BIOTROPICA 32(4b): 842–850 2000

Frugivory by Toucans (Ramphastidae) at Two Altitudes in the Atlantic Forest of Brazil[1]

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ABSTRACT

Toucans are prominent components of the tropical American avifauna. Although these birds are very conspicuous, there are few ecological studies focusing on them. In this study, the diets of four sympatric toucans (*Ramphastos vitellinus, R. dicolorus, Selenidera maculirostris,* and *Baillonius bailloni*) were assessed by recording feeding bouts at two altitudes in the Atlantic Forest of southeast Brazil. Our results show that toucans are predominantly frugivorous birds (96.5% of the 289 feeding bouts were on fruits). In the lowlands (70 m elev.), only fruits (48 species, 27 families) were recorded, while in the highlands (700 m elev.), toucans were observed feeding on fruits (25 species, 22 families), flowers, leaves, and insects. Non-fruit items were recorded only in the highlands, most of them eaten by *B. bailloni. Cecropia glaziovii* and *Euterpe edulis,* two abundant plants in the highland and lowland sites, respectively, and *Virola oleifera,* a plant that produces lipid-rich arillate fruits, were eaten heavily by the toucans. The number of feeding bouts recorded for *R. vitellinus* in the lowlands was positively correlated with lipid content of the fruits eaten. The diameters of fruits eaten by toucans varied greatly (range = 0.4–25.0 mm). While the large *Ramphastos* species not only ate tiny fruits (*e.g., Hyeronima alchorneoides*) but also large ones (*e.g., Virola gardneri*), the toucanets ate piecemeal the large fruits that exceeded their gape width, suggesting that gape size did not limit the use of any fruit by the toucans at our study sites.

RESUMO

Os tucanos formam um importante grupo de aves americanas pelo papel que desempenham como dispersores de sementes. Embora sejam conspícuas, há relativamente poucos estudos ecológicos sobre estas aves. Neste estudo, a dieta de quatro espécies simpátricas de tucanos *(Ramphastos vitellinus, R. dicolorus, Selenidera maculirostris,* and *Baillonius bailloni*) foi investigada através do registro de eventos de alimentação em duas áreas localizadas em diferentes altitudes da Mata Atlântica do sudeste do Brasil. Os resultados mostraram que os tucanos são aves predoninantemente frugívoras (96.5% dos 289 eventos de alimentação registrados foram em frutos). Na área de baixada (700 m a.n.m.), somente frutos (48 espécies, 27 famílias) foram registrados na dieta, enquanto na área montana (700 m a.n.m.) os tucanos foram observados alimentando-se de frutos (25 espécies, 22 famílias), flores, folhas e insetos. Itens alimentares diferentes de frutos foram registrados somente na área montana, a maioria deles foram consumidos por *B. bailloni. Cecropia glaziovii* e *Euterpe edulis,* duas espécies de plantas abundantes nas áreas montana e de baixada, respectivarnente, e *Virola oleifera* que produz frutos arilados ricos em lipídeos, foram altamente consumidos pelos tucanos. 0 número de eventos de alimentação registrado para *R. vitellinus* na área de baixada esteve positivamente correlacionado com o conteúdo lipídico dos frutos consumidos. Os diâmetros dos frutos consumidos pelos tucanos variou consideravelmente (0,4–25,0 mm). Enquanto as espécies de maior porte *(Ramphastos* spp.) consumiram não somente frutos pequenos (*e.g., Hyeronima alchomeoides*) mas também frutos grandes (*e.g., Virola gardneri*), as espécies menores (*S. maculirostris* e *B. bailloni*) comeram aos pedaços os frutos cujos diâmetros excederam a largura de seus bicos, mostrando que a largura do bico em si não limita o consumo de nenhum fruto pelos tucanos nas áreas estudadas.

Key words: Atlantic Forest; frugivory; gape size; Ramphastidae; seed dispersal; toucan.

