SEASONAL FOOD HABITS OF FIVE SYMPATRIC FOREST MICROCHIROPTERANS IN WESTERN MADAGASCAR

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We determined the foods habits of 5 species of microchiropteran bats (*Hipposideros commersoni*, *Triaenops rufus*, *Triaenops furculus*, *Myotis goudoti*, and *Miniopterus manavi*) in the austral winter and summer in a dry deciduous forest in western Madagascar using fecal analysis. We also assessed food availability and bat activity in 4 forest microhabitats. Despite overlap in dietary composition, *H. commersoni* consumed mainly Coleoptera; *M. goudoti* consumed mainly Hymenoptera, Neuroptera, and Araneae; *M. manavi* consumed mainly Hemiptera; and *T. rufus* and *T. furculus* consumed mainly Lepidoptera. Diptera were the most abundant insects in traps but were rarely encountered in feces. *H. commersoni* was not netted during the austral winter, but the other 4 species changed their diet according to seasonal availability, with lepidopterans the most important diet items in winter and coleopterans in summer. We consistently trapped a higher abundance of potential bat prey at the forest edge, whereas the forest interior was low in both food availability and bat activity. The 5 microchiropterans studied partitioned the available food mainly through dietary specialization, although spatial and temporal partitioning also may play a role. More research is needed to assess levels of dependency on forest by these bats, and to investigate the seasonal ecology of *H. commersoni* and interspecific competition between *T. rufus* and *T. furculus*.

Key words: bats, competition, food habits, *Hipposideros commersoni*, Madagascar, *Miniopterus manavi*, *Myotis goudoti*, *Triaenops furculus*, *Triaenops rufus*

Microchiropteran bats are prolific consumers of invertebrate prey and differences in wing morphology and echolocation characteristics facilitate the existence of many species in the same habitat through interspecific variation in prey selection and habitat use (Arlettaz et al. 1997; Barlow 1997; Fenton and Thomas 1980; Findley and Black 1983; Rydell and Yalden 1997). An understanding of prey selection and diet in microchiropterans is necessary to explain patterns of habitat selection and also for predicting how major changes in invertebrate communities associated with deforestation will impact bats. Madagascar is an international conservation priority because its endemic mammals are mostly restricted to the remaining intact forests that are under chronic pressure from other land uses (Brooks et al. 2002). A few investigations have described niche partitioning in endemic Malagasy land mammals and provided helpful insights into the relationship between habitat–food requirements and tolerance to forest disturbance (e.g., Ganzhorn 1988, 1989; Lehtonen et al. 2001; Stephenson 1993, 1995; Yamashita 2002) but the chiropteran fauna has received relatively little attention in this regard.

An upsurge of interest in the bat fauna of Madagascar since the late 1990s has resulted in a much better understanding of the ecology and conservation of fruit bats (e.g., Andriafidison et al. 2006; Bollen and Van Elsacker 2002; MacKinnon et al. 2003) and significant advances in our understanding of the distribution (Goodman et al. 2005a) and taxonomy of microchiropterans (e.g., Goodman et al. 2005b; Goodman and Cardiff 2004; Goodman and Ranivo 2004). Yet, with the exception of a single study based on analysis of stomach contents (Razakarivony et al. 2005), there have been no attempts to describe the diet of Malagasy forest microchiropterans.

We investigated the food habits of 5 microchiropteran species in Parc National Tsingy de Bemaraha, western Madagascar, during 2 seasons. Additionally, we evaluated bat

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habitat use and prey abundance in 4 forest microhabitats. Previous assessments of diet and morphology have shown that species with a similar morphology forage in similar habitats and therefore have similar diets (e.g., Aldridge and Rautenbach 1987; Findley and Black 1983). We assessed whether dietary specialization was evident in the bat community together with spatial and temporal patterns of prey abundance and composition.

MATERIALS AND METHODS

Study area.—Fieldwork was conducted in the Parc National Tsingy de Bemaraha (18°12′–19°07′S, 44°34′–44°57′E) situated near Antsalova, in the Province de Mahajanga of western Madagascar (Rasoloarison and Paquier 2003). The park lies within a limestone karst belt that stretches from northwestern to southwestern Madagascar. The climate has a distinct wet season (austral summer) from November to April and a dry season (austral winter) from May to November. Rainfall is greatest in February, at approximately 456 mm. Our study periods were during July and November 2003.

