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The diet of three synanthropic bats (Chiroptera: Molossidae) from eastern Madagascar

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We analysed 890 faecal samples from 145 molossid bats in eastern Madagascar during the austral summer and winter. Coleoptera, Hemiptera, Lepidoptera and Diptera were the most important sources of food for *Mops leucostigma*, *Mormopterus jugularis* and *Chaerephon pumilus*. The percentage volume of Hemiptera and Lepidoptera were similar in the diet, pooled across season, for all species but significant differences were found for Diptera and Coleoptera. *Mops leucostigma*, however, had the highest volume of Diptera and *M. jugularis* of Coleoptera. Hemiptera were an important food source for all species during both seasons, whereas Coleoptera were prevalent in the diet only during the summer. Diptera were rarely eaten by *M. jugularis* but constituted a major source of food for the other two species during the winter. Although there was little evidence of strong interspecific dietary partitioning, *M. jugularis* appeared to have a more limited dietary composition at the ordinal level. Major differences in dietary composition were between season rather than species at the ordinal level. Further investigations are recommended to assess the potential role of molossids in consuming economic pests of cotton in Madagascar.

Key words: *Chaerephon*, *Mops*, *Mormopterus*, dietary overlap, Madagascar, molossid, prey selection, roost

Introduction

Most molossid species known from Madagascar are known to live synanthropically and four, *Mormopterus jugularis, Chaerephon pumilus, Chaerephon leucogaster*, and *Mops leucostigma* are relatively widespread (Goodman and Cardiff, 2004). There is no information available on the feeding ecology and diet of molossids in Madagascar and this reflects a general paucity of ecological study on Malagasy microchiropterans (Goodman and Benstead, 2005), although advances have recently been made in their taxonomy (e.g., Goodman and Ranivo, 2004; Goodman *et al*., 2005), diet (Razakarivony *et al*., 2005) and biogeography (e.g., Yoder *et al*., 2005).

There is growing appreciation of the potential role that molossid bats play in predation on crop pests (e.g., Whitaker *et al*., 1996; Lee and McCracken, 2005). Molossids in Madagascar frequently roost in large colonies in municipal buildings or houses, and often close to agricultural land. Therefore, in addition to the objective of describing the diet of Madagascar's endemic mammals, a better understanding of the dietary preference of molossid bats in rural settings may provide clues as to their potential as predators of crop pests. In this study we investigated seasonal and interspecific variation in the diet of three sympatric molossids (*M. jugularis*, *M. leucostigma* and *C. pumilus*) from an agricultural setting near mid-elevation dense humid forest in eastern Madagascar.

Materials and Methods

The study was conducted in the small town of Andasibe on the fringes of Parc National de Mantadia and Reserve Spéciale d'Analamazaotra (18°54'S, 48°25'E; altitude: 980 m a.s.l.). The town is situated on the banks of the Sahatandra River and major land use includes rice cultivation, *Eucalyptus* spp. plantations and vegetable crops. A significant amount of mid-elevation dense humid forest is also found in the area. Populations of three free-tailed bat species (*Mormopterus jugularis*, *Mops leucostigma* and *Chaerephon pumilus*) were studied in seven roosts located in buildings in the town. *Mormopterus jugularis* and *M. leucostigma* are Malagasy endemics (Peterson *et al*., 1995) and *C. pumilus* is widespread in Africa (Hutson *et al*., 2001).

Faecal pellets were used to determine the diet of trapped bats. We conducted our work during the austral summer (1–15th February) and austral winter (10–15th July) of 2003. Bats were trapped in mist nets placed outside the entrances to their roosts as they returned from evening foraging bouts. Emergence was usually completed before 19:30 hour and all trapped bats were caught between 20:00–00:00 hour. Three people attended the nets continuously and extracted the bats immediately upon capture. Individual bats were kept in cloth bags from one to three hours (usually less than one hour) in order to obtain faecal samples. Five of the largest intact faecal pellets were retained for analysis (e.g., Whitaker *et al*., 1996; Lee and McCracken, 2005) and stored in 70% alcohol.

