in the Brazilian atlantic forest (Pizo *et al.* 1995). It occurs from Bahia to Rio Grande do Sul, southern Mato Grosso in Brazil and Uruguay, Paraguay and Argentina. This medium-sized

parakeet weigh about 72-94 g and is 29 cm long. Besides fruits this species is also known to eat insect galls (Martuscelli 1994).

Pionopsitta pileata (Red-capped Parrot, Cuiú-cuiú) - This species is a medium-sized parrot (98-120 g, 21 cm) and it occurs from southern Bahia to Rio Grande do Sul, Argentina (Misiones) and Paraguay (Sick 1993). This parrot was observed eating fruits of *Podocarpus* and *Myrcia* sphaerocarpa (Sick 1993) and *Gallesia gorazema* (Guix 1995). The reproduction of this parrot has been studied by Scherer-Neto and Muller (1984). The ecology of this genus is poorly documented and there are scanty data about their feeding behavior (Eitniear *et al.* 1994).

Pionus maximiliani (Scaly-headed Parrot, Maitaca) - The Scaly-headed Parrot is the second largest psittacid at Saibadela (233-293 g, 27 cm). It occurs in north-east and east to southern Brazil, also in Bolivia, Paraguay and Argentina. This species is a generalist and also eats large amounts of flowers. The diet of the Scaly-headed Parrot in a semi-deciduos forest in Brazil was studied by Galetti (1993).

Triclaria malachitacea (Blue-bellied Parrot, Sabiá-cica) - The Blue-bellied Parrot is considered one of the most secretive parrot (Pizo *et al.* 1995). It is a relatively large parrot (110-155 g, 29 cm). It occurs from southern Bahia and Minas Gerais to Argentina (Misiones) (Sick 1993, Whitney 1996). Collar *et al.* (1992) considered this species to be associated to *Euterpe edulis* palms. The rapid decline of this parrot population is due to the over-harvesting of *Euterpe* palm, their main food source (Collar *et al.* 1992, 1994). Altidudinal migration is suggested by Collar *et al.* (1992), Sick (1993) and Whitney (1996).

Seasonal abundance of psittacids. Parrots are highly mobile and an accurate census is extremely difficult (see Bibby *et al.* 1992, Pizo *et al.* 1995, 1997). Also, their green camouflage makes them very difficult to detect in the forest canopy.

Most methods used for psittacid censuses rely on the index of abundance rather than on density estimates. In general, five methods have been widely used to estimate parrot density (or abundance): counts from vantage points (Lambert 1993), variable circular plots (Marsden 1992, 1995), transect counts or encounter rates (Pizo *et al.* 1995, 1997), counts at roosts (Chapman *et al.* 1989) and capture-mark release (Cannon 1984).

The seasonal abundance of parrot species at Saibadela was assessed by encounter rates along transects. Eight different transects were walked each month, ranging from one to 10 km. Each encounter (visual or aural) with an individual or a flock was recorded as one encounter. The overall abundance was estimated by frequency of encounter hour or field work. This method does not provide an accurate estimate of parrot density, because it does not distinguish differences in flock size. The aim in this study was, however, to detect marked seasonal fluctuations of intra-specific abundance throughout the year, rather than estimating parrot densities. Because of the poor visibility of the flocks it was assumed that flock size did not differ between seasons, although this is probably bias (see Pizo *et al.* 1997).

Diet and fruit availability. The diet of parrots and parakeets was based on observed feeding bouts. Each time that a single parrot or a flock was observed eating a determined plant species it was recorded as one feeding bout. If the birds moved to another food source, a new independent bout was recorded (Galetti 1993, Pizo *et al.* 1995). For each feeding bout, the number of birds foraging, the plant consumed, and the part eaten (e. g., seeds, pulp, flowers) were recorded. The stratum used by each species for fruit foraging was recorded. Four main strata used by parrots for foraging were distinguished: forest edge (along rivers), canopy (emergent trees over 20 m), subcanopy (trees between 10 to 20 m height) and understory (trees below 10 m) vegetation.

