

Gleaning bats as underestimated predators of herbivorous insects: diet of *Micronycteris microtis* (Phyllostomidae) in Panama

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Abstract: Predators of herbivorous insects play important roles in tropical ecosystems as herbivory may affect structure and diversity of plant populations. Although insectivorous bats are particularly abundant and diverse in the tropics, their impact on herbivorous insects is little understood. To assess prey consumption, we observed the gleaning bat *Micronycteris microtis* (Phyllostomidae) continuously for 3 mo including 16 full nights at a nightly feeding roost on Barro Colorado Island in Panama using infrared videotaping combined with collection of prey remains. Individual bats consumed about 61–84% of their body mass in arthropods per night. Diet analysis revealed a high percentage of herbivorous insects, constituting more than half (51%) of all prey and over 70% of prey biomass. Dominant prey were caterpillars (33% of prey biomass), and other herbivores including crickets, katydids, scarab beetles and phasmids. Furthermore, a novel feeding behaviour was observed as *M. microtis* selectively discarded parts of intestines of phytophagous insects before consumption, probably to avoid intake of plant material either for ballast reduction and/or for protection from secondary plant compounds. Combined with estimated feeding rates of insects in sympatric bat species, our data suggest that gleaning bats are important predators of herbivorous insects and might be underestimated reducers of herbivory in the tropics.

Key Words: Chiroptera, feeding rate, herbivory, infrared videotaping, insectivory, predation

INTRODUCTION

Herbivorous insects play a central role in the ecology of tropical forests. The regulation of plant populations, maintenance of diversity, and evolution of plant chemical defence all depend in part on the strong selection pressure from herbivorous insects (Coley & Barone 1996, Connell 1971, Janzen 1970, Leigh & Smythe 1978). The impact of herbivorous insects on tropical forests has led to a corresponding appreciation of predators such as birds and insects, that control herbivore populations and thus reduce levels of herbivory (Atlegrim 1989, Greenberg *et al.* 2000, Marquis & Whelan 1994, Strong *et al.* 2000, Van Bael *et al.* 2003). However, to date, no study has explicitly addressed the potential impact of insectivorous bats (Microchiroptera) as predators of herbivorous insects

in tropical forests, probably because so few data are available on diet, feeding rates and prey biomass.

Bats are characterized by high local abundance and species richness, especially in the Neotropics, where more than 100 species may co-exist (Kalko 1997, Patterson *et al.* 2003, Simmons & Voss 1998). Although bats are trophically diverse, most bat species are insectivorous and catch insects by foraging on the wing (aerial insectivores), or taking them from substrate (gleaning insectivores) (Findley 1993, Schnitzler & Kalko 1998, 2001). Probably to escape diurnal predators such as birds and primates, many insects in the tropics are active at night (Meyer *et al.* 2004, Windsor 1978) where they suffer increased exposure to bats. This applies in particular for katydids (Orthoptera: Tettigoniidae) that form a substantial part of the diet of gleaning insectivorous bats (Belwood 1988, Belwood & Morris 1987, Giannini & Kalko 2004, Humphrey *et al.* 1983, LaVal & LaVal 1980, Wilson 1971) and are very important and diverse herbivores in most

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tropical forests compared to temperate forests. Hence, gleaning insectivorous bats could play a previously underestimated role in the reduction of herbivorous insects.

Despite such suggestive data, methodological constraints have so far limited our knowledge of the foraging ecology of tropical bats. Assessing the potential impact of gleaning insectivorous bats on herbivorous insects requires a detailed dietary analysis of the bats and feeding rates. However, most published data of diets of gleaning insectivorous bats are based on faecal analysis and/or analysis of prey remains under night roosts, and both methods suffer several limitations (Arlettaz 1996, Swift & Racey 2002, Whitaker 1988). Many bats use several night roosts, so not all of the prey remains or faecal pellets are usually available for analysis at one roost. Additionally, mixed species assemblages at the same roost are common and impede correct assignment of faecal pellets and prey remains to relevant bat species. Detailed faecal analysis is difficult as insectivorous bats chew their prey very thoroughly. This way, insects with hard exoskeletons may be overrepresented because their remains are more likely to pass through the digestive system of the bats (Rabinowitz & Tuttle 1982, Whitaker 1988). Collection of wings underestimates wingless prey, as well as prey that gets eaten whole. Furthermore, insect remains at feeding roosts often get easily lost due to wind, rain or detritivores such as ants or cockroaches that quickly transport them away.

