DOI 10.1515/mammalia-2012-0103 — Mammalia 2014; 78(1): 93–101

Renata Lara Muylaert*, Dalva Maria da Silva Matos and Marco Aurelio Ribeiro Mello

Interindividual variations in fruit preferences of the yellow-shouldered bat *Sturnira lilium* (Chiroptera: Phyllostomidae) in a cafeteria experiment

Abstract: In studies on frugivory and seed dispersal, it is frequently assumed that individual frugivores of the same population behave as equivalents. However, there is growing evidence from dietary studies pointing out that, in many natural populations, individuals use different subsets of the total resource pool. As heterogeneity in foraging behavior and food selection may affect the outcome of the seed dispersal process, we tested whether yellow-shouldered bats *Sturnira lilium* (E. Geoffroy St.-Hilaire, 1810), the key neotropical seed dispersers, show interindividual variations in fruit preferences. Thirty individuals were submitted to cafeteria trials in a flight tent, when they were offered fruits of *Solanum variabile* Mart. (Solanaceae) *Cecropia pachystachya* Trec. (Urticaceae), and *Piper aduncum* L. (Piperaceae), which belong to the favorite genera consumed by *S. lilium*. Although *S. variabile* had the highest consumption rates on average, there were variations among individuals in the fruits consumed in the second and third places. These findings, together with interindividual differences in foraging areas observed in the same population, may be interpreted as preliminary evidence of individual specialization. As a possible consequence, frugivorous bats of the same population, despite being all legitimate dispersers, may differ in their efficiency.

Keywords: animal-plant interactions; cafeteria trials; food choice; frugivory; Phyllostomidae.

***Corresponding author: Renata Lara Muylaert,** Departamento de Ecologia, Universidade Estadual Paulista, Avenida 24A, 1515, 13506-900 Rio Claro, SP, Brazil, e-mail: renatamuy@yahoo.com.br
Dalva Maria da Silva Matos: Departamento de Botânica, Universidade Federal de São Carlos, Rodovia Washington Luís, km 235, 13565-905 São Carlos, SP, Brazil
Marco Aurelio Ribeiro Mello: Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos, 6.627, 31270-901 Belo Horizonte, MG, Brazil

Introduction

Seed dispersal is a vital ecosystem function (Isbell et al. 2011), especially in the tropics, where approximately 90% of the tree species depend on animals for their sexual reproduction (Muscarella and Fleming 2007). The first stage of seed dispersal by animals is fruit choice, which follows a hierarchy of mechanisms at different scales, from the plant species to the fruits of an individual plant (Sallabanks 1993). Therefore, decisions made by frugivores at this stage determine the outcome of the whole seed dispersal process, and we need to understand some key aspects, such as which fruit species are preferred by a given frugivore, where are most seeds carried to, and how many of them establish and reproduce (Wang and Smith 2002). It is also important to understand fruit choice at different organization scales, from the whole frugivore community to the individuals within a population (Mello et al. 2011).

However, most of what is known about seed dispersal is based on the community and population levels, as many studies in Ecology assume that individuals of the same population are ecologically equivalent (Bolnick et al. 2003). Growing evidence points out, though, that many natural populations are composed of individuals that use different subsets of the resource pool used by the population as a whole (Bolnick et al. 2002), and this may be true for seed dispersers, too. An individual whose niche is substantially narrower than the population's niche, due to factors that are not related to sex, age, size, or morphotype, is an individual specialist (Bolnick et al. 2003). Evidences of individual specialization have been found in populations of several animals, such as mollusks (West 1986), birds (Smith 1990), otters (Estes et al. 2003), and fish (Araújo et al. 2008). Direct and indirect evidence of interindividual variations in foraging, roosting, and diet has been also obtained in populations of insectivorous bats (Cryan et al. 2012), bird-eating bats (Fortuna et al. 2009), and fishing bats (Barclay 1985). Nevertheless, only one

Brought to you by | Universidade Estadual Paulista - Sao Paulo
Authenticated
Download Date | 10/9/14 6:24 PM

single study, so far, assessed individual specialization in a population of frugivorous bats (Rogeri 2011). Individual specialization has important implications for ecological interactions and evolutionary processes because, when individuals of the same population make different sets of interactions, this may result in polymorphism (Werner and Sherry 1986, Araújo et al. 2008) or, ultimately, in sympatric speciation (Bolnick et al. 2003).

The stenodermatine bat *Sturnira lilium* (E. Geoffroy St.-Hilaire, 1810) has a broad geographic distribution. In South America, it is found in a variety of habitats (Gannon et al. 1989) and feeds on at least 80 plant species of 20 families, although it shows a preference for Solanaceae, observed in studies based on fecal analysis and direct observation (Uieda and Vasconcellos-Neto 1985, Marinho-Filho 1991, Giannini 1999, Passos et al. 2003, Mello et al. 2008a, Lobova et al. 2009). In general, bats of the subfamily Stenodermatinae (Chiroptera: Phyllostomidae), specialized frugivores (Rojas et al. 2011), are good models to study individual specialization because many species in this group have a broad diet, but the set of items consumed by a given species varies among local populations (Lobova et al. 2009). Considering this feeding plasticity, it is reasonable to assume variations also within a population. These characteristics make *S. lilium* a good model for studying interindividual variations. Furthermore, these bats are considered as legitimate and efficient seed dispersers, as they do not harm seeds and transport them over several hectares in a single night (Mello et al. 2008b). They can feed almost entirely on fruits (Herrera et al. 2001), although most previous studies were based only on fecal analysis, and it remains unclear if fruits of Solanaceae are the most frequently observed in the natural diet of *S. lilium* due to preference or opportunism (Mello et al. 2008a). In one of the few experimental studies with this species carried out in a Costa Rican rainforest, Bonaccorso and Gush (1987) offered fruits of the genera *Piper* and *Cecropia* to *S. lilium*, which did not show any selectivity; however, fruits of Solanaceae were not included in their experiment.

