

**Diet, reproduction and roosting habits of the Madagascar
free-tailed bat, *Otomops madagascariensis* Dorst, 1953
(Chiroptera: Molossidae)**

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Otomops madagascariensis is a large (24–27 g) molossid bat endemic to Madagascar. Unlike its congener *O. martiensseni*, in nearby mainland Africa, little is known about its ecology although it appears to roost only in caves. It is only known from a few sites in the west and occupies a small percentage of the available caves. We studied roosting colonies in seven vertical erosion domes in the roof of a cave in Parc National Tsingy de Bemaraha during July and October 2003. We also captured bats as they emerged from and returned to a roost cave in the south. Female bats examined in the west during October and in the south during November were pregnant. In the roosting colonies, one group contained 57 pregnant females and five adult males. Most other groups also consisted of both sexes but three male-only groups were encountered in October. Diet consisted mainly of Lepidoptera and Coleoptera and there was variation between sites and study locations in the contribution of these prey types. *Otomops madagascariensis* is an obligate cave dweller that appears to be rare within its known range and should be a target species for conservation and research.

Key words: breeding, caves, *Otomops*, diet, Madagascar, Molossidae, reproduction

INTRODUCTION

Otomops madagascariensis is endemic to Madagascar and is thought to be an obligate cave-dweller, unlike the closely related *Otomops martiensseni* from the African mainland which forms colonies in houses (Fenton *et al.*, 2002). The distribution of *O. madagascariensis* covers western Madagascar, from north to south, and appears to

be associated with sites on limestone or sandstone where it roosts in caves (Goodman *et al.*, 2005). Although *O. martiensseni* has been the subject of a number of studies (Mutere, 1973; Rydell and Yalden, 1997; Fenton *et al.*, 2002, 2004), there are few data available on the biology of *O. madagascariensis*. Here we report on the population structure of *O. madagascariensis* from sites in western and southern Madagascar

and investigate patterns of seasonality in food habits and reproduction.

MATERIALS AND METHODS

We studied roosting bats in Anjohikinakina cave (19°0.59'S, 44°46.06'E, 100 m a.s.l.) in the Parc National (PN) Tsingy de Bemaraha, Province de Mahajunga, between 12 and 15 August and 29 and 30 October 2003. Bats roosted in circular erosion domes in the ceiling and we assigned numbers to individual domes that were retained throughout the study. We used long-handled sweep nets to collect all roosting individuals within each erosion dome.

At Namaza canyon on 29 April 2003, PN d'Isalo, Province de Fianarantsoa (22°32.4'S, 45°22.8'E, 800 m a.s.l.) we trapped flying bats using a 12 m mist net set over a small river. In the south of Madagascar, at Ambanalia cave near Sarodrano village, Province de Toliara, bats were trapped using a 9-m mist net erected across a cave entrance. The captures were undertaken as bats left their cave roost on 15 June 2003 and as they returned to it after foraging on 25 November 2003 and 23 February 2004 (23°32.40'S, 43°44.76', 1 m a.s.l.). We were unable to enter the cave at Ambanalia because of local taboos. Bats were kept in cloth bags for a short time in order to collect faeces for diet analysis. Each bat was weighed (Pesola balance, nearest 0.5 g), measured (forearm, nearest mm) and aged (adult or juvenile based on ossification of phalanges) and sexed before release.

Bat faeces were stored in plastic vials with 70% ethanol. Faecal pellets were teased apart with dissecting needles, with the aid of a binocular microscope (10–20×) in a Petri dish. All potentially identifiable arthropod remains were removed, mounted in glycerin on a slide, sealed with nail varnish and examined with a binocular microscope (40–400×). Identification was achieved using generic keys for bat faeces together with other keys and monographs on invertebrate morphology (Delvare and Alberlanc, 1989; Scholtz and Holm, 1989). We visually estimated percentage volume of major prey types following the methods of Whitaker (1988).