We selected the small (5–7 g) gleaning insectivorous bat *Micronycteris microtis* (Phyllostomidae) to quantify for the first time consumption of herbivorous arthropods in a neotropical lowland forest with disturbance-free infrared videotaping as well as traditional methods of collecting prey remains at a night roost. *Micronycteris microtis* is well-suited for diet analysis because individuals show high roost fidelity and consistently return with food to a permanent night roost where they discard parts of their mostly large and herbivorous insect prey (LaVal & LaVal 1980). From our recordings, we assessed type and size of prey, estimated biomass of food, as well as feeding rates per night of individual bats, and documented details of the prey-handling behaviour.

METHODS

Study site and period

The study was conducted for 3 mo (1 March – 31 May 2001) in a tropical lowland, semi-deciduous moist forest on Barro Colorado Island (BCI), the field station of the Smithsonian Tropical Research Institute, in Panama (9°9'N, 79°51'W). The 15.6-km² island receives an average of 2600 mm of rain annually, about 90% of which falls during the rainy season from May–December

(Leigh 1999). The year of our study (2001) was characterized by an extended dry season. Monthly rainfall totalled 14.5 mm for March, 26.5 mm for April and 182.8 mm for May (Paton 2001).

Study animal

Micronycteris microtis (*sensu* Simmons 1996) (Phyllostomidae) occurs from northern Mexico to southern Brazil (Reid 1997). All previous studies of *M. megalotis* in Central America (e.g. LaVal & LaVal 1980) actually refer to *M. microtis* (see Simmons 1996). It is the smallest of nine insectivorous gleaning bats known on BCI (Belwood 1988, Kalko *et al.* 1996), with a body mass of 5–7 g and a body length of 55–65 mm. Unlike most other gleaning insectivorous bats, *M. microtis* shows high site fidelity in the use of night roosts for prey consumption (Kalko, unpubl. data, LaVal & LaVal 1980).

Infrared videotaping

We recorded activity per night of *M. microtis* at its feeding roost located under the outside stairs of a residential building on BCI for 16 full nights corresponding to about 200 h of videotaping. The interval between recording nights was 4–5 nights. A digital S/W Infrared CCD-Camera (Type VK-121/IR) with a motor-zoom was mounted on a tripod about 1.2 m from the night roost of the bats. Three custom-made infrared-panels, each equipped with 32 LEDs (TS AlGaAs infrared 875 nm, 5 mm Ø, HSDL-4230) were used as light sources. A Sony Video-Walkman with LCD monitor (DC-VQ800) connected to the camera was placed about 12 m from the roost around the corner of the house. With the exception of the camera and the infrared panels, equipment and observer were hidden from the bats. To zoom in on individual bats for identification of consumed prey, we adjusted the lens (Eneo DC-Motorzoom Lens EC-Series, F1, 8/8–80 mm) with a remote control. Presence of camera and operation of the motor-zoom did not noticeably affect the behaviour of the bats.

The observed roost was located about 2 m from the forest edge and has been consistently used by *M. microtis* since 1991 when the buildings were constructed (Kalko, *pers. obs.*). A group of five individuals used this roost every night for social interactions, resting, and consumption of prey throughout the entire study period. Videotaping began at 18h00 before arrival of the first bat and ended about 12.5 h later, shortly before sunrise, after the last bat had left the roost. Moon phase was recorded for each filmed night. On 21 April, one adult male and two palpably pregnant females were caught, weighed with a Pesola spring balance (precision 0.1 g), forearm

Table 1. Mass, forearm length and reproductive status of three *Micronycteris microtis* captured at their night roost under the staircase of a building on BCI (21 April 2001).

Animal	Sex	Mass (g)	Forearm length (mm)	Reproductive status
M	male	5.5	32.4	non-reproductive
W1	female	7.5	33.5	pregnant
W2	female	7	34	pregnant

was measured with a ruler to the nearest mm, and individuals were marked by clipping a patch of fur on their back (Table 1). These marks were necessary for assessing individual duration of foraging flights as well as entire activity per night at the night roost. An adult male was radio-tracked for 4 nights (21–25 April), using a 0.48-g one-stage transmitter (Holohil Systems Ltd, Ontario, Canada), to obtain additional data on activity. The transmitter represented 11.4% of the body mass of the bat. This is around the 10% mass threshold suggested by Brander & Cochran (1969) as a limit for radiotracking but above the 5% mass threshold proposed by Aldridge & Brigham (1988) where transmitter mass may affect foraging behaviour of animals. As the male in our study did not differ noticeably in foraging time and capture success from the two females observed at the night roost and from other individuals that were tracked with similar-sized transmitters in a subsequent study (van de Sand, *pers. comm.*) and considering that small bats can carry heavier loads relative to their body mass than larger species (Norberg & Rayner 1987), we conclude that the transmitter mass did not negatively affect flight performance of the tagged individual.