Evidence of individual specialization in the use of foraging areas in the same population of *Sturnira lilium* analyzed in the present study was obtained by Rogeri (2011), who observed that different individuals flew more frequently within some habitat types than expected based on the relative area occupied by these habitat types in our study area. These differences among individuals in the use of space may be a consequence of differences in fruit preferences and uneven distribution of food-plants. Therefore, in the present study, we made the first test of the hypothesis of individual specialization in fruit preferences in a *S. lilium* population. If this hypothesis is correct, we expected that different individuals should have different rankings of preference for fruits of the main plant genera consumed by *S. lilium* in the study area, if offered equal amounts of these fruits. We also expected to find Solanaceae fruits always at the first place in the ranking, as currently assumed based on fecal analysis.

Materials and methods

Study area

Our study was carried out in a cerrado remnant in a reserve within the campus of the Federal University of São Carlos (UFSCar), São Carlos, state of São Paulo, southeastern Brazil (21°58′S, 47°52′W). The cerrado biome, also known as Brazilian savanna, is considered as one of the world's biodiversity hotspots (Myers et al. 2000). The study area is composed of a mosaic of cerrados, gallery forests, plantations of *Pinus* and *Eucalyptus*, anthropogenic areas such as dams, trails, and abandoned fields, and semi-deciduous forests around the reserve (Paese 1997). The climate is classified as Cwa (tropical of altitude) according to the Köppen system (Center of weather research CEPAGRI – UNICAMP).

Bat capture and handling

We captured wild individuals of *Sturnira lilium* in gallery forest and forest edges within the reserve. These bats were used in cafeteria trials inside a flight tent. In the capture and handling of bats, we followed the guidelines for the care and use of mammals in research suggested by the American Society of Mammalogists (Sikes et al. 2011). Fieldwork was carried out under research permits granted by the Chico Mendes Institute for Conservation and Biodiversity (SISBIO #11093-2, #19335-1). Our study was also approved by the Committee for Ethics in Animal Research of UFSCar (#013/2007), and access to the reserve was granted by the Campus Administration of UFSCar (#022/07 DISG/PU).

Captures were made with mist nets (model 716/7P, 7×2, 5 m; denier 70/2, mesh 16×16 mm; Ecotone Inc., Gdynia, Poland) set up for 6 h from sunset, as neotropical frugivorous bats tend to concentrate their activity in the first hours of the night (Aguiar and Marinho-Filho 2004, Esbérard and Bergallo 2005). Therefore, all bats submitted to the experiment were captured before 22:00 h, and the experiment was always started before midnight.

Brought to you by | Universidade Estadual Paulista - Sao Paulo
Authenticated
Download Date | 10/9/14 6:24 PM

Bats were identified using a combination of taxonomic keys (Vizotto and Taddei 1973, Gannon et al. 1989, Emmons and Feer 1997, Gardner 2007). Voucher specimens were deposited in the mammal collection of the Zoology Museum of São Paulo University. The two *Sturnira* species that occur in the area, *Sturnira lilium* and *Sturnira tildae*, were distinguished through tooth morphology, muzzle shape, and forearm length (following Simmons and Voss 1998). To create adequate conditions for bats in captivity, even considering short stays of 2 nights at most, we followed recommendations given in specialized publications (Barnard 1995) and by the specialists, Susan Barnard and Ariovaldo Cruz-Neto.

Cafeteria trials

For the cafeteria trails, we built a flight tent (a 2×2×3 m wooden structure, covered with shading material with a density of 50%) in the experimental garden of the Botanical Department of UFSCar. We offered, one individual at a time, the fruits of the species *Cecropia pachystachya* Trec. (Urticaceae), *Piper aduncum* L. (Piperaceae), and *Solanum variabile* Mart. (Solanaceae), which belong to the main plant genera recorded in the diet of *Sturnira lilium* all over its geographic range (Mello et al. 2008a). We chose these species for the experiment because they are the most abundant of their respective genera in the study area (Rogeri 2011) and have already been recorded in the diet of *S. lilium* (Lobova et al. 2009). Furthermore, these plants follow a steady-state fruiting strategy (sensu Gentry 1974), as typical zoochoric plants offering a reduced number of ripe fruits per day in several months. So all three species were available throughout the year. It would not have been feasible to carry out the cafeteria trials with additional plant species, as each species has a different timing of fructification in the area, which makes it virtually impossible to have enough amounts of ripe fruits of several species on all experimental rounds.