Study species.—*Hipposideros commersoni* is a large microchiropteran bat with forearm length ranging between 85.5 and 97.3 mm (Peterson et al. 1995). The 2 other hipposiderids in the study community, *Triaenops rufus* and *T. furculus*, are smaller with forearms in the range of 49.0–56.0 mm and 42.9–47.0 mm, respectively (Peterson et al. 1995). *H. commersoni* is relatively widespread at lower elevations. *T. furculus* is restricted to southern and western Madagascar (Goodman et al. 2005a), whereas *T. rufus* has a wider distribution but is thought to be rare in the east (Eger and Mitchell 2003). *Miniopterus manavi* and *Myotis goudoti* are small vespertilionids, with forearm measurements ranging from 37.5 to 40.5 mm and 34.5 to 40.0 mm, respectively (Peterson et al. 1995), and are widely distributed species in Madagascar (Eger and Mitchell 2003; Goodman et al. 2005a). All of these species roost in caves, often in mixed colonies.

Bat trapping.—Mist nets were placed across potential flyways to intercept foraging bats in 4 forest habitats: forest interior, forest clearing with a rocky substratum, riparian forest, and forest edge (interface between forest and agricultural–degraded habitats). We conducted a total of 60 h of mistnetting in July and 60 h in November. Mistnetting effort in different habitats was the same in each period, with 12 h in both forest interior and forest clearings, 20 h in riparian forest, and 16 h at the forest edge. Nets typically were placed low to the ground and traversed trails, streams, and clearings, or were placed perpendicular to edges. Between 36 and 42 m of mist nets were set each night, and were open for 4 h from dusk (approximately 1800 h) until 2200 h. Nets were regularly checked for captured bats, usually at 5-min intervals for the 1st trapping hour and every 15 min thereafter. Captured bats were placed in cloth bags for a maximum of 30 min to collect deposited feces. Individuals captured soon after emergence from day roosts were quickly processed and released. Species were identified using Peterson et al. (1995) and Russ et al. (2003). Bats were handled according to

guidelines approved by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Invertebrate sampling.—Invertebrates were sampled in the same 4 habitat types as described above using light traps and malaise traps. Light traps consisted of a white cotton sheet (200 × 100 cm) set between 2 poles and suspended 50 cm above the ground. A gas light (Petromax, Tower Pressure Lantern, Huangdai Town, Suzhou, China) was placed in front of the sheet with the bulb level with the middle of the cotton sheet. All macroinvertebrates that alighted on the sheet were collected with a jar or suction tube. Light trapping was conducted for 20 min every hour between 1800 and 2200 h and the samples were preserved in 70% ethanol. A single malaise trap was used to sample invertebrates at each sampling site (1800–2200 h). Samples of invertebrates were identified to order using Delvare and Aberlenc (1989).

Bat detectors.—We assessed the foraging habitats of bats by listening for feeding buzzes from a series of point counts. Feeding buzzes are the characteristic noises produced as foraging bats hone in on their prey and are distinct from the sounds made by searching bats (e.g., Vaughan et al. 1997). We listened for bats during 5-min intervals with Duet (Stag Electronics, Steyning, West Sussex, United Kingdom) broadband bat detectors at points located throughout the study site in the 4 habitat categories described earlier. Recordings in frequency division lasting the duration of the point count were made onto minidisks and the number of feeding buzzes was later counted with the use of headphones and a tally counter. Recordings from individual bat species were not analyzed separately but were pooled for a general assessment of foraging activity. We used the number of feeding buzzes per recording interval as our sampling unit and each point count was treated as an independent data point.

Fecal analysis.—Although other workers have used gut contents from sacrificed bats (e.g., Razakarivony et al. 2005) and the use of insect fragments has some shortcomings (e.g., Kunz and Whitaker 1983), we used fecal analysis to investigate dietary differences between species and seasons because this is standard procedure for microchiropteran studies (e.g., Whitaker 1988, 2004). All fecal pellets produced by captured bats were collected and stored in plastic vials containing 70% ethanol representing each individual animal. A maximum of 10 pellets per bat were selected for analysis and thus our independent replicates were from individual bats using data pooled from a series of fecal samples for each animal (see Whitaker 2004). Bat fecal pellets were softened in 70% ethanol and teased apart in a petri dish with dissecting needles, under a binocular microscope (10–20×). All identifiable items were removed, mounted on a slide in glycerine, sealed with nail varnish, and examined under a binocular microscope (40–400×). Identification was made using generic keys for bat feces (Shiel et al. 1997; Whitaker 1988), together with other keys and works on invertebrate morphology (Delvare and Aberlanc 1989; Scholtz and Holm 1989). Further, the reference collection of invertebrates from the malaise and light traps provided additional comparative material that was useful in this regard. The

TABLE 1.—Summary of microchiropteran captures from mist nets set in 4 different forest microhabitats in Parc National Tsingy de Bemaraha during the austral winter (July) and summer (November).