Diet analysis

The diet of *M. microtis* was determined by combining all-night video recordings with subsequent collection of insect remains at the feeding roost. In video analysis, we counted all visible prey brought by the bats to the roost. Prey from videotaped feeding events and food remains was taxonomically identified to order and whenever possible also to lower levels (Aiello, *pers. comm.*, Borror & White 1987). Prey remains were collected from the feeding roost at the end of each night. Initially, we also collected faecal pellets for comparison. However, preliminary analysis of some samples with a dissecting microscope revealed that the prey had been chewed so thoroughly that species identification was very difficult or impossible. Prey size was estimated from the videotapes in comparison to the head length of the bats and assigned to one of five size classes (class of prey body length: I: < 1 cm, II: 1–2 cm, III: 2–3 cm, IV: 3–4 cm, and V: > 4 cm). Head length of *M. microtis* (20.1 ± 0.2 mm SD; $n = 3$) was measured from caught individuals as distance between the anterior-most point of pre-maxillae and hind-most point of skull.

In order to assess wet mass of prey consumed by *M. microtis*, we collected and weighed representative insects of all size classes and used data given in Belwood (1988). We multiplied amount of consumed prey of a given size class recorded on film by average mass for insects of that taxon and size class to estimate prey biomass. In 18% of all cases we observed that *M. microtis* was chewing when it entered the roost but could not clearly distinguish any prey item. These food items were so small that the bats probably already started feeding while they flew back to the night roost. We therefore may have somewhat underestimated consumption of smaller prey since we only used recordings of clearly visible feeding events for final analysis.

RESULTS

Foraging flights and activity

The first individual of the group entered the roost 16 ± 10 min ($n = 16$ nights) after local sunset. The entire activity period per night of individual bats from first arrival until last departure at the roost encompassed $10.5 \text{ h} \pm 28$ min ($n = 18$; 6 nights for three marked bats). The time the last bat left the roost was significantly correlated with local sunrise (linear regression, $R = 0.912$; $P < 0.0001$), preceding it by 6 ± 5 min ($n = 16$ nights). The radio-tracked male *M. microtis* from the observed roost was in continuous flight all the time it was outside the roost.

All resting phases coincided with videotaped returns to the night roost, suggesting that this individual did not use any other night roost. The filmed activity of the other bats in the roost resembled the activity pattern of the radio-tracked individual. Therefore we assume that all members of the observed group used the roost under the stairwell as their main roost for prey consumption. This might have overestimated flight time in a few cases because a subsequent study revealed that occasionally, *M. microtis* may briefly use individual, temporary night roosts within their foraging area (van de Sand, unpubl. data). However, as this happened only rarely and for a short period of time, we are confident that it did not affect the overall picture of foraging activity in *M. microtis* for our study. We interpret the time *M. microtis* spent outside of its night roost as foraging flights because the majority of the returns of the radio-tagged bat were associated with successful captures and subsequent processing of prey. Duration of foraging flights ranged from 15 s to 51 min ($n = 241$). About half (49%) of the flights were shorter than 5 min, 23% were between 5–10 min, 17.5% between 10–20 min, and 10.5% exceeded 20 min. Individual *Micronycteris microtis* conducted 1.7 ± 0.5 foraging flights per hour ($n = 176$) and spent 14.1 ± 5.3 min h^{-1} searching for

prey ($n = 180$ h). The bats were active throughout the whole night and showed no distinctive activity peaks. Number and duration of foraging flights as well as size, quantity and biomass of prey eaten at hourly intervals did not show significant differences in temporal distribution throughout the night (one-way ANOVAs, $P > 0.05$). In 61% of all flights *M. microtis* returned to the roost with prey.

Diet and feeding rates

We observed 778 feeding events for five bats in 16 nights. Individual *M. microtis* consumed 1.1 ± 0.6 prey items per hour ($n = 176$ h). They processed prey immediately after landing in the roost followed by grooming for about 5 min and a resting phase of variable length (10–30 min) before the bats resumed foraging after a second grooming period.