RESULTS

In total, we captured 427 *O. madagascariensis* during the study, 196 in PN Tsingy de Bemaraha, 229 at Sarodrano and two in PN d'Isalo. There was no significant difference in forearm length between bats from

PN Tsingy de Bemaraha and Sarodrano sites but males were significantly larger than females (in mm, $\bar{x} \pm \text{SE}$), 61.9 ± 0.15 , and 60.9 ± 0.11 , respectively (2-way ANOVA, site — $F_{1,421} = 3.5$, $P \gg 0.05$, sex — $F_{1,421} = 33.2$, $P < 0.001$, interaction — $F_{1,421} = 0.3$, $P \gg 0.05$). At PN Tsingy de Bemaraha, male and female body mass (in g) differed significantly between seasons (2-way ANOVA, sex — $F_{1,192} = 1.2$, $P > 0.05$, month — $F_{1,290} = 22.5$, $P < 0.001$) and increased between August ($\delta \delta$ — 25.6 ± 0.74 , $\phi \phi$, 25.1 ± 0.33) and October ($\delta \delta$ — 27.8 ± 0.38 , $\phi \phi$ — 27.3 ± 0.33). At Sarodrano, both sex and month and the interaction were significant factors (2-way ANOVA, sex — $F_{1,223} = 4.5$, $P < 0.05$, month — $F_{2,223} = 32.8$, $P < 0.001$, interaction — $F_{2,223} = 9.6$, $P < 0.01$). Male body mass was lower in February (23.0 ± 0.32) than in June (26.3 ± 0.62) or November (26.8 ± 0.39). Females by contrast attained lowest body mass in June (22.9 ± 0.63) and peaked in November (26.6 ± 0.41) before decreasing again in February (24.0 ± 0.31). There were no pregnant females in August at PN Tsingy de Bemaraha, but 95% of the 80 females were pregnant in October. At Sarodrano, no pregnancies were noted in June and February but 45% of the 53 females netted in November were pregnant.

In Sarodrano, 54% of the 28 captures in June and 63% of the 67 captures in November were female. This pattern was similar to Anjohikinakina cave where 54% of the 93 bats caught in August and 75% of the 106 captures in October were female. At the latter site, where we were able to trap all roosting individuals, the sex ratio ($\delta \delta : \phi \phi$) changed from 1:1.1 in June to 1:3.1 in October without a major change in colony size.

At PN Tsingy de Bemaraha we captured all individuals in each roosting group and no other *O. madagascariensis* was found in the cave. We sampled the same seven roosting groups during the two study

TABLE 1. Summary of the population structure of *O. madagascariensis* from seven erosion domes used as roosts in the ceiling of a cave in Parc National Tsingy de Bemaraha, Madagascar during August and October 2003

Roost hole	Month	Total bats	♂ ♂	♀ ♀	% ♂ ♂
1	August	48	19	29	40
	October	22	4	18	18
2	August	19	2	17	11
	October	1	1	0	100
3	August	19	18	1	95
	October	8	4	4	50
4	August	7	5	2	71
	October	7	6	1	86
5	August	0	0	0	0
	October	3	3	0	100
6	August	0	0	0	0
	October	3	3	0	100
7	August	0	0	0	0
	October	62	5	57	8

periods, ranging in size from 7 to 48 individuals in August and 1 to 62 individuals in October (Table 1). The erosion domes in which the bats were roosting were approximately 15–20 m from the ground. All seven erosion domes were occupied by bats in October but only four were occupied August. In August, the sex ratio was almost equal, with 47% males and 53% females but it was more female-biased in October with only 33% males (Table 1).

In August, roosting groups consisted of mostly males in holes 3 and 4, whilst females were most numerous in holes 1 and 2. During this month, all four occupied holes had males and females with the percentage

of males varying from 11% to 95%. In October the composition of hole 1 changed markedly to 82% female. Hole 7, which was unoccupied in July contained 62 bats in October, 92% of which were female. Small numbers of males were found in holes 2–6 and only in hole 1 were males common (Table 1). All four holes with females in October contained pregnant bats.

Based on percentage volume, the diet of *O. madagascariensis* is comprised mainly of Coleoptera and Lepidoptera with other orders making a minor contribution (Table 2). There were few differences in diet between the sexes although the percentage volume of dipterans was significantly higher in female diet (Table 2). In PN Tsingy de Bemaraha, Lepidoptera and Coleoptera were the most common prey items by volume, but Diptera were also important in October (Table 3). Seasonal differences were more pronounced from Sarodrano in southern Madagascar, with most Coleoptera in the faeces during February and Lepidoptera in November (Table 3).