RAMPHASTIDAE (TOUCANS AND TOUCANETS) IS AMONG THE OLDEST AVIAN LINEAGES with living descendants (Sibley & Ahlquist 1990), and is the symbol of the tropical American forests. Since naturalists first visited the tropics, toucans have attracted attention due to their large body size, flamboyant colors, and long and bizarre beaks (Bates 1863, Goeldi 1894, Van Tyne 1929, Gould & Rutgers 1972). In spite

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of their conspicuousness, however, toucans are very difficult to study in the wild because they live in the forest canopy, are rarely captured in mist nets, and usually have large territories (Terborgh *et al.* 1990). Of the 42 extant species, we have more than a minimum knowledge of ecology and natural history for only a few species, mainly those inhabiting Costa Rica and Panama (Skutch 1944, 1958, 1971, 1972; Stiles & Skutch 1989; Beltran 1992; Riley & Smith 1992). Toucans have a broad diet that includes mainly fruits, but also flowers, arthropods, and small vertebrates (Remsen *et al.* 1993). Based on stomach contents recorded on museum specimen labels, Remsen *et al.* (1993) found that 93.5 percent of the 326 stomachs analyzed contained only fruit remains; however, few systematic data regarding the foods taken by toucans in the wild are available.

In the Neotropics, toucans, as well as cotingas, represent a model of large canopy fruit-eating birds (Snow 1976). Their widespread distribution over different habitats and altitudes makes them particularly interesting for investigating inter- and intraspecific differences in diet and foraging strategies at different altitudes. These birds have been considered "specialist" seed dispersers that provide "high-quality" seed dispersal (McKey 1975, Snow 1981), but we have few data on frugivory by toucans (*c.f.* Howe 1977, 1981, 1993).

Five species of toucans occur in the Brazilian Atlantic Forest (Sick 1993). We investigated the diets of four of these species (*Ramphastos vitellinus, R. dicolorus, Selenidera maculirostris,* and *Bailonius bailloni*) occurring in two sites located at different altitudes in a Brazilian Atlantic Forest reserve. We were especially interested in answering the following questions: (1) what are the contributions of fruit and non-fruit items to the diets of toucans?; (2) how do diets of toucans vary altitudinally?; and (3) is gape size an important determinant of fruit selection by the toucans? For the lowlands, where we determined the chemical composition of fruits eaten by toucans, we additionally asked (4) is the contribution of fruits to the diet of toucans associated with the lipid, protein, and carbohydrate contents of the fruits?

STUDY SITES AND METHODS

This study was carried out at Parque Estadual Intervales (hereafter PEI; 24°16'S, 48°25'W), a 490-km^2 forest reserve in the Serra de Paranapiacaba mountains of southeast Brazil (Aleixo & Galetti 1997). Two sites located at different altitudes were chosen to investigate the diet of toucans. The study sites, Saibadela and Carmo Research Stations, were located at 70 and 700 m elevation encompassing lowland and highland areas of the reserve, respectively. Extensive areas of pristine forest surrounded the sites. Straight-line distance between the two sites is *ca* 25–30 km.

The vegetation at the lowland site consisted of primary forest and small patches of secondary growth near human settlements (Almeida-Scabia 1996). The highland vegetation, in contrast, was mainly late secondary with patches of primary forest (Pizo *et al.* 1996). The lowland site was subjected to higher temperature (annual mean *ca* 24°C, range 3–42°C) and precipitation (4000 mm/yr) than the highland site (annual mean temperature *ca* 17°C, range 4–38°C; annual precipitation 1600 mm/yr). Both sites experienced a period of dry–cold weather from April to August (more pronounced at the highland site), and a wet–hot period from September to March.

Five toucan species were found at PEI: (1) the Spot-billed Toucanet or "araçari-poca" (*Selenidera maculirostris*: 33 cm total length; 140 g body weight; gape width of 24.6 ± 1.2 mm). Lengths, weights, and gape widths were taken from Sick (1993), Dunning (1993), and Laps (1996), respectively, and the species occured in both study sites but was more common in the lowlands; (2) the Saffron Toucanet or "araçari banana" (*Baillonius bailloni*: 35 cm total length; 139 g body weight; gape width of 23.8 ± 0.8 mm) which was observed commonly in the highlands but was rare in the lowlands, where it occured mainly in forest edges and secondary forests (Aleixo & Galetti 1997); (3) the Green-billed Toucan or "tucano de bico verde" (*Ramphastos dicolorus*: 48 cm total length; 400 g body weight; gape width of 30.0 ± 1.1 mm) which was common in the highlands and was a winter migrant in the lowlands, where invariably it was observed in mixed flocks with *R. vitellinus*; (4) the Channel-billed Toucan or "tucano de bico preto" (*Ramphastos vitellinus*: 46 cm total length; 390 g body weight; gape width of 31.1 ± 1.6 mm) which was almost restricted to the lowlands, occurring at the highlands only as a sporadic visitor; and (5) the "araçari de bico branco" (*Pteroglossus aracari*) which was observed only once in the highlands and not included in this study.