All prey items of *M. microtis* documented on infrared video or as prey remains under the feeding roost were arthropods (Table 2). The most common prey types were Lepidoptera (26%) half of which were caterpillars, frequently covered by long hairs or prominent spines. The bats captured nocturnal moths (e.g. Noctuidae) as well as diurnal butterflies (e.g. Papilionidae). Orthoptera (Tettigoniidae, Gryllidae and Acrididae) and Coleoptera (predominantly Scarabaeidae) were also frequently eaten. A fifth of all Orthoptera (20%) lacked wings or were nymphs. *Micronycteris microtis* captured both sexes of Orthoptera in about equal quantities as assessed by presence of ovipositors or stridulatory organs. Dragonflies (Odonata: Anisoptera) and cockroaches (Blattoidea) constituted other important prey taxa of

M. microtis ($> 10\%$ each). A smaller proportion of the prey of *M. microtis* ($< 5\%$) was composed of cicadas (Homoptera, mostly Cicadidae), flies (Diptera, mostly Asilidae), spiders (Arachnida), Hymenoptera (Apoidea, Formicidae, including swarming leaf-cutter reproductives and ichneumonid wasps) and stick insects (Phasmidae). Occasionally ($< 1\%$), *M. microtis* captured lacewings (Neuroptera) and termites (Isoptera).

Biomass and size of prey

Caterpillars constituted about a third (33%) of total biomass (wet mass) consumed by *M. microtis* throughout the study period, despite being only 12% of prey items. Biomass of other orders did not differ substantially from their relative proportion in the diet of the bats (Table 2). Individual prey that was visible on film or found in prey remains ranged from 0.2 g (small moth) to 2 g (large caterpillar), spanning 0.3% to 31% mass of an average sized *M. microtis* (6.5 g). Prey body length varied from small (0.4 mm) beetles (Coleoptera) up to very long (9 cm) stick insects (Phasmidae). Almost half (47%) of prey ranged between 1–2 cm body length (size classes II) and a small portion (11%) exceeded with 4 cm and more (size classes IV and V) the bat's body length (Table 2). Caterpillars spanned all size classes from small (size class I) to very large (size class V). Almost half (45%) of the consumed caterpillars were longer than 3 cm. Overall, individual *M. microtis* consumed an estimated 4.6 ± 1.6 g (wet mass) equivalent to 61–84% of their own body mass of arthropods per night.

Effects of moonlight and seasonality on diet

Moonlight had no significant effect on foraging activity measured as number and duration of foraging flights, and on number, type or biomass of consumed prey (one-way ANOVAs, $P > 0.05$). However, of the six major groups of prey taxa taken by *M. microtis*, all but dragonflies (Anisoptera) showed significant variation in capture frequency across the 3 mo of the study, which covered the end of the dry season (March), transition to wet season (April) and onset of wet season (May) (Figure 1). Lepidoptera, both as caterpillars ($\chi^2 = 34.2$, $df = 2$, $P < 0.001$) and as adults ($\chi^2 = 36.5$, $df = 2$, $P < 0.001$), represented the major food source at the beginning of the study period during the dry season, then declined throughout April and May. Beetles ($\chi^2 = 130$, $df = 2$, $P < 0.001$) were only a minor food source of *M. microtis* at the end of the dry season, but dominated at the onset of the rainy season, when they accounted for almost half (46%) of all prey. Consumption of orthopterans ($\chi^2 = 20.3$, $df = 2$, $P < 0.001$) and

Table 2. Number (arranged in descending order), biomass and size of prey based on infrared videotaping of *Micronycteris microtis* feeding at a night roost on BCI. Size classes of prey body length: I: < 1 cm, II: 1–2 cm, III: 2–3 cm, IV: 3–4 cm, V: > 4 cm.

Insect order	Prey (N)	Prey (%)	Biomass (g)	Biomass (%)	Size classes (%)				
					I	II	III	IV	V
Coleoptera	149	19.2	49.4	15.4	34	61	5	–	–
Orthoptera	144	18.5	65.4	20.4	6	51	37	5	1
Lepidoptera (moth)	106	13.6	7.8	2.4	22	55	23	–	–
Blattodea	98	12.6	35	10.9	2	84	14	–	–
Lepidoptera (caterpillar)	96	12.3	106.6	33.2	6	18	30	21	25
Anisoptera	82	10.5	33.9	10.5	0	–	30	70	–
Homoptera	30	3.9	4.4	1.4	12	88	–	–	–
Diptera	23	3.0	4.9	1.5	5	30	45	20	–
Arachnida	20	2.6	5	1.6	18	82	–	–	–
Hymenoptera	16	2.1	2.9	0.9	14	57	29	–	–
Phasmidae	9	1.2	4.9	1.5	–	–	–	11	89
Neuroptera	4	0.5	1	0.3	–	–	25	75	–
Isoptera	1	0.1	0.1	–	100	–	–	–	–
Total	778	100	321.3	100	–	–	–	–	–