The collected fruit eaten by parrots were weighed, measured and the number of seeds, fruit size, and fruit hardness were recorded (Galetti 1996). Fruit hardness was categorized as soft (berries, arils and drupes, such as Myrtaceae, Burseraceae), medium (*Ficus gomeleira, Ficus insipida*) and hard (leguminous pods, such as *Inga*, and capsules, such as *Sloanea*).

Fruit availability. To estimate the fruitfall availability in Saibadela forest, 30 fruit traps of 0.25 m^2 were distributed along forest trails, spaced every 25 m, from June 1994 to January 1996. Each trap consisted of a fiber box with a fine mesh to collect even tiny seeds (0.1 mm), such a *Ficus* spp.

Once a month all the fruits found in the traps were collected, identified up to the highest possible taxonomic level and weighed (wet weight). Non-zoochoric fruits were rare, but when present in the traps they were not included in the sample weighed. Monthly fruitfall is based on the sum of fruit weigh of all 30 traps and then extrapolated to kilograms per hectar.

Statistical analysis. The distribution of the monthly abundance of each parrot species was tested for normality using Wilk-Shapiro test. Because all species, abundances were found to be statistically different from a normal distribution, non-parametric statistics were used in all analyses. Spearman-rank correlation was used to relate parrot abundance to rainfall, temperature and fruit production. Producto momentum correlation (Pearson) was used to relate fruit hardness to percentage of such fruits in the diet of parrots.

All statistics used followed Sokal and Rohlf (1995) and were analyzed using the Statistical Package for Social Sciences-SPSS (Norusis 1994).

RESULTS

Fruit availability. Fruitfall in the Saibadela forest was estimated to be 625.2 kg/ha/year (figure 2). Peak fruit availability ocurred during the winter (April-August) and declined in the spring (August-October; the short dry season). In June and July 1994 frost ocurred when

temperatures dropped to 3° and 5° C, and fruit production was lower in 1994 than in 1995.

Fruitfall was higher in winter (252 kg/ha) than in summer (116 kg/ha; complete annual data for 1995 only). There was a statistical difference in fruitfall between seasons (log-transformed data, t-test, $t = 4.18$, d.f. = 6, $p = 0.005$). Most fruits collected in the winter were *Euterpe edulis* fruits (about 80 % of the fruit biomass). Fruits of Myrtaceae made a substantial contribution to the fruitfall biomass during the winter.

Abundance and seasonality. A total of 1,306 contacts with parrots were recorded during the 20-month study period. The most abundant species was *B. tirica*, followed by *P. maximiliani, T. malachitacea, P. frontalis, F. crassirostris* and *P. pileata.*

The number of contacts per hour was higher in the second year (1995) than in the first year (1994), both in the winter and in the breeding season (table 1). Most of the species were more abundant in winter 1995 than in winter 1994. The lowest fluctuation was in *P. maximiliani* (twice) and the highest in *P. frontalis* (6.3 times). During the breeding season (August to December) all species were more abundant in 1995. *Pyrrhura frontalis* was 1.6 times more abundant in this year and *T. malachitacea* was 3.1 times more abundant.

It was impossible to have an accurate estimate of the flock size detected due to the poor visibility, but *T. malachitacea* generally ocurred in small flocks (2-5 birds/flock), *F. crassirostris* (4-6 birds/flock), *P. frontalis* (6-12 birds/flock), *P. maximiliani* (2-12 birds/flock), and *B. tirica* (6-10 birds/flock).

There was a negative correlation between *Forpus* abundance in each month and mean temperature ($r_s = -0.58$, $p < 0.05$), and minimum temperature ($r_s = -0.628$, $p < 0.001$). *Brotogeris* abundance per month showed a positive correlation with maximum temperature ($r_s = 0.501$, $p < 0.05$). The abundance of other parrot species did not show any correlation with the parameters analyzed (temperature, rainfall, fruitfal and number of fruiting plants). *Forpus* was more abundant in the winter and spring (September-November), declining in the summer (figure 4). Because *P. pileata* had an extremely low abundance it is not shown in figure 4.

