

FRUIT CHARACTERISTICS ASSOCIATED WITH FRUIT PREFERENCES IN FRUGIVOROUS BATS AND SADDLE-BACK TAMARINS IN PERÚ

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Abstract. Many zoochorous fruit species evolved so-called fruit syndromes in order to attract certain dispersers on the basis of a combination of fruit traits. We evaluated visual (color) and chemical (compound composition) fruit traits associated with fruit preferences of free-ranging Neotropical frugivorous bats and saddle-back tamarins (*Saguinus nigrifrons*) living in sympatry. We documented 29 seed morphospecies carried by bats and report for the first time chiropterochorous dispersal of the plant genus *Schefflera*. Saddle-back tamarins fed on 15 species of fruits and overlapped with five species of fruits within the bats' diet. Generally, bats tended to prefer greenish fruits and *S. nigrifrons* selected mainly yellow fruits. The yellow color might enhance the visibility of the fruits against the dark foliage for the mainly visually-orienting tamarins. Bats, in contrast, rely more on olfactory cues for detection of fruits. Overall composition of fruit compounds did not differ between fruits eaten by saddle-back tamarins, by bats, or by both. Only fruits exclusively consumed by saddle-back tamarins were classified correctly to 100% by a discriminant function analysis pointing to similar chemical composition. These fruits were characterized by significantly lower lipid concentration and marginally lower protein concentration than fruits that were (also) eaten by bats. As bats show an energy-intense feeding strategy and cover their protein requirements largely by fruits, they might rely on fruits with higher protein and lipid concentration than saddle-back tamarins that complement their fruit diet more regularly with animal prey.

Key words: Stenodermatinae, Carollinae, *Saguinus nigrifrons*, fruit chemistry, fruit preferences, seed dispersal, Peruvian Amazon

INTRODUCTION

To maximize reproductive success, plants need to ensure that their seeds reach suitable sites for germination and establishment. Therefore many plants have evolved strategies that facilitate seed dispersal. Examples are explosive fruits that allow self-dispersal (autochory), hairy or slimy fruits that are adapted to water-dispersal (hydrochory) or fleshy fruits that promote dispersal by animals (zoochory) (Howe & Smallwood 1982, Willson 1993, Willson & Traveset 2000). Adaptations of zoochorous fruits to their main dispersers is reflected in fruit characteristics or syndromes that facilitate attraction and removal by dispersers including presentation, size, and color as well as odor and time of maturation (Knight &

Siegfried 1983, Kalko *et al.* 1996a, Korine *et al.* 2000, Schaefer & Schmidt 2004, Thies & Kalko 2004).

Most zoochorous plants enclose their seeds in fleshy fruit pulp to attract frugivorous animals. In tropical ecosystems, bats, birds, and primates are important vertebrate seed dispersers (Terborgh 1986, Chapman 1995, Kalko *et al.* 1996a, Korine *et al.* 2000). In the Neotropics, colors of fruits mainly dispersed by bats tend to be greenish (van der Pijl 1957, Gautier-Hion *et al.* 1985, Gorchov *et al.* 1995, Korine *et al.* 2000) in contrast to colorful fruits in red, yellow, and purple that are mostly taken by birds or primates (Janson 1983, Voigt *et al.* 2004). Such colorful fruits may visually indicate the contents of macronutrients or secondary compounds and thus influence, for example, fruit choice by birds (Schaefer

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& Schmid 2004, Schaefer *et al.* 2008). Some bat-dispersed fruits are presented on pendulous peduncles (flagellichory) or as erect spikes, thus facilitating detection and localization by echolocation and approach in flight (van der Pijl 1957, Kalko & Condon 1998). Often, bat-dispersed fruits produce a characteristic odor that promotes detection by frugivorous bats (Thies *et al.* 1998, Korine *et al.* 2000, Hodgkinson *et al.* 2007).

In contrast to syndromes of fruits mainly consumed by Neotropical bats, where olfaction and to a limited degree also echolocation are the main cues for fruit detection, it is more difficult to define specific syndromes for fruits that are primarily dispersed by the mostly visually-orienting primates. Overall, primates are more flexible in foraging behavior and hence utilize a larger array of fruit sizes, colors, and forms (Dew & Wright 1998, Lambert & Garber 1998) than bats. This may be one of the causes leading to inconsistent results in studies focusing on primate fruit choice. Whereas Gautier-Hion *et al.* (1985) found Gabonese primates to feed on yellow, orange, or red fruits and to avoid green and brown ones, primates in Cameroon (Poulsen *et al.* 2002) and Malagasy lemurs (Dew & Wright 1998) tended to select green and brown fruits.