Species	July				November			
	Clearing	Edge	Interior	Riparian	Clearing	Edge	Interior	Riparian
Hipposideros commersoni	0	0	0	0	2	14	6	15
Triaenops rufus	5	14	19	14	0	1	12	3
T. furculus	1	1	8	9	0	0	2	3
Miniopterus manavi	0	2	55	28	0	11	20	18
Myotis goudoti	0	1	11	18	1	1	3	2
Total	6	18	93	69	2	26	43	41
Total/effort (h)	0.3	1.1	7.8	3.5	0.1	1.6	7.2	2.1

percentage volume of each invertebrate taxon was visually estimated using the methods described in Whitaker (1988).

Statistical analysis.—Two-way analysis of variance (AN-OVA) was used on log-transformed insect abundance to test for differences between seasons (July and November) and habitats (forest clearing, edge, riparian, and interior). Data on bat feeding buzzes were not normally distributed and differences between habitat and season were tested using Kruskal–Wallis and Mann–Whitney tests. Arcsine transformed percentage volume data for major prey items were compared for each bat species using ANOVA. Chi-square analysis was used on all capture frequencies, pooled for both seasons, to investigate associations with habitat.

RESULTS

Capture rates, seasonality, and feeding activity of bats.—We captured a total of 37 *H. commersoni*, 68 *T. rufus*, 24 *T. furculus*, 134 *M. manavi*, and 37 *M. goudoti*. Captures were not evenly distributed among habitats ($\chi^2 = 38.4$, $d.f. = 12$, $P < 0.001$), with the highest capture rate from the forest interior (Table 1). Trap sites in clearings and edges accounted for only 13% and 25% of bats captured in July and November, respectively. *H. commersoni* was significantly more abundant in November (ANOVA, $F = 6.0$, $d.f. = 23$, $P < 0.001$), whereas the seasonal variation in the abundance of the other 4 species was not statistically significant (ANOVA, all $P > 0.05$). Captures of *T. rufus* generally were restricted to the forest interior in November compared to July, when bats also were captured regularly at the forest edge and in riparian habitats (Table 1). The feeding activity of microchiropterans was significantly different among habitats (Kruskal–Wallis $H = 29.1$, $P < 0.001$) and was lowest in the forest interior (Fig. 1). There was no significant difference in the number of feeding buzzes between July and November across all habitats (Mann–Whitney $U = 11487$, $P > 0.05$).

Diet.—Fecal analysis from 120 bats revealed the most important prey items by percent volume were Coleoptera, Hemiptera, and Lepidoptera. The percent volume of Coleoptera differed significantly among species (ANOVA, $F = 6.0$, $d.f. = 4, 111$, $P = 0.002$) and was highest in the feces of *H. commersoni* (Table 2). The percent volume of hemipterans also differed significantly among species (ANOVA, $F = 4.2$, $d.f. = 4, 111$,

$P = 0.003$) with post hoc tests revealing significant differences between *M. manavi* and the other 4 species. There were no interspecific differences in percent volume of Diptera (ANOVA, $F = 1.78$, $d.f. = 4, 111$, $P = 0.14$) or Dictyoptera ($F = 0.8$, $d.f. = 4, 111$, $P = 0.50$). Percent volume of Lepidoptera varied significantly among species (ANOVA, $F = 20.10$, $d.f. = 4, 111$, $P < 0.001$) and was very low in the diet of *H. commersoni*. Neither Ephemeroptera (ANOVA, $F = 1.2$, $d.f. = 4, 111$, $P = 0.28$) nor Neuroptera (ANOVA, $F = 2.23$, $d.f. = 4, 111$, $P = 0.06$) showed interspecific differences. Significant differences among species in Hymenoptera ($F = 5.9$, $d.f. = 4, 111$, $P = 0.002$) and Araneae ($F = 24.1$, $d.f. = 4, 111$, $P < 0.001$) were associated with the occurrence of these prey items in the diet of *M. goudoti*. There was evidence of dietary specialization in the bat community studies; *H. commersoni* fed mainly on Coleoptera, the 2 *Triaenops* on Lepidoptera, *M. manavi* on Hemiptera, and *M. goudoti* on Araneae and Hymenoptera.

Assessing the food habits at the family level for Coleoptera and Hemiptera revealed that *H. commersoni* and *M. goudoti* had the most distinctive diets (Table 3). Some coleopteran families (e.g., Carabidae, Chrysomelidae, Cucujoidae, and Scarabidae) and the hemipteran family Cicadellidae were found
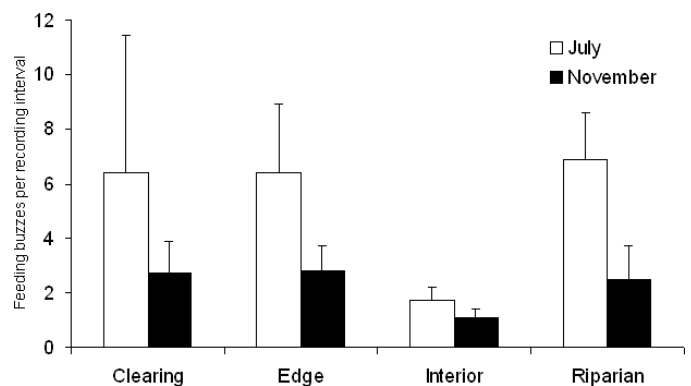

