

# The implications of food hardness for diet in bats

L. F. AGUIRRE\*†, A. HERREL‡, R. VAN DAMME‡ and E. MATTHYSEN‡

\*Centro de Biodiversidad y Genetica, Universidad Mayor San Simon, PO Box 538, Cochabamba, Bolivia, and

‡University of Antwerp, Department Biological Sciences, Universiteitsplein 1, B-2610 Belgium

## Summary

1. Neotropical bat communities are characterized by a broad species diversity, which can be achieved and maintained only through partitioning of the available resources.
2. Here patterns of trophic resource utilization within a single neotropical savanna bat community are investigated. Moreover, the physical properties of food items (i.e. hardness), its variation with food size, and whether food hardness differs between items consumed by the bats in this community are investigated experimentally.
3. The results show that food hardness increases with the size of the food item, and that distinct differences exist in the amount of force needed to crush different food items (beetles *vs* other insects *vs* fruits).
4. Using previously published data on bite forces from species in the same community it is explored whether food hardness may play a role in shaping the diets of the bats in the community. The combined data on bite forces and food hardness indicate that food hardness can both directly and indirectly limit dietary diversity in bats.
5. The results also indicate that dietary specialization may potentially result in a decrease in trophic breadth for some species through its effect on bite performance.

*Key-words:* Bite force, Chiroptera, feeding

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## Introduction

Over the past few decades, several studies have demonstrated the broad diversity of bats in the neotropics, with single sites harbouring up to, or even over, 70 species of bats (Koepcke 1987; Timm *et al.* 1989; Handley, Wilson & Gardner 1991; Medellín 1993; Patterson, Pacheco & Solari 1996; Simmons & Voss 1998; Lim & Engstrom 2001). Such diversity can probably only be achieved and maintained through an intricate partitioning of the available resources. Both spatial (e.g. where animals forage) and temporal (when animals forage) patterns of resource utilization are clearly major factors structuring these communities (Heithaus, Fleming & Opler 1975; Bonaccorso 1979; Findley & Black 1983; Fleming 1986). Within the three-dimensional habitat matrix, bats can specialize on a certain spatial component thereof, thus reducing or even avoiding competition with the rest of the community (Heithaus *et al.* 1975; Arlettaz, Perrin & Hausser 1997; Kalko 1997; Bernard, Albernaz & Magnusson 2001; Kalko & Handley 2001). Bats have done this to a large degree and consequently slow fliers, hoverers, gleaners and fast fliers, all with a specialized wing design and flight pattern, are typically part of a bat community (see Norberg 1994). Other spatial aspects such as the use

and selection of roosts and temporal differences in foraging patterns have been demonstrated to be important elements of resource partitioning in bat communities (Heithaus *et al.* 1975; Fenton 1982; Fenton & Rautenbach 1986).

Given the considerable diversity of trophic niches in New World bat communities, partitioning of food resources is probably one of the major elements structuring the community. The explosive, adaptive radiation of certain groups such as phyllostomid bats into previously unexplored trophic niches lies, at least partly, at the basis of the tremendous diversity and complexity of bat communities in the neotropics (Dumont 1999; Freeman 2000). Previous studies have documented how neotropical bats can be grouped into feeding guilds such as insectivores, carnivores, piscivores, sanguivores, nectarivores and omnivores, which partition the available food resources (see for example Bonaccorso 1979; McKenzie & Rolfe 1986; Neuweiler 1989; Fenton 1990; Findley 1993; Kalko 1997). Yet, most feeding guilds are represented by several species of bats, all specializing on similar food items. As within insectivorous, omnivorous and frugivorous guilds many species coexist (e.g. a typical community can have five or more frugivorous bats and might have up to 15 or more insectivores, see Heithaus *et al.* 1975; Aguirre, Hanagarth & de Urioste 1996; Medellín 1993; Dumont 1999; Simmons & Voss 1998), food resource partitioning at these lower levels must take place too.

Although members of a guild are, at first glance, utilizing the same prey (e.g. insects or fruits), food items differ in many aspects, which may shape resource utilization patterns of bats. Not only do food items differ in spatial and temporal availability (Kalko, Herre & Handley 1996b; Kalko, Handley & Handley 1996a; Julien-Laferrière 1999), but the behavioural and physical properties of the food, such as its size, evasiveness and resistance to mechanical deformation, can also differ drastically for seemingly similar prey. Recently, Dumont (1999) showed how fruit hardness has a pronounced impact on the feeding behaviour, and might ultimately even determine the food items selected and utilized by frugivorous phyllostomid bats. Other authors (e.g. Freeman 1979; Sosa, De Asenção & Soriano 1996) suggest an important role for prey size and hardness in prey selection in insectivorous bats. Moreover, Goldman & Henson (1977) have observed how certain species of bats were unable to eat beetles (i.e. were not able to crush them), although they were capable of capturing these prey. These observations indicate that food hardness might be important in determining food resource use and food partitioning at lower organizational levels (i.e. within guilds), potentially resulting in decreased competition between members of the same guild.

Theoretical considerations (see Lucas 1979; Lucas & Luke 1984) suggest that the physical properties of food items are indeed different between 'hard-shelled' prey, such as beetles, and other insects (Currey 1970; Freeman 1979, 1984; Lucas, Corlett & Luke 1985). Similarly, fruits can be grouped into hard and soft categories based on the structural properties of the outer skin (Freeman 1988; Dumont 1999). However, whereas many authors have speculated about food hardness and how it may affect prey use, dental and cranial morphology, and niche segregation (Freeman 1979, 1984; Sosa *et al.* 1996), the hardness of food items has rarely been tested (but see Dumont 1999). Moreover, the relations between food hardness and size remain unexplored to date, but may have an important impact upon food selection (but see Herrel *et al.* 1999, 2001). As previously suggested by Dumont (1997, 1999), the assessment of the physical properties of food items (size, hardness, toughness) could offer tremendous insights into the range of variation in cranial and mandibular morphology and food utilization patterns among frugivores. If food items do show large differences in physical properties, the demands thereof on the cranial morphology and the performance of the feeding apparatus are probably strong (e.g. Freeman 1979, 1988, 1995).

In the present study we investigate patterns of food resource partitioning in a previously studied Neotropical bat community. Moreover, we wanted to test whether food items consumed by the species, at the community and guild levels, show marked differences in physical properties such as size and hardness, which might help to improve our understanding of resource

partitioning. We do so by assessing food hardness experimentally for a wide range of food items naturally eaten by bats in the community. Finally, by combining these data with previously published data on bite forces for bats from the same community, we explore how food hardness may play a role in shaping the diet of different species, and whether trophic specialization comes at the expense of a reduced trophic breadth as suggested previously (Aguirre *et al.* 2002).