The five pellets were first softened and then carefully teased apart with a dissecting needle. A few drops of glycerine were added to the middle of the slide to separate individual items (Shiel *et al*., 1997). All insect fragments items were removed by working systematically up and down the slide. Under a binocular microscope the prey items were identified to the ordinal level using keys and illustrations (Whitaker, 1988; Delvare and Aberlanc, 1989; Scholtz and Holm, 1989; Shiel *et al*., 1997) and reference collections made in the field by collecting insects using a light traps ('Petromax' petrol-powered light) during trapping sessions on 28th March and 8th July 2003.

We visually estimated the percentage volume of each prey type for each individual bat (Whitaker, 1988) using five pellets per bat as one sample. We used individual bats as our sample unit rather than individual faecal pellets to avoid pseudoreplication. Percentage frequency was calculated as the percentage of bats containing a particular food type in each season. We tested for differences in dietary composition between season using Mann-Whitney *U*-tests on mean percentage volume of major prey types, with each individual bat representing an independent replicate. All percentage values were arcsine transformed before analysis.

Results

Faecal samples (five pellets per bat) were analysed from 145 bats. Sixty two bats were captured during the austral winter and 83 during the summer. The overall composition of our captures was made up of 54 *C. pumilus,* 48 *M. leucostigma* and 43 *M. jugularis*. The most abundant prey types in the faeces measured by percentage volume for the three species combined were Coleoptera ($\bar{x} = 45.8 \pm 3.34$ SE), Hemiptera (20.2 ± 2.06), Lepidoptera (15.0 ± 1.32) and Diptera (8.1 ± 1.33). The percentage volume of Hemiptera and Lepidoptera were similar when pooled across season (Kruskal Wallis, Hemiptera: $H = 3.5$, *d.f.* = 2, $P = 0.17$; Lepidoptera: $H = 4.0$, *d.f.* = 2, $P = 0.13$; see Table 1). The volume of Diptera varied significantly between species ($H = 10.1$, *d.f.* = 2, $P < 0.01$) and was highest for *M. leucostigma*. The volume of Coleoptera also differed significantly between species ($H = 6.3$, *d.f.* = 2, $P < 0.05$) and was highest in the diet of *M. jugularis* contained the highest volume of Coleoptera (Table 1).

The diet of all three species varied with season (Table 2). Hemiptera and Lepidoptera were important prey for *C. pumilus* during both seasons with Diptera only

TABLE 1. Mean percentage volume (± SE) of four invertebrate orders in the diet of three molossid species from eastern Madagascar. Sample sizes of bats are shown in parentheses

Order	*Chaerephon pumilus* (54)	*Mops leucostigma* (48)	*Mormopterus jugularis* (43)
Coleoptera	40.3 ± 5.07	39.6 ± 5.93	60.5 ± 6.30
Hemiptera	19.3 ± 2.58	21.7 ± 3.70	19.9 ± 4.78
Lepidoptera	17.6 ± 2.01	15.3 ± 2.64	11.3 ± 2.14
Diptera	6.6 ± 1.46	15.2 ± 3.39	2.7 ± 1.60
Hymenoptera	0.7 ± 3.12	0.3 ± 0.23	0.0
Ephemeroptera	0.0	1.1 ± 0.59	0.0
Trichoptera	0.7 ± 0.46	0.0	0.0

making a notable contribution in the winter and Coleoptera prevalent only during the summer. Hemiptera and Diptera were most common in the diet of *M. leucostigma* during the winter, with the summer diet characterised by a high coleopteran presence. Hemiptera, in the winter, and Coleoptera, in the summer, were the main dietary components of *M. jugularis*. Diptera constituted an important food source *M. leucostigma* in the winter but were less common in the diet of *C. pumilus* and only rarely encountered in the diet of *M. jugularis* (Table 2). Other invertebrate orders such as Trichoptera, Ephemeroptera and Hymenoptera were infrequently detected in the faecal samples.

