The food habits of a Malagasy Giant: *Hipposideros commersoni* (E. Geoffroy, 1813)

Andrinajoro A. Rakotoarivelo[1,2], Mahefatiana Ralisata[2], Olga Ramilijaona Ravoahangimalala[2], Marlène R. Rakotomalala[2], Paul A. Racey[3] and Richard K. B. Jenkins[2,3]*

[1]*Département de Biologie Animale, Faculté des Sciences, Université d'Antananarivo, B.P. 906, Antananarivo (101), Madagascar,* [2]*Madagasikara Voakajy, B. P. 5181, Antananarivo (101), Madagascar and* [3]*School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, U.K.*

Abstract

Hipposideros commersoni is a large microchiropteran bat endemic to Madagascar. We analysed fragments of its prey from faeces and from underneath feeding perches to describe its diet from four sites. Diet was similar across sites and Coleoptera was the main prey item by percentage volume (75%), followed by Hemiptera (13%). Carabidae and Scarabidae were the most frequent coleopterans found in the diet. Direct observations (n = 3) were made of bats flying short distances from perches along forest trails to prey on Cicadidae (*c.* 20 mm in length) located on tree trunks. There were differences in the composition of faecal samples collected form netted bats and pellets collected under feeding perches, with the latter consisting of more Blattoptera (Blattellidae 'cockroaches'). *Hipposideros commersoni* appears to have a unique foraging behaviour and diet among Malagasy microchiropterans and its preference for certain Coleoptera and other large invertebrates may account for reported seasonal variation in body fattening and activity.

Key words: diet, foraging, *Hipposideros,* Madagascar, Microchiroptera

Résumé

Hipposideros commersoni est une grande chauve-souris microchiroptère endémique de Madagascar. Nous avons analysé des fragments de proies à partir des excréments et sous les perchoirs où elle se nourrit pour décrire son régime alimentaire sur cinq sites. Le régime était semblable sur tous les sites, et les coléoptères constituent les proies principales en pourcentage du volume (75%), suivis par les hémiptères (13%). Les carabidés et les scarabidés sont les coléoptères trouvés le plus fréquemment dans le régime alimentaire. Des observations directes (n = 3) ont été faites de chauves-souris volant sur de courtes distances à partir de leur perchoir le long de pistes forestières pour attraper des cicadidés (env. 20 mm. de long) posés sur des troncs d'arbres. Il y avait des différences dans la composition des échantillons de crottes récoltés à partir de chauves-souris capturées dans des filets et celle des pelotes récoltées sous les perchoirs, ces dernières contenant plus de Blattoptères (Blattellides – cancrelats). *Hipposideros commersoni* semble avoir un comportement et un régime alimentaires uniques parmi les microchiroptères malgaches, et sa préférence pour certains coléoptères et pour d'autres grands invertébrés pourrait intervenir dans les variations saisonnières rapportées du taux de graisse dans le corps et de l'activité.

Introduction

The genus *Hipposideros* contains some of the largest extant microchiropteran species and can attain body weights of 180 g (Kingdon, 1974; Vaughan, 1977). The life history and evolution of large-bodied hipposiderids is of interest to biologists because of the adaptations required by these large bats to persist in seasonal, tropical environments (Vaughan, 1977; McWilliam, 1982; Cotterill & Fergusson, 1999). *Hipposideros vittatus* from mainland Africa has a large gape and powerful bite (Cotterill & Fergusson, 1999) and it is a specialized predator of large arthropod prey with hard exoskeletons (Vaughan, 1977). Seasonal fluctuations in prey abundance for large African hipposiderids, which results in temporary food shortage during the cool dry

*Correspondence: E-mail: jenkins@moov.mg and r.jenkins@abdn.ac.uk

season, is a major determinant of life history and has been invoked to explain local migrations to areas rich in food (Vaughan, 1977; McWilliam, 1982) or lower metabolic rates during periods of food shortage (Churchill, Draper & Marais, 1997).