## Materials and methods

### STUDY SITE AND SPECIES

We studied feeding habits of bats from a community belonging to the Espiritu Wildlife Refuge, a seasonally flooded savanna located in the central-north of the 'Llanos de Moxos' (Beni, Bolivia). The 23 species of bats of which dietary data were collected (Table 1) constitute more than 60% of the total bat community of the area (Aguirre *et al.* 1996). All dietary data were collected at the end of the dry season (August–October) which precludes us from assessing seasonal variability in diet. Bats were captured inside, or in the surroundings of, forest islands within the savanna using mist nets. After capture, bats were evaluated for age, sex and reproductive status. Adult bats were distinguished from sub-adults by the degree of ossification in the metacarpal-phalangeal joint of the third finger and reproductive females were determined by direct palpation of the abdomen.

### STOMACH CONTENT ANALYSES

Depending on their abundance, up to eight individuals per species (only adults and non-reproductive females) were captured and preserved for stomach content analyses (see Appendix). Stomachs were removed and stored in a 75% aqueous ethanol solution for analysis. The contents was removed, placed in a Petri dish and analysed under a Zeiss binocular microscope (Carl Zeiss Inc., Chester, USA). Insects in the samples were determined to the family level using descriptions in Borror, Triplehorn & Johnson (1989) and by comparison with a reference collection of arthropods collected by the first author at the sites where the bats were captured. Where possible, the size (length) of the insects was determined by comparing the remains in the stomach with insects from the reference collection. All prey were classified as belonging to one of five length categories (Table 2). The stomach contents of frugivorous species (containing mainly seeds) was identified by comparison with seeds contained in a reference collection at the Bolivian National Herbarium. As the identification of diet in frugivorous bats was based purely on the presence of seeds in the stomach, it might be biased towards smaller fruits (seeds of large fruits may not be ingested).

**Table 1.** Summary morphometrics of the species sampled in the present study. Nomenclature follows Aguirre *et al.* (1996). Table entries are means. The acronyms for the species are composed of the first letter of the genus and the first three letters of the species name. Bite force data were taken from Aguirre *et al.* (2002). See Aguirre *et al.* (2002) for sample sizes of bite force data

Bat species	Acronym	Mass (g)	Forearm length (mm)	Skull length (mm)	Bite force (N)
<i>Artibeus jamaicensis</i>	AJAM	46.60	63.10	3.10	24.96
<i>Carollia perspicillata</i>	CPER	18.10	41.80	22.80	6.65
<i>Desmodus rotundus</i>	DROT	32.50	58.20	12.50	8.60
<i>Eptesicus furinalis</i>	EFUR	8.50	38.60	15.00	7.30
<i>Eumops glaucinus</i>	EGLA	30.10	57.10	23.70	–
<i>Eumops hansae</i>	EHAN	17.30	39.20	18.20	–
<i>Glossophaga soricina</i>	GSOR	20.10	33.70	20.20	2.25
<i>Micronycteris minuta</i>	MMIN	9.20	37.20	19.20	2.18
<i>Molossops temminckii</i>	MTEM	6.90	31.60	14.60	–
<i>Molossus molossus</i>	MMOL	21.70	41.60	18.60	8.34
<i>Molossus rufus</i>	MRUF	26.60	48.40	20.50	8.40
<i>Myotis albescens</i>	MALB	5.60	33.60	13.60	2.18
<i>Myotis nigricans</i>	MNIG	4.60	33.10	13.20	1.27
<i>Myotis simus</i>	MSIM	10.00	38.10	14.40	2.88
<i>Noctilio albiventris</i>	NALB	29.70	59.70	21.60	11.91
<i>Noctilio leporinus</i>	NLEP	76.10	88.50	28.90	19.90
<i>Phyllostomus discolor</i>	PDISC	37.70	63.30	30.20	21.61
<i>Phyllostomus elongatus</i>	PELO	42.50	66.10	29.50	14.78
<i>Phyllostomus hastatus</i>	PHAS	88.20	78.30	38.40	68.00
<i>Platyrrhinus lineatus</i>	PLIN	25.10	46.80	24.80	25.40
<i>Rhynchonycteris naso</i>	RNAS	6.00	33.80	12.60	–
<i>Sturnira lilium</i>	SLIL	21.60	42.10	22.70	7.72
<i>Tonatia sylvicola</i>	TSIL	26.00	52.50	26.00	21.63

**Table 2.** Range of lengths of the insects found in the stomachs of insectivorous and omnivorous bats at the study site. Insect lengths were estimated based on a reference collection of insects sampled at the same site. Table entries are the absolute number of prey of that size category found for each species

Species	N	Range size (mm)				
		1–5	5–10	10–15	15–20	20–25
<i>P. hastatus</i>	4				2	3
<i>P. elongatus</i>	3		2	2	1	1
<i>P. discolor</i>	3			1		1
<i>T. silvicola</i>	5			2		
<i>N. albiventris</i>	8	14	64	11	3	3
<i>E. furinalis</i>	5	2	8	1	1	
<i>M. simus</i>	2	5	4	1		
<i>M. temminckii</i>	1	2	4			
<i>M. ater</i>	5	1	1	2		2
<i>M. molossus</i>	4		1	1		3

#### FOOD HARDNESS

To investigate the force needed to crush food items consumed by the various bats in the community, a wide variety of arthropods and fruits were collected at the field site to represent the entire variety of prey available to the bats (Table 3). None of the fruits tested was selected on the basis of ripeness. Our hardness values are thus a general indication of the hardness of that fruit type at the end of the dry season. The linear dimensions (length and width) and masses of all food items were recorded before crushing. Food hardness or

crushing strength of food items was measured using an isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland) connected to a Kistler charge amplifier (type 5995, Kistler Inc.; see Herrel *et al.* 2001 for a description of the set-up). A long screw with a flattened free end (surface area of 3 mm<sup>2</sup>) was mounted on the force transducer, and pushed onto the food item until mechanical failure of its external surface occurred. For insects the resistance of different parts of the prey was measured, and the maximal resistance encountered was recorded (usually for the head and the pro-thorax). A similar procedure was used to record the resistance to mechanical failure for fruits. Fruits were tested at several positions along the fruit and the highest forces were recorded as indicating the maximal amount of force an animal would need to reduce that fruit. For *Piper* fruits, the amount of force needed to 'strip' the fruits from the stalk, as well as the amount of force needed to crush a single fruit was recorded.