FIG. 1.—Mean number of bat feeding buzzes per 5-min recording interval (± 1 *SE*) recorded with a frequency division bat detector in 4 different forest microhabitats Parc National Tsingy de Bemaraha during the austral winter (July) and summer (November). Sample sizes in July were 15 (clearing), 18 (edge), 84 (forest interior), and 44 (riparian forest), and during November were 17 (clearing), 37 (edge), 91 (forest interior), and 14 (riparian forest).

TABLE 2.—Major orders of insects and arachnids recorded in the diet of 5 species of bats in Parc National de Bemaraha, western Madagascar (data are mean percentage volume $\pm$ *SE*). Post hoc (Fisher's probable least-squares difference) test results are indicated by superscript letters, with either bat species that differed significantly ([a]) or those with similar amounts of each prey type in the diet ([b]).

	Hipposideros commersoni (n = 18)	*Triaenops furculus* (n = 22)	*T. rufus* (n = 19)	*Myotis goudoti* (n = 24)	*Miniopterus manavi* (n = 27)
Coleoptera	86.3 ± 4.2[a]	21.4 ± 5.3	22.8 ± 5.7	40.5 ± 6.4	33.9 ± 5.3
Hemiptera	9.5 ± 4.2[b]	7.5 ± 1.7[b]	18.7 ± 5.4[b]	8.3 ± 2.0[b]	30.7 ± 4.7[a]
Diptera	0.3 ± 0.3[a]	1.7 ± 0.7[b]	1.5 ± 0.8[b]	7.4 ± 3.0[a]	3.1 ± 1.1[b]
Dictyoptera	1.8 ± 0.9	4.2 ± 1.4	3.9 ± 1.3	9.1 ± 3.1	6.3 ± 1.8
Lepidoptera	1.1 ± 0.6[a]	58.7 ± 7.7[b]	46.1 ± 6.9[b]	14.9 ± 3.1[a]	23.0 ± 4.9[a]
Ephemeroptera	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Hymenoptera	0.0 ± 0.0[b]	0.0 ± 0.0[b]	0.9 ± 0.6[b]	5.2 ± 1.7[a]	0.7 ± 0.6[b]
Neuroptera	0.0 ± 0.0[b]	0.0 ± 0.0[b]	0.0 ± 0.0[b]	2.6 ± 1.7[a]	0.0 ± 0.0[b]
Araneae	0.0 ± 0.0[b]	0.0 ± 0.0[b]	0.0 ± 0.0[b]	14.4 ± 3.7[a]	0.0 ± 0.0[b]

in the diet of all 5 microchiropteran species. Seven of the 21 (33%) families of Coleoptera and Hemiptera in the diet of *H. commersoni* were not recorded for any other bat species (Table 3). Similarly, 6 (43%) of the 14 families were exclusive to the diet of *M. goudoti*. Values for the other 3 species of bats were 2 (11%) of 18 for *M. manavi*, 1 (7%) of 14 for *T. rufus*, and 2 (15%) of 13 for *T. furculus*. Overlap was greatest between *Triaenops* and *M. manavi* (Table 3), although a complete assessment is not possible because lepidopterans were important prey items for these species of bats and because it was not possible to identify that order to family level.

There were significant shifts in the food habits of the 4 small microchiropteran species between the samples from July and November. There was no significant difference in the percent volume of Coleoptera ($F = 0.42$, *d.f.* = 1, 21, $P = 0.52$), Hemiptera ($F = 0.43$, *d.f.* = 1, 21, $P = 0.52$), or Lepidoptera ($F = 0.03$, *d.f.* = 1, 21, $P = 0.95$) between seasons in the diet of *T. rufus* (Fig. 2a). Percent volume of dictyopterans was significantly higher in November ($F = 5.10$, *d.f.* = 1, 21, $P = 0.03$). The diet of *T. furculus* (Fig. 2b) contained a higher percent volume of Coleoptera ($F = 6.65$, *d.f.* = 1, 16, $P = 0.02$) and Dictyoptera ($F = 14.29$, *d.f.* = 1, 21, $P < 0.001$) in November but percent volume of Lepidoptera was highest in July ($F = 11.89$, *d.f.* = 1, 21, $P = 0.003$). In general, the seasonal fluctuations in relative contributions of each prey type were similar for *T. rufus* and *T. furculus* (Figs. 2a and 2b). The diet of *M. manavi* (Fig. 2c) did not differ seasonally in the percent volume of Coleoptera ($F = 1.45$, *d.f.* = 1, 25, $P = 0.49$), Hemiptera ($F = 0.48$, *d.f.* = 1, 25, $P = 0.50$),

Dictyoptera ($F = 0.38$, *d.f.* = 1, 25, $P = 0.54$), or Diptera ($F = 0.52$, *d.f.* = 1, 25, $P = 0.86$), but Lepidoptera was highest in July ($F = 4.86$, *d.f.* = 1, 21, $P = 0.04$). The diet of *M. goudoti* (Fig. 2d) contained a significantly higher percent volume of Coleoptera in November ($F = 27.96$, *d.f.* = 1, 27, $P < 0.001$) and of Lepidoptera in July ($F = 9.8$, *d.f.* = 1, 27, $P = 0.004$).