Data were collected during 43 months at the highland site (December 1989–December 1991 and August 1992–January 1994) and 24 months at the lowland site (January 1994–December 1995). The method used to quantify the diet of

toucans was based on feeding bouts (Galetti 1993, 1996). This method consisted of walking along trails, and every time that a flock or a single bird was observed feeding, a "bout" was recorded irrespective of the time spent feeding. If the bird/flock moved to another plant, a new bout was recorded. The feeding behavior and the item eaten, either of plant or animal origin, were recorded. When plant identification was not immediately possible, the plant was flagged for later collection. Samples of the fruits eaten also were collected, weighed (with spring scales to the nearest 0.5 g), and measured (with calipers to the nearest 0.1 mm). At both sites, we walked along several trails and unpaved roads during the morning (0600–1200 h) that crossed the forest.

Chemical analyses of the fruits eaten by toucans in the lowlands were made using recently fallen fruits from which seeds were removed, except for *Phytolacca dioica, Coussarea contracta,* and *Guapira opposita* (which were not included in overall protein analysis). Fruits were preserved frozen until the analyses were performed. Proteins and lipids were analyzed according to the methods described by the American Association of Cereal Chemists (AACC 1995, method #46-13) and Bligh and Dyer (1959). Ash content was determined by incinerating the samples in a muffle furnace until the weight had stabilized. Total carbohydrates (*i.e.,* structural plus soluble carbohydrates) were obtained by difference.

RESULTS

General diet.—A total of 289 feeding bouts (151 at the lowland site and 128 at the highland site), most of them on 60 plant species (35 families, 97.6% of the feeding bouts) and a few on insect adults and larvae (2.4%), was recorded (Table 1). A larger number of plant species was recorded in the lowlands compared to the highlands (48 and 25 species, respectively). Overall, the diets of toucanets (*Selenidera* and *Baillonius*) included a greater range of items than those of the two species of *Ramphastos* (Table 1). Toucanets were observed consuming insects, flowers, and leaves only in the highlands. In contrast, the only non-fruit item recorded in the lowlands was a fledgling of the Red-necked Tanager (*Tangara cyanocephala,* Emberezidae) eaten by *S. maculirostris* (V. Zipparro, pers. comm.).

In the highlands, three species of fruits (*Cecropia glaziovii, Virola oleifera,* and *Euterpe edulis*) were particularly important to toucans, together comprising 59 percent of the feeding bouts recorded at that site. Only *E. edulis* was eaten heavily by toucans (22% of the feeding bouts) in the lowlands. The chemical content of the fruits eaten by toucans in the lowland forest varied greatly, especially in the lipid component (Table 2).

Toucanets, especially *S. maculirostris,* tended to forage more frequently in the understory than the two *Ramphastos* species, which were restricted more to the canopy. This behavior allows toucanets to eat understory berries, such as those of the Rubiaceae and Melastomataceae.

Selenidera maculirostris.—This toucanet was recorded eating fruits of 40 and 9 plant species in the lowlands (105 feeding bouts) and highlands (31 feeding bouts), respectively. At both sites, the most important food item for this toucanet was fruits of *E. edulis* (22 and 35% of the feeding bouts in the lowland and highland sites, respectively). The second most consumed fruits were *C. glaziovii* in the highlands (26%), and *Psychotria mapoureoides* (6.7%), an understory shrub, in the lowlands (Table 1). There was no correlation among the major chemical components of the fruits (lipids, proteins, and carbohydrates) and the number of bouts recorded for *S. maculirostris* feeding on them in the lowlands (Spearman's rank correlation, all $P > 0.20$; no chemical data available for the highlands).