We sliced each fruit or infructescence in pieces and placed them on separate dishes on the floor inside the flight tent. In preliminary experiments carried out in the same area with the species *Artibeus lituratus*, *Carollia perspicillata*, and *Sturnira lilium*, we observed that *S. lilium* bats respond better to cafeteria trials, when fruits are offered sliced and on dishes, instead of in their original shape in a set up simulating natural conditions. For instance, Andrade (2008) used 13 *S. lilium* in his cafeteria trials simulating natural conditions (whole fruits hung on tree branches inside the flight tent), but only one individual fed on the fruits. The reasons for that are unclear, but the percentage of bats that reacted to our experiment was much higher. Better responses, using sliced fruits in flight tent experiments with small phyllostomids, have also been obtained by Thies (1998). Furthermore, we wanted to make the fruits of different species more comparable, by controlling form and presentation, as these two factors affect fruit choice (Kalko and Condon 1998). Fruits were offered in equal amounts per night, according to their availability in the field. The amount of fruits varied for some individuals: for 26 individuals, we offered at least 7 g of each fruit species, and for only four individuals, we offered between 3 and 7 g; the total amount varied from 3 to 25 g of each fruit species (mean=12.51±1.49). We used only fresh and ripe fruits in the experiment, collected on the same day when they were used; fruit ripeness was assessed visually through color and texture.

To start the experiment, we released one bat inside the tent, hanging it on the top, opposite to the entrance, 1.8 m distant from the dishes. There were no perches inside the flight tent, and the bats could easily hang on its top. The dishes with fruits were placed on the ground, each kind of fruit on a separate dish at fixed positions aligned 10 cm distant from each other, were always *Cecropia pachystachya*, *Piper aduncum*, *and Solanum variabile*. Temperature and humidity in the flight tent were not controlled, and experiments with different individuals were made on different days and in different months, from January 2010 to April 2011, during all seasons. Bats stayed in the flight tent for 1 whole day and were marked and released on the following night. After each experimental round (1 night), we weighed the amount of fruits remaining and subtracted it later from the amount offered in each dish, in order to calculate the consumption rate (amount consumed/amount offered in g). The activity of each individual was filmed in infrared for 1 h with a handheld Sony mini-DV camcorder (model DCR-HC26 with nightshot function), in order to record additional details of feeding behavior.

Thirty bats were subjected to a single round of the experiment (1 night), in order to test our main working hypothesis. Additionally, 11 bats were subjected to a second round of the experiment in the following night, in order to test whether fruit choice was consistent for each individual.

Statistical analysis

First, we considered, in our experimental design, the main factors assumed to cause differences among individuals (Bolnick et al. 2003): age, sex, and morphotype. In

Brought to you by | Universidade Estadual Paulista - Sao Paulo
Authenticated
Download Date | 10/9/14 6:24 PM

a preselection of individuals, we checked their sex, age, reproductive status, forearm length, and weight (following Kunz 1988). We controlled for age in the experiment by using only adults (bats with all wing epiphyses ossified, following Kunz 1988); reproductive individuals were also excluded. Another factor suggested by Bolnick et al. (2003), morphotype, does not vary in *Sturnira lilium*, as all *S. lilium* have the same morphology, and there is also no marked sexual dimorphism in this species (Gannon et al. 1989).

To test the hypothesis of individual specialization, we used a two-step procedure. First, to test whether bats consumed different amounts of the three fruit species, we calculated a repeated measures general linear mixed-effects model with bootstrapping (10,000 iterations). We chose a repeated measures model, in order to consider the consumption rates of *Cecropia*, *Piper*, and *Solanum* of each individual as non-independent treatments. In our mixed model, the response variable was fruit consumption rate (consumption), the fixed variables were fruit species (fruit) and sex of the bat (sex), and the random variables were body mass (mass) and amount of fruits offered (amount). Therefore, we assumed that fruit consumption rate depended mainly on fruit species, but could also differ between sexes; the amount of fruits consumed by a given individual could be also affected at a minor degree by its body mass (larger bats eat supposedly a higher amount of fruits) and by the amount of fruits offered. In order to test for the consistency of fruit choice by individual bats, we analyzed data for 11 bats that underwent the experiment twice, using an additional repeated measures general linear mixed-effects model with bootstrapping (10,000 iterations), in which the response variable was fruit consumption rate (consumption), and the fixed variables were fruit species (fruit) and experimental round (round). On average, the 30 *Sturnira lilium* bats used in the experiment weighed 21±8 g (Table 1).

Table 1 Individual bats of *Sturnira lilium* submitted to cafeteria trials in the Federal University of São Carlos, southeastern Brazil.

Individual	Sex	Weight (g)	Number of experimental rounds	Amount of fruits offered (g)	Year	Month
1	F	21	2	9	2011	January
2	M	24	2	9	2011	January
3	M	18	2	12	2010	April
4	M	20	2	15	2010	May
5	M	18	2	18	2011	January
6	M	20	2	18	2010	August
7	M	15	2	21	2010	August
8	F	21	2	21	2010	July
9	F	23	2	21	2010	November
10	M	20	2	21	2010	May
11	M	20	2	21	2010	November
12	M	22	1	21	2010	October
13	F	19	1	21	2011	January
14	F	20	1	21	2010	June
15	F	20	1	21	2010	July
16	M	20	1	21	2011	January
17	F	23	1	21	2011	January
18	M	26	1	33	2010	October
19	M	23	1	75	2010	November
20	M	27	1	51	2011	January
21	M	24	1	51	2011	January
22	M	20	1	60	2011	January
23	M	20	1	60	2011	February
24	F	22	1	75	2011	February
25	M	22	1	75	2011	February
26	M	23	1	75	2011	February
27	F	24	1	75	2011	January
28	M	20	1	75	2010	November
29	M	23	1	75	2011	February
30	F	17	1	75	2011	March