Diet. The parrot community at Saibadela was observed to consume 31 plant species of 19 families (table 2). Most feeding bouts were on fruit pulp or seeds and only one on flowers (*B. tirica* eating *Pseudobombax* sp., Bombacaceae). No animal matter was observed being ingested by any parrot species.

Forpus was observed eating only seeds or pulps of soft fruits, while *Brotogeris* consumed pulp/aril in 61 %, flowers in 8.5 % and seeds in 30.4 % of feeding bouts. *Pyrrhura* consumed pulp (50 % of feeding bouts) and seeds (50 %). The larger parrots (*Triclaria* and *Pionus*), on the other hand, rarely consumed pulp and their diets were based mainly on seeds.

Pulp of *Cryptocarya moschata* (Lauraceae) was a particulary important food source for both parakeets, comprising 30 % of their diets. *Brotogeris tirica* can forage for up to one hour eating *Cryptocarya* pulp, dropping the intact seeds below the fruiting tree. *Cryptocarya moschata* bears ripe fruits in the winter and is important for large arboreal frugivores (capuchin and woolly spider monkeys) (pers. obs.) Pulp was also ingested by *Triclaria* and *Forpus*, but comprised a minor part of their diets (7.7 % and 16.7 % respectively).

Brotogeris tirica was observed consuming 12 species (23 feeding bouts), *P. frontalis* 12 species (20 feeding bouts), *P. maximiliani* seven species (14 feeding bouts), *T. malachitacea* eigth species (13 bouts), *F. crassirostris* four species (six bouts) and *P. pileata* only one species (one feeding bout) (table 2). The number of species observed in the diet of each parrot is correlated with the number of feeding bouts ($r_s = 0.87$, $p = 0.05$), suggesting that the overall diet of all species is far from the being complete for any psittacid species. The low number of feeding bouts for some species (*Forpus* and *Pionopsitta*) constrain any further analysis.

Apparently, none of the parrot species showed strict specialization to a plant species or a family, as observed in macaws (see discussion). Nevertheless, Myrtaceae was the family most used by parrots, especially for *T.*

Table 1. Annual and seasonal differences in parrot abundance (contact/hour) at Saibadela forest.

	1994		1995			
Parrot species	Winter[1]	Breeding[2]	Winter[1]	Breeding[2]	Total contacts	Contacts/h
Brotogeris tirica	1.40	2.41	2.89	2.92	840	2.30
Pionus maximiliani	0.35	0.68	0.52	0.73	203	0.56
Triclaria malachitacea	0.21	0.25	0.25	0.79	97	0.27
Pyrrhura frontalis	0.08	0.21	0.50	0.34	82	0.22
Forpus crassirostris	0.11	0.21	0.27	0.28	58	0.16
Pionopsitta pileata	0.15	0.08	-	-	26	0.07

[1]Winter: May to August
[2]Breeding season: September to December

Table 2. Characteristics of plant species eaten by parrots and parakeets at Saibadela, Parque Estadual Intervales.