In October 1994, a nest was found with three young. Inside the nest, several regurgitated seeds of *Geonoma elegans* and *C. glaziovii* were found. No remains of animal matter were found in the nest. In another nest found in January 1995, toucanets were observed feeding their nestling with two other fruit species (*G. opposita* and an unidentified Lauraceae).

Baillonius bailloni.—This toucanet, endemic to the Atlantic Forest, was observed eating 4 and 17 fruit species in the lowlands (4 feeding bouts) and highlands (71 feeding bouts), respectively (Table 1). The most frequent food item recorded in the latter site was fruits of *C. glaziovii* (20% of the feeding bouts), closely followed by the large arillate seeds of *V. oleifera* (18%). *B. bailloni* was the only species observed eating flowers (2 feeding bouts) and leaves (1 feeding bout), as well as the species most often recorded eating insects (5 feeding bouts), which they frequently captured in epiphytic bromeliads.

Ramphastos vitellinus.—This toucan was recorded only in the lowland site, where it ate the fruits

TABLE 1. *Diet of the four toucan species studied at two different altitudes in the Parque Estadual Intervales, southeast Brazil.*

Plant family	Plant species	Toucan species[a]	Part eaten[b]	Percent of feeding bouts: Lowlands (N = 151)	Percent of feeding bouts: Highlands (N = 128)
Anacardiaceae	*Tapirira guianensis*	Rd	Fr		11.5
Araceae	*Heteropsis oblongifolia*	Sm	Fr	1.0	
	Philodendron sp.	Sm	Fr	3.8	
	Undetermined	Bb	Fr	25.0	
Araliaceae	*Dendropanax* sp.	Sm	Fr	3.8	
		Rv	Fr	2.8	
	Didymopanax sp.	Sm	Fr		3.2
Arecaceae	*Euterpe edulis*	Sm	Fr	21.9	35.5
		Bb	Fr		12.6
		Rv	Fr	19.4	
		Rd	Fr	50.0	7.7
	Geonoma elegans	Sm	Fr	1.0	
Boraginaceae	*Cordia sylvestris*	Sm	Fr	2.9	
Burseraceae	*Protium widgrenii*	Sm	Fr	4.8	3.2
		Rv	Fr	2.8	
Caesalpiniaceae	*Copaifera trapezifolia*	Rd	Fr		15.4
		Rv	Fr	2.8	
		Bb	Fr	25.0	
Cecropiaceae	*Cecropia glaziovii*	Sm	Fr	3.8	25.8
		Rd	Fr		11.5
		Rv	Fr	11.1	
		Bb	Fr	25.0	19.7
Celastraceae	*Maytenus aquifolia*	Sm	Fr	1.0	
	M. ligustrina	Sm	Fr	1.9	
	M. robusta	Sm	Fr	1.9	
	Maytenus sp.	Sm	Fr		3.2
Clusiaceae	*Clusia parviflora*	Sm	Fr	2.9	
Combretaceae	*Combretum* sp.	Bb	Fl		1.4
Elaeocarpaceae	*Sloanea guianensis*	Bb	Fr	25.0	
Euphorbiaceae	*Alchornea glandulosa*	Sm	Fr	1.0	
		Bb	Fr		1.4
	Hyeronima alchorneoides	Sm	Fr	1.9	
		Rv	Fr	2.8	
		Bb	Fr		1.4
	Margaritaria nobilis	Rv	Fr	2.8	
Lauraceae	*Cryptocarya aschersoniana*	Sm	Fr	1.0	
	Ocotea sp.	Sm	Fr	1.0	
		Bb	Fr		1.4
	Undetermined	Sm	Fr	2.9	3.2
		Rv	Fr	8.3	
		Bb	Fr		2.8
Loranthaceae	*Psittacanthus* sp.	Bb	Fr		2.8
Marcgraviaceae	*Marcgravia polyantha*	Sm	Fr	1.0	
Melastomataceae	*Leandra* sp.	Bb	Fr		1.4
	Miconia cabucu	Bb	Fr		2.8
Meliaceae	*Cabralea canjerana*	Sm	Fr	1.0	
		Rd	Fr		3.8
Menispermaceae	*Hiperbaena* sp.	Sm	Fr	1.0	
Moraceae	*Brosimum* sp.	Sm	Fr	1.0	
	Ficus glabra	Bb	Fr		1.4
		Bb	Le		1.4
	Ficus sp. 1	Sm	Fr	1.0	
	Ficus sp. 2	Sm	Fr	1.0	
Myristicaceae	*Virola gardneri*	Sm	Fr	4.8	
		Rv	Fr	13.9	
	V. oleifera	Sm	Fr	4.8	19.4
		Rd	Fr		38.5
		Rv	Fr	11.1	
		Bb	Fr		18.3