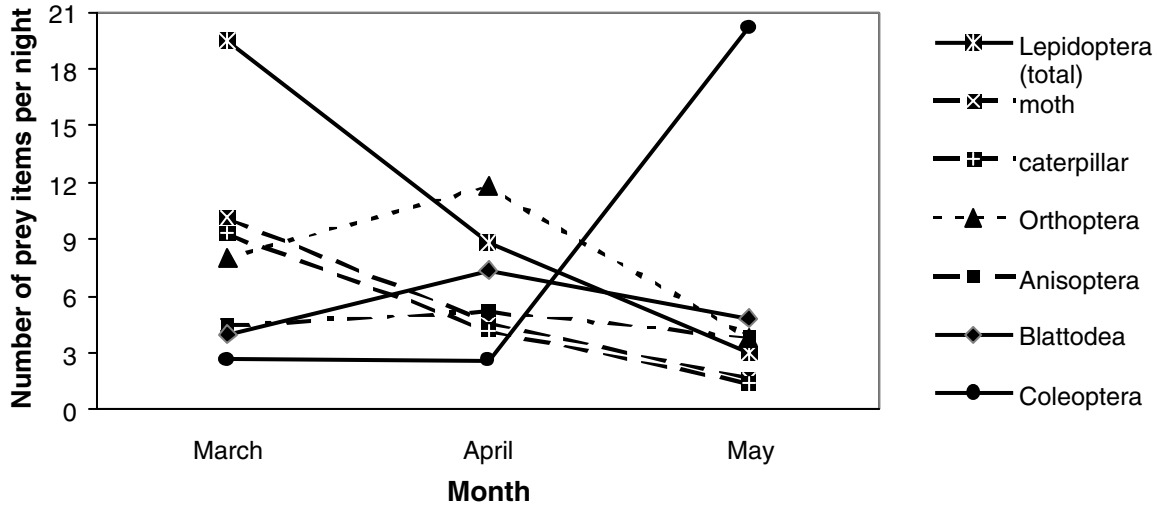


Figure 1. Monthly variation in average number of dominant prey (n = 778) caught by *Micronycteris microtis* per night.

cockroaches ($\chi^2 = 6.3$, $df = 2$, $P = 0.04$) peaked in the April transitional period.

Handling of prey

Micronycteris microtis generally bit off and discarded wings and legs of prey before consumption. In some prey, the bats also selectively spit out parts of the intestines. Most notably, *M. microtis* discarded those components only in the case of phytophagous and detritivorous prey taxa, namely caterpillars, beetles, crickets, katydids, phasmids, cockroaches and in one case

also a moth, but not in carnivorous groups including dragonflies, hymenopterans, robberflies, spiders and lacewings (Figure 2). The bats either dropped part of the abdomen, or separated it from the exoskeletons by rapid head movements. Discarding parts of the intestines was most conspicuous in caterpillars, where fewer than 5% of all individuals, all less than 1.5 cm in body length, were eaten whole. Unlike most other prey items, *M. microtis* mostly did not use its thumb claws to push caterpillars towards its mouth but handled them almost exclusively with its lips and teeth only, repeatedly and quickly moving the caterpillars from one side to the other. The bat then squeezed out or bit off parts of the intestines and dropped