Most studies on fruit characteristics have been limited to comparisons of selected morphological traits. However, chemical fruit composition is another important factor that is likely to reflect adaptations between plants and their main dispersers. High concentrations of nutrients can enhance the removal probability of fruits whereas secondary compounds may deter removal (Schaefer *et al.* 2003). Some bird species show distinct preferences for certain nutritional compounds by selecting fruits rich in lipids or carbohydrates (Fuentes 1994, Wittmer & van Soest 1998). Hence, when focusing on fruit compounds it is particularly interesting to include different sympatric taxa of frugivores with distinct fruit preferences to assess whether the chemical composition of fruits varies depending on the main disperser group. So a comparison between bats and primates holds promise in finding such differences since dietary overlap should be low for those taxa (Gorchov *et al.* 1995). We therefore analyzed and compared the composition of fruits that are primarily consumed by the saddle-back tamarin (*Saguinus nigrifrons*, previously *Saguinus fuscicollis nigrifrons* (see Matauschek *et al.* 2011)) with those that are primarily eaten by bats. We focus on *S. nigrifrons*, one of 12 primate species

at our study site (Heymann 1993), as its feeding behavior is well known (*e.g.* Knogge & Heymann 2003). This provides excellent conditions for comparison with bats. Because bats and tamarins differ in activity rhythm (nocturnal versus diurnal), sensory systems (olfaction, echolocation versus vision), and show a fundamental difference in locomotion during foraging (flight versus scansorial searches), we expected clear differences in fruit syndromes, including the chemical composition of preferred fruits.

In order to reveal differences between fruits according to their main disperser, we compared color and nutritional characteristics of fruits consumed by frugivorous bats and the saddle-back tamarin at a study site in the Peruvian Amazon. Specifically, we examined (1) dietary composition of fruit resources consumed by frugivorous bats; (2) potential overlap between the fruit species taken by bats and by sympatric saddle-back tamarins, and (3) potential differences in characteristics such as color and nutritional compounds of primarily bat-dispersed fruits and those mostly consumed by saddle-back tamarins.

METHODS

All parts of data collection in the field were carried out simultaneously during a three-month period from September to November 2007 in the Tahuayo River basin in Peru.

Study area. The study was conducted at the “Estación Biológica Quebrada Blanco” (EBQB), a field site operated by the German Primate Center (DPZ). The area that is associated with the field station encompasses 123 ha and is located approximately 90 km southeast of Iquitos (4°21'S, 73°09'W) at 120 m a.s.l. (Tirado Herrera *et al.* 2003). Mean annual rainfall averaged about 3000 mm, measured at the meteorological station in Tamshiyacu (1980-1989), 40 km north-east of the EBQB (Heymann 1995). The climate is seasonal, with December to May as the wettest months and July to August as the driest (Tirado Herrera *et al.* 2003). The vegetation is dominated by primary rainforest.

Mist-netting of bats. We mist-netted bats during 46 nights using two to six ground nets (6 x 2.5 m or 12 x 2.5 m) that were complemented with one to two nets in the subcanopy at a height of 8 to 12 m during eight nights. Nets were open from sunset until at the latest 01:00 h and occasionally between 04:00 and 06:00 h. In total the mist-netting effort added up to 22 288.75 m² x h. Bat identification was based on

morphological characteristics following an unpublished key by Sampaio, Mello, Wilson, Kalko, and Handley.