TABLE 1. *Continued.*

Plant family	Plant species	Toucan species[a]	Part eaten[b]	Percent of feeding bouts: Lowlands (N = 151)	Percent of feeding bouts: Highlands (N = 128)
Myrsinaceae	*Rapanea ferruginea*	Bb	Fr		1.4
		Rd	Fr		3.8
Myrtaceae	*Eugenia oblongata*	Sm	Fr	1.0	
	E. handroana	Sm	Fr	1.0	
	Gomidesia spectabilis	Sm	Fr	1.9	
	Undetermined 1	Rv	Fr	2.8	
		Bb	Fr		9.8
	Undetermined 2	Sm	Fr	1.0	
Nyctaginaceae	*Guapira opposita*	Sm	Fr	1.9	
Phytolaccaceae	*Phytolacca dioica*	Rv	Fr	2.8	
		Rd	Fr	16.7	
Poaceae	*Merostachis* sp.	Sm	Fr		3.8
		Bb	Fr		1.4
Rosaceae	*Prunus sellowii*	Rd	Fr		3.8
		Bb	Fr		1.4
Rubiaceae	*Amaioua guianensis*	Sm	Fr	1.0	
	Coussarea contracta	Sm	Fr	1.0	
	Psychotria astrellantha	Sm	Fr	1.0	
	P. mapoureoides	Sm	Fr	6.7	
		Rv	Fr	2.8	
	Rudgea recurva	Sm	Fr	1.9	
	Zanthoxyllum rhoifolium	Sm	Fr	1.0	
Sapindaceae	*Cupania oblongifolia*	Rd	Fr	16.7	
		Bb	Fr		2.8
	Matayba elaeognoides	Sm	Fr	2.9	
		Rv	Fr	2.8	
Sapotaceae	*Chrysophyllum flexuosum*	Rv	Fr	2.8	
Solanaceae	*Solanum mauricianum*	Bb	Fl		1.4
Symplocaceae	*Symplocos uniflora*	Sm	Fr	1.0	
Ulmaceae	*Trema micrantha*	Sm	Fr	1.9	3.2
		Bb	Fr		5.6
Verbenaceae	*Citharexyllum myrianthum*	Sm	Fr	1.9	
		Rd	Fr	16.7	
		Rv	Fr	8.3	
INSECTS		Sm			3.2
		Bb			7.0
		Rv			3.8

[a] Toucan species: Sm = *Selenidera maculirostris,* Bb = *Bailonius bailloni,* Rd = *Ramphastos dicolorus,* Rv = *R. vitellinus.*
[b] Part eaten: Fr = fruits, Fl = flowers, Le = leaves.

of 16 plant species (Table 1). The most frequently recorded item was the fruit of *E. edulis* (19% of 36 feeding bouts), but it also often was recorded consuming the arillate fruits of both *Virola* species (25% of the feeding bouts). It was never observed ingesting animal matter. This species used both primary and secondary vegetation, and was usually observed along gallery forests consuming fruits of *Citharexyllum myrianthum* and *C. glaziovii.*

The number of feeding bouts recorded for *R. vitellinus* in the lowlands was positively correlated with lipid content of the fruits (r_s = 0.80, N = 10, P = 0.005), but negatively associated with carbohydrates (r_s = −0.75, N = 9, P = 0.02). No significant correlation was found for proteins (r_s = −0.43, N = 10, P = 0.21).