#### ANALYSES

To investigate relationships between the food dimensions and hardness, all data were log<sub>10</sub>-transformed and hardness was regressed against mass, length or width of the food item tested. All food items were subsequently classified as belonging to one of five categories: hard arthropods (i.e. beetles), soft arthropods, hard fruits (figs) and soft fruits (*Piper*). *Solanum* fruits were included into the analyses as a separate category as no *a priori* predictions regarding their hardness could be made. To test whether these functional food

**Table 3.** Size and hardness of potential food items collected at the study site (Espiritu, Bolivia). Many of the food items measured are eaten by the bats in the community (see Tables 2 and 3)

Food items	<i>N</i>	Mass (g)	Length (mm)	Width (mm)	Max. force (N)
<b>Arthropods</b>					
<b>COLEOPTERA</b>					
Scarabaeidae					
Melolontinae					
sp. 1	13	2.12 ± 0.89	30.62 ± 4.13	16.00 ± 2.27	34.02 ± 11.35
sp. 2	25	0.24 ± 0.21	18.20 ± 2.08	9.84 ± 1.07	7.86 ± 3.51
sp. 3	12	0.10 ± 0.05	12.25 ± 1.91	6.42 ± 0.90	3.47 ± 1.35
Rutellinae	5	0.94 ± 0.13	24.60 ± 0.55	13.60 ± 0.89	24.78 ± 2.00
Aphodiinae	8	0.63 ± 0.13	18.50 ± 1.12	11.63 ± 1.22	14.48 ± 2.27
Hydrophilidae	2	0.97 ± 0.06	40.67 ± 1.15	19.00 ± 0.00	20.83 ± 6.51
Dytiscidae sp. 1	4	0.05 ± 0.00	13.75 ± 4.92	5.25 ± 2.50	2.25 ± 0.31
Elateridae	5	0.13 ± 0.15	17.20 ± 6.14	5.40 ± 2.07	7.22 ± 5.24
Tenebrionidae	1	0.00	11.00	4.00	3.00
Cerambycidae	1	0.10	19.00	3.00	10.00
Curculionidae	1	0.10	16.00	5.00	20.40
Dytiscidae sp. 2	1	0.30	19.00	10.00	8.90
<b>ODONATA</b>					
sp. 1	1	0.30	4.80	6.00	1.60
sp. 2	8	0.07 ± 0.03	14.25 ± 2.31	5.63 ± 1.30	2.71 ± 0.69
<b>ORTHOPTERA</b>					
Blattidae	1	0.40	36.00	18.00	3.40
Acrididae	4	0.73 ± 0.68	53.25 ± 17.17	6.25 ± 1.71	7.45 ± 3.20
Tettigoniidae	2	0.10 ± 0.14	22.50 ± 6.36	4.50 ± 0.71	2.65 ± 0.49
<b>LEPIDOPTERA</b>					
Noctuidae	8	0.28 ± 0.47	18.75 ± 11.96	6.25 ± 2.82	1.75 ± 1.24
<b>HOMOPTERA</b>					
Cicadidae	3	0.08 ± 0.03	15.00 ± 1.00	5.33 ± 0.58	1.67 ± 0.38
<b>ARACHNIDAE</b>					
Theraphosidae	3	3.15 ± 0.64	33.50 ± 3.54	14.00 ± 0.00	2.35 ± 2.05
<b>Fruits</b>					
<i>Ficus obtusifolia</i>	11	1.47 ± 0.23	14.83 ± 0.88	16.27 ± 0.90	4.23 ± 0.54
<i>Ficus trigona</i>	2	2.80 ± 0.00	23.00 ± 0.00	28.00 ± 0.00	2.00 ± 0.00
<i>Ficus eximia</i>	11	8.22 ± 2.80	27.17 ± 2.64	26.50 ± 2.74	5.19 ± 1.99
<i>Dipterix odorata</i>	6	15.30 ± 0.00	44.00 ± 0.00	34.00 ± 0.00	16.95 ± 1.90
<i>Piper aduncum</i>	7	1.03 ± 0.30	10.60 ± 2.20	0.44 ± 0.05	0.83 ± 0.44
<i>Solanum wrightii</i>	7	0.33 ± 0.11	7.97 ± 0.64	8.91 ± 0.76	4.70 ± 1.31

categories differed from one another, food hardness was regressed against food mass (both  $\log_{10}$ -transformed), residuals were calculated and used in an analysis of variance, and subsequent *post-hoc* test (Duncan test). All analyses were performed in Statistica (Version 5.0, Statsoft Inc.)

## Results

### DIET

The bats used for dietary analysis in the present study represented a subsample (62%) of the total community found in Espiritu (Aguirre *et al.* 1996). Because only mist netting was used to capture bats, aerial insectivores are probably under-represented in our sample. In total, dietary data were collected for 23 out of the 37 species present in the area (Table 1). Although all trophic guilds were included in our sample, carnivorous bats are under-represented in the analysis. From this group, only *Noctilio leporinus* was examined. All three individuals contained only fish in their stomachs. Fish

were strongly chewed and only small, white fleshy remains and crushed fish scales could be recovered from the stomachs. Consequently no estimate of fish size was possible.

A large portion of the insectivorous bat community was analysed for diet (68%) and arthropods belonging to two classes and nine orders were represented (see Appendix). More than half the insects eaten by bats in the community were beetles (Coleoptera). Other important items consumed by insectivorous bats were Diptera (especially individuals of the suborder Nematocera, comprising 10% of all arthropods), ants (Formicidae) and crickets (Gryllidae). Molossid bats (*Eumops glaucinus*, *Molossus rufus* and *M. molossus*) and *Noctilio albiventris* were the only species to prey on damselflies (Zygoptera). Within the insectivorous guild, *Noctilio albiventris* was the species including the largest arthropod diversity into its diet, with coleopterans constituting more than half of its diet (see Appendix). As mentioned, crickets were consumed frequently by bats, with *Tonatia sylvicola* showing a distinct preference for them (together with scarabaeid beetles). On

the other hand, vespertilionid and molossid bats did not seem to be very selective and ate a wide proportion of the available spectrum, but typically in low quantities.

Among the omnivorous bats, *Phyllostomus hastatus* ate a large number of arthropods, predominantly beetles (96%). The other two omnivores, *P. discolor* and *P. elongatus*, both ate a wider variety of arthropod prey (see Appendix). Both the frugivorous and nectarivorous bats in the sample studied here typically had a low diversity of food items in their stomach (see Appendix). Among the frugivores, *Platyrrhinus lineatus* and *Artibeus jamaicensis* were eating mostly figs. *Sturnira lilium* and *Carollia perspicillata*, on the other hand, were found to eat only *Solanum* and *Piper* fruits, respectively. *Glossophaga soricina* seemed to be an exclusively nectarivorous species at our field site at the time of study, as no other food was found in its stomach. The last species in the community, the Common Vampire Bat *Desmodus rotundus*, was mainly feeding on blood, although an intact small (<2 mm) water beetle (Dytiscidae) was found in the stomach of one of the individuals examined. As the beetle was not chewed, it might have been ingested accidentally.