Dietary composition. Composition of the diet of the frugivorous bat species *Carollia perspicillata*, *C. brevicauda*, *C. castanea*, *Rhinophylla pumilio*, *R. fisherae*, *Artibeus obscurus*, *A. gnomus*, *Sturnira tildae*, *Vampyressa thuyone*, *Platyrrhinus helleri*, *Uroderma bilobatum*, and *Mesophylla macconelli* was examined during the 3-month period. We collected fecal material from individuals captured in the field by keeping them for up to two hours in soft cloth bags. Fecal samples were surveyed to extract seeds. To collect larger seeds dropped by bats after feeding on the surrounding mesocarp, we set seed traps (~ 0.5 m² of cotton cloth between four wooden stakes, 1 m high) underneath a total of ten roosts, in particular leaf tents that were used by frugivorous bats as shelter during the day and feeding roosts at night. The roosts were occupied occasionally by individuals of the species *Rhinophylla pumilio*, *Mesophylla macconelli*, *Uroderma bilobatum* and further small stenodermatine species, probably of the genera *Artibeus* or *Vampyressa*. We used the traps in the field for 30 to 50 days and checked them weekly. To find the respective fruits associated with the seeds obtained, we opportunistically collected fruits in the study area and assembled a seed reference collection. Once seeds obtained from bat feces or from roosts matched one of our reference samples, we collected the respective mature fruits directly from the plant for chemical analysis, as well as leaves for further identification and documentation. Seeds that could not be readily assigned to a plant species were used for germination experiments. We deposited untreated seeds in plastic boxes on moist paper towels for germination (modified after Tang *et al.* 2007). After successful germination, the seedlings were identified to family or genus by Ricardo Zárate, a local botanist at the "Instituto de Investigaciones de la Amazonia Peruviiana" (IIAP). Main identification was based on the characteristic pattern of the venation of the first leaves that emerged after the cotyledons.

Fruits taken by saddle-back tamarins. Troops of *S. nigrifrons* were followed from sunrise to late afternoon and observed with binoculars during feeding in order to determine the spectrum of utilized fruits. In addition we collected fruit material that was dropped. An experienced field assistant identified the plant species used by tamarins, based on information

generated in earlier studies (Knogge & Heymann 2003). The tamarins were observed for 48 days during their periods of activity throughout the entire field season.

Fruit analysis. Color of ripe fruits was categorized into the following classes: black/brown, green, purple, reddish, or yellow. We separated pulp from seeds and other plant parts, such as peduncles or husks, to process only the fruit parts actually digested by the animal(s) concerned. The remaining fruit material was weighed and dried at 50-55°C for about 2-5 h. After drying, the samples were stored in Zip-Lock® bags with silica gel to minimize microbial infestation.

Chemical analyses were performed in January 2008 at the Institute of Zoology, Department of Ecology and Conservation, University of Hamburg, Germany, in the laboratory of Jörg Ganzhorn. Samples (5 g dry matter per species) were frozen at -18°C, ground, and passed through a 2-mm sieve. Analyses were conducted for soluble protein (BioRad protein assay, Bradford 1976), total nitrogen (Kjeldahl procedure, Horwitz 1975), soluble sugar (Kates 1972), lipids (Soxhlet method), condensed tannins (butanol method, Oates *et al.* 1977), total phenolics (Folin & Ciocalteu 1927), and fiber (acid detergent fiber (ADF) and neutral detergent fibre (NDF), ANKOM Technology, Macedon, New York).

To compare fruit compounds within and between the respective group(s) of dispersers we performed a principal component analysis (PCA). We reduced eight classes of compounds (soluble proteins, soluble sugar, lipids, total nitrogen, condensed tannins, total phenolics, ADF, and NDF) to three components. We then conducted a discriminant function analysis (DFA) on the basis of the resulting principal components with an eigenvalue higher than 1.0. The standardized discriminant function coefficients and the factor loadings of the PC's after varimax rotation (Kaiser 1958) were used to assess the importance of single classes of compounds. The PCA and DFA were run in SPSS 13.0 and all other statistical tests in SigmaStat 3.5.

RESULTS

Frugivorous bats and their diet. We obtained 122 fecal samples from 227 frugivorous bats; 95 fecal samples from 12 bat species contained seeds. The seeds were assigned to 17 morphotypes, of which six could be identified to species and two to genus level (Table 1). All seeds in the fecal material were smaller than 5 mm.

TABLE 1. Frequency of seed morphospecies extracted from fecal material of 12 frugivorous bat species; Cp = *Carollia perspicillata*; Cb = *C. brevicauda*; Cc = *C. castanea*; Rp = *Rhinophylla pumilio*; Rf = *R. fischeriae*; Ao = *Artibeus obscurus*; Ag = *A. gnomus*; St = *Sturnira tildae*; Vt = *Vampyressa thuyone*; Ph = *Platyrrhinus helleri*; Ub = *Uroderma bilobatum*; Mm = *Mesophylla macconelli*.