The percentage volume of lepidopterans was significantly different between season for *C. pumilus* ($U = 211$, $n = 54$, $P < 0.01$), *M. leucostigma* ($U = 181$, $n = 48$, $P < 0.05$) and *M. jugularis* ($U = 121$, $n = 43$, $P < 0.05$). Expressed as percentage frequency, lepidopterans were frequently encountered in the diet and appeared to be an important food source for all species (Table 2). Coleoptera were regularly found in the faeces of all three species during the summer but were less common and very rare in the case of *M. jugularis*, in the winter (Table 2). Seasonal variation in the percentage volume of Coleoptera was significant for all species (*C. pumilus*: $U = 0.0$, $n = 54$, $P < 0.001$; *M. leucostigma*: $U = 0.0$, $n = 48$, $P < 0.001$; *M. jugularis*: $U = 0.0$, $n = 43$, $P < 0.001$) and was highest in the summer (Table 2). Diptera were an important food source during the winter only and this was reflected in a significant seasonal difference in percentage volume for *C. pumilus* ($U = 171$, $n = 24$, $P < 0.001$) and *M. leucostigma* ($U = 72$, $n = 48$, $P < 0.001$). Diptera were never common in the diet of *M. jugularis*. Hemipterans were commonly found in the diet of all three species and especially during the winter (Table 2) and seasonal differences in percentage volume were significant (*C. pumilus*: $U = 208$, $n = 54$, $P < 0.001$; *M. leucostigma*: $U = 40$, $n = 48$, $P < 0.001$; *M. jugularis*: $U = 25$, $n = 4$, $P < 0.01$).

DISCUSSION

Diet of Molossid Bats

As high, fast flying bats that hawk over open areas using relatively long, narrowband echolocations molossids are adapted to feeding on large, flying insects. The diet of molossid bats in our study consisted mainly of Coleoptera followed by Hemiptera, Lepidoptera and Diptera. This is consistent with other descriptions of molossid diet. For example, *Tadarida brasiliensis* has a diet of mainly Coleoptera, Lepidoptera and Hemiptera (Whitaker *et al.*, 1996; Lee and McCracken, 2005), although the exact composition varies according to the time of foraging (Whitaker *et al.*, 1996; Lee and McCracken, 2005). In east Africa however, *C. pumilus* diet was made up of Hemiptera,

TABLE 2. Percentage ($\bar{x} \pm SE$) volume (Vol.) and frequency (Freq.) of invertebrate orders in the diet of microchiropterans from eastern Madagascar. Sample sizes of bats caught during each season are given in parentheses (number of pellets analyzed for each species is 5 × bat sample size)

Order	*Chaerephon pumilus*				*Mops leucostigma*				*Mormopterus jugularis*			
	Winter (24)		Summer (30)		Winter (25)		Summer (23)		Winter (13)		Summer (30)	
	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.
Hemiptera	28.1 ± 4.19	92	10.4 ± 2.02	67	36.9 ± 5.29	100	5.1 ± 1.97	44	58.1 ± 9.19	92	3.4 ± 1.22	33
Lepidoptera	24.2 ± 2.35	87	10.9 ± 2.82	47	18.2 ± 3.26	80	12.0 ± 4.19	61	16.9 ± 3.65	77	8.9 ± 2.55	57
Diptera	13.1 ± 2.39	50	0.03 ± 0.03	0	31.1 ± 5.07	68	0.04 ± 0.04	0	8.5 ± 5.04	23	0.20 ± 0.17	3
Coleoptera	3.3 ± 1.18	33	77.3 ± 3.02	100	3.0 ± 0.76	44	79.5 ± 4.2	100	1.5 ± 1.54	8	86.1 ± 2.72	100
Hymenoptera	1.3 ± 0.79	8	0.1 ± 0.07	7	0.6 ± 0.44	8	0.0	0	0.0	0	0.0	0
Ephemeroptera	0.0	0	0.0	0	2.2 ± 1.08	12	0.0	0	0.0	0	0.0	0
Trichoptera	1.3 ± 0.92	4	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0
Unidentified taxa	28.8 ± 2.48	100	1.3 ± 0.57	17	11.5 ± 1.65	80	3.3 ± 1.7	22	15.0 ± 3.92	85	1.5 ± 0.75	20