Hipposideros commersoni is endemic to Madagascar and occurs throughout the forested areas to an altitude of 850 m (Eger & Mitchell, 2003). Its diet in western Madagascar consists mainly of Coleoptera (Razakarivony, Rajemison & Goodman, 2005; Rakotoarivelo *et al.*, 2007) and seasonal variation in its activity and diet has been recorded (Kofoky *et al.*, 2007; Rakotoarivelo *et al.*, 2007). In southern Madagascar, *H. commersoni* is eaten by local people to supplement their diet during periods of food shortage when the bats have large fat deposits (Goodman, 2006). In this paper we report on the diet of *H. commersoni* from four sites and describe its food habits based on faecal samples collected from netted bats and under feeding perches.

Materials and methods

Study area

Our work was conducted in three national parks in western Madagascar and a forest reserve in the east. The deciduous forests of Parc National Tsingy de Bemaraha (PNTB; 19°08′S, 44°48′E, 120 m a.s.l.) and PN de Namoroka (PNN; 16°24′S, 45°18′E, 220 m a.s.l) are on karstic rock and have a high chiropteran richness (16 and 10 species, respectively) which is thought to be related to the abundance of cavity roosting sites (Goodman *et al.*, 2005). The forest of PN d'Ankarafantsika (PNA; 16°19′S, 46°48′E, 160 m a.s.l.) is on a sandstone substratum and nine bat species are known from the site (Goodman *et al.*, 2005). Tampolo forest reserve (TFR; 7°16′S, 49°25′E, 10 m a.s.l.) is a large fragment of littoral forest in eastern Madagascar (de Gouvenain & Silander, 2003) from where three microchiropteran species have been recorded (Ifticene, Razafimanahaka & Goodman, 2005). For further details of the study sites see Nicoll & Langrand (1989), Alosno *et al.* (2002), Rasoloarison & Paquier (2003), Ratsirarson & Goodman (2005) and Kofoky *et al.* (2007). Our fieldwork was conducted during the austral summer between the months of October and April; 10–27 October 2003 (PNTB), 22 February–21 March 2005 (TFR), 21–28 October 2004 (PNN) and 27 February–3 April 2004 (PNA).

Bat capture

Bats were netted along trails and gaps in the forest. Mist nets were placed at ground level and bats were extracted immediately upon capture. Trapping occurred between 1800 h and 2200 h. Bats were kept for a maximum of 30 min in cloth bags at the capture site. Before release, all bats were aged, sexed and their weight (g) and forearm length (mm) were measured with a pesola balance and dial calipers, respectively. Faeces were collected from the cloth bags after the release of the bats and stored in individual plastic vials for later identification. At TFR, a night-feeding perch was located and faecal material was collected each morning. For this site, our dietary data therefore consisted of faeces from flying and resting bats. The invertebrate fauna at each of the four sites was collected using malaise and light traps and was used as reference material for the identification of prey fragments.

Faecal analysis

Ten faecal pellets were selected at random from each bat, softened and teased apart with a dissecting needle. All insect fragments were removed and prey items were identified to the ordinal or family levels using keys (Delvare & Aberlanc, 1989; Scholtz & Holm, 1989) and field reference collections. We visually estimated the percentage volume of each prey type for each individual bat (Whitaker, 1988). Percentage frequency was also calculated for Coleoptera families.

Results

The biometrics of 60 netted bats were recorded and male forearm length (92.1 mm ± SE 0.45, n = 30) was significantly larger than females (84.3 mm ± SE 0.45, n = 30; ANOVA $F_{1,\,58}$ 165, $P < 0.001$). We collected faecal samples from 61 bats during our study and further 26 samples from beneath a night-feeding perch. Expressed as percentage volume, *H. commersoni* diet comprised mostly of Coleoptera, with Hemiptera the second most important food item (Table 1). Together these two orders accounted for 88% volume of the invertebrate fragments with the remaining 12% from eight other taxa and unidentified pieces.

Coleoptera was the most voluminous order in the diet of *H. commersoni* from all four study sites and was highest in the two karst national parks, PNTB and PNN (Table 2).