Family/Species	Habit	Part eaten	Fruit hardness	Fruiting	Density	Parrot	% Diet
ARACEAE							
Heteropsis oblongifolia	E	seeds	S	Jan-Feb	-	Tr	*
ARALIACEAE							
Dendropanax sp.	T	seeds	S	Feb	-	Pi	7.14
BOMBACACEAE							
Pseudobombax sp.	T	flowers	-	-	>1.9	Br	4.34
Spirotheca passifloroides	E	seeds	S	Aug-Nov	-	Br	4.34
						Py	*
BORAGINACEAE							
Cordia sylvestris	T	seeds	S	Feb-Apr	1.9	Py	5
BURSERACEAE							
Protium widgreni	T	seeds	H	Dec-Jan	>1.9	Pi	7.14
						Py	5
CECROPIACEAE							
Cecropia pachystachia	T	seeds	S	Jan-Apr	1.9	Fo	66.7
						Br	8.7
Pouroma guianensis	T	seeds	S	Feb	5.8	Pi	7.14
ELAEOCARPACEAE							
Sloanea monosperma	T	seeds	H	Jul	9.6	Tr	15.4
EUPHORBIACEAE							
Alchornea triplinervia	T	seeds	H	Nov-Jan	25	Py	10
Hyeronima alchorneoides	T	seeds	S	Jan-Mar	21.1	Py	*
Margaritaria nobilis	T	seeds	H	Jan-Apr	>1.9	Pi	14.3
Tetrorchidium rubrivernium	T	seeds	H	Dec-Jan	7.7	Py	*
LAURACEAE							
Cryptocarya moschata	T	pulp	S	May-Jul	15.4	Py	30
						Br	30.43
						Tr	7.7
LEGUMINOSAE-CAESALPINIACEAE							
Copaifera trapezifolia	T	seed	S	Jun-Oct	>1.9	Br	4.34
LEGUMINOSAE-MIMOSOIDAE							
Inga edulis	T	seeds	H	Jan		Pi	28.6
						Py	5
MARCGRAVIACEAE							
Macgravia polyantha	L	pulp?	S	May-Jun	6	Fo	16.7
MENISPERMACEAE							
Abuta selloana	L	seeds	H	Apr-Jul	-	Br	13
Hiperbaema sp.	L	seeds	S	Aug-Oct	-	Br	4.34
MORACEAE							
Brossimum sp.	T	seeds	S	all year	3.8	Br	*
Ficus insipida	T	pulp/seeds	M	Oct-Apr	1.9	Py	10
Ficus obtusiuscula	T	pulp/seeds	M	-	1.9	Py	5
						Br	8.7
Ficus enormis	T	pulp	M	Feb	-	Fo	16.7
						Py	5
Sorocea bomplandii	T	seeds	S	Nov-Dec	7.7	Tr	*

Table 2. Continued.

Family/Species	Habit	Part eaten	Fruit hardness	Fruiting	Density	Parrot	% Diet
MYRISTICACEAE							
Virola oleifera	T	capsule	H	May-Aug	9.6	Tr	7.7
MYRTACEAE							
Campomanesia neriiflora	T	seeds	S	Jan-Feb	7.7	Tr	23
Campomanesia sp.	T	seeds	S	Dec	>1.9	Tr	15.4
Eugenia sp1	T	seeds	S	-	-	Tr	7.7
Eugenia sp2	T	seeds	S	-	-	Br	4.34
Eugenia cambucarana	T	seeds	S	Sep	-	Pi	7.14
Eugenia multicostata	T	pulp	S	Feb-May	5.8	Br	4.34
Myrceugenia reitzii	T	seeds	S	Aug-Nov	1.9	Tr	7.7
PALMAE							
Euterpe edulis	T	seeds	S	May-Sep	255.6	Py	15
						Br	8.7
					Tr	15.4	
PHYTOLACCACEA							
Phytolacca dioica	T	seeds	S	Mar-Apr	>1.9	Pp	100
						Py	5
SAPINDACEAE							
Matayba elaeognoides	T	aril	H	Dec-Jan	-	Br	4.34
ULMACEAE							
Trema micrantha	T	seed	S	Nov-Mar		Fo	16.7
						Py	5

Habitat: T = tree, S = srub, E = epiphyte, L = liana.
Fruit hardness: S = soft, H = hard, M = medium.
Density = individual/ha (from Almeida-Scabbia 1996).
Parrot species: Fo = *Forpus crassirostris*, Pp = *Pionopsitta pileata*, Br = *Brotogeris tirica*, Py = *Pyrrhura frontalis*, Tr = *Triclaria malachitacea*, Pi = *Pionus maximiliani*.
* = species recorded by local people or Pizo *et al.* (1995).

malachitacea (54 % of the diet). This family is also the most diverse and abundant in the Saibadela forest (Almeida-Scabbia 1996).