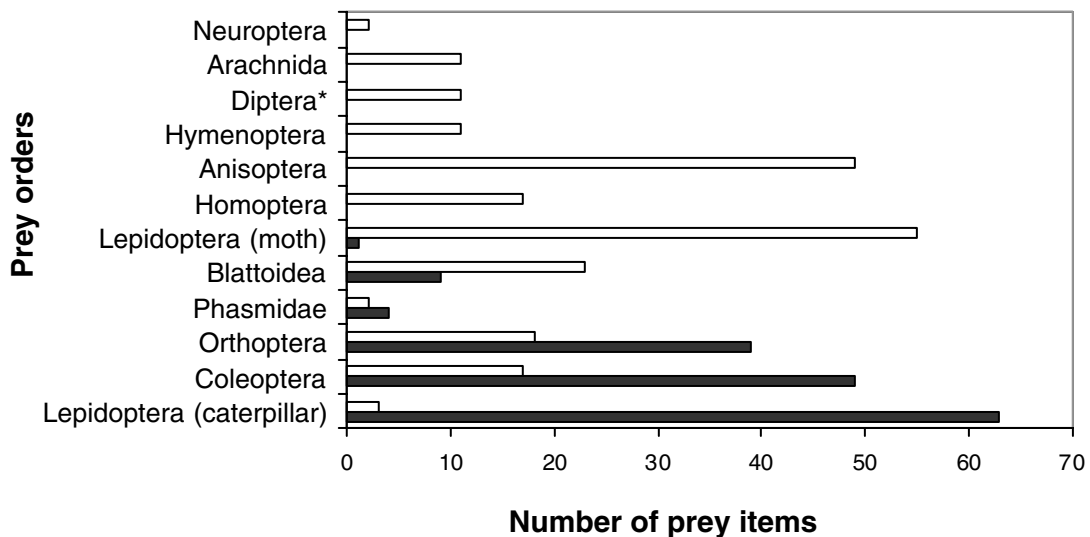


Figure 2. Processing of prey by *Micronycteris microtis* as observed on selected film sequences with (black bars) and without (white bars) manipulation. Lepidoptera (caterpillar): n = 66, Orthoptera: n = 57; Phasmidae: n = 6; Coleoptera: n = 66; Lepidoptera (moth): n = 56; Blattodea: n = 32; Anisoptera: n = 49; Homoptera: n = 17; Hymenoptera: n = 11; Diptera: n = 11 (*mostly Asilidae); Arachnida: n = 11; Neuroptera: n = 2.



Figure 3. Selective prey manipulation by *Micronycteris microtis* processing a hairy caterpillar at the night roost on BCI. Arrows indicate parts of intestines that have been squeezed out by the bat.

them (Figure 3). The dropped parts mostly came from the abdominal region of the caterpillars, but in some cases also originated from frontal areas. Examination with a dissecting microscope revealed that the round or elliptical parts were often filled with greenish material and showed fine vascularizations. We assume that the discarded fragments were parts of intestines filled with plant material. Surprisingly, the bats ingested most hairs and all of the skin of caterpillars.

Comparison of diet determination in bats

To evaluate methods, we compared our collection of prey remains at the night roost of *M. microtis* with our simultaneous infrared videotaping (Table 3). Half (45%) of all prey that the bats carried into the night roost was

Table 3. Filmed prey items of *Micronycteris microtis* that were missed (number in descending order and %) in the parallel collections of prey remains from the feeding roost on BCI.

Insect order	Number filmed	Number missed	Per cent missed
Coleoptera	149	43	29
Orthoptera	144	92	64
Lepidoptera (moth)	106	31	29
Blattodea	98	27	28
Lepidoptera (caterpillar)	96	96	100
Anisoptera	82	18	22
Homoptera	30	7	23
Diptera	23	6	26
Arachnida	20	20	100
Hymenoptera	16	6	38
Phasmidae	9	6	67
Neuroptera	4	1	25
Isoptera	1	0	0
Total	778	353	45

not detected in the prey remains. The missing groups were mostly wingless prey taxa such as caterpillars. However, even among winged taxa, 26% of all consumed individuals were not recorded in the collection of prey remains at the feeding roost. Furthermore, the majority of orthopterans (64%) and phasmids (67%) also remained undetected by analysis of prey remains alone.

DISCUSSION

Diet of *Micronycteris microtis*

We documented diet, feeding rate and processing of food by a group of *M. microtis* with infrared taping at a night roost. The core diet of *M. microtis* in our study consisted mainly of lepidopterans followed by beetles, crickets, katydids, dragonflies, cockroaches and cicadas and thus is in accordance with previous studies (Belwood 1988, LaVal & LaVal 1980). However, we recorded a much wider array of prey taxa. The new method allowed us to document for the first time regular consumption of phasmids, large spiders, and large numbers of caterpillars. We are confident that the prey spectrum is representative of the natural diet of the bat at our study site given that the radio-tracked male as well as individuals of *M. microtis* that were radio-tracked in a subsequent study on BCI (*M. van de Sand*, unpubl. data) foraged exclusively in the forest and did not use the lights of the field station for gleaning insects off the walls. Similar to LaVal & LaVal (1980), but in contrast to other studies (reviewed in Alonso-Mejía & Medellín 1991, Gardner 1977) we found no evidence of fruit consumption in *M. microtis*. Previous observations of fruit remains below *M. microtis* roosts may be a result of sharing feeding roosts with frugivorous bats

such as *Carollia perspicillata*, which we observed at other times of the year in the night roost of *M. microtis* on BCI (Schweiger, *pers. comm.*).