Family	Plant species	Cp	Cb	Cc	Rp	Rf	Ao	Ag	St	Vt	Ph	Ub	Mm	total
Cyclanthaceae	<i>Asplundia peruviana</i>				7				1					8
Cecropiaceae	<i>Cecropia sciadophylla</i>						1				1			2
Moraceae	<i>Ficus</i> sp. 1									1			3	4
Moraceae	<i>Ficus</i> sp. 2						4	2				1		7
Marcgraviaceae	<i>Marcgravia longifolia</i>				4	1								5
Piperaceae	<i>Piper dumosum</i>	3												3
Piperaceae	<i>Piper lanceolatum</i>	8		2		1								11
Clusiaceae	<i>Vismia angusta</i>	16	2		1	1						1		21
	Morphospecies I				7	2								9
	Morphospecies II	1			4	1			1					7
	Morphospecies III	2												2
	Morphospecies IV						1							1
	Morphospecies V	4			1	2						1		8
	Morphospecies VI	2				1								3
	Morphospecies VII	2												2
	Morphospecies VIII	1												1
	Morphospecies IX	1												1

Overall, the fecal samples of *Carollia perspicillata* (n = 40) harbored the highest abundance and species richness of seeds. The seeds included three identifiable plant species and seven morphospecies (Table 1). The fecal material of *Rhinophylla fischeriae* and *R. pumilio* also revealed a wide spectrum of fruits with six and seven morphospecies, respectively, four of which were identified to species. *Rhinophylla pumilio* mainly ate fruits of an epiphyte (*Asplundia peruviana*, Cyclanthaceae) and a liana (*Marcgravia longifolia*, Marcgraviaceae). *Vismia sciadophylla* (Clusiaceae), a pioneer plant, was the most common seed type found in the fecal samples of the bats (Table 1; n = 5 bat species; n = 21 samples), most of them in the fecal material of *C. perspicillata* (n = 16 samples).

We documented synzoochorous dispersal for 12 morphotypes, five of which we identified to genus level or species (Table 2). A seed of the palm *Socratea exorrhiza* was carried into the net by *Artibeus obscurus*. Additionally we collected 180 synzoochorously dispersed seeds from seed traps. More than half of all seeds collected were identified as *Schefflera megacarpa* (n = 106 seeds) followed by seeds of two *Licania* species (n = 29 seeds). Fruits of *S. megacarpa* con-

sisted of a fleshy pulp coating five flat, radially arranged seeds. Twenty-four unidentified seeds belonged to seven morphospecies.

Diet of the saddle-back tamarin. Observations of the feeding behavior of *S. nigrifrons* revealed fruits of 15 species (Table 2). Five of the 15 species were also utilized by bats. We observed that the tamarins regularly fed on invertebrates (mainly katydids, Orthoptera) and occasionally on small vertebrates like lizards.

Differences in fruit colors. Most ripe fruits from the bats' diet were green (45%, n = 5) followed by yellow (27%, n = 3) and reddish or purple fruits (n = 2 and 1, respectively; Table 2). The diet of saddle-back tamarins was primarily composed of yellow fruits (47%, n = 7) followed by green, reddish, brown/black or purple (13% each, n = 2, respectively). However, preferences for fruit colors were not significantly different (Fisher's Exact Test, p = 0.37).

Chemical analyses of fruit compounds. Fruit pulp from 13 plant species was analyzed. Five of these fruit species were exclusively consumed by bats, and three by saddle-back tamarins. Five species were eaten by both

TABLE 2. Life form, dispersal mode (syn = synzoochorously dispersed, endo = endozoochorously dispersed) and color of fruits taken by fruit-eating bats (C = Carollinae, S = Stenodermatinae) and saddle-back tamarins (T). For some plant species information on life form, dispersal mode, and/or fruit color was not available (na).