#### PREY DIMENSIONS

Although all bats (with the possible exception of *Desmodus*) chew their food thoroughly, for arthropods, the size of the prey item could often be estimated using a reference collection of arthropods captured at the same site. Whereas vespertilionid bats (*Myotis* sp., *Eptesicus* sp.) typically ate small prey, *Phyllostomus hastatus* and *P. elongatus* consumed mostly medium to large prey (Table 2). *Noctilio albiventris* apparently utilized the entire spectrum of prey sizes with a dominance of small prey in its diet. The two molossid species for which prey size could be estimated seemed to eat intermediate-sized prey as well as some very large prey (note that all large prey were grasshoppers). Both *Tonatia sylvicola* and *P. discolor* had intermediate-sized prey in their stomachs. Several *Artibeus jamaicensis*, captured in mist nets carried figs which were recovered and measured, allowing an estimate of their size. On average, *Artibeus* carried figs of  $7.4 \pm 3.3$  g and  $26.5 \pm 2.9$  mm in diameter ( $N = 7$ ). Although there thus seems to be a general trend for the larger bats to eat larger prey, some of the smaller species (e.g. *M. molossus*) also ate large prey and some big species such as *N. albiventris* also ate very small prey (see Table 2).

#### FOOD HARDNESS

Food hardness estimates indicated that within each food group, significant relationships between food item mass and its linear dimensions were observed (i.e. longer or wider items being heavier; see Table 4). Moreover, for all prey groups a significant relationship between the size of the food item (as indicated by either mass, length or width) and its hardness was observed

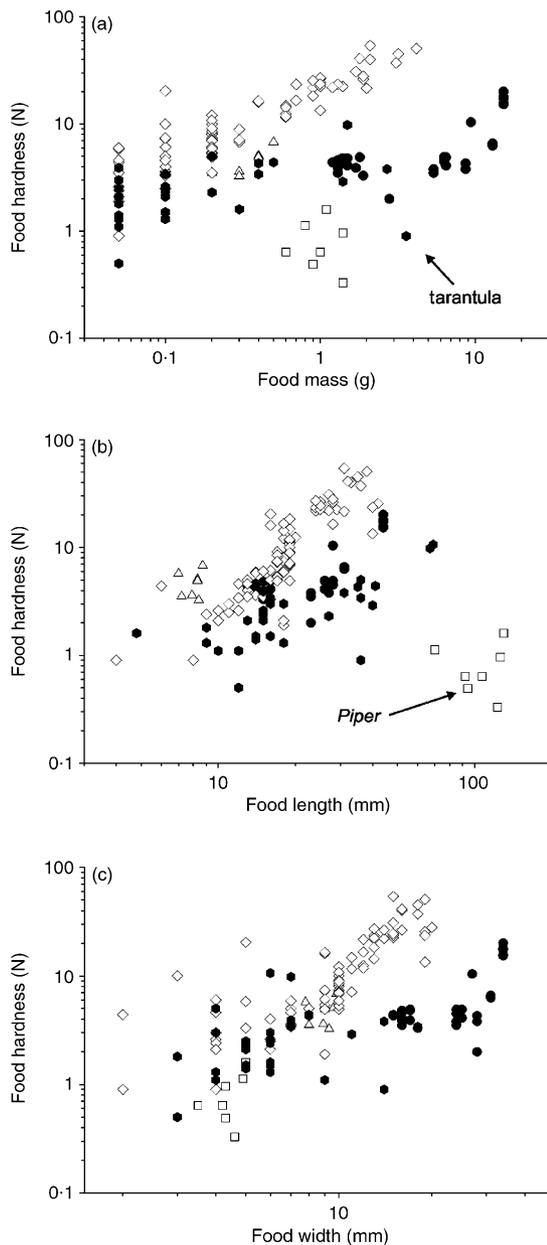
**Table 4.** Results of the regression analyses performed on the food hardness data

	Slope	Intercept	$r^2$
<b>Regressions of food item mass vs. its linear dimensions</b>			
<i>Piper</i> ( $N = 7$ )			
Length	0.55	2.02	0.56*
Width	0.21	0.64	0.28
<i>Solanum</i> ( $N = 7$ )			
Length	0.22	1.01	0.87**
Width	0.92	0.03	0.95**
Figs ( $N = 30$ )			
Length	0.41	1.10	0.94**
Width	1.33	-0.45	0.93**
Beetles ( $N = 81$ )			
Length	0.27	1.42	0.69**
Width	0.34	1.15	0.74**
Other arthropods ( $N = 29$ )			
Length	0.33	1.52	0.53**
Width	0.24	0.99	0.51**
<b>Regressions of food dimensions vs. food hardness</b>			
Figs			
Length	1.12	-0.79	0.54**
Width	1.22	-0.92	0.34*
Mass	0.45	0.46	0.48**
Beetles			
Length	1.91	-1.47	0.73**
Width	1.45	-0.44	0.63**
Mass	0.67	1.32	0.82**
Other arthropods			
Length	0.73	-0.57	0.46**
Width	0.41	0.05	0.07
Mass	0.18	0.49	0.15*

\*Regression significant at the  $\alpha = 0.05$  level; \*\*significant at the  $\alpha = 0.01$  level.

(Fig. 1, Table 4). For beetles, mass was the best predictor of hardness ( $R^2 = 0.82$ ), and the  $\log_{10}$  of hardness increased strongly positively with the  $\log_{10}$  of mass (intercept: 1.32; slope: 0.67). For all other arthropods combined, a significant positive relation between hardness and mass, and hardness and prey length was present. Here prey length was the best predictor of hardness (intercept: -0.57, slope: 0.73;  $R^2 = 0.46$ ). For figs, a similar highly significant and positive relationship was observed between hardness on one hand and mass and fig diameter on the other hand, with the diameter being the best predictor of hardness (intercept: -0.79, slope: 1.12;  $R^2 = 0.54$ ). As the size ranges of the *Piper* and *Solanum* collected were small, no regression analysis was performed.

An analysis of variance performed on the residual hardness data (hardness regressed against mass, both  $\log_{10}$ -transformed) indicated that food categories differed significantly from each other in hardness ( $F_{4,149} = 57.01$ ;  $P < 0.001$ ). *Post-hoc* tests indicated that beetles were significantly harder than all other prey (see also Table 3). *Solanum* fruits were softer than beetles but, quite unexpectedly, significantly harder than all other food categories. Hard fruits, including figs, were similar to the non-coleopteran arthropods in hardness, but significantly softer than *Solanum* and beetles. *Piper*



**Fig. 1.** Relationship between food hardness and food dimensions. Food items were classified as belonging to one of five categories based on their hardness: beetles (white diamonds), other arthropods (black hexagons), figs (black circles), *Piper* (white squares) and solanum (white triangles). For all categories for which a size range was tested a significant relationship between food size (as indicated by mass, length or width) and hardness was observed (see also Table 4). Note how tarantulas are very soft for their mass. For *Piper*, the length of the frutescence was measured, explaining the low hardness to length ratio.

fruits were significantly softer than all other food items tested (see also Fig. 1).

## Discussion

### DIET ANALYSIS

The dietary data gathered here indicate that the bat community at Espiritu can be grouped into a number

of distinct guilds as previously described for other Neotropical bat communities (Willig 1986; Medellín 1993; Kalko 1997). Most species seemed to belong to a single dietary guild. However, it should be noted that sample sizes were low for some species and that samples were only taken at a single time period (end of the dry season). Consequently, as it has been documented that the availability of fruit and insect prey changes seasonally (e.g. see Bonaccorso 1979), we probably underestimated the true trophic diversity of the species in the community.