Lepidoptera and Hymenoptera but the primary food source was Blattodea taken from inside the roost (Aspetsberger *et al*., 2003). *Tadarida plicata* in Thailand fed on mainly Homoptera, Lepidoptera and Coleoptera (Leelapaibul *et al*., 2005). Fenton *et al.* (1998) reported Coleoptera as the main dietary component of the large *Molossus ater* (body mass 30–45 g) in Mexico. The diet of the European free-tailed bat *Tadarida teniotis* consisted mainly of Lepidoptera and Neuroptera (Rydell and Arlettaz, 1994) but this species has an unusually low echolocation frequency (11–12 kHz) and is proposed to be a specialist on tympanate insects.

Overlap and Competition

Our study presents the first description of the diet of two endemic Malagasy bats *M. leucostigma* and *M. jugularis.* These species roosted synanthropically with *C. pumilus* in the low roofs of buildings at the edge of a mid-elevation dense humid forest. If food resources were limited we might expect a mechanism of resource partitioning to be present. At the ordinal level there was considerable overlap between the dietary composition of the three bat species within each of the two study periods. Dietary composition changed according to the season but this shift was consistent across the diet of all bat species, although there were a few interspecific differences in the percentage frequency of Diptera and Lepidoptera. It appears that interspecific competition for food is not strong, although we acknowledge that there may have been undetected spatial segregation of foraging areas that could reduce levels of competition or selection of different prey size (e.g., Zhang *et al*., 2005). Another possibility is that there was interspecific variation in the composition of Lepidopterans in the diet, due in part to foraging techniques associated with echolocation characteristics, but this was not detected during our analyses because of the difficulty in analysing soft lepidopteran parts from faeces. The agriculture-forest landscape in our study area appears to provide ample insect food for molossid bats and changes in dietary composition probably followed seasonal patterns of insect availability.

Pest Control?

There is growing interest in the role that insectivorous bats play in predation upon insect pests (e.g., Lee and McCracken, 2005; Leelapaibul *et al*., 2005; Zhang *et al*., 2005). Lepidopterans are significant economic pests of Madagascar's cotton crop and in particular, larvae of *Helicoverpa armigera* and *Spodoptera littoralis* have been identified as serious pests and are targetted by the annual application of insecticide. Although our study site was in eastern Madagascar**,** away from the island's main cotton producing areas, some molossid bats (e.g., *C. leucogaster, M. leucostigma*) are occur within both the western and southern cotton producing regions. Lepidopterans were an important food source for molossid bats in our study and further investigation is now required into the quantity and composition of invertebrates consumed by microchiropterans in order to assess their economic and environmental role in Madagascar.

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LITERATURE CITED

ASPETSBERGER, F., D. BRANDSEN, and D. S. JACOBS. 2003. Geographic variation in the morphology, echolocation and diet of the little free-tailed bat, *Chaerephon pumilus* (Mollosidae). African Zoology, 38: 245–254.

DELVARE, G., and H. P. ABERLANC. 1989. Les insectes d'Afrique et d'Amérique tropicale. Clés pour la reconnaissance des familles. PRIFAS, CIRAD-GERDAT, Montpellier, France, 302 pp.