Family	Plant species	Main disperser			Life form	Dispersal mode	Fruit color
		C	S	T			
Araceae	<i>Heteropsis</i> sp.			X	epiphyte	endo	yellow
Araliaceae	<i>Schefflera megacarpa</i>		X		treelet	syn	purple
Arecaceae	<i>Socratea exorrhiza</i>		X		tree	syn	yellow
Chrysobalanaceae	<i>Licania</i> sp. 1		X		tree	syn	green
Chrysobalanaceae	<i>Licania</i> sp. 2		X		tree	syn	na
Clusiaceae	<i>Vismia angusta</i>	X	X		tree	endo	green
Cyclanthaceae	<i>Asplundia peruviana</i>	X	X	X	epiphyte	endo	yellow
Cecropiaceae	<i>Cecropia sciadophylla</i>		X	X	tree	endo	yellow
Fabaceae	<i>Inga</i> sp.			X	tree	na	yellow
Moraceae	<i>Brosimum</i> sp.		X		tree	syn	na
Moraceae	<i>Ficus</i> sp. 1		X	X	epiphyte	endo	reddish
Moraceae	<i>Ficus</i> sp. 2		X	X	epiphyte	endo	green
Marcgraviaceae	<i>Marcgravia longifolia</i>	X		X	liana	endo	reddish
Melastomataceae	<i>Tococa guianensis</i>			X	shrub	endo	purple
Menispermaceae	<i>Abuta</i> sp.			X	tree	endo	yellow
Nyctaginaceae	<i>Neea verticillata</i>			X	tree	endo	purple
Piperaceae	<i>Piper dumosum</i>	X			shrub	endo	green
Piperaceae	<i>Piper lanceolatum</i>	X			shrub	endo	green
Rubiaceae	<i>Psychotria</i> sp.			X	shrub	endo	brown/black
Violaceae	<i>Leonia</i> sp.			X	tree	endo	green
	Morphospecies X			X	tree	endo	yellow
	Morphospecies XI			X	tree	endo	brown/black
	Morphospecies XII			X	tree	endo	yellow

groups. Seven more fruit species taken by *S. nigrifrons* could not be preserved for further analysis through drying because almost no solid substances remained of the thin gelatinous mesocarp after desiccation. We obtained relative proportions of eight different fruit compounds (Table 3).

Comparison of fruit compounds. We performed a PCA with the relative proportions of eight fruit compounds. Three PCs with an eigenvalue > 1 accounted for 81.1% of total variance. The first component was represented strongest by protein concentration, explaining almost half of total variance (Table 4). Components two and three were dominated by ADF and lipids, respectively. We subsequently used the three components as variables for a discriminant function analysis to determine whether they separate the

fruits preferred by the three categories of dispersers (bats, saddle-back tamarins, and both). We obtained two discriminant functions (DF), where the first function accounted for 55.5% of total variability among the groups (eigenvalue = 0.539) and the second for 44.5% (eigenvalue = 0.431).

The two DFs did not distinguish the three disperser categories based on the selected compound composition of the consumed fruits (DF1: $df = 6$, $\chi^2 = 7.106$, $p = 0.311$; DF2: $df = 2$, $\chi^2 = 3.228$, $p = 0.199$; Figure 1). DF1 was most heavily weighted on the PCA component 1 (loading 0.967) and DF2 on component 3 (loading 0.964), indicating that protein and fat content most likely separated the two groups; 76.9% of the original grouped cases were correctly classified. Group 3 was classified correctly to 100%,

TABLE 3. Fruit compounds (in %) in 13 fruit species from two dispersers, bats and tamarins. Values refer to dry matter; n indicates number of fruits; ADF = acid detergent fiber, NDF = neutral detergent fiber; all fruits originated from individual plants except *M. longifolia*, *A. peruviana* (two plants each) and two *Piper* species (at least five plants were sampled per species).