RAMPHASTOS DICOLORUS.—This toucan was observed eating 4 and 8 fruit species in the lowlands (6 feeding bouts) and highlands (26 feeding bouts), respectively (Table 1). The arillate seeds of *V. oleifera* were by far the most frequently recorded item in the diet of *R. dicolorus* in the highlands (38% of the feeding bouts). Besides the insect recorded once during this study, *R. dicolorus* also was observed preying upon nestlings of *Pitangus sulphuratus* (Tyrannidae) in the highlands (F. Olmos, pers.

TABLE 2. *Chemical characteristics of the fruits eaten by Ramphastidae at the lowland forest of the Parque Estadual Intervales, southeast Brazil. At least 10 g of pulp/aril collected from one to three individuals were analyzed.*

Family	Species[a]	Percent water	Percent dry weight			
			Lipids	Protein	TC[b]	Ash
Araceae	*Heteropsis oblongifolia*	83.0	2.1	15.5	76.0	6.5
Arecaceae	*Euterpe edulis*	30.8	19.7	7.5	69.5	2.7
	Geonoma gamiova	87.8	2.2	4.9	—	—
Boraginaceae	*Cordia sylvestris*	81.0	1.6	7.8	83.9	6.8
Burseraceae	*Protium widgrenii*	58.4	2.7	6.6	88.1	2.6
Caesalpiniaceae	*Copaifera trapezifolia*	74.8	2.7	7.2	87.4	2.7
Celastraceae	*Maytenus aquifolia*	82.2	9.2	13.4	74.9	2.4
Clusiaceae	*Clusia parviflora*	44.6	53.2	14.2	—	—
Elaeocarpaceae	*Sloanea guianensis*	90.9	2.5	6.9	87.7	2.9
Euphorbiaceae	*Alchornea glandulosa*	43.3	68.4	7.6	21.7	2.4
	Hyeronima alchorneoides	74.3	7.9	6.3	—	—
Lauraceae	*Cryptocarya archersoniana*	89.9	2.2	7.2	86.7	3.9
Marcgraviaceae	*Marcgravia polyantha**	82.6	11.0	6.4	80.2	2.4
Meliaceae	*Cabralea canjerana*	47.7	70.8	10.3	16.5	2.3
Myristicaceae	*Virola gardneri*	72.3	88.8	4.9	5.3	1.0
	V. oleifera	62.7	61.8	4.6	32.1	1.4
Myrtaceae	*Eugenia handroana*	77.8	4.1	4.3	87.8	3.7
	E. oblongata	90.8	18.8	9.1	67.4	4.7
	Gomidesia spectabilis	76.4	5.6	6.1	84.2	4.1
Nyctaginaceae	*Guapira opposita**	68.4	3.0	19.1	72.1	5.8
Phytolaccaceae	*Phytolacca dioica**	34.2	5.7	15.3	72.6	6.3
Rubiaceae	*Coussarea contracta**	14.8	1.1	10.5	80.5	7.8
	Psychotria mapoureoides	88.5	4.2	8.9	86.7	4.2
Sapindaceae	*Cupania oblongifolia*	56.0	62.6	11.0	24.6	1.7
Sapotaceae	*Chrysophyllum flexuosum*	16.7	3.5	9.6	82.1	4.7
Verbenaceae	*Citharexylum myrianthum*	81.4	6.3	6.8	82.7	4.1

[a] An asterisk denotes that seeds were included in the chemical analyses.
[b] TC = total (*i.e.*, soluble plus structural) carbohydrates.

comm.). In fact, this toucan is often mobbed by small passerines during the avian breeding season.

All observations of *R. dicolorus* in the lowlands were made during the winter in mixed flocks with *R. vitellinus*. No agonistic behavior was observed between the species when they were feeding at the same fruiting tree. Also, the Red-ruffed Fruitcrow *Pyroderus scutatus* (Cotingidae) was observed following the mixed flocks formed by these toucans.

There was high overlap in gape width between both toucanets and between the two *Ramphastos* species, but none between the toucans and the toucanets (Fig. 1). This suggests that diet partitioning between these two groups might be based on fruit diameter, since the small toucanets cannot ingest fruits > 25 mm in diameter; however, at least in the lowlands, most of the fleshy fruits were small (mean diameter = 17.6 ± 12.0 mm, $N = 101$; Galetti 1996; no data available for the highlands) and could be consumed by toucanets. Moreover, the toucanets can eat piecemeal the large fruits which are swallowed whole by the toucan species (*e.g., Virola gardneri*). Thus, gape width does not seem to limit the use of any fruit by the toucans at PEI.