Table 1 Dietary composition of 61 *Hipposideros commersoni* from Madagascar expressed as mean ± standard error of estimated percentage volume of nine invertebrate taxa in faecal samples

Taxa	Per cent volume
Coleoptera	75.2 ± 2.04
Hemiptera	13.4 ± 1.79
Blattoptera	4.2 ± 0.91
Trichoptera	0.2 ± 0.12
Diptera	0.6 ± 0.21
Hymenoptera	0.8 ± 0.31
Lepidoptera	0.4 ± 0.21
Ephemeroptera	0.7 ± 0.26
Neuroptera	1.6 ± 0.51
Psocoptera	0.2 ± 0.16

The volume of Hemiptera varied between sites and was highest in PNN and lowest in TFR. The contribution to the diet from other taxa was generally low (<5% mean volume) with the exception of Blattoptera fragments which were found mostly in bats from TFR and PNA.

Because of the important contribution of Coleoptera to the diet we identified these fragments to the family level and expressed them as percentage frequency. Scarabidae was the most common coleopteran family and was recorded in 60 of the 61 faecal samples (Table 3). Carabidae was the next most common one at PNA and PNTB, while Chrysomeloidea featured frequently in the diet of bats from PNN, and Curculionidae in TFR. Dietary diversity of coleopteran families was highest in TFR and a number of families found in the diet at this site were rare elsewhere (Table 3).

There were noticeable differences between the percentage volume of major prey types collected from perching and flying bats (Fig. 1). While differences between the least common food types were imperceptible from our samples sizes, the percentage volume of Coleoptera and Blattoptera clearly differed. The volume of Coleoptera was highest in the faeces collected from bats netted while foraging. In contrast, Blattoptera fragments were rare in the faeces of foraging bats but were common in the remains found underneath a night-feeding perch.

We made three opportunistic observations of *H. commersoni* feeding at PNTB. On each occasion the bats used a perch in a forest clearing or along a trail and were observed in natural light at dusk. Each bat flew 3–4 m from its perch and captured a single cicada (Hemiptera, Cicadidae) from a tree trunk before returning to its original perching site. These cicadas were estimated to be *c.* 20 mm in length. Cicada fragments were found in 1/19 (5%) fecal samples collected from netted bats in PNTB and in 1/26 (4%) of the samples under a feeding perch from TFR.

Discussion

Hipposideros commersoni is sexually dimorphic and feeds mainly on Coleoptera (Scarabaeidae, Carabidae, Chrysomelidea and Curculionidae). This was consistent across seasons and study sites and other invertebrate taxa were rare in the diet, suggesting that this bat is a specialized beetle predator.

There have been few other studies on the diet of Malagasy microchiropterans. Andrianaivoarivelo *et al.* (2006) described the diet of three molossid bats roosting together in a synanthropic setting in eastern Madagascar but there is relatively little information about forest species, such as

Table 2 Dietary composition of 61 *Hipposideros commersoni* from Parc National d'Ankarafantsika (PNA), Parc National Tsingy de Bemaraha (PNTB), Parc National de Namoroka (PNN) and Tampolo Forest Reserve (TFR) in Madagascar expressed as mean ± standard error of estimated percentage volume of nine invertebrate taxa in faecal samples

	PNA n = 23	PNTB n = 19	PNN n = 12	TFR n = 7
Coleoptera	64.1 ± 1.46	86.6 ± 4.21	80.0 ± 4.26	72.1 ± 1.4
Hemiptera	15.4 ± 1.37	8.9 ± 4.15	20.0 ± 4.77	7.8 ± 4.06
Blattoptera	6.9 ± 1.62	1.8 ± 0.87	0.0 ± 0.00	7.8 ± 2.14
Diptera	1.3 ± 0.47	0.26 ± 0.26	0.0 ± 0.00	0.0 ± 0.00
Hymenoptera	1.2 ± 0.65	0.0 ± 0.00	0.0 ± 0.00	2.9 ± 1.49
Lepidoptera	0.2 ± 0.22	1.0 ± 0.61	0.0 ± 0.00	0.0 ± 0.00
Ephemeroptera	0.9 ± 0.40	0.26 ± 0.26	0.0 ± 0.00	2.1 ± 2.1
Neuroptera	2.2 ± 0.99	0.0 ± 0.00	3.3 ± 1.42	0.0 ± 0.00
Psocoptera	0.0 ± 0.00	0.0 ± 0.00	0.8 ± 0.83	0.0 ± 0.00

n, number of bats.