Second, to test for interindividual variations in consumption rates of the three fruit species, we used an analysis of complementary specialization based on network theory: the H_2' index of Blüthgen et al. (2006). This index measures, in a bipartite network, how much the vertices differ from each other in their weighed pattern of connections. Values of H_2' range from zero (all vertices are connected to the same partners with equal intensity) to one (every vertex has a different pattern of weighed interactions). We organized the results of our experiment as an adjacency matrix, in which individual bats were represented as vertices on the one side, and fruit species were represented as vertices on the other side of the network. Links between vertices were established, whenever an individual bat was fed on a particular fruit species during the cafeteria trial. Furthermore, we added to each link a weight, based on the consumption rate recorded. As the network index used in this analysis is based on integers (Blüthgen et al. 2006), we transformed each consumption rate into an index that varies from 0 to 11, based on the ranges of the actual values recorded (0=no consumption, 1=0.1%–10%, 2=10.1%–11%, 3=11.1%–20%, 4=20.1%–30%, 5=30.1%–40%, 6=40.1%–50%, 7=50.1%–60%, 8=60.1%–70%, 9=70.1%–80%, 10=80.1%–90%, 11=90.1%–100%), using a similar approach as in the widely used herbivory index of Dirzo and Miranda (1991). The weighed matrix was then analyzed, and graphs were drawn in the package bipartite 1.17 for R (Dormann et al. 2008), to calculate the index H_2'. The significance of H_2' was estimated with an online software written by Nils Blüthgen and Nico Blüthgen (http://rxc.sys-bio.net/),

Brought to you by | Universidade Estadual Paulista - Sao Paulo
Authenticated
Download Date | 10/9/14 6:24 PM

using a Monte Carlo procedure with 10,000 randomizations based on the null model Patefield (the weight of a link is proportional to its row and column totals). We analyzed H_2' for the complete network with all three fruit species and also for the network without *Solanum variabile*, in case the mixed model showed significant differences in consumption rates among fruit species. We did it so because it was possible that *S. variabile*, supposedly the preferred species (Mello et al. 2008a), could mask interindividual variations in consumption rates of the other two fruit species.

Percentages (e.g., fruit consumption rates) were arcsine transformed prior to analysis. All statistical analyses followed those of Zar (1996) and Manly (2007) and were made in SPSS 20.0 for Mac.

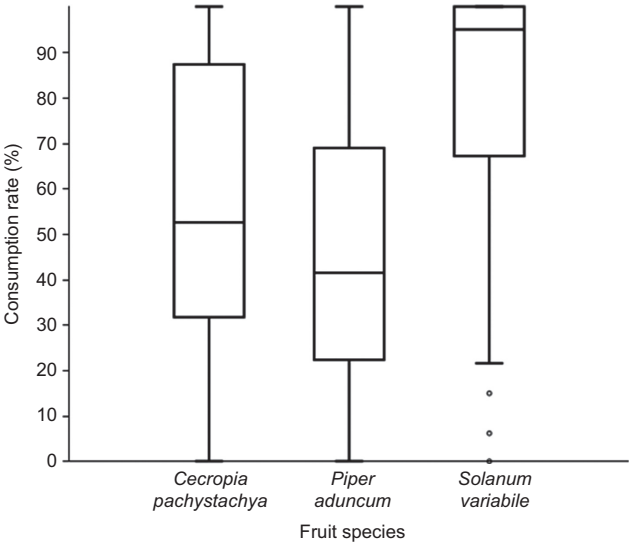

Figure 1 Consumption rate of three fruits in cafeteria trials carried out with 30 *Sturnira lilium* individuals in the Federal University of São Carlos, southeastern Brazil. The circles are outliers, the bars represent maximum and minimum values, and the middle bar represents the median and interquartile.

Results

Between January 2010 and April 2011, we used 30 *Sturnira lilium* bats in the cafeteria trials (20 males and 10 females). All the bats responded positively to the cafeteria trials. As the experimental rounds were started, the bats stood still where they had been placed, before starting to fly in circles ca. 1.5 m above the ground. They waited for only 15–40 min to start feeding. After a bat first landed on the ground, it limited its activity to short flights at lower heights, inspecting the dishes. Then, it landed on the dish or reached the dish crawling and, then, started to feed, usually eating right on the ground or picking a piece of fruit and eating it at the cage's top. Bats did not necessarily land more frequently near the dish with their preferred fruit. This pattern was observed in all the individuals.

Bats fed on 58±32% (mean±s.d.) of the *Cecropia pachystachya* fruits, 46±30% of the *Piper aduncum* fruits, and 80±30% of the *S. variabile* fruits. The first mixed model (N=30, r^2=0.22, p=0.005, Power=0.94) pointed out that *Solanum variabile* were the preferred fruits on average (fruit: F=8.75, η^2=0.18, p<0.001) and that sex (sex: F=1.20, η^2=0.01, p=0.28), body mass (mass: F=0.60, η^2=0.01, p=0.44), and amount of fruits offered (amount: F=1.50, η^2=0.02, p=0.22) played no role in fruit selection (Figure 1). The second mixed model (N=11, r^2=0.11, p=0.05, Power=0.75) pointed out that there were no differences in fruit choice between the first and the second experimental rounds (round: F=1.84, η^2=0.03, p=0.18) for the 11 bats tested twice, with *S. variabile* being always the preferred fruit species (fruit: F=5.05, η^2=0.15, p=0.009).