Invertebrate community.—Our samples were numerically dominated by Diptera and Lepidoptera, making up 48% and 21% of the total numbers of individuals trapped. The next most common orders, making up 14% and 13%, respectively, were Hemiptera and Coleoptera. Eleven other invertebrate orders were identified (e.g., Hymenoptera, Trichoptera, and Orthoptera) but statistical comparisons were not undertaken on these taxa because they only represented 3% of the total.

Coleopteran abundance differed significantly between season and habitat, based both on light traps ($F_{season} = 4.38$, *d.f.* = 1, 32, $P < 0.05$; $F_{habitat} = 7.07$, *d.f.* = 3, 32, $P < 0.001$) and malaise traps ($F_{season} = 5.52$, *d.f.* = 1, 32, $P < 0.05$; $F_{habitat} = 3.05$, *d.f.* = 3, 32, $P < 0.05$) and abundance was highest in November and along the forest edge (Figs. 3a and 3b). There were no significant differences in dipteran abundance from malaise traps between season ($F_{season} = 0.06$, *d.f.* = 1, 32, $P > 0.05$) but samples from light traps contained significantly more invertebrates in July ($F_{season} = 24.9$, *d.f.* = 1, 32, $P < 0.001$). Dipteran abundance from both trap types differed significantly between habitats (light $F_{habitat} = 6.31$, *d.f.* = 3, 32, $P < 0.001$; malaise $F_{habitat} = 9.03$, *d.f.* = 3, 32, $P < 0.001$), with the highest abundance at the forest edge (Figs. 3a and 3b). There was no significant difference in hemipteran abundance between the

TABLE 3.—Richness of Coleoptera and Hemiptera families in the diet of 5 microchiropteras from Parc National Tsingy de Bemaraha. Single-taxon prey are the families found in the feces of only 1 species of bat.

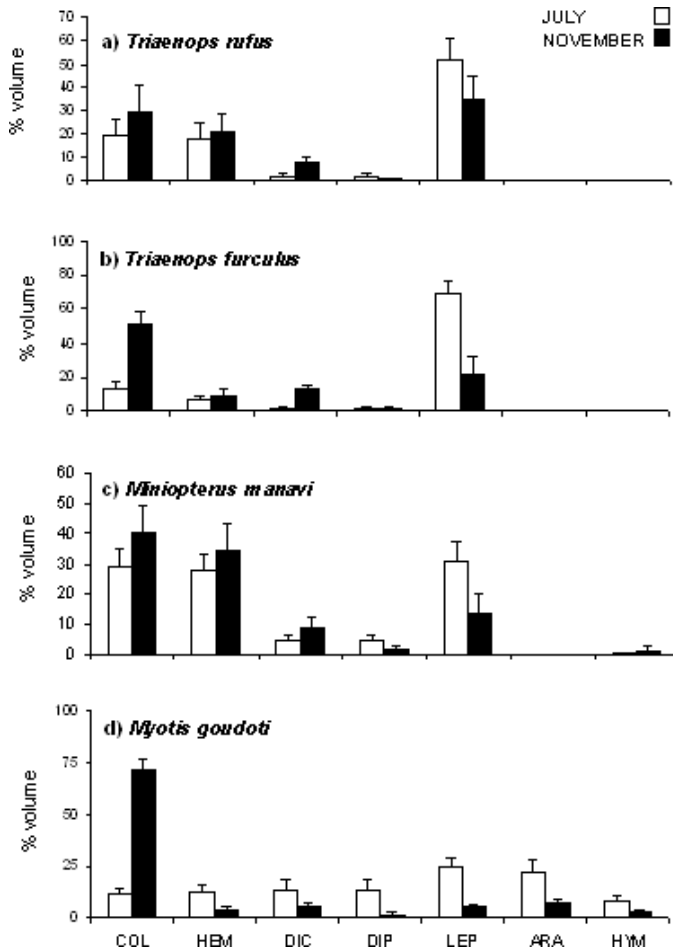|	Taxon richness	Single-taxon prey	Taxon overlap (number of Coleoptera and Hemiptera families)				
			Hipposideros commersoni	*Triaenops rufus*	*T. furculus*	*Miniopterus manavi*	*Myotis goudoti*
H. commersoni	21	7	NA[a]	9	6	9	7
T. rufus	14	1		NA	9	12	6
T. furculus	13	2			NA	10	8
M. manavi	18	2				NA	6
M. goudoti	14	6					NA

[a] NA, not applicable.