Triclaria malachitacea, which was previously considered to be dependent on *E. edulis* fruits (Collar *et al.* 1992) was rarely observed eating this palm in this study. Although palms are very abundant in the study site (mainly *E. edulis*, 255 individuals/ha) their fruits were moderately consumed, varying from 8.7 % (for *Brotogeris*) to 5.4 % (for *Triclaria*). Even the *Ficus* species were not so heavily consumed by parrots, as observed elsewhere (Janzen 1981, Jordano 1983).

Fruit characteristics. The fruits eaten by parrots ranged from tiny berries (*Hyeronima alchorneioides*, 0.5 cm lenght) to large pods (*Inga edulis*, 11 cm length). The proportion of hard fruits in the parrot diet was correlated with parrot body mass ($r = 0.90$, $p = 0.032$), but body mass was not correlated with soft ($r = -0.539$) and medium fruits ($r = 0.355$) (figure 4). This suggests that hard fruits (such as Leguminosae and capsules) can be consumed only by large parrots, but soft fruits are also exploited by large parrots. Seeds of hard fruits, such as *Inga* and *Protium*, are eaten by large species (*Pionus*). Smaller species such as the parakeets can consume dehiscent hard fruits only when the capsules are open, ingesting the aril or even the seed (e. g., *Matyba* and *Copaifera*).

Habitats used for foraging varied among species, although both parakeets (*Brotogeris* and *Pyrrhura*) orverlapped in proportional use the habitats (figure 5). *Forpus crassirostris* was observed eating only at the forest edge. *Triclaria malachitacea* is the only psittacid that was observed feeding on the understory (Myrtaceae berries) and also using orchards to consume the seeds of oranges (Pizo *et. al.* 1995, pers. obs.).

DISCUSSION

The main characteristics allowing the coexistence of six parrots in the lowland Atlantic forest were the differences in fruit diet and stratum used. Although there were a high overlap of habitat use and fruit hardness in both parakeets with similar body mass (*Brotogeris* and *Pyrrhura*), their diets were divergent in terms of species consumed. Only three fruit species were consumed by both parakeets, but