When examining published dietary data for the species within the frugivorous guild, it becomes clear that these species in general are not as selective as suggested by the data gathered in the present study. However, despite the much wider variety of food items typically consumed by these bats, the fruits found in their stomach in the present study are a predominant part of the diet (see Bonaccorso 1979; Bonaccorso & Humphrey 1984). Insect eaters such as *T. sylvicola* also seem to be more generalized in certain areas compared with our study site (Humphrey *et al.* 1983; Kalko *et al.* 1996b). Although the molossid are also true insect specialists (e.g. Freeman 1981a), they consumed a wider variety of insect prey than typically reported. Whereas *M. molossus* is sometimes referred to as a durophagous species eating largely Coleopterans (Freeman 1979, 1981a, 1981b), the individuals in this study ate a wide variety of prey, including ants, flies, Zygotera, Orthoptera, Hemiptera and Homoptera, with Coleoptera comprising only about 30% of the total prey.

Unexpectedly, we found only insect prey in the stomachs of those species generally considered omnivores (*P. hastatus*, *P. discolor* and *P. elongatus*). Nevertheless, other studies have demonstrated that in many cases species such as *P. hastatus* predominantly consume fruit, pollen and insects (Humphrey *et al.* 1983; Kalko *et al.* 1996b; Kalko & Condon 1998). *Noctilio albiventris* seems to be a strict insectivore eating a wide variety of insects (see also Kalko *et al.* 1996b) and *N. leporinus* was eating exclusively fish at our site. The presence of an insect in the stomach of one of the *D. rotundus* was rather surprising and may have been incidental (but see Arata, Vaughan & Thomas 1967).

The overall pattern that seems to be appearing by comparing our data with previously published accounts on diet in the same species is that at our study site at the end of the dry season trophic niches seem to be more restricted. As food availability may be limited at this time, competition for resources, and thus also the partitioning thereof, can be expected to be strongest. Additionally, at these periods of food limitation, selection on functional properties that may reduce competition are expected to be strongest. Thus any limitations imposed by food hardness on diet should be reflected by an interaction of diet, food hardness, food item size and bite forces for the species in the community.

Interestingly, the data gathered in the present study as well as data previously gathered for fruits by Dumont (1999) indicate that food items of similar linear dimensions or mass may differ strongly in the force needed to reduce them. As has been demonstrated by Dumont (1999), fresh figs are fairly hard and require more force to crush than other foods such as papaya. Our data for natural food items indicate that *Solanum*, rather unexpectedly, is even harder for a given mass. *Piper*, on the other hand can be considered a soft fruit, which does not require a lot of force to be reduced. Interestingly, Dumont (1999) showed that *Carollia*, a *Piper* specialist, showed no behavioural adaptations in its feeding behaviour that would allow it to efficiently utilize hard fruits such as figs. Fruit hardness might thus play an important role in structuring frugivorous bat guilds. Although the degree of ripeness of fruits was not specifically assessed in the present study, this may have a considerable effect on fruit hardness. As bats typically prefer ripe fruits to unripe ones, it would be most interesting to test whether this is correlated with differences in hardness.

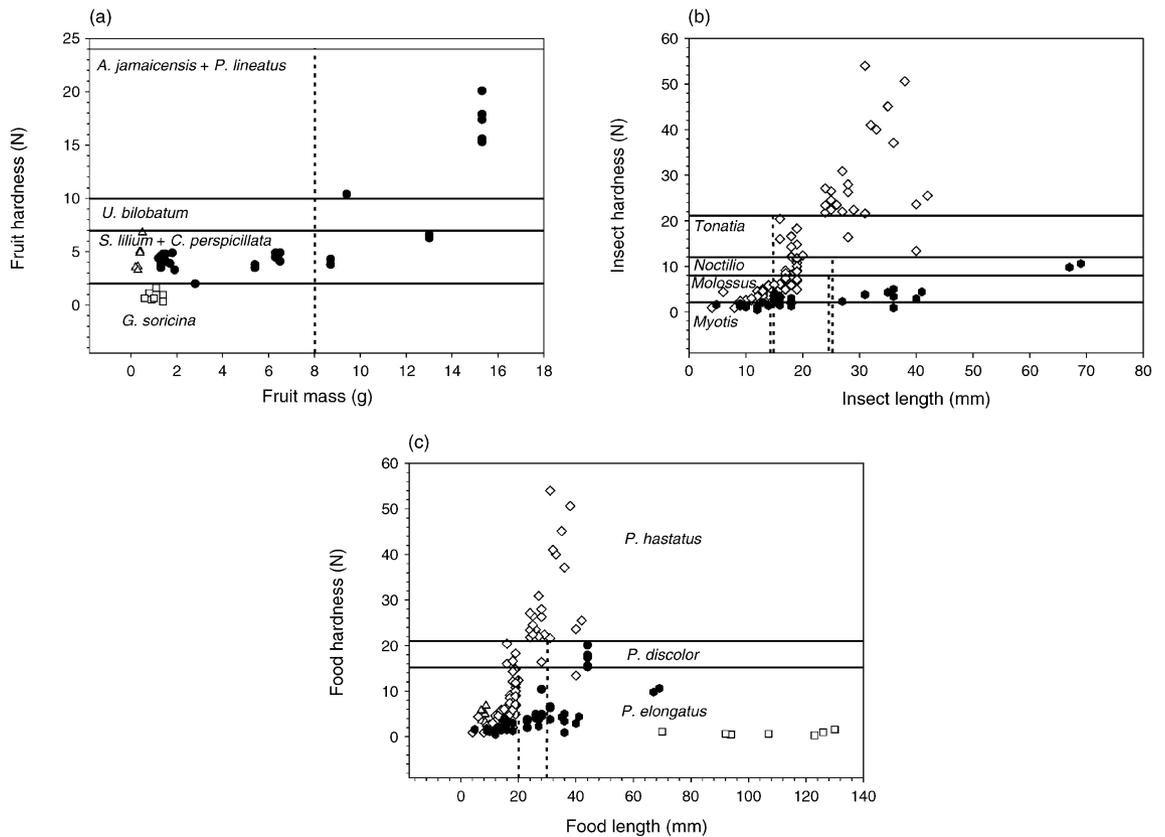
However, there is considerable variation in food hardness also within arthropods. As suggested by previous authors (Freeman 1979, 1981a,b) beetles are indeed much harder than other arthropods for a given size. Additionally, beetle hardness increases much more rapidly with mass than for any other food item tested (see Table 4). For a small insectivorous bat, non-coleopteran arthropods will be much more beneficial as they require less mechanical work to reduce for a given size (but see La Val & La Val 1980). Indeed, our data indicate that, whereas nearly all insectivores will include coleopterans into their diet, only the larger species of bats, such as the three *Phyllostomus* and *N. albiventris*, will prey on large (>15 mm) coleopterans (Table 4). The large insects recovered from the stomachs of *T. sylvicola*, *M. rufus* and *M. molossus* were all non-coleopterans (Table 2). Clearly also within the insectivorous guild food hardness may play a role in prey selection and ultimately in trophic niche partitioning.