Fruit species	n	Total nitrogen (%)	Soluble sugar (%)	NDF (%)	ADF (%)	Lipids (%)	Soluble protein (%)	Phenolics (%)	Cond. tannins (%)	Consumer
<i>P. dumosum</i>	20	1.15	7.3	41.6	12.5	32.89	0.89	0.3	0.11	bat
<i>P. lanceolatum</i>	23	2.4	13.26	46.9	22.6	3.01	4.82	0.9	0.19	bat
<i>S. exorrhiza</i>	16	1.27	61.55	27.4	16.2	1.45	9.63	1.71	4.07	bat
<i>S. megacarpa</i>	7	0.58	73.64	17.5	14.6	1.76	4.05	0.73	0.42	bat
<i>V. angusta</i>	20	0.51	27.77	47.7	11.5	5.12	4.76	0.26	0.35	bat
<i>C. sciadophylla</i>	10	0.83	84.4	11.9	8.1	2.03	7.64	3.1	1.68	bat/tamarin
<i>A. peruviana</i>	2	1.11	23.93	34.7	28.9	1.65	11.34	4.49	1.93	bat/tamarin
<i>Ficus</i> sp. 1	20	1.18	13.79	43.5	32.5	3.47	3.01	2.08	0.26	bat/tamarin
<i>Ficus</i> sp. 2	24	0.85	37.63	33.3	24.5	1.88	5.22	1.84	0.78	bat/tamarin
<i>M. longifolia</i>	15	0.92	67.87	12.2	6.4	6.44	13.42	7.98	4.04	bat/tamarin
<i>T. guianensis</i>	11	0.57	59.22	13.9	10.2	1.68	1.81	0.77	1.14	tamarin
Morphospecies I	10	0.48	31.63	53.1	44	0.72	2.3	1.91	0.5	tamarin
<i>Psychotria</i> sp.	15	1.34	76.59	21.1	15.7	0.82	1.72	0.74	1.45	tamarin

TABLE 4. Principal component analysis of the chemical composition of 13 fruit species. Factor loadings > 0.25 are shown.

	PC1	PC2	PC3
Soluble protein	0.950		
Total phenolics	0.892		
Condensed tannins	0.833		
ADF		0.907	
NDF		0.853	0.282
Lipids			0.850
Total nitrogen		0.284	0.528
Cumulative proportion of variance	44.7	65.4	81.1

pointing to similar compound composition within the fruits consumed exclusively by saddle-back tamarins but not by bats. Evaluation of single compounds revealed that the fruits solely eaten by tamarins (group 3) had significantly lower lipid concentrations (U-test: $T = 8.000$, $p = 0.035$) than the remaining fruits that were taken by bats or bats and tamarins. Relative amounts of protein were marginally lower in fruits of group 3 (U-test: $T = 9.000$, $p = 0.052$). Concentrations of the remaining compound

classes (sugar, fiber, nitrogen, and secondary compounds) did not differ significantly between the two groups.

DISCUSSION

Fecal analysis revealed 17 morphospecies dispersed by bats. Congeners at least of all identified fruit plants have previously been described as being dispersed by bats, in particular *Ficus* and *Piper* species (Thies & Kalko 2004, Olea-Wagner *et al.* 2007, da Silva *et al.* 2008) are dispersed by a range of bat species (*Ficus* sp.: *Artibeus* sp., *Vampyressa* sp.; Piperaceae: *Carollia* sp.; Kalko *et al.* 1996a,b; Lobova & Mori 2004, Thies & Kalko 2004, Delaval *et al.* 2005). Our study also confirms chiropterochory of *Asplundia* sp. (Rinehart & Kunz 2006) and *Marcgravia* sp. by *R. pumilio* (Gorchov *et al.* 1995), *Cecropia* sp. by *A. obscurus* and *P. helleri* (reviewed in Lobova *et al.* 2003), and *Vismia* by *C. perspicillata* (Sampaio *et al.* 2003, Lobova *et al.* 2009).

The collection of seeds below bat roosts yielded 12 synzoochorously dispersed morphotypes, five of which could be identified at least to genus level. *Socratea exorrhiza*, *Licania* sp., and *Brosimum* sp. have been previously reported to be dispersed by bats (van der Pijl 1957, Romo 1996, Estrada & Coates-Estra-