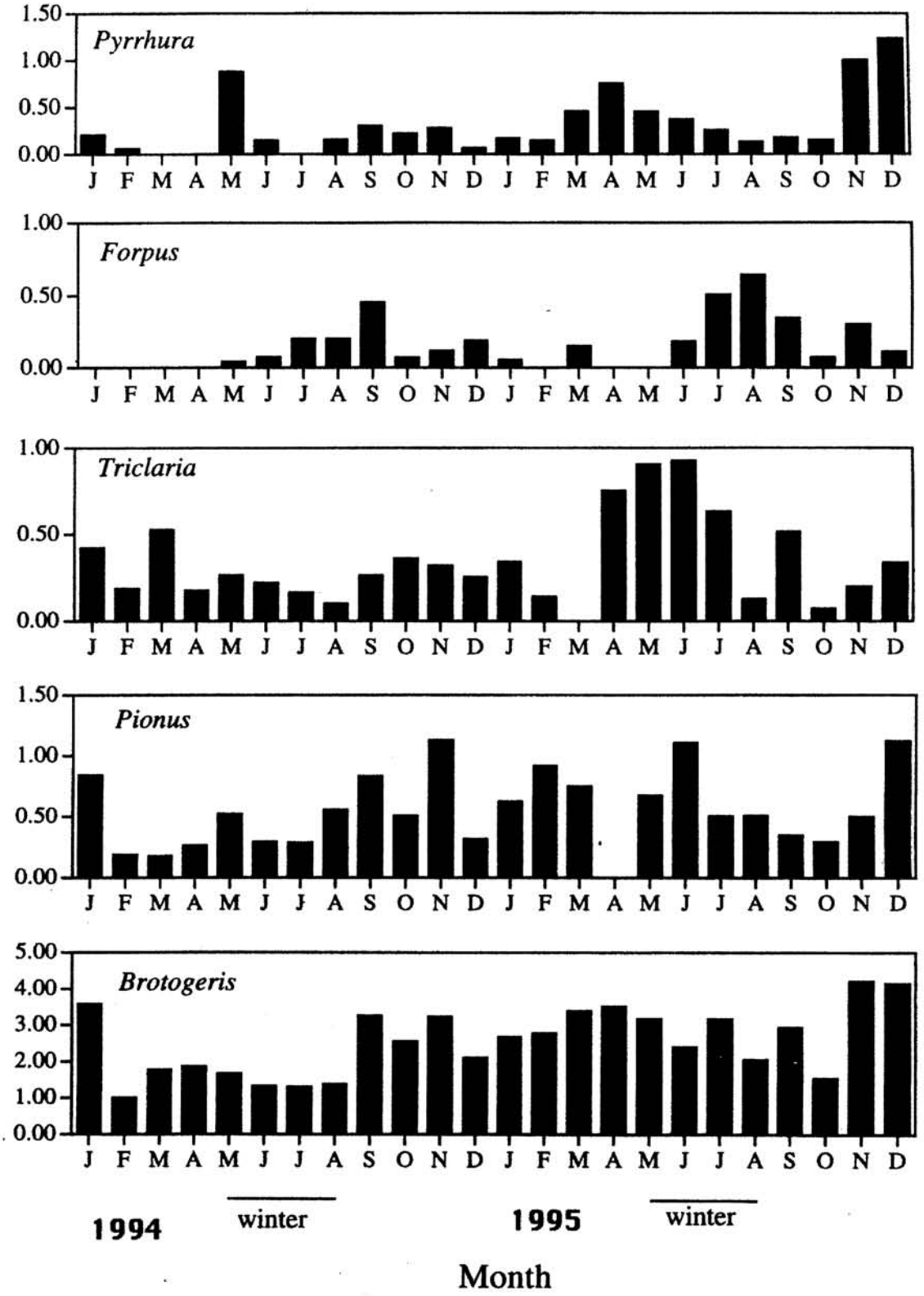

Figure 3. Seasonal fluctuation in psittacid abundance at Saibadela site.

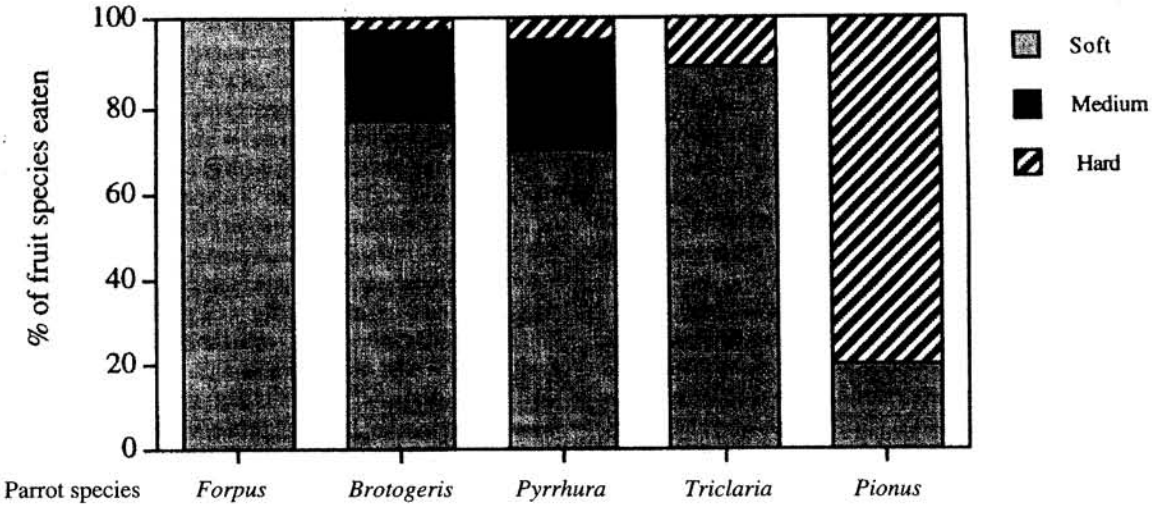

Figure 4. Percentage of fruit hardness in the diet of the Psittacidae at Saibadela (body size increase from *Forpus* to *Pionus*).