The complete network with all 30 individual bats and three fruit species showed a low and nonsignificant level of specialization (H_2'=0.05, p=0.27) (Figure 2). However, the network without *Solanum variabile*, the preferred species according to the mixed model, showed a higher and significant level of specialization (H_2'=0.09, p=0.04), evidencing interindividual differences in the consumption of *Cecropia pachystachya* and *Piper aduncum*.

Discussion

Results of our experiment carried out with bats from a wild population of *Sturnira lilium* provided the first evidence of interindividual variations in fruit preferences among the phyllostomid bats. Although most individuals tested in the cafeteria trials fed on at least two fruit species and, on average, preferred fruits of *Solanum variabile* in the first place, they differed in their secondary preferences for fruits of the species *Cecropia pachystachya* and *Piper aduncum*. Probably, individuals of this population do also differ in how they complement their natural diets, what may have great importance in times of scarcity of their preferred fruits. Therefore, our findings may be interpreted as preliminary evidence of individual specialization in fruit preferences in *S. lilium*.

The observed preference of *Sturnira lilium* for a fruit to the detriment of other fruit species does not corroborate the experimental results obtained by Bonaccorso and

Brought to you by | Universidade Estadual Paulista - Sao Paulo
Authenticated
Download Date | 10/9/14 6:24 PM

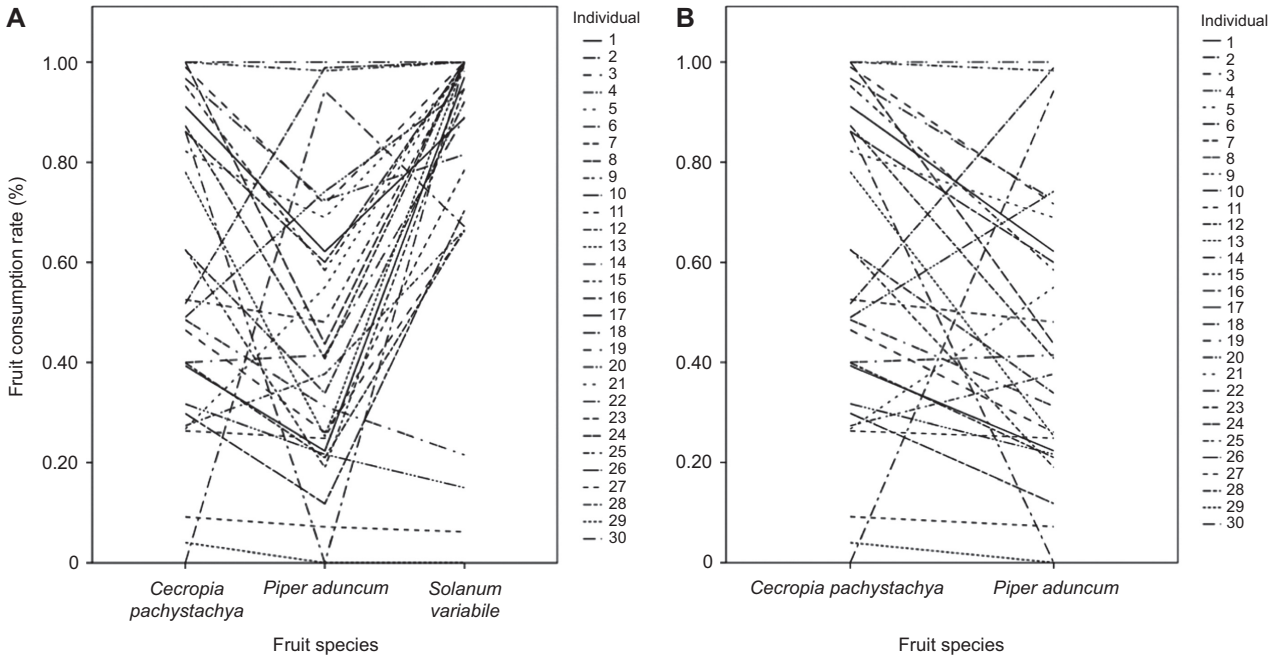

Figure 2 Most individual bats of the *Sturnira lilium* population preferred to feed on fruits of *Solanum variabile*, when offered together with two other fruit species in cafeteria trials (A). However, there were some interindividual variations in the preference for secondary and tertiary fruits of *Cecropia pachystachya* and *Piper aduncum* (B). Each line represents an individual bat used in the experimental rounds.