Miconycteris microtis showed great dietary flexibility in prey class and size. They captured minute prey, as well as caterpillars up to 31% of their own body mass. Over the course of our study, the bats alternately focused on Lepidoptera, both adults and caterpillars, Orthoptera and beetles. Adult beetles form the dominant diet of *M. microtis* at the beginning of rainy season when the first rains trigger mass emergence of fat-rich scarab beetles. The seasonal change in dietary preference is supported by a 2.5-y study at the same night roost on BCI from 1991–1993 where we found similar patterns for all taxa that can be determined by analysis of prey remains (Kalko, unpubl. data). Because these seasonal changes in diet also reflect general patterns of insect abundance on BCI (Smythe 1982, Wolda 1978), we believe that *M. microtis* is largely an opportunistic forager.

Methodological implications

Our infrared recordings showed that about half of the diet of *M. microtis* consisted of immature stages of arthropods including caterpillars and nymphs as well as of wingless, often soft-bodied prey which would have been largely missed when looking at prey remains only. Remains were missing because the bats ate some arthropods entirely, in particular small and less-sclerotized prey. Further, discarded prey items were quickly carried away at the night roost by ants and other insects (Belwood 1988, Kalko, unpubl. data), or they were blown away by wind. This is the first study to document caterpillars as a primary food of a neotropical bat although traces of caterpillars have been found in faeces of other bats, for example *Thyroptera tricolor* (Dechmann, unpubl. data.), *Myotis nattereri* (Beck 1995) and in larger amounts also in *Nycteris thebaica* (Whitaker & Black 1976). We propose that, in light of these findings, caterpillars may be important food items for other gleaning insectivorous bats as well.

Selective prey handling – protection against secondary plant compounds?

In general, *M. microtis* bit off wings and occasionally also legs of its prey prior to consumption. However, certain prey types were treated further, resulting in selective separation of additional internal body parts from the abdominal region. Because *M. microtis* showed this behaviour only in phytophagous but not in carnivorous taxa, we believe that the bats avoided consumption of plant material in intestines of its prey. The origin

of the spat-out fragments as well as their structure and coloration support this hypothesis. Intestines of herbivorous insects are often filled with fibrous material that is probably not very valuable for bats. Avoiding consumption of those parts might reduce unnecessary weight that could hinder flight, a strategy well known from frugivorous bats which squeeze fruits for the nutritious juice and discard the leftovers as almost dry pellets (Handley *et al.* 1991).

Miconycteris microtis also may avoid eating plant matter due to its chemical composition. Many plants contain chemicals that are either directly toxic or reduce efficiency of digestion as a defence against herbivores (reviewed in Coley & Barone 1996). Nevertheless, these plants are still consumed by specialized herbivores that are able to tolerate those toxins and, in some cases, may use them for their own defence. Thus the guts of herbivorous insects may contain considerable amounts of secondary plant compounds that are detrimental to predators. For instance, *M. microtis* discarded gut fragments of phasmids feeding on Piperaceae that are known to contain alkaloids and to show insecticidal activity (Srivastava 1970, J. Berger, *pers. comm.*). Future studies with controlled feeding trials combined with chemical analysis of prey and discarded parts will be necessary to determine whether the behaviour of the bats is a response to chemical composition of the plants.

Gleaning bats: underestimated reducers of herbivorous insects?

Herbivory by insects is a major constraint on plant growth and reproduction (Coley & Barone 1996, Leigh & Smythe 1978, Marquis & Whelan 1994) and a strong force in the maintenance of tropical diversity (Connell 1971, Janzen 1970). For instance on BCI, herbivorous insects destroy about 20% of the entire annual leaf production (Leigh & Windsor 1982). Exclosure experiments in the tropics increasingly reveal the importance of birds and other taxa including ants and lizards as predators on herbivorous insects (Atlegrim 1989, Gradwohl & Greenberg 1982, Greenberg *et al.* 2000, Marquis & Whelan 1994, Murakami & Nakano 2000, Philpott *et al.* 2004, Strong *et al.* 2000, Van Bael *et al.* 2003). The impact of bat predation on herbivorous insects still remains unknown, because exclosure studies in the tropics did not distinguish between diurnal and nocturnal predation, and thus attributed reductions in herbivorous insects primarily to birds.