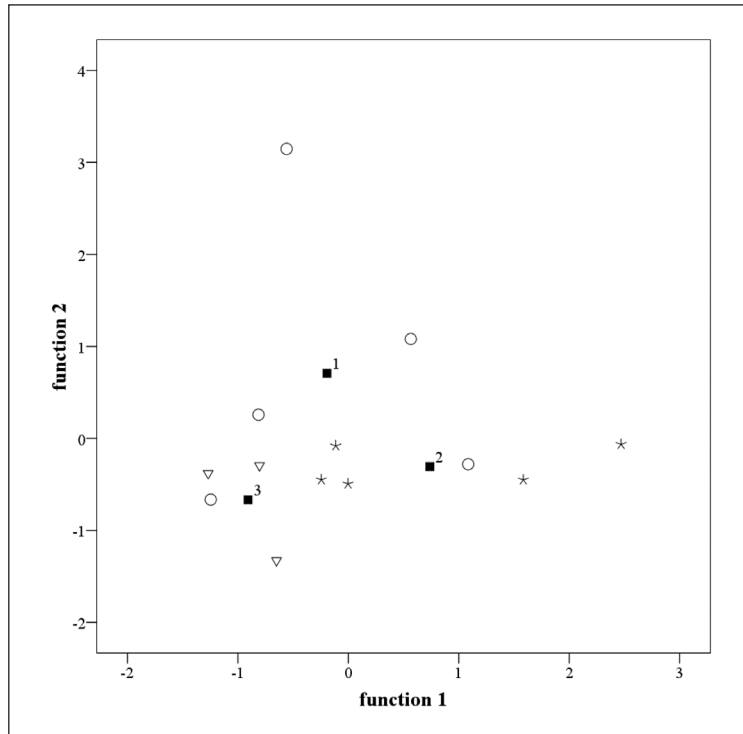


FIGURE 1: Comparison of fruits taken by bats (1, O, $n = 5$), bats and tamarins (2, *, $n = 5$), and tamarins (3, ∇, $n = 3$) in relation to the composition of their nutritional components, using canonical discriminant function analysis (DFA); ■ = group centroid.

da 2002). By contrast, plants of the genus *Schefflera* (Araliaceae) were not known to be visited by bats. They were previously only observed to be dispersed by birds (Burrows 1994). In our study area *S. megacarpa* was heavily utilized by small Stenodermatinae. The presentation of fruits on extended peduncles (pendulichory) of this small tree (Gentry 1981) could favor dispersal by bats, as this fruit position facilitates approach by flying dispersers (van der Pijl 1957).

Only five out of 29 fruit morphospecies consumed by bats overlapped with 15 morphospecies that were taken by tamarins. Dietary overlap may clearly be different in different months, since fruit availability varies throughout the year and we only provide data on a three-months period. Nevertheless, the results are in line with literature predicting low numbers of utilized plant genera shared by bats and primates, since fruit syndromes associated with these two disperser groups are distinct (Gorchov *et al.* 1995). One reason for the limited dietary overlap in our particular case may be the tamarins' capacity to swallow larger seeds of fruits holding only a very thin

layer of pulp that is mechanically difficult to remove (Garber 1986, Garber & Kitron 1997, Knogge & Heymann 2003). Such fruit types constituted almost half of the tamarins' fruit diet, but seem unattractive to bats since the seeds are too large to be swallowed and difficult to be processed in alternative ways.

We could not find statistically significant differences in the preference for fruit colors among bats and saddle-back tamarins. However, this might be accounted for by the low sample size, as we observed tendencies that are in accord with former studies. Bats tended to prefer greenish fruits, as observed in previous studies (van der Pijl 1957, Fleming 1979, Gauthier-Hion *et al.* 1985, Gorchov *et al.* 1995, Korine *et al.* 2000). Since Neotropical bats are nocturnal, chiropterochorous plants attract their dispersers by non-visual cues, including odor and fruit presentation which facilitates detection by echolocation (Kalko & Condon 1998, Thies *et al.* 1998, Korine & Kalko 2005). However, according to Knogge & Heymann (2003) a large proportion of fruit species in the diet of the saddle-back tamarins

was characterized by yellow coloration that provided a higher visual contrast against the foliage. Those findings support studies on birds and primates demonstrating that the visual abilities of dispersers are likely to shape fruit traits (Lomáscolo & Schaefer 2010, Lomáscolo *et al.* 2010). Beyond improved detectability, Schaefer & Schmidt (2004) suggested dietary content as another important motive for selection of yellow fruits, since yellow and orange colors may signal high protein concentration. Our results partly support these findings, as three of the four yellow fruit species analyzed (*A. peruviana*, *C. sciadophylla*, *S. exorrhiza*) had very high protein concentrations compared with non-yellow fruits. Only the red fruits of *M. peruviana* showed an even higher protein concentration.