For both arthropods and fruits, significant relationships between the dimensions of the food item and its hardness could be demonstrated. Bigger food items will thus typically require higher crushing forces, and may thus be excluded from the diet in species with low bite forces. Moreover, the scaling of food hardness with food dimensions may be different for different food types (Table 4, Fig. 1). Interestingly, among frugivores, a correlation of bat size with fruit size has been demonstrated (Bonaccorso 1979; Kalko *et al.* 1996b). As previously gathered data for bite performance in bats (Aguirre *et al.* 2002) indicate that bite forces increase with bat size, this implies that here food hardness might be driving this relationship between bat size and food size. Big fruits might just be too hard for small bats to chew.

The fact that larger bats do seem to select larger prey, and that only the larger bats will eat large coleopterans suggests that food hardness has major consequences for diet selection. As extensive food processing before swallowing is a part of chiropteran feeding behaviour (all prey were strongly reduced in the stomachs of the animals examined in the present study; see also Kallen & Gans 1972; Czarnecki & Kallen 1980; De Gueldre & De Vree 1984, 1988; Dumont 1999), it is likely that food hardness will place constraints on the diet of the animals. Moreover, harder prey will require more extensive food processing (De Gueldre & De Vree 1984, 1988) and will thus be energetically more demanding. Moreover, larger prey will probably require more time to chew which cannot be spent hunting for more prey, or for other activities.

That food hardness is ecologically relevant, and may in fact be limiting the dietary scope, in bats is illustrated in Fig. 2. Here, the bite forces of the bats (see Aguirre *et al.* 2002) in the community are superimposed on the prey hardness graphs. Additionally, the largest prey found in the stomach is indicated on the figure. Whereas at first sight, little correlation among the maximal food item size, its hardness and the bite forces of the frugivores in the community seems present, for the insectivorous and omnivorous bats in the community clear and strong interactions among food hardness, maximal food size and bite force can be observed. Especially for the two smaller omnivores (*P. elongatus* and *P. discolor*), the maximal size of prey found in the stomach corresponds well to the maximal size of beetle that they could potentially eat based on their bite forces. Also for some of the insectivorous bats (e.g. *Tonatia*, *Myotis*) the largest size of prey found in the stomach seems to be determined by food hardness and bite force. Other insectivorous bats such as the two *Molossus* species and *N. albiventris* seem to be eating bigger prey than predicted by their maximal bite capacity. However, the largest prey classes found in the stomachs were non-coleopteran arthropods which are significantly softer for their size (see black hexagons on Fig. 2). Only for the largest species (*P. hastatus*) does food hardness not seem to be imposing limits to diet selection.

Why no correlations were found among size, hardness and bite force for frugivores cannot be answered by the data gathered here. Either food hardness is not determining prey size at all in these animals or other factors such as the energy or time spent chewing prey interact with prey hardness making it less favourable to eat the largest fruits that could still be physically reduced (i.e. chewed). One other potentially important factor determining fruit size might be the energetic requirements of flight. Frugivores such as *A. jamaicensis* often take fruits and will transport them over considerable distances before eating them (L. F. Aguirre *et al.* personal observation). As the transport of heavy food



**Fig. 2.** Relationships between food hardness, food dimensions and bat bite forces (see Table 1). (a) The hardness of the fruits measured relative to their mass. Superimposed upon this graph are the bite forces of the frugivores in the community (solid horizontal lines). For one species (*A. jamaicensis*) the size of the fruits actually eaten could be determined and is represented by the dashed vertical line. Whereas food hardness does not seem to be limiting diet in some of the larger frugivores, it clearly restricts diet in some of the smaller species. The nectar-eating species *G. soricina* seems to be restricted to the smallest and least hard fruits. (b) Insect hardness vs insect length. Superimposed are bite forces (solid lines) for the insectivorous bats in the community and the estimated maximal lengths of the prey recovered from the stomachs (dashed vertical lines). In contrast to what was observed for frugivores, the maximal prey size consumed by these animals seems largely determined by the hardness of beetles. Whereas it seems that both *Noctilio albiventris* and both species of *Molossus* are eating larger prey than predicted by their bite forces (dashed vertical lines are situated to the right of the intersection of beetle hardness and the bat bite force curves), the diet data (Tables 2 and 4) show how these species switch to softer prey categories above 20 mm. (c) The relationships between food hardness vs food length for all prey tested. As in the other two graphs bite forces (solid line) and the maximal size (dotted line) of prey in the stomach are superimposed for the omnivorous bats in the community. Whereas the largest species (*P. hastatus*) can eat all prey available, for the other two species, the largest prey recovered from the stomach (which was a beetle) is clearly determined by the interaction of prey hardness and bite force. White diamonds, beetles; black hexagons, other arthropods; black circles, figs; white squares, *Piper*; white triangles, *Solanum*. prey tested. As in the other two graphs bite forces (solid line) and the maximal size (dotted line) of prey in the stomach are superimposed for the omnivorous bats in the community. Whereas the largest species (*P. hastatus*) can eat all prey available, for the other two species, the largest prey recovered from the stomach (which was a beetle) is clearly determined by the interaction of prey hardness and bite force. White diamonds, beetles; black hexagons, other arthropods; black circles, figs; white squares, *Piper*; white triangles, *Solanum*.

items is energetically demanding, this may be limiting the size of prey actually consumed by these animals.

That food hardness is an ecologically relevant variable becomes obvious when considering bite forces for some of the smaller species. For these animals, a large part of the available dietary spectrum is not available as they are not able to crush these prey (e.g. *Myotis* species). These data also illustrate that trophic specializations leading to a reduced bite performance (as in the case of *G. soricina* or *D. rotundus*; see Aguirre *et al.* 2002) will have strong ecological consequences. As illustrated on Fig. 2, *G. soricina* can thus only exploit the smallest and/or softest prey available (i.e. *Piper* and

small non-coleopterans), suggesting that trophic specialization may lead to an obligatory reduction in niche breadth.

In conclusion, food hardness in itself may clearly be limiting dietary scope in bats, excluding large portions of the available dietary spectrum from small animals (e.g. Vespertilionids, nectar-eating bats). Food items differ in many aspects, which may all play an important role in determining the selection of food by predators. Based on the data in the present study we would like to suggest that experimental measures of food hardness, although often ignored in bat community analysis (but see Dumont 1999), might further our understanding

of these complex communities. As demonstrated here, the combination of measurements of food hardness and *in vivo* bite forces for bats from the same community might prove especially insightful.