FENTON, M. B., I. L. RAUTENBACH, J. RYDELL, H. T. ARITA, J. ORTEGA, S. BOUCHARD, M. D. HOVOROKA, B. LIM, E. ODGREN, C. V. PORTFORS, W. M. SCULLY, D. M. SYME, and M. J. VONHOF. 1998. Emergence, diet, echolocation and foraging behaviour of *Molussus ater* (Chiroptera: Molossidae). Biotropica, 30: 314–320.

GOODMAN, S. M., and J. P. BENSTEAD. 2005. Updated estimates of biotic diversity and endemism for Madagascar. Oryx, 39: 73–78.

GOODMAN, S. M., and S. G. CARDIFF. 2004. A new species of *Chaerephon* (Molossidae) from Madagascar with notes on other members of the family. Acta Chiropterologica, 6: 227–248.

GOODMAN, S. M., and J. RANIVO. 2004. The taxonomic status of *Neoromicia somalicus malagasyensis*. Mammalian Biology, 69: 434–438.

GOODMAN, S. M., R. K. B. JENKINS, and F. H. RATRIMOMANARIVO. 2005. A review of the genus *Scotophilus* (Mammalia, Chiroptera, Vespertilionidae) on Madagascar, with the description of a new species. Zoosystema, 27: 867–882.

HUTSON, A. M., S. P. MICKLEBURGH, and P. A. RACEY. 2001. Microchiropteran bats — global status survey and conservation action plan. IUCN/SSC Chiroptera Specialist Group, Gland, 258 pp.

LEE, Y.-F., and G. F. MCCRACKEN. 2005. Dietary variation of Brazilian free-tailed bats links to migratory populations of pest insects. Journal of Mammalogy, 86: 67–76.

LEELAPAIBUL, W., S. BUMRUNGSRI, and A. PATTANAWIBOON. 2005. Diet of the wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially acting as biological pest control agents. Acta Chiropterologica, 7: 111–119.

PETERSON, R. L., J. L. EGER, and L. MITCHELL. 1995. Chiroptères. Vol. 84. Faune de Madagascar. Muséum National d'Histoire Naturelle, Paris, 204 pp.

RAZAKARIVONY, V. R., B. RAJEMISON, and S. M. GOODMAN. 2005. The diet of Malagasy Microchiroptera based on stomach contents. Mammalian Biology, 70: 312–316.

RYDELL, J., and R. ARLETTAZ. 1994. Low-frequency echolocation enables the bat *Tadarida teniotis* to feed on tympanate insects. Proceedings of the Royal Society of London, 257B: 175–178.

SCHOLTZ, C. H., and E. HOLM. 1989. Insects of Southern Africa. Butterworths, Durban, 502 pp.

SHIEL, C. C., C. M. MCANEY, J. SULLIVAN and J. S. FAIRELY. 1997. Identification of arthropod fragments in bat droppings. Mammal Society, London, 56 pp.

WHITAKER, J. O. 1988. Food habits and analysis of insectivorous bats. Pp. 171–189, *in* Ecological and behavioural methods for the study of bats (T. H. KUNZ, ed.). Smithsonian Institution Press, Washington D.C., 503 pp.

WHITAKER, J. O., C. NEEFUS, and T. H. KUNZ. 1996. Dietary variation of the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). Journal of Mammalogy, 77: 716–724.

YODER, A. D., L. E. OLSON, C. HANLEY, K. L. HECKMAN, R. M. RASOLOARISON, A. L. RUSSELL, J. RANIVO, V. SOARIMALALA, K. P. KARANTH, A. P. RASELIMANANA, and S. M. GOODMAN. 2005. A multidimensional approach for detecting species patterns in Malagasy vertebrates. Proceedings of the National Academy of Sciences, 102: 6587–6954.

ZHANG, L., G. JONES, S. ROSSITER, G. ADES, B. LIANG, and S. ZHANG. 2005. Diet of flat-headed bats, *Tylonycteris pachypus* and *T. robustula*, in Guangxi, South China. Journal of Mammalogy, 86: 61–66.

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