Gush (1987), who observed no selectivity in this species when offered fruits of *Ficus* and *Muntingia*. Moreover, Bonaccorso and Gush (1987) suggested that *S. lilium* could be an extreme generalist among obligate frugivores. However, in their study, no *Solanum* fruits were offered at all, and only one individual was tested. In turn, we observed a strong preference of *S. lilium* for the fruits of *Solanum*, what has been observed in several dietary studies under natural conditions based on fecal analysis (e.g., Marinho-Filho 1991, Giannini 1999, Mello et al. 2008a, Lobova et al. 2009, Sánchez et al. 2012). It is interesting to notice that the preference for *Solanum* observed in the present study was as marked as the previously cited studies based on the fecal samples collected in the natural habitat, even though we offered sliced fruits to the bats, which evidences the strong association between *S. lilium* and *Solanum*. Furthermore, the results obtained were consistent not only for one experimental round, but for two consecutive rounds, which increases their reliability.

As there was no effect of the amount of fruits offered on their consumption rates, probably, when the fruits are offered in a standardized way (sliced and in equal amounts), the energetic costs of different fruit species become similar, and *S. lilium* bats feel free to focus on their favorite fruits, although they still consume other fruits. Therefore, as *lilium* bats can feed almost exclusively on fruits in some localities (Thomas 1984, Mello et al. 2008a), they probably need to diversify the plant species included in their natural diet, in order to meet their nutritional requirements. Diet complementation has already been observed in other stenodermatine bats, which, for instance, need to drink muddy water frequently to obtain important minerals that are not abundant in fruits (Bravo et al. 2010).

Like all stenodermatines, *Sturnira lilium* is a specialized frugivore (Mello et al. 2008a). The species of *Sturnira* seem to have a strong preference for *Solanum* and to be the main seed dispersers of some species of this genus (Lobova et al. 2009), although there are *Solanum* species that are dispersed mainly by birds or by different vectors combined (Jacomassa and Pizo 2010). In addition, although the toxicity of *Solanum variabile* is low (Antonio et al. 2004), future studies could investigate which morphological and physiological adaptations or exaptations allow *Sturnira* bats to explore other species of *Solanum* that contain toxic secondary compounds, so that these fruits can be the core of their diet.

Interindividual differences in the preference for secondary and tertiary fruits, although small, probably mean that fruits of the genera *Cecropia* and *Piper* may be equally important to the population as a whole, but differences occur at the individual level. We suggest that these differences in fruit consumption be explained by differences in

Brought to you by | Universidade Estadual Paulista - Sao Paulo
Authenticated
Download Date | 10/9/14 6:24 PM

the efficiency of obtaining or digesting each kind of fruit and may be even a mechanism of competition relaxation, but these mechanisms have not been investigated in the present study. Learning could also play an important role, as mothers teach their young how to find fruits, and so they may influence their future preferences as adults (Altringham 1996). The consistency of those differences as well as the mechanisms behind them remains to be studied in the future. In addition, considering the interindividual differences observed (Figure 2) and the positive responses to cafeteria trials, it would be interesting for future studies to investigate nestedness in individual diets. In other words, in some natural populations, individuals may not only feed on different subsets of the total resource pool. Sometimes, individuals with a narrower diet feed on a subset of the items consumed by individuals with a broader diet, what could be interpreted as evidence of an optimal diet (Howell and Hartl 1980, Pyke 1984), as the items in the population's diet could be ranked according to their cost-benefit relationship from preferred to occasional. The most important items would be present in the diets of most individuals, while the least consumed items would appear only in the diet of the most generalistic individuals (see, for instance, Pires et al. 2011).

Finally, we conclude that interindividual variations in diet may be one of the mechanisms behind differences in foraging areas observed in the same population (Rogeri 2011). Different habitats can be safe or unsafe for seed germination and seedling establishment, and the density of the three plant species used in the experiment varies largely among habitat types in the study area (Rogeri 2011). If different individuals have different fruit preference, and these differences lead them to forage in different habitats, where their preferred fruits are more abundant, ultimately, individual specialization in diet and use of foraging areas can lead to differences among individuals in dispersal efficiency (Schupp et al. 2010). The consequences for the seed dispersal service rendered by these bats probably depend on how strong these interindividual variations are and on the proportion of safe and unsafe habitats where the seeds are carried to.

Acknowledgments: We thank many colleagues who helped us in this study. Ariovaldo Cruz-Neto, Elisabeth Kalko, and Susan Barnard helped us with invaluable information about maintaining bats in captivity, building flight tents, and setting up behavioral experiments. Vinicius Kavagutti, Lucas Sacilotto, Débora Motta, Patrícia Rogeri, Pavel Dodonov, and Tiago Andrade assisted us in the field and the experiments. Márcio Araújo helped us with the literature and discussions about individual specialization. Marcelo R. Nogueira helped us in bat identification. Plants were identified by Maria I. S. Lima. Carsten Dormann, Nico Blüthgen, and Vladimir Batagelj advised us on the use of their network software. Kirstin Übernickel gave us suggestions for the statistical analysis. The Federal University of São Carlos and EMBRAPA Pecuária Sudeste provided us with fieldwork infrastructure. The Brazilian Research Council (CNPq, 123569/2010-9), the São Paulo Research Foundation (Fapesp, 2006/00265-0), and the Alexander von Humboldt Foundation (AvH, 1134644) funded our study. This study is dedicated to the memory of our great mentor and friend Elisabeth Kalko.

Received September 19, 2012; accepted May 24, 2013; previously published online July 4, 2013

References

Aguiar, L.M.S. and J. Marinho-Filho. 2004. Activity patterns of nine phyllostomid bat species in a fragment of the Atlantic Forest in Southeastern Brazil. Rev. Brasil. Zool. 21: 385–390.