We did not find significant differences in overall nutritional composition of consumed fruits between the two groups of dispersers. This result is in accordance with a study carried out in South Africa and Madagascar, where fruit color was more important for food selection by birds and lemurs than chemical fruit traits (Voigt *et al.* 2004). Interestingly, however, the fruits that were exclusively consumed by tamarins and not by bats (group 3) were classified correctly to 100%, pointing towards similar compound composition. The associated discriminant functions 1 and 2 of the DFA were weighted most heavily on protein and lipid concentration. Indeed the concentration of lipids was significantly lower and protein marginally lower in these fruits than in all other fruits that were also or exclusively consumed by bats. This pattern suggests that bats may avoid fruits with lipid or protein concentrations below a certain threshold, while saddle-back tamarins still feed on them.

A certain concentration of lipids, which provide a relatively high caloric value, may be important to phyllostomid bats, since they mainly do not feed directly within a fruiting tree, but carry fruits away to roosting sites for feeding (Kalko *et al.* 1996b, Bizerril & Raw 1998). Higher energy content per food item should reduce the total number of commutes between fruiting tree and feeding roost necessary to satisfy their energy demands. Feeding directly in a fruiting tree in tamarins (Garber 1988) should lower costs for locomotion and might allow them to feed on fruits with lower energy content per unit weight than bats.

That the protein concentration tended to be higher in fruits consumed by bats than in those only taken by *S. nigrifrons* might be associated with the

respective body mass of the consumers. It has been shown that smaller animals select items with a higher protein concentration (Ganzhorn 1988). Even the body mass of the heaviest frugivorous bats in our sample (*Artibeus lituratus*, ≤ 68 g) is distinctly lower than that of the observed tamarin species *S. nigrifrons* (ca. 350 g; Smith & Jungers 1997). Additionally, tamarins regularly prey on protein-rich animal food (Nickle & Heymann 1996, Heymann *et al.* 2000), which complements their fruit diet. While frugivorous bats may occasionally also feed on insects (Gardner 1977, Gorchov *et al.* 1995), they must obtain most of their dietary protein from fruits (Herbst 1986, Herrera *et al.* 2001).

Phenolic compounds and tannins have been shown to reduce mammalian herbivory *e.g.* by moose or hare (Tahvanainen *et al.* 1985, Stolter *et al.* 2005). Interestingly, we found high concentrations of phenolic compounds in fruits of *M. longifolia* and *A. peruviana*, fruits which were mainly found within the diet of the frugivorous bat *Rhinophylla pumilio* and in *Sturnira tildae*. The latter is well known to regularly feed on *Solanum* fruits (Passos *et al.* 2003), which contain high amounts of secondary compounds that have been shown to deter certain potential consumers such as birds (Cipollini & Levey 1997). *Asplundia peruviana* is known to cause diarrhea in *S. nigrifrons* (Knogge *et al.* 1998). This feeding strategy might be worth further investigation on possible physiological adaptations of *R. pumilio* and *S. tildae*, since exploitation of fruits with high phenolic content might require a specific enzyme equipment. Various plant-feeding mammals have been found to produce proline-rich proteins in their salivary glands that may bind and deactivate detrimental effects of secondary plant compounds, *e.g.* tannins (Chapman & Chapman 2002, Stolter *et al.* 2005). Furthermore, folivorous *Colobus* monkeys have a gut flora that enables them to detoxify some toxins in their diet (Chapman & Chapman 2002). Perhaps the two bat species *R. pumilio* and *S. tildae* might reveal similar physiological adaptations towards a diet rich in secondary compounds, which in turn may have opened up a feeding niche which other sympatric bat species cannot exploit. Unfortunately we were not able to analyze the fruits' mineral compounds, which might also play an important role in the detoxification of secondary compounds (Voigt *et al.* 2008).

To summarize, bats and saddle-back tamarins tended to choose green and yellow fruits, respectively, but their preferences for fruit colors were not

significantly different. Similarities in overall nutrient composition could not be used to assign fruits to the associated disperser group. However, specific compounds, in particular proteins and lipids, seemed to influence fruit preferences in bats. Data on nutritional ecology of zoochorous fruits is scarce, but in combination with phenological traits immensely important in understanding the mechanism of how plants assure that their seeds get dispersed. The huge variety of adaptations among fruiting plants and their dispersers makes a substantial contribution to the high diversity of tropical rainforests. As frugivores play a pivotal role in maintenance and regeneration processes in the tropics, it is essential to understand the intricacies of animal-plant interactions to protect and restore this highly diverse ecosystem.

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