FIG. 2.—Mean percentage volume (± 1 *SE*) of major food items of 4 microchiropteran species from Parc National Tsingy de Bemaraha during the austral winter (July) and summer (November). Coleoptera (COL), Hemiptera (HEM), Dictyoptera (DIC), Diptera (DIP), Lepidoptera (LEP), Aranae (ARA), Hymenoptera (HYM).

FIG. 3.—Mean abundance (± 1 *SE*) of 4 invertebrate orders from 4 different forest microhabitats Parc National Tsingy de Bemaraha during the austral winter (July) and summer (November).

July and November sample periods for either trap type (light $F_{season} = 3.74$, $d.f. = 1, 32$, $P > 0.05$; malaise $F_{season} = 0.21$, $d.f. = 1, 32$, $P > 0.05$) but habitat was a significant factor (light $F_{habitat} = 5.24$, $d.f. = 3, 32$, $P < 0.01$; malaise $F_{habitat} = 3.88$, $d.f. = 3, 32$, $P < 0.05$) with highest abundance recorded from the forest edge (Fig. 3). Lepidopteran abundance differed significantly between seasons from the malaise ($F_{season} = 6.45$, $d.f. = 1, 32$, $P < 0.01$) but not the light traps ($F_{season} = 2.92$, $d.f. = 1, 32$, $P > 0.05$) and abundance was higher in November. The abundance of Lepidoptera from malaise traps ($F_{habitat} = 11.33$, $d.f. = 3, 32$, $P < 0.001$) differed significantly between habitats but not from light traps ($F_{habitat} = 2.67$, $d.f. = 3, 32$, $P > 0.05$) and was highest at the forest edge (Figs. 3a and 3b).

In general, the abundance of the main types of invertebrate prey found in the diets of 5 bat species was greater in November than July. Diptera were most abundant in July but were not an important food item for the bat species studied. The forest edge consistently produced the highest abundance of invertebrates, although riparian forest and edges were notable for the high abundance of dipterans.
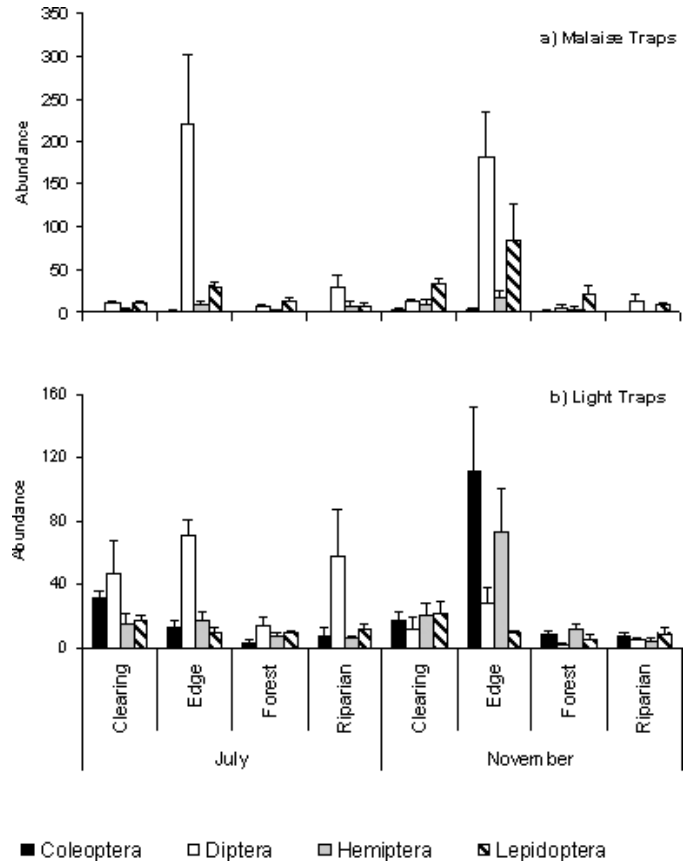
DISCUSSION

The only previous study on microchiropteran diet in Madagascar analyzed stomach contents of 81 individuals of 5 species from 5 different sites in the north and west (Razakarivony et al. 2005). These authors concluded that there was no pronounced dietary specialization in the microchiropterans of western Madagascar, but that food habitats varied temporally according to fluctuations in availability. Yet, given different body size, echolocation, foraging methods, and the fact that forests in western Madagascar may have at least 10 sympatric microchiropteran species (Goodman et al. 2005a), some degree of dietary resource partitioning would be expected if food is limited. Our study showed that although Coleoptera, Lepidoptera, and Hemiptera are the most frequent food items in the diet of all 5 species, there were considerable interspecific and temporal differences in dietary composition.