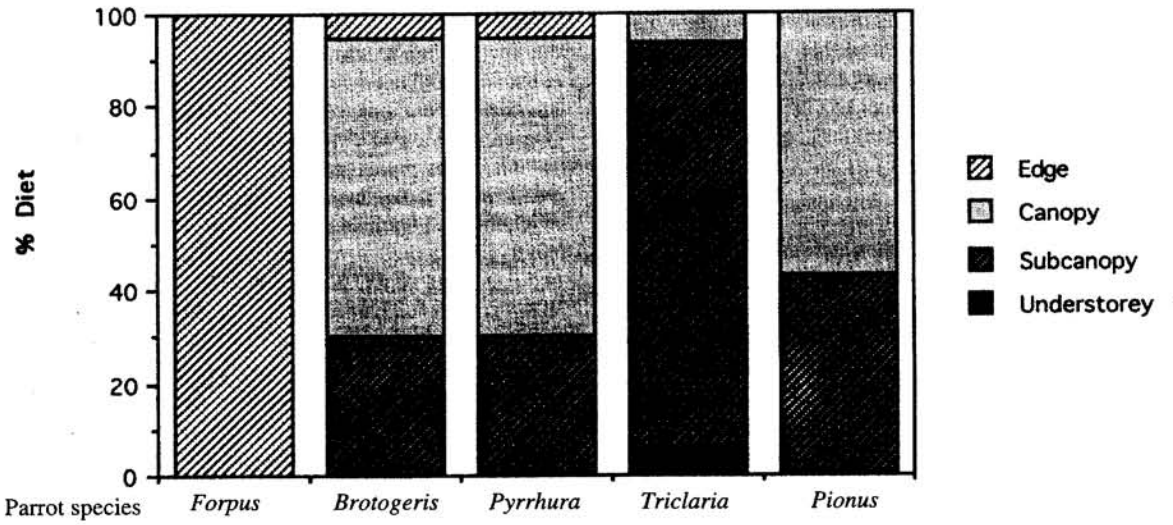

Figure 5. Percentage of the diet in each vegetation strata of the parrots of Saibadela.

all of them produce large fruit crops (*C. moschata, E. edulis* and *Ficus* spp.).

The results presented here indicate that it is very difficult to determine psittacid diet in dense primary forest and many years are needed to detect most of fruits used by the parrot community. It seems likely, however, that larger parrots may include a wider diversity of fruit in their diets and they can use both hard and soft fruits, but smaller species appear to be restricted to consuming seeds of berries and soft drupes. Roth (1984) studied niche overlap among 16 sympatric psittacid species in Amazon forests and also found the same pattern. Both differences in body mass and habitat use seem to be the predominant characters that allow the coexistence of phygenetically related species (Diamond 1973, Crome 1975, Schoener 1982).

Fruit hardness has been found to be important in dietary divergence among large seed predator specialists, such as peccaries and Pithecine monkeys (Kiltie 1982, Kinsey and Norconk 1993). The same relationship was expected to occur among parrots. Abbott *et al.* (1977)

found that seed hardness was important in determining diet divergence in Darwin's finches. In fact, parrot beak size is correlated with body mass, large psittacids with strong beaks are the only psittacids that can exploit very hard fruits such as palm nuts (Roth 1984). This allows large species (e. g. macaws) to specialize on fewer plant species (Yamashita and Valle 1993). It is also known that granivorous finches choose the seeds based on their nutritive values (Díaz 1994, 1996), but this character was not assessed in this study.