Table 3 The Coleopteran diet of 61 *Hipposideros commersoni* expressed as percentage frequency of occurrence for 16 families

Coleoptera	PNA n = 23	PNTB n = 19	PNN n = 12	TFR n = 7
Anthicidae	0.0	0.0	0.0	14.3
Bruchidae	0.0	0.0	0.0	28.6
Buprestidae	0.0	10.5	8.3	28.6
Carabidae	47.8	52.6	16.7	28.6
Cerambicidae	4.3	5.3	0.0	0.0
Ceratocanthidae	13.0	0.0	0.0	0.0
Chrysomeloidea	17.4	31.6	33.3	0.0
Cucujoidea	26.1	5.3	25.0	28.6
Curculionidae	13.0	15.8	8.3	42.9
Dermestidae	0.0	0.0	0.0	14.3
Elateridae	17.4	0.0	0.0	0.0
Meloidae	0.0	0.0	0.0	42.9
Passalidae	0.0	21.1	0.0	42.9
Ptinidae	0.0	0.0	0.0	14.3
Scarabaeidae	95.7	100.0	100.0	100.0
Trogidae	0.0	0.0	8.3	0.0
Taxon richness	8	8	7	11

n, number of bats; PNA, Parc National d'Ankarafantsika; PNTB, Parc National Tsingy de Bemaraha; PNN, Parc National de Namoroka; TFR, Tampolo Forest Reserve.

vespertilionid and hipposiderid bats. Razakarivony *et al.* (2005) analysed the stomach contents of five forest bats species, including 11 individuals of *H. commersoni* from PNTB. They found coleopterans as the most frequently encountered prey items, present in 64% of the stomachs analysed. The next most common prey item was Isoptera, found in 36% of the samples.

Our results are consistent with dietary studies from elsewhere which report that large *Hipposideros* species are primarily beetle predators, e.g. *Hipposideros lankadiva* (Eckrich & Neuweiller, 1988), *Hipposideros diadema* (Pavey & Burwell, 1997) and *H. vittatus* (Vaughan, 1977). Samples collected under feeding perches of *H. commersoni* in Kenya were mainly from four coleopteran families, Cerambycidae, Elateridae, Scarabaeidae and Chrysomelidae (Vaughan, 1977). *Hipposideros commersoni* in Madagascar fed mainly on scarabeids but carabeids were also an important source of food in all sites. There are unconfirmed reports that *H. commersoni* feeds on small frogs (cited in Eger & Mitchell, 2003), and carnivory has been reported from *Hipposideros* species smaller than *H. commersoni*, such as *H. diadema* (32–57 g; Pavey & Burwell, 1997). Although there was no evidence of carnivory from the current study, it cannot be ruled out.

While other microchiropterans in Madagascar also feed on Coleoptera (Razakarivony *et al.*, 2005; Andrianaivoarivelo *et al.*, 2006) it appears that the foraging behaviour and diet of *H. commersoni* is distinct from other species. Like the observations of Vaughan (1977) on *H. vittatus*, *H. commersoni* appears to be a sit-and-wait predator that makes short sallies to catch large, hard-bodied prey. *Hipposideros vittatus* in Kenya fed mainly on flying beetles but occasionally gleaned prey from vegetation. We observed prey capture of nonaerial prey when large cicadas were plucked from the surface of tree trunks at night.

As reported elsewhere there are biases involved with the interpretation of faecal material from microchiropterans and small soft-bodied prey are usually under-represented (Dickman & Huang, 1988). For bats that feed on large invertebrates and small vertebrates the collection and analysis of culled parts under feeding roosts is an important method for assessing diet (e.g. Fenton *et al.*, 1990,