Altringham, J.D. 1996. Bats: biology and behaviour. Oxford: Oxford University Press, UK. pp. 262.

Andrade, T.Y. 2008. Hierarquia de seleção de frutos por morcegos filostomídeos nos níveis de espécies e indivíduos. Bachelor's dissertation. Universidade Federal de São Carlos. Departamento de Botânica, São Carlos, Brazil.

Antonio, J.M., J.S. Gracioso, W. Toma, L.C. Lopez, F. Oliveira and A.R.M. Souza Brito. 2004. Antiulcerogenic activity of ethanol extract of *Solanum variabile* (false "jurubeba"). J. Ethnopharmacol. 93: 83–88.

Araújo M.S., P.R. Guimarães Jr., R. Svanbäck, A. Pinheiro, P.R. Guimarães, S.F. Reis and D.I. Bolnick. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. Ecology 89: 1981–1993.

Barclay, R.M.R. 1985. Foraging behavior of the African insectivorous bat, *Scotopilus leucogaster*. Biotropica 170: 65–70.

Barnard, S. 1995. Bats in captivity. Wild Ones Animal Books, Springville, UT. pp. 194.

Blüthgen, N., F. Menzel and N. Blüthgen. 2006. Measuring specialization in species interaction networks. BMC Ecol. 6: 1–12.

Bolnick, D.I., I.L.H. Yang and J.A. Fordyce. 2002. Measuring individual-level resource specialization. Ecology 10: 2936–2941.

Bolnick, D.I., R. Svanbäck, J.A. Fordyce, L.H. Yang, J.M. Davis, C.D. Hulsey and M.L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. Am. Nat. 161: 1–28.

Brought to you by | Universidade Estadual Paulista - Sao Paulo
Authenticated
Download Date | 10/9/14 6:24 PM

Bonaccorso, F.J. and T.H. Gush. 1987. Feeding behaviour and foraging strategies of captive Phyllostomid fruit bats: an experimental study. J. Anim. Ecol. 56: 907–920.

Bravo, A., K.E. Harms and L.H. Emmons. 2010. Puddles created by geophagous mammals are potential mineral sources for frugivorous bats (Stenodermatinae) in the Peruvian Amazon. J. Trop. Ecol. 26: 173–184.

Cryan, P.M., C.A. Stricker and M.B. Wunder. 2012. Evidence of cryptic individual specialization in an opportunistic insectivorous bat. J. Mammal. 93: 381–389.

Dirzo, R. and A. Miranda. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. In: (P.W. Price, T.M. Lewinsohn, G.W. Fernandes, W.W. Benson, eds.) Plant-animal interactions: evolutionary ecology in tropical and temperate regions. Wiley and Sons Pub, New York, NJ. pp. 273–287.

Dormann, C.F., B. Gruber and J. Fründ. 2008. Introducing the bipartite package: analyzing ecological networks. R News 8: 8–11.

Emmons, L.H. and F. Feer. 1997. Neotropical rainforest mammals: a field guide. The University of Chicago Press, Chicago, IL. pp. 396.

Esbérard, C.L.L. and H.G. Bergallo. 2005. Sampling bats for six or twelve hours in each night? Rev. Bras. Zool. 22: 1095–1098.

Estes, J.A., M.L. Riedman, M.M. Staedler, M.T. Tinker and B.E. Lyon. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. J. Anim. Ecol. 72: 144–155.

Fortuna, M.A., A.G. Popa-Lisseanu, C. Ibañez and J. Bascompte. 2009. The roosting spatial network of a bird-predator bat. Ecology 90: 934–944.

Gannon, M.R., M.R. Willig and J.J. Knox-Jones.1989. *Sturnira lilium*. Mamal. Spec. 333: 1–5.

Gardner, A.L. 2007. Mammals of South America, Volume 1. Marsupials, xenarthrans, shrews, and bats. University of Chicago Press, Chicago, IL. pp. 669.

Gentry, A.H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. Biotropica 6: 64–68.

Giannini, N. 1999. Selection of diet and elevation by sympatric species of *Sturnira* in an Andean rainforest. J. Mammal. 80: 1186–1195.

Herrera, L.G., K.A. Hobson, A. Manzo, D. Estrada, V. Sanchez-Cordero and C. Mendez. 2001. The role of fruits and insects in the nutrition of frugivorous bats: evaluating the use of stable isotope models. Biotropica 33: 520–528.

Howell, D.J. and D.L. Hartl. 1980. Optimal foraging in Glossophaginae bats: when to give up. Am. Nat. 115: 696–704.

Isbell, F., V. Calcagno, A. Hector, J. Connolly, W.S. Harpole, P.B. Reich, M. Scherer-Lorenzen, B. Schmid, D. Tilman, J. van Ruijven, A. Weigelt, B.J. Wilsey, E.S. Zavaleta and M. Loreau. 2011. High plant diversity is needed to maintain ecosystem services. Nature 477: 199–202.

Jacomassa, F.A.F. and M.A. Pizo. 2010. Birds and bats diverge in the qualitative and quantitative components of seed dispersal of a pioneer tree. Acta Oecol. 36: 493–496.

Kalko, E.K.V. and M.A. Condon. 1998. Echolocation, olfaction and fruit display: how bats find fruit of flagellichorous cucurbits. Funct. Ecol. 12: 364–372.