Roth (1984) divided the community of psittacids in Amazon into three groups: diet specialists (*Ara manilata*), partial specialists (*Brotogeris chrysopterus, Pionopsitta barrabandi, Ara ararauna* and *A. severa*) and generalists (*Amazona ochrocephala, A. farinosa, Aratinga weddellii, A. leucophthalmus,* and *Deroptyus acciptrinus*). At Saibadela, there were no diet specialist, mainly because there is no fruit that is produced all year round. All species showed a generalist diet but some trends seemed evident.

Fifty-four percent of the diet of the *Triclaria* parrot was composed of seeds of the Myrtaceae family. This family is the most abundant in the Atlantic forest (Mori *et. al.* 1983) and at least one species bears fruits each month. It is difficult to know if *Triclaria* is a specialist on Myrtaceae fruits, or if they are just using the most abundant resource. Collar *et al.* (1992) suggested that *T. malachitacea* is dependent on fruits of the palm *E. edulis*, but no evidence was found in this study. Bencke (1996) also found that *Euterpe* fruits are not important for *T. malachitacea* in Rio Grande do Sul, but that Myrtaceae fruits were more common in the diet.

Another intriguing point was that seeds of the genus Campomanesia (Myrtaceae), which are considered toxic for vertebrates (Landrum 1986), were commonly consumed by *T. malachitacea.* As pointed out by Bozinovic and Martínez del Rio (1996), other aspects such as physiology and anatomy of the birds, must be considered in foraging studies.

Seeds comprise an important source of carbohydrates, but are usually poor in lipids and protein (Díaz 1996). Therefore, it is expected that parrots should look for lipids in the fruit pulp of arillate fruits, such as *Virola* spp. The only fruit pulp consumed frequently by parrots (*C. moschata*), however, is rich in carbohydrates (84 % of the pulp dry mass), and poor in lipids (4.17 %) and proteins (1.2 %) (Galetti 1996). Proteins could be obtained from invertebrates and has indeed been recorded for some species studied here (Martuscelli 1994). It is not known where the parrots studied can obtain enough lipids since there are no data on seed chemical compositon of the study site.

Although some authors considered parrots as seed dispersers (Fleming *et al.* 1985, Bohning-Gaese *et al.* 1995), here they acted mainly as seed predators by destroying the seeds or by dropping the fruits below the parent tree.

Altitudinal differences. Pizo *et al.* (1995) carried out a similar study on the diet and abundance of psittacids in the highlands (c. 900 m a.s.l.) of Parque Estadual Intervales. One of the main differences observed in the diet of parrots in the lowland is that flowers were rarely used. This difference, however, could be an artefact of the sample size. In seasonal dry forests, parrots consume large amounts of flowers when fruits are not available (Galetti 1993, Wermundsen 1997). Fruit (and consequently seeds) were available throughout the year in the study site and there was no extreme fuit scarcity for seed predators.

Altitudinal migratory movements due to fruit availability is well known for some frugivorous birds in Costa Rica (Blake and Loiselle 1991, Loiselle *et al.* 1991). A similar pattern has been suggested for frugivorous birds in the Brazilian Atlantic forest, but there is no study that has addressed this question in detail. *Triclaria malachitacea* is the only parrot species considered to make altitudinal migration (Collar *et al.* 1992, Sick 1993, Whitney 1996), but the species was never studied year round. In fact, the evidence presented here shows that *T. malachitacea* is a year round resident, and the same result was found by Benche (1996) studying this parrot in Rio Grande do Sul.

Forpus crassirostris showed marked fluctuation in abundance between seasons in the study site being more common during the winter in the lowlands when compared to the highlands. *Brotogeris tirica* and the *F. crassirostris*, however, are more common during the wet season (December-March) (Pizo *et al.* 1995).

The data presented here indicate that the parrot community in the lowland Atlantic forest has similar mechanisms to allow coexistence among species as observed elsewhere in bird communities, such as body size and foranging strata (Wiens 1989). Seasonal fluctuations in abundance of parrot species in the lowlands is less marked than in the highlands of Serra de Paranapiacaba and such fluctuations seem to be related more to an abiotic (temperature and rainfall) than to a biotic (fruit/seeds availability) factor.

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