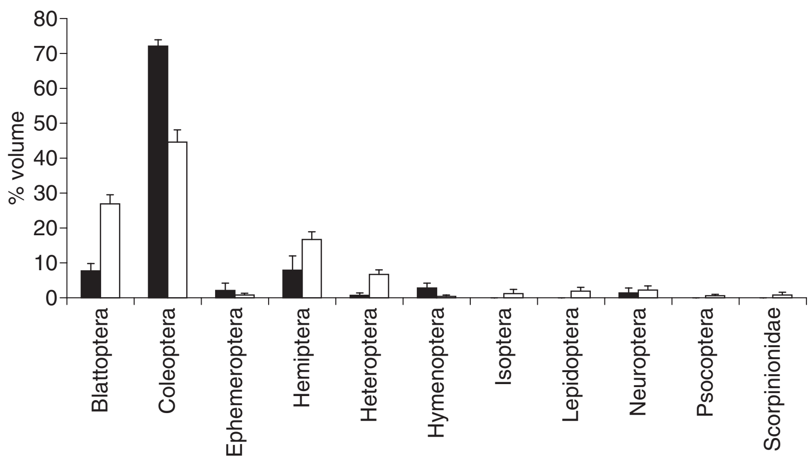

Fig 1 The food habits (mean percentage volume ± standard error) of *Hipposideros commersoni* from Tampolo Forest Reserve in eastern Madagascar: (□), faeces collected under a single night-feeding perch, n = 26; (■), faeces collected from trapped bats, n = 7

1993). Further dietary studies of *H. commersoni*, using both faecal analysis and direct observations of foraging bats, will better determine the key prey types and permit an assessment of whether seasonal shortages of these invertebrates coincides with shifts in abundance or the sex ratio of bat populations. Kofoky *et al.* (2007) reported that *H. commersoni* was abundant in PNTB in October but very rare in the same area during July. Similarly, hunting of *H. commersoni* by local people in southern Madagascar coincides with the period when the bats have high fat deposits (Goodman, 2006). These observations suggest that *H. commersoni* undergoes seasonal changes in activity, distribution or metabolism.

Acknowledgements

The authors are grateful to their partners, the Département de Biologie Animale, Université d'Antananarivo and ANGAP. This work was authorized by the Ministry of Environment, Water and Forest. Funding was provided by the Darwin Initiative (#162/10/024), Fauna and Flora International, National Geographic Society (#C23-02) and the British Ecological Society (#2159). The authors are also grateful to Daudet Andriafidison, Amyot F. Kofoky, Lorraine Marshall-Ball, Tsibara Mbohoahy, Nicolas Ranaivoson, Roseline Rampilamanana, Félicien H. Randrianandrianina, Fanja H. Ratrimomanarivo and Hanta Julie Razafimanahaka for their assistance.

References

Alosno, L.E., Schulenberg, T.S., Radilofe, S. & Missa, O. (2002) *Evaluation rapide de la diversité biologique de reptiles et amphibians de la Reserve Naturelle Integrale d'Ankarafantsika*. RAP Bulletin of Biological Assessment No. 23. Conservation International, Washington, D.C.

Andrianaivoarivelo, R.A., Ranaivoson, N., Racey, P.A. & Jenkins, R.K.B. (2006) The diet of three synanthropic bats (Chiroptera: Molossidae) from eastern Madagascar. *Acta Chiropter.* **8,** 439–444.

Churchill, S., Draper, R. & Marais, E. (1997) Cave utilization by Namibian bats: population, microclimate and roost selection. *S. Afr. J. Wildl. Res.* **27,** 44–50.

Cotterill, F.P.D. & Fergusson, R.A. (1999) Reproductive ecology of Commerson's leaf nosed bats *Hipposideros commersoni* (Chiroptera: Hipposideridae) in south-central Africa: interactions between seasonality and large body size; and implications for conservation. *S. Afr. J. Zool.* **34,** 53–63.

Delvare, G. & Aberlanc, H.P. (1989) *Les Insectes d'Afrique et d'Amérique Tropicale Clés Pour La Reconnaissance Des Familles*. CIRAD, Département GERDAT, Laboratoire de Faunistique, Acridologie opérationnelle – Ecoforce Internationale, France.

Dickman, C.R. & Huang, C. (1988) The reliability of faecal analysis as a method for determining the diet of insectivorous mammals. *J. Mammal.* **69,** 108–113.

Eckrich, M. & Neuweiller, G. (1988) Food habits of the sympatric insectivorous bats *Rhinolophus rouxi* and *Hipposideros lankadiva* from Sri Lanka. *J. Zool.* **215,** 729–737.

Eger, J.L. & Mitchell, L. (2003) Chiroptera, Bats. In: *The Natural History of Madagascar* (Eds S. M. Goodman and J. P. Benstead). University of Chicago Press, Chicago.