Insectivorous bats may play an important role as predators because many herbivorous insects in the tropics are active mainly at night and hide during the day, probably to avoid heat and to escape diurnal predators. In Guanacaste, Costa Rica, four times more herbivorous

insects were found foraging on vegetation at night than during the day (Windsor 1978). Although rather well protected during the day, these insects suffer increased exposure to predation by gleaning insectivorous bats at night.

Our video recordings revealed that more than half of the arthropods (51%) in the diet of *M. microtis* were herbivores. This number increases to 65% including adult Lepidoptera, which are not herbivorous but produce caterpillars, and to 69% including Homoptera which feed on plant sap. Herbivores contributed to more than two thirds (70%) of prey biomass. The proportion of herbivores in the diet of *M. microtis* may be even higher later in the wet season, when herbivore populations peak in response to new leaf production (Barone 1998, Coley & Aide 1991, Janzen 1988, Smythe 1982, Wolda 1978).

Potential impact of gleaning insectivorous bats on herbivory rates on BCI

A radio-tracking study of *M. microtis* on BCI revealed average home ranges of about 1–2 ha for individual bats with large overlap between group members (van de Sand, *pers. comm.*). With a conservative estimate of 600 *M. microtis* on BCI (1560 ha) that each feed on roughly 4.6 g (wet mass) of arthropod biomass per night, of which about 70% are herbivorous insects, *M. microtis* would capture a minimum of about 700 kg y⁻¹ (wet mass) of herbivorous insects.

On BCI, the eight co-occurring insectivorous gleaning bats all surpass *M. microtis* in body mass (Kalko *et al.* 1996) and thus consume higher amounts of insect biomass per individual. For instance, the three medium-sized (25–35 g) gleaners *Lophostoma silvicolium* (following Lee *et al.* 2002 for taxonomy and spelling), *Tonatia saurophila* and *Trachops cirrhosus* with an estimated population size of at least 300 individuals each (Kalko *et al.* 1999, E. Kalko, unpubl. data) are likely to consume at least 50% of their body mass in arthropods each night of which an estimated 70% or more are likely to be herbivorous, including many herbivorous katydids (Tettigoniidae). Based on an average body mass of 30 g for these three bat species and our data from *M. microtis*, we calculated a minimum feeding rate of 5200 kg y⁻¹ of herbivorous insects on BCI for those four gleaners alone.

Combining the above conservative estimated feeding rates with the assumption that it takes about 10 kg of fresh leaves to produce 1 kg of insects (Leigh & Windsor 1982), our estimates suggest that predator pressure of the four gleaners alone may 'save' more than 52 000 kg of fresh leaves per year. In the context of overall production of leaf-biomass on BCI, which augments to an estimated 6 tons dry weight of leaves ha⁻¹ y⁻¹ (Leigh 1999), this appears little. However, if we take into account that these

gleaners represent only four of the nine insectivorous gleaners and the more than 20 species of insectivorous bats known on BCI (Kalko 1997), overall feeding rates of bats are likely to be comparable or may exceed those of insectivorous birds on BCI which have been estimated to eat about 37 500 kg y⁻¹ of folivorous insects (Leigh 1999). The estimates on birds are conservative as they do not take into account factors such as increased predation rates of birds during reproduction. However, given that bird predation affects herbivory in a tropical forest near BCI (Van Bael *et al.* 2003), we predict that similar or higher levels of bat predation will also influence herbivory rates. Until we know more about actual population sizes of insectivorous bats, their diets and feeding rates, as well as production of plant biomass and how it is affected by herbivores, our estimates must remain speculative. Nevertheless, we can say that in the case of *M. microtis*, herbivorous insects comprise a much higher percentage of its diet than previously appreciated. Our preliminary estimates point to a potentially substantial role of neotropical bats as predators of herbivorous insects. Exclosure studies which explicitly measure and separate nocturnal from diurnal predation, combined with more in-depth studies on bat diets and foraging behaviour will help to quantify the impact gleaners may have on the biomass of herbivorous insects and hence on insect herbivory. Such studies will refine our current thinking about herbivory as a factor promoting regeneration and maintaining plant diversity in tropical forests.

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