DISCUSSION

Although direct observations of bird diet may be biased toward large and identifiable food items, the data we gathered confirm the findings of Remsen *et al.* (1993) based on museum specimen labels, namely that animal matter forms a minor proportion of the items ingested by toucans in general. The species we studied were mainly frugivorous, and the only species to include a considerable proportion of non-fruit items in its diet was *B. bailloni,* which ate insects, flowers, and leaves (11.3% of the feeding bouts recorded for this species in the highlands). All of the non-fruit items ($N = 10$) were recorded at the highland site, which may reflect the low availability of fruits at that site during the dry season (Laps 1996). Non-fruit records, however, were not restricted to the dry season and seemed to be distributed evenly throughout the year. Riley and Smith (1986) also noted that flower

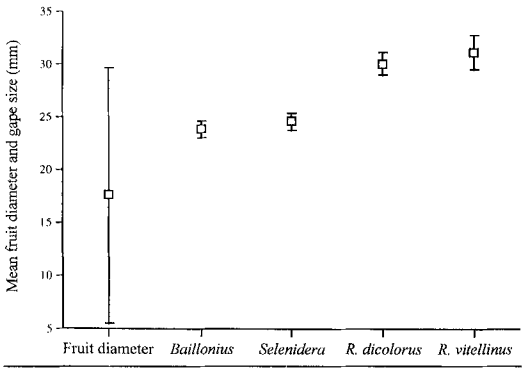

FIGURE 1. Mean gape diameter (±SD) of the four Ramphastidae species studied, and fruit diameter (±SD of the fleshy fruits (N = 101) in the lowland forest of Parque Estadual Intervales, southeast Brazil. Ten estimates were measured for each toucan species.

eating by *Aulacorhyncus prasinus* in Costa Rica was not related to fruit scarcity. Thus, it seems that toucans eat non-fruit items on a regular basis, but in small amounts, which can increase during the breeding period (Riley 1986).

A high proportion of feeding observations was made on common plants at both study sites. *E. edulis,* for example, is one of the dominant plant species in intact areas of the southeast Brazilian Atlantic Forest (Veloso & Klein 1957). At our lowland site, it occured at a density of 255 individuals/ha (Almeida-Scabia 1996). Each individual annually produces one to five bunches with hundreds of fruits that are eaten heavily by toucans at both study sites (Laps 1996). Galetti and Aleixo (1998) found that *R. vitellinus* was less abundant in palm-harvested forest than in pristine forest. *C. glaziovii,* a pioneer tree having fruits that also are eaten frequently by toucans, was very common in late secondary vegetation in the highlands. At this site, toucans took advantage of the staggered fruiting season of *C. glaziovii* (December–May), *E. edulis* (April–September), and *V. oleifera* (July–December), relying heavily upon their fruits as food (59% of the feeding bouts recorded at the highland site; M. A. Pizo, pers. obs.). Among these species, *V. oleifera* was not an especially common tree (9.6 individuals/ha at the lowland site; Almeida-Scabia 1996) but was eaten avidly by toucans. This plant, however, produces large fruits with lipid-rich arils. Possibly due to their nutritional value, lipid-rich fruits are important food items for frugivorous birds (Stiles 1993), which may have accounted for the frequent consumption of *V. oleifera* (and also *V. gardneri*) recorded during this study. Laps (1996) also noticed in the highlands of PEI that *R. dicolorus* and several other frugivorous birds switched to *V. oleifera* when ripe fruits of this species became available.