Fenton, M.B., Swanepoel, C.M., Brigham, R.M., Cebek, J. & Hickey, M.B.C. (1990) Foraging behaviour and prey selection by large-slit faced bats (*Nycteris grandis* Chiroptera: Nycteridae). *Biotropica* **22,** 2–8.

Fenton, M.B., Rautenbach, I.L., Chipese, D., Cumming, M.B., Musgrave, M.K., Taylor, J.S. & Volpers, T. (1993) Variation in foraging behaviour, habitat use and diet of large slit-faced bats (*Nycteris grandis*). *Z. Säugetierkd.* **58,** 65–74.

Goodman, S.M. (2006) Hunting of Microchiroptera in south western Madagascar. *Oryx* **40,** 225–228.

Goodman, S.M., Andriafidison, D., Andrianaivoarivelo, R.A., Cardiff, S.G., Ifticene, E., Jenkins, R.K.B., Kofoky, A., Mbohoahy, T., Rakotondravony, D., Ranivo, J., Ratrimomanarivo, F., Razafimanahaka, J., Razakarivony, V. & Racey, P.A. (2005) The distribution and conservation of bats in the dry regions of Madagascar. *Anim. Cons.* **8,** 153–165.

de Gouvenain, R.C. & Silander, J.A. (2003) Littoral Forest. In: *The Natural History of Madagascar* (Eds S. M. Goodman and J. P. Benstead). The University of Chicago Press, Chicago.

Ifticene, E., Razafimanahaka, J.H. & Goodman, S.M. (2005) Les Chiroptères. In: *Suivi de la biodiversité de la Forêt Littorale de Tampolo* (Eds J. Ratsirarson and S. M. Goodman). Recherches pour le Développement.

Kingdon, J. (1974) *Mammals of Africa: An Atlas of Evolution in Africa*, **Vol. 2a**. Academic Press, London.

Kofoky, A., Andriafidison, D., Ratrimomanarivo, F.H., Razafimanahaka, J.H., Rakotondravony, D., Racey, P.A. & Jenkins, R.K.B. (2007) Habitat use, roost selection and conservation of bats in Tsingy de Bemaraha National Park, Madagascar. *Biodiv. Cons.* **16,** 1039–1053.

McWilliam, A.N. (1982) Adaptive responses to seasonality in four species of insectivorous bats in coastal Kenya. Ph.D thesis. University of Aberdeen, UK.

Nicoll, M.E. & Langrand, O. (1989) *Madagascar: revue de la conservation et des aires protegees*. World Wide Fund for Nature, Gland, xvii + 374 pp.

Pavey, C.R. & Burwell, C.J. (1997) The diet of the diadem leaf--nosed bat *Hipposideros diadema*: confirmation of a morphologically-based prediction of carnivory. *J. Zool.* **243,** 295–303.

Rakotoarivelo, A.A., Ranaivoson, N., Ramilijaona, O.R., Kofoky, A.F., Racey, P.A. & Jenkins, RK.B. (2007) Seasonal food habits of five sympatric forest microchiropterans in western Madagascar. *J. Mammal.* **88,** 959–966.

Rasoloarison, V. & Paquier, F. (2003) Tsingy de Bemaraha. In: *The Natural History of Madagascar* (Eds S. M. Goodman and J. P. Benstead). University of Chicago Press, Chicago and London.
Ratsirarson, J. & Goodman, S.M. (2005) *Suivi de la biodiversité de la Forêt Littorale de Tampolo*. Recherches pour le Développement.
Razakarivony, V.R., Rajemison, B. & Goodman, S.M. (2005) The diet of Malagasy Microchiroptera based on stomach contents. *Mammal. Biol.* **70**, 312–316.
Scholtz, C.H. & Holm, E. (1989) *Insects of Southern Africa*. Johannesburg
Vaughan, T.A. (1977) Foraging behaviour of the giant leaf-nosed bat (*Hipposideros commersoni*). *E. Afr. Wildl. J.* **15**, 237–249.
Whitaker, J.O. (1988) Food habits and analysis of insectivorous bats. In: *Ecological and Behavioural Methods for the Study of Bats* (Ed T. H. Kunz). Smithsonian Institution Press, Washington D.C.

(Manuscript accepted 13 December 2007)

doi: 10.1111/j.1365-2028.2008.00947.x