Inherent biases in the use of fecal analysis to determine diets of bats, because of the different digestibility and body size of invertebrate prey, may have influenced our results. In particular, hard-bodied prey may be overrepresented because of their indigestibility, whereas remains of soft-bodied prey, such as lepidopterans, are more difficult to count and identify because they are easily digested. These shortcomings may have ob-

scured interspecific differences in *Triaenops* but are unlikely to have masked major interspecific dietary differences.

Dietary partitioning.—There was strong evidence for interspecific partitioning in the diet of the 5 microchiropterans. Although >69% of the feces from all 5 species contained Coleoptera, the composition by percent volume showed that only *H. commersoni* fed predominantly on this order. This result is consistent with other studies in Madagascar where Coleoptera were found in 90% of 11 stomachs of *H. commersoni* (Razakarivony et al. 2005). *H. commersoni* fed on 7 families that were not present in the prey of the other bats and these included large-bodied taxa such as Cicadidae, Lucanidae, and Passalidae. In eastern Africa, large-bodied Coleoptera were reported as the main prey of *Hipposideros gigas*, a species similar in size to *H. commersoni* (Vaughan 1977). Preliminary observations in Madagascar reveal that foraging behavior of *H. commersoni* involves short hunting flights from night perches (e.g., A. Rakotoarivelo, in litt.; Russ et al. 2003). There is little available information on the foraging behavior of other Malagasy microchiropterans but it seems that the large body size and large teeth, constant-frequency echolocation calls of 64 kHz (Russ et al. 2003), and foraging strategy make *H. commersoni* the coleopteran specialist in the bat community.

Lepidopterans were the most important food source for both species of *Triaenops* and these bats therefore had a diet distinct from other sympatric species, although it is less clear how *T. rufus* and *T. furculus* partition resources. *T. furculus* is less frequently netted or detected than *T. rufus* and data are insufficient to assess whether these bats forage in the same habitats.

Myotis goudoti was the only species that fed on Araneae and Neuroptera and fragments of spiders were present in 55% of the fecal samples. Razakarivony et al. (2005) found Araneae in 2% of stomachs of *M. manavi* and 27% of stomachs of *M. goudoti*. Other *Myotis* bats are known to glean from vegetation, and remains of spiders frequently are found in fecal samples (e.g., Swift and Racey 2002; Whitaker 2004). Although *M. goudoti* cannot be considered a spider specialist because it feeds predominantly on Coleoptera, the regular occurrence of Araneae provides evidence for gleaning, and potential interspecific competition from *Miniopterus* or other species may be reduced by feeding on or close to vegetation. The presence of Hymenoptera and Neuroptera almost exclusively in the diet of *M. goudoti* further supports the conclusion that this species is a gleaner. Additionally, we detected strong differences in the composition of the coleopteran and hemipteran component of the diet compared to the other species. In a macroanalysis of the morphology of 129 *Myotis* specimens, *M. goudoti* was classified as an intermediary species, likely to use both gleaning and aerial foraging (Fenton and Bogdanowicz 2002) and our results confirm that this species feeds on nonaerial prey. Both *M. goudoti* and *M. manavi* are small bats that frequently share roosts. There is considerable difference in the echolocation calls between the species; calls of *M. goudoti* consist of a single frequency-modulated sweep from 75 kHz to 55 kHz, whereas *M. manavi* consist of a frequency-modulated sweep that terminates in a constant-frequency portion with maximum energy around 57 kHz (Russ et al. 2003). The diet of *M. manavi* con-

tained more hemipterans than *M. goudoti* or the other species. In the absence of field observations on foraging behavior, predictions based on echolocation and morphology suggest that *M. goudoti* is better adapted to foraging in cluttered areas and may therefore have a closer association with forest vegetation.

Seasonal variation in diet.—The food habits of the bat community differed significantly between seasons for the 4 species present during the 2 study periods. Diptera were most abundant in July but were rarely encountered in the diet of bats. All other invertebrate orders were most abundant in November and the percent volume of Coleoptera in the diet of *T. rufus*, *T. furculus*, *M. goudoti*, and *M. manavi* was greater in November than July. Therefore, the bats seemed to avoid feeding on the abundant dipteran prey and adjusted their relative consumption of other invertebrate families according to availability. Changes in the contribution of lepidopterans were the most pronounced because moths seemed to be an important prey type in July for all species, but only the feces of *T. rufus* contained a high percent volume of moths in November. Razakarivony et al. (2005) reported dietary switching in response to short-term superabundance of food such as Isoptera. The ability of small insectivorous bats to alter their dietary composition in different seasons is presumably an adaptation to the temporal variation in food supply and enables the bats to remain present and active throughout the year. Highly specialized predators are more vulnerable to periods of low food abundance. *H. gigas* undertakes seasonal movements in central Africa (Cotterill and Fergusson 1999), and *H. commersoni* was not trapped during our study in July, although it is not clear whether the species had moved from the area or was present but inactive. This suggests that there are insufficient local food resources to sustain this large microchiropteran during the austral winter.