The fruits eaten by toucans vary widely, both in chemical composition and size. The contribution of the different species of fruits to the diet of *R. vitellinus,* as indicated by the number of feeding bouts, was positively associated with lipid content, suggesting that this toucan may track lipid-rich fruits throughout its home range (estimated to be *ca* 40–50 ha for *Ramphastos* spp. in the Peruvian Amazon: Terborgh *et al.* 1990). The negative correlation obtained for carbohydrates should be interpreted with caution because of the usual negative association between lipids and carbohydrates in the fleshy portion (pulp or aril) of fruits in general (Jordano 1992, Galetti 1996), and in our fruit sample in particular ($r_s = -0.74$, $N = 23$, $P < 0.001$). Thus, the negative association between number of feeding bouts and carbohydrates is an artifact rather than indicative of any real fruit preference by *R. vitellinus.* It is important to note that a method more precise than the feeding bouts used here to quantify the diet of toucans should be used to properly investigate the influence of the chemical composition of fruits in the diets of these birds.

Gape size usually determines the upper size limits of fruit ingested by birds (Wheelwright 1985), but frugivorous birds with large beaks, such as toucans (the beak width of the species studied here ranged from 23.8 mm in *B. baillonius* to 31.1 mm in *R. vitellinus*), can consume small fruits as well (Moermond & Denslow 1985). This accounted for the broad range of fruit diameters consumed by toucans (ranging from 0.4 mm in *Hyeronima alchorneoides* to 25 mm in *V. gardneri*) at the study sites. In fact, the largest fruit eaten by *Ramphastos* toucans (*V. gardneri*) also was eaten by toucanets (although they do not swallow the seeds), while small fruits were eaten by *Ramphastos* (*e.g., H. alchorneoides*). A similar wide range of fruits is eaten by *A. prasinus* in Costa Rica, where they ingest fruits ranging from 3 to 22 mm in diameter (Wheelwright *et al.* 1984).

Most of the fruits eaten by toucans are dispersed, but the "quality" (*sensu* Schupp 1993) of seed dispersal for some species is doubtful. *S. maculirostris,* for instance, can spend more than one hour eating *E. edulis* fruits, regurgitating the seeds below the parent plant every 10–15 minutes. Moreover, toucanets may act as "fruit thieves" of large fruits, such as *V. gardneri,* consuming the aril and dropping the seed beneath the parent plant.

Large toucans (*Ramphastos*), on the other hand, act as one of the main seed dispersers of several large fruits such as *Virola* species in Central America (Howe 1977, 1981, 1993), and probably in the Atlantic Forest as well.

There are few studies that have compared fruit availability at different altitudes (Loiselle & Blake 1991). Djojosudharmo and van Schaik (1992) found a notable decline in the availability of fleshy fruits and greater fruiting seasonality in the mountain slopes than at lower elevations in a tropical forest of Sumatra. In the highlands of PEI, there is a marked seasonality of rainfall and fruit production (Laps 1996), while in the lowlands, seasonality is less severe (Morellato *et al.* 2000). As a result, toucans may track fruits over large territories that encompass areas of different altitudes. A similar behavior also was noted in *Aceros* hornbills tracking figs and fruits of Myristicaceae in tropical forests of southeast Asia (Leighton & Leighton 1983, Kinnaird *et al.* 1996). This hypothesis needs to be confirmed with banded birds; however, we suggest that *R. dicolorus* may track fruits over different altitudes, associating in mixed flocks with *R. vitellinus* in the lowlands when fruit production is depressed in the highlands. As a resident, *R. vitellinus* probably knows the spatial and temporal location of fruit resources in its home range. Thus, the migratory *R. dicolorus* may maximize its searching efforts by tagging along with *R. vitellinus*.

ACKNOWLEDGMENTS

We are grateful to Fundação Florestal do Estado de São Paulo for logistical support. We thank R. Almeida-Scabia for plant identification, V. Zipparro, M. Paschoal, J. Vieira, and Mr. Lauro for field assistance, and F. Olmos, M. Rodrigues, C. Bosque, and an anonymous referee for critical suggestions on the manuscript. Financial support was provided by the Wildlife Conservation Society, World Wildlife Fund, John and Catherine T. MacArthur Foundation (through Fundação O Boticário de Proteção à Natureza), the U.S. Fish and Wildlife Service (through ICBP-PACS), and FMB. M. Galetti and R. Laps received a fellowship from CNPq, and M. A. Pizo received a fellowship from FAPESP. This paper was written while M. Galetti was supported by a FAPESP fellowship (Proc. 96/10464-7) and CNPq (Proc. 300025/97-).

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