DISCUSSION

All known roosts of *O. madagascariensis* are inside caves, with colonies reported from Sarodrano, PN Tsingy de Bemaraha and RS Ankarana (Cardiff, 2006; Kofoky *et al.*, 2007). *Otomops martiensseni* usually roosts in caves in East Africa (Kingdon, 1974) but frequently uses houses in South

TABLE 2. The percentage volume ($\bar{x} \pm \text{SE}$) of six invertebrate orders in the diet of 22 males and 33 females of *O. madagascariensis* from Madagascar. *F*-values and significance are given for ANOVAs on arcsine transformed percentages

Order	All bats	♂ ♂	♀ ♀	<i>F</i> -value
Lepidoptera	43.5 $\pm$ 3.37	44.3 $\pm$ 3.77	42.9 $\pm$ 5.06	0.58
Coleoptera	38.9 $\pm$ 2.86	40.1 $\pm$ 3.77	38.1 $\pm$ 2.86	0.07
Diptera	5.5 $\pm$ 1.06	2.4 $\pm$ 1.07	7.5 $\pm$ 1.53	6.10*
Hemiptera	3.3 $\pm$ 1.25	4.4 $\pm$ 2.18	2.6 $\pm$ 1.51	0.50
Heteroptera	1.50 $\pm$ 0.76	1.52 $\pm$ 0.89	1.36 $\pm$ 1.36	0.16
Ephemeroptera	1.2 $\pm$ 0.84	0.00	1.9 $\pm$ 1.39	1.27

* — $P < 0.05$

TABLE 3. The percentage volume ($\bar{x} \pm \text{SE}$) of six invertebrate orders in the diet of *O. madagascariensis* from two sites during different seasons. Number of individual bats in parentheses

Order	PN Tsingy de Bemaraha		Sarodrano	
	October (11)	August (14)	February (13)	November (15)
Lepidoptera	31.0 $\pm$ 4.60	41.1 $\pm$ 4.55	28.5 $\pm$ 5.86	72.6 $\pm$ 3.30
Coleoptera	44.2 $\pm$ 4.58	42.8 $\pm$ 4.67	48.3 $\pm$ 6.50	19.9 $\pm$ 2.97
Diptera	15.2 $\pm$ 3.30	2.6 $\pm$ 1.35	2.4 $\pm$ 1.07	2.5 $\pm$ 0.62
Hemiptera	0.9 $\pm$ 0.91	3.2 $\pm$ 1.45	9.8 $\pm$ 4.64	0.0
Heteroptera	3.6 $\pm$ 2.53	2.4 $\pm$ 2.14	0.0	0.7 $\pm$ 0.54
Ephemeroptera	0.0	0.0	4.9 $\pm$ 3.45	0.0

Africa (Fenton *et al.*, 2002). Other members of the genus are hole and cavity roosting bats (e.g., Ramakrishna *et al.*, 2003).

There is little published information on the roosting ecology of *O. madagascariensis* although Cardiff (2006) reported a preference for caves with a large entrance and high ceiling in northern Madagascar. In a survey of *O. martiensseni* roosts in Durban, Fenton *et al.* (2002) reported a mean colony size of 11.2 individuals from 24 attics. However, in caves in coastal Kenya Mutere (1973) captured between 20 and 848 bats per year from two caves indicating that *O. martiensseni* roosts in colonies of various sizes, which may be determined by the volume of the cavity. In their five study colonies, only 6 of 84 bats were adult males and a male with a well-developed gular gland occupied each building (Fenton *et al.*, 2002). This harem organization may also be present in larger roosting aggregations but may be more difficult for biologists to detect (Fenton *et al.*, 2002). There was no direct evidence of a harem mating system in our study cave because no roosting group consisted of a single large male with females and sub-adults. In August most males were found in two erosion domes, both of which contained females. Erosion domes 1 and 2 contained 19 and 18 males respectively but corresponding female numbers 29 and 1. In October, when most of the females were obviously pregnant, three domes contained only males and another six males and a female. One dome contained

57 pregnant females and 5 males, giving a ratio of 1 male to 11 females, which is similar to the reported sex ratio of *O. martiensseni* (Fenton *et al.*, 2002). Male-only groups present during October were presumably unattached 'bachelor' males. The relative size and suitability of each erosion dome may determine the breeding system. As Fenton *et al.* (2002) studied *O. martiensseni* in January, when females were lactating, further studies on *O. madagascariensis* are needed especially as another roosting colony in PN Tsingy de Bemaraha, in a cave near Antsalova (R. K. B. Jenkins, personal observations), appears to have a different roosting formation, consisting of a single group of 100–300 individuals surrounded by satellite groups in circular depressions in the cave roof.