Spatial patterns of prey abundance.—At Parc National Tsingy de Bemaraha, high capture rates from mistnetting inside the forest during the early evening are associated with bats exiting day roosts and flying along forest trails (Kofoky et al. 2007). Mist nets set across trails and rivers are likely to be more successful in capturing bats than those on edges or in clearings because they limit options for evasion that are available to bats in more open habitats. Acoustic assessments of bat activity (Kofoky et al. 2007) and feeding (this study) strongly suggest that forest edges are the most important foraging areas. Forest trails had the lowest abundance of invertebrate prey and these areas may be used by bats commuting to more profitable foraging sites such as forest edges and clearings. Our assessment of bat activity, based on mist-net captures and acoustic detections, may have underestimated bats that mainly forage in the canopy or have quiet echolocation calls. Furthermore, our assessments of feeding activity were probably more efficient at detecting vespertilionids than hipposiderids.

We found the highest abundance of all invertebrates and of those commonly occurring in the diets of bats at the forest edge, although we acknowledge that light and malaise traps may not have adequately sampled the entire range of bat prey available at the sites. Although edges of intact forest are usually viewed negatively by conservation biologists because the

habitat structure and microclimate is radically different from the more intact interior zones to which many forest-dependent species are restricted, they likely represent important habitats for bats. At least in Parc National Tsingy de Bemaraha, the forest edge is formed naturally by geology, with the forest restricted mainly to the rocky karst outcrops occurring inside the reserve. The myriad roosting locations associated with karst outcrops provide ideal habitats for bats and it seems likely that the bats in our study were roosting in crevices and caves inside the forest, using trails for commuting, and using edges and riparian habitats for feeding. Rivers and other linear landscape features (e.g., Racey 1998; Verboom and Spoelstra 1999) are known to be important habitats for bats in Europe by providing connecting flyways, shelter, and food.

RESUME

Nous avons identifié l'habitude alimentaire des chauves-souris microchiroptères dans une forêt sèche caducifoliée dans l'ouest de Madagascar durant l'hiver austral et l'été austral grâce à l'analyse des fèces de ces animaux. Aussi, nous avons estimé la disponibilité de la nourriture et les activités des chauves-souris dans quatre micro habitats forestiers. Le régime de toutes les 5 espèces (*Hipposideros commersoni*, *Triaenops rufus*, *Triaenops furculus*, *Myotis goudoti* et *Miniopterus manavi*) étudiées contient souvent des Coléoptères, des Hémiptères et des Lépidoptères. Malgré la similarité de la composition alimentaire, des différences d'habitudes alimentaires ont été observées chez chaque espèce; ainsi, *H. commersoni* consomme surtout des Coléoptères, *M. goudoti* principalement des Hyménoptères, des Neuroptères et Araneae, *M. manavi* principalement des Hémiptères et *T. rufus* et *T. furculus* consomment surtout des Lépidoptères. *H. commersoni* et *M. goudoti* ont adopté un régime plus spécifique de coléoptères et d'hémiptères avec 41% et 54% des familles dans leur régime respectif que l'on ne trouve pas dans les fèces des autres espèces. Les Diptères ont été les insectes les plus abondants dans les pièges mais rarement rencontrés dans les fèces. *Hipposideros commersoni* n'a pas pu être capturée durant l'hiver austral, peut-être à cause du manqué de nourriture dans la zone d'étude. Les quatre autres espèces ont changé d'habitat selon la disponibilité de la nourriture durant chaque saison, les lépidoptères étant les plus abondants durant l'hiver et les coléoptères pendant l'été. Nous avons en conséquence capturé une grande quantité de proies potentielles chassées par les chauves-souris à la lisière de la forêt; cependant, à l'intérieur de la forêt, la nourriture disponible n'était pas abondante et à l'activité des chauves-souris était faible. Les 5 microchiroptères étudiés ont notamment partagé les nourritures disponibles grâce à leur spécialisation alimentaire respective, bien que les zones d'interaction suggèrent la possibilité d'un rôle que joue la répartition spatiale et temporelle. Des recherches plus poussées sur l'habitude de recherche alimentaire et l'emploi de l'habitat sont nécessaires pour évaluer le niveau de dépendance de la forêt et pour étudier l'écologie saisonnière chez *H. commersoni* et la concurrence entre les espèces *T. rufus* et *T. furculus*.

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