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### References

- Aguirre, L.F., Hanagarth, W. & de Urioste, R.J. (1996) Mamíferos del refugio de vida silvestre Espiritu, Dpto. Beni, Bolivia. *Ecología En Bolivia* **28**, 29–44.
- Aguirre, L.F., Herrel, A., Van Damme, R. & Matthysen, E. (2002) Ecomorphological analysis of trophic niche partitioning in a tropical savanna bat community. *Proceedings of the Royal Society of London B* **269**, 1271–1278.
- Arata, A.A., Vaughan, J.B. & Thomas, M.E. (1967) Food habits of certain Columbian bats. *Journal of Mammalogy* **48**, 653–655.
- Arlettaz, R., Perrin, N. & Hausser, J. (1997) Trophic resource partitioning and competition between two sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology* **66**, 897–911.
- Bernard, E., Albernaz, A.L.K.M. & Magnusson, W.E. (2001) Bat species composition in three localities in the Amazon basin. *Studies on Neotropical Fauna and Environment* **36**, 177–184.
- Bonaccorso, F.J. (1979) Foraging and reproductive ecology in a Panamanian bat community. *Bulletin of the Florida State Museum, Biological Sciences* **24**, 359–408.
- Bonaccorso, F.J. & Humphrey, S.R. (1984) Fruit bat niche dynamics: their role in maintaining tropical forest diversity. *Tropical Rainforest* (eds A.C. Chadwick & S.L. Sutton), pp. 169–183. Leeds Philosophical and Literary Society, Leeds.
- Borror, D.J., Triplehorn, C.A. & Johnson, D.M. (1989) *An Introduction to the Study of Insects*. Saunders College Publishing, Montréal.
- Currey, J.D. (1970) *Animal Skeletons*. Edward Arnold, London.
- Czarnecki, R.T. & Kallen, F.C. (1980) Craniofacial, occlusal and masticatory anatomy in bats. *Anatomical Record* **198**, 87–105.
- De Gueldre, G. & De Vree, F. (1984) Movements of the mandibles and tongue during mastication and swallowing in *Pteropus giganteus* (Megachiroptera): a cineradiographical study. *Journal of Morphology* **179**, 95–114.
- De Gueldre, G. & De Vree, F. (1988) Quantitative electromyography of the masticatory muscles of *Pteropus giganteus* (Megachiroptera). *Journal of Morphology* **196**, 73–106.
- Dumont, E.R. (1997) Cranial shape in fruit, nectar, and exudate feeders: implications for interpreting the fossil record. *American Journal of Physical Anthropology* **102**, 187–202.
- Dumont, E.R. (1999) The effect of food hardness on feeding behaviour in frugivorous bats (Phyllostomidae): an experimental study. *Journal of Zoology, London* **248**, 219–229.
- Fenton, M.B. (1982) Echolocation calls and patterns of hunting and habitat use of bats (Microchiroptera) from Chillagoe, north Queensland. *Australian Journal of Zoology* **30**, 417–425.
- Fenton, M.B. (1990) The foraging behavior and ecology of animal-eating bats. *Canadian Journal of Zoology* **68**, 411–422.
- Fenton, M.B. & Rautenbach, I.L. (1986) A comparison of the roosting and foraging behavior of three species of African insectivorous bats (*Rhinolophus hildebrandti* – Rhinolophidae, *Scotophilus borbonicus* – Vespertilionidae, and *Tadarida midas* – Molossidae). *Canadian Journal of Zoology* **64**, 2860–2867.
- Findley, J. (1993) *Bats: A Community Perspective*. Cambridge University Press, Cambridge.
- Findley, J.S. & Black, H.L. (1983) Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology* **64**, 625–630.
- Fleming, T.H. (1986) Opportunism versus specialisation: the evolution of feeding strategies in frugivorous bats. *Frugivores and Seed Dispersal* (eds A. Estrada & T.H. Fleming), pp. 105–118. Dr W. Junk, Dordrecht.
- Freeman, P.W. (1979) Specialized insectivory: beetle-eating and moth-eating molossid bats. *Journal of Mammalogy* **60**, 467–479.
- Freeman, P.W. (1981a) A multivariate study of the family Molossidae (Mammalia: Chiroptera): morphology, ecology, evolution. *Fieldiana Zoology* **7**, 1–173.
- Freeman, P.W. (1981b) Correspondence of food habits and morphology in insectivorous bats. *Journal of Mammalogy* **62**, 166–173.
- Freeman, P.W. (1984) Functional analysis of large animalivorous bats (Microchiroptera). *Biology Journal of the Linnean Society* **21**, 387–408.
- Freeman, P.W. (1988) Frugivorous and animalivorous bats (Microchiroptera): dental and cranial adaptations. *Biological Journal of the Linnean Society* **33**, 249–272.
- Freeman, P.W. (1995) Nectarivorous feeding mechanisms in bats. *Biological Journal of the Linnean Society* **56**, 439–463.
- Freeman, P.W. (2000) Macroevolution in Microchiroptera: recoupling morphology and ecology with phylogeny. *Evolutionary Ecology Research* **2**, 317–335.
- Goldman, L.J. & Henson, O.W. Jr (1977) Prey recognition and selection by the constant frequency bat, *Pteronotus p. parnellii*. *Behavioural Ecology and Sociobiology* **2**, 411–419.
- Handley, C.O., Wilson, D.E. & Gardner, A.L. (1991) Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panama. *Smithsonian Contributions to Zoology* **511**, 1–173.
- Heithaus, E.R., Fleming, T.H. & Opler, P.A. (1975) Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* **56**, 841–854.
- Herrel, A.L., Sptihoven, R. & Van Damme & De Vree, F. (1999) Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Functional Ecology* **13**, 289–297.
- Herrel, A., Van Damme, R., Vanhooydonck, B. & De Vree, F. (2001) The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology* **79**, 662–670.
- Humphrey, S.R., Bonaccorso, F.J. & Zinn, T.L. (1983) Guild structure of surface-gleaning bats in Panama. *Ecology* **64**, 284–294.
- Julien-Laferrrière, D. (1999) Foraging strategies and food partitioning in the neotropical frugivorous mammals *Cahuromys philander* and *Potos flavus*. *Journal of Zoology, London* **247**, 71–80.
- Kalko, E.K.V. (1997) Diversity in tropical bats. *Tropical Biodiversity and Systematics* (ed. H. Ulrich), pp. 13–43.

- Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.
- Kalko, E.K.V. & Condon, M.A. (1998) Echolocation, olfaction and fruit display: how bats find fruit of flagelliferous cucurbits. *Functional Ecology* **12**, 364–372.
- Kalko, E.K.V. & Handley, C.O. Jr (2001) Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology* **153**, 319–333.
- Kalko, E.K.V., Handley, C.O. Jr & Handley, D. (1996a) Organisation, diversity, and long-term dynamics of a neotropical bat community. *Long-term Studies of Vertebrate Communities* (eds M. Cody & F. Smallwood), pp. 503–553. Academic Press, London.
- Kalko, E.K.V., Herre, E.A. & Handley, C.O. Jr (1996b) Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *Journal of Biogeography* **23**, 565–576.
- Kallen, F.C. & Gans, C. (1972) Mastication in the little brown bat, *Myotis lucifugus*. *Journal of Morphology* **136**, 385–420.
- Koepcke, J. (1987) *Ökologische Studien an Einer Fledermaus-Artengemeinschaft Im Tropischem Regenwald Von Peru*. PhD Thesis, University of Munchen, Munchen.
- La Val, R.K. & La Val, M.L. (1980) Prey selection by a neotropical foliage-gleaning bat, *Micronycteris megalotis*. *Journal of Mammalogy* **61**, 327–330.
- Lim, B.K. & Engstrom, M.D. (2001) Species diversity of bats (Mammalia: Chiroptera) in Iwokrama Forest, Guyana and the Guianan subregion: implications for conservation. *Biodiversity and Conservation* **10**, 613–657.
- Lucas, P.W. (1979) The dental-dietary adaptations of mammals. *Neues Jahrbuch Geologie und Paläontologie* **8**, 486–512.
- Lucas, P.W. & Luke, D.A. (1984) Chewing it over: basic principles of food breakdown. *Food Acquisition and Processing in Primates* (eds D.J. Chivers, B.A. Wood & A. Bilsborough), pp. 283–301. Plenum Press, New York.
- Lucas, P.W., Corlett, R.T. & Luke, D.A. (1985) Plio-pleistocene hominid diets: an approach combining masticatory and ecological analysis. *Journal of Human Evolution* **14**, 187–202.
- McKenzie, N.L. & Rolfe, J.K. (1986) Structure of bat guilds in the Kimberley mangroves, Australia. *Journal of Animal Ecology* **55**, 401–420.
- Medellín, R.A. (1993) Estructura y diversidad de una comunidad de murciélagos en el trópico húmedo mexicano. *Avances En El Estudio de Los Mamíferos de México* (eds R.A. Medellín & G. Ceballos), pp. 333–354. Asociación Mexicana de Mastozoología, A.C., México, D.F.
- Neuweiler, G. (1989) Foraging ecology and audition in echolocating bats. *Trends in Ecology and Evolution* **6**, 160–166.
- Norberg, U.M. (1994) Wing design, flight performance and habitat use in bats. *Ecological Morphology* (eds P.C. Wainwright & S.M. Reilly), pp. 205–239. University of Chicago Press, Chicago.
- Patterson, B.D., Pacheco, V. & Solari, S. (1996) Distribution of bats along an elevational gradient in the Andes of south-eastern Peru. *Journal of Zoology, London* **240**, 637–658.
- Simmons, N.B. & Voss, R.S. (1998) The mammals of Paracou, French Guiana: a Neotropical rainforest fauna. Part I: Bats. *Bulletin of the American Museum of Natural History* **237**, 1–219.
- Sosa, M., De Asenção, A. & Soriano, P.J. (1996) Dieta y patrón reproductivo de *Rhogeessa minutilla* (Chiroptera: Vespertilionidae) en una zona árida de los Andes de Venezuela. *Revista de Biología Tropical* **44**, 867–875.
- Timm, R., Wilson, D.E., Clauson, B.L., La Val, R.K. & Vaughan, C.S. (1989) Mammals of La Selva-Braulio Carrillo Complex, Costa Rica. *US Department of the Interior Fish and Wildlife Service* **75**, 1–161.
- Willig, M.R. (1986) Bat community structure in South America: a tenacious chimera. *Revista Chilena de Historia Natural* **59**, 151–168.

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**Appendix**

Prey items consumed by bats in Espiritu

Species	NLEP	DROT	GSOR	PLIN	AJAM	SLIL	CPER	RNAS	NALB	MMIN	TSIL	PDIS	PELO	PHAS	MALB	MNIG	MSIM	EFUR	MTEM	EGLA	EHAN	MRUF	MMOL
	(3)	(8)	(3)	(4)	(7)	(4)	(6)	(1)	(8)	(2)	(5)	(3)	(3)	(4)	(1)	(7)	(2)	(5)	(1)	(4)	(1)	(5)	(4)
ARTHROPODA									5							2							
EPHEMEROPTERA																							
ODONATA																							
Zygoptera									2											2		1	1
ORTHOPTERA																							
Blattidae												1											
Gryllidae										1	4	1	1	1		1	2	3	1		1	3	3
Indet												2								2			
HEMIPTERA																							
Corixidae									8								5						
Belostomidae									1													1	
Reduviidae									1														
Indet									17				1			1			2			1	1
HOMOPTERA																							
Cercopidae																2							
Cicadelidae									10							1	1		3				1
Delphacidae									1								1	6	4				
Fulgoridae									5														1
Indet									8							1	4	3					1
COLEOPTERA																							
Carabidae									33				1	2		3	2	2	1				1
Dytiscidae		1							11								6		3			1	
Hydrophilidae									20		2	1	2			4		3	1	3		3	2
Staphylinidae									5								1						
Scarabaeidae									7		6	2	3	44		3	1	1				5	2
Elateridae									3											1			
Cucujidae																						1	
Chrysomelidae																		1					
Curculionidae									6			2	1			1	7	1	1				2
Indet									48	1		3	1	30		1	4	16	2	2		3	2

(Continued overleaf)

Appendix Continued

Species																								
	NLEP (3)	DROT (8)	GSOR (3)	PLIN (4)	AJAM (7)	SLIL (4)	CPER (6)	RNAS (1)	NALB (8)	MMIN (2)	TSIL (5)	PDIS (3)	PELO (3)	PHAS (4)	MALB (1)	MNIG (7)	MSIM (2)	EFUR (5)	MTEM (1)	EGLA (4)	EHAN (1)	MRUF (5)	MMOL (4)	
LEPIDOPTERA							1		1						1	5	1	5	1	1				
DIPTERA																								
Nematocera									18							3	5	15	2				12	
Brachycera									2							1		1						
HYMENOPTERA																								
Formicidae									40			1	2										2	
Indet									3									2						
ARACHNIDA															1			1						
<b>Fruits</b>																								
<i>Ficus eximia</i>				3	1																			
<i>Ficus</i> sp.					1																			
<i>Solanum wrightii</i>						3																		
<i>Piper aduncum</i>							4																	
<i>Piper</i> sp.							1																	
Indet ( <i>Cecropia</i> ?)					1																			
Fish	3																							
Blood		8																						
Nectar			3																					
<b>Unidentified</b>								6		1	1		2		4	1	2		3	1	1		2	

Arthropod orders are indicated in capitals, families in lower case. Sample sizes are indicated in parentheses under the species abbreviation. Table entries are absolute numbers of arthropods retrieved from the stomachs. For fruits, fish, blood and nectar table entries are the number of stomachs containing those food items. See Table 1 for a list of species abbreviations.