Kunz, T.H. 1988. Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, DC. pp. 556.

Lobova, T.A., C.K. Geiselman and S.A. Mori. 2009. Seed dispersal by bats in the Neotropics. Botanical Garden Press, New York, NJ. pp. 465.

Manly, B.F.J. 2007. Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall/CRC, Laramie, WY, USA. pp. 455.

Marinho-Filho, J.S. 1991. The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. J. Trop. Ecol. 7: 59–67.

Mello, M.A.R., E.K.V. Kalko and W.R. Silva. 2008a. Diet and abundance of the bat *Sturnira lilium* (Chiroptera) in a Brazilian montane Atlantic forest. J. Mammal. 89: 485–492.

Mello, M.A.R., E.K.V. Kalko and W.R. Silva. 2008b. Movements of the bat *Sturnira lilium* and its role as a seed disperser of Solanaceae in the Brazilian Atlantic forest. J. Trop. Ecol. 24: 225–228.

Mello, M.A.R., F.M.D. Marquitti, P.R. Guimarães Jr., E.K.V. Kalko, P. Jordano and M.A.M. Aguiar. 2011. The missing part of seed dispersal networks: structure and robustness of bat-fruit interactions. PloS One 6: e17395.

Muscarella, R. and T.H. Fleming. 2007. The role of frugivorous bats in tropical forest succession. Biol. Rev. 82: 573–590.

Myers N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Paese, A. 1997. Caracterização e análise ambiental do campus da Universidade Federal de São Carlos (UFSCar), São Carlos, SP. MSc Dissertation. DSc. Universidade Federal de São Carlos. Departamento de Hidrobiologia, São Carlos, Brazil.

Passos, F.C., W.R. Silva, W.A. Pedro and M.R. Bonin. 2003. Frugivoria em morcegos (Mammalia, Chiroptera) no Parque Estadual Intervales, sudeste do Brasil. Rev. Brasil. Zool. 20: 511–517.

Pires, M.M., P.R. Guimarães, M.S. Araújo, A.A. Giaretta, J.C.L. Costa and S.F. dos Reis. 2011. The nested assembly of individual-resource networks. J. Anim. Ecol. 80: 896–903.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. Ann. Rev. Ecol. Syst. 15: 523–575.

Rogeri, P.K. 2011. Especialização individual no uso do espaço em morcegos frugívoros. Master's dissertation. Universidade Estadual de Campinas Universidade Federal de São Carlos. Instituto de Biologia, Campinas, Brazil.

Rojas, D., A. Vale, V. Ferrero and L. Navarro. 2011. When did plants become important to leaf-nosed bats? Diversification of feeding habits in the family Phyllostomidae. Mol. Ecol. 20: 2217–28.

Sallabanks, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. Ecology 74: 1326–1336.

Sánchez, M.S., L.V. Carizo, P.N. Giannini and R.M. Barquéz. 2012. Seasonal patterns in the diet of frugivorous bats in the subtropical rainforests of Argentina. Mammalia 76: 269–275.

Schupp, E.W., P. Jordano and J.M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytol. 188: 333–353.

Sikes, R.S., W.L. Gannon and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal. 92: 231–253.

Simmons, N. and R. Voss. 1998. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna: Bats. Bull. Am. Mus. Nat. Hist. 237: 1–219.

Brought to you by | Universidade Estadual Paulista - Sao Paulo
Authenticated
Download Date | 10/9/14 6:24 PM

Smith, T.B. 1990. Resource use by bill morphs of an African finch: evidence for intraspecific competition. Ecology 71: 1246–1257.

Thies, W. 1998. Resource and habitat use in two frugivorous bat species (Phyllostomidae: *Carollia perspicillata* and *C. castanea*) in Panama: mechanisms of coexistence. PhD dissertation. Eberhard Karls Universität Tübingen, Tübingen, Germany.

Thomas, D.W. 1984. Fruit intake and energy budgets of frugivorous bats. Physiol. Zool. 57: 457–467.

Uieda, W. and J. Vasconcellos-Neto. 1985. Dispersão de *Solanum* spp. (Solanaceae) por morcegos, na região de Manaus, AM, Brasil. Rev. Brasil. Zool. 2: 449–458.

Vizotto, L.D. and V.A. Taddei. 1973. Chave para determinação de quirópteros brasileiros. Editora da Universidade Estadual de São Paulo, São José do Rio Preto, Brazil. pp. 72.

Wang, B.C. and T.B. Smith. 2002. Closing the seed dispersal loop. Trends Ecol. Evol. 17: 379–385.

Werner, T.K. and T.W. Sherry. 1986. Behavioral feeding Specialization in *Pinaroloxias inornata*, the "Darwin's finch" of Cocos Island, Costa Rica. Proc. Natl. Acad. Sci. USA 84: 5506–5510.

West, L. 1986. Interindividual variation in prey selection by the snail *Nucella* (= *Thais*) *emarginata*. Ecology 67: 798–809.

Zar, J.H. 1996. Biostatistical analysis. Third ed. Prentice-Hall, Upper Saddle River, NJ. pp. 662.

Brought to you by | Universidade Estadual Paulista - Sao Paulo
Authenticated
Download Date | 10/9/14 6:24 PM