Mutere (1973) recorded peak male testis mass in August just before the onset of pregnancy in females. We were unable to follow the breeding condition of a single colony but pregnancy was noted in October and November in western and southern Madagascar respectively. Differences in the proportion of pregnant females between sites could be attributed to the difference in the timing of breeding between latitudes. Another possibility is that as we trapped bats leaving the roosts in the south but captured bats inside the roost in the west, our results may have been influenced by the behaviour and activity patterns of pregnant females, as only active bats were sampled from Sarodrano.

Increases in female body mass between the austral winter (June and August) and the austral summer (October and November) are associated with pregnancy. There was no clear pattern of male mass change during the same periods but this may be associated with breeding status. In a harem system, the energy budget of harem masters (i.e. those that control access to groups of females) is likely to be different to subordinate males.

As large bodied bats with narrow wings, *Otomops* typically fly high and fast and take flying insects on the wing. Studies on *O. martiensseni* have shown it forages at least 3 km from roosts (Fenton *et al.*, 2002) and feeds almost exclusively on large moths (Rydell and Yalden, 1997). *Otomops madagascariensis* fed mostly on Coleoptera and Lepidoptera but seasonal variation was evident from both study sites, particularly for the latter order. Kingdon (1974) and Mutere (1973) suggest that *O. martiensseni* migrates during periods of food shortage, although there is at present no evidence of this from Madagascar. However, major changes to the proportion of males and females at Anjohikinakina cave between August and October points to seasonal movements and the existence of other colonies. Such movements are likely to depend on the local availability of prey and in Madagascar this may vary according to geographical region. The diet of three other Malagasy molossids is made up predominantly of Lepidoptera and Hemiptera, with Diptera and Coleoptera important seasonally (Andrianaivoarivelo *et al.*, 2006). However, this study was conducted in the humid east of Madagascar and little is known about the diet of the molossid species that occur sympatrically with *O. madagascariensis*.

Otomops madagascariensis was found in seven of the 13 sites surveyed recently in western Madagascar (Goodman *et al.*, 2005). In two of these, despite an

abundance of caves, only a few were found to contain roosting *O. madagascariensis* (Cardiff, 2006; Kofoky *et al.*, 2007). Therefore, as an obligate cave species, known from only a small proportion of caves that have been surveyed for bats, the conservation status of *O. madagascariensis* will depend on the degree of protection afforded to these caves.

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LITERATURE CITED

- ANDRIANAIVOARIVELO, R. A., N. RANAIVOSON, P. A. RACEY, and R. K. B. JENKINS. 2006. The diet of three synanthropic bats (Chiroptera: Molossidae) from eastern Madagascar. *Acta Chiropterologica*, 8: 439–444.
- CARDIFF, S. G. 2006. Bat cave selection and conservation in Ankarana, northern Madagascar. MSci. Thesis, Columbia University, New York, 73 pp.
- DELVARE, G., and H. P. ABERLANC. 1989. Les insectes d'Afrique et d'Amérique-Tropicale. Clés pour la reconnaissance des familles. CIRAD (Centre de Coopération Internationale en Recherche Agronomique pour le Développement), Montpellier, 302 pp.
- FENTON, M. B., P. J. TAYLOR, D. S. JACOBS, E. J. RICHARDSON, E. BERNARD, S. BOUCHARD, K. R. DEBAEREMAEKER, H. TER HOFSTEDE, L. HOLLIS,

- C. L. LAUSEN, J. S., LISTER, D. RAMBALDINI, J. M. RATCLIFFE, and E. REDDY. 2002. Researching little-known species: the African bat *Otomops martiensseni* (Chiroptera: Molossidae). *Biodiversity and Conservation*, 11: 1583–1606.
- FENTON, M. B., D. S. JACOBS, E. J. RICHARDSON, P. J. TAYLOR, and W. WHITE. 2004. Individual signatures in the frequency-modulated sweep calls of African large-eared, bats *Otomops martiensseni* (Chiroptera: Molossidae). *Journal of Zoology* (London), 262: 11–19.
- GOODMAN, S. M., D. ANDRIAFIDISON, R. ANDRIANAIVOARIVELO, S. G. CARDIFF, E. IFTICENE, R. K. B. JENKINS, A. KOFOKY, T. MBOHOAHY, D. RAKOTONDRAVONY, J. RANIVO, F. RATRIMOMANARIVO, J. RAZAFIMANAHAKA, V. RAZAKARIVONY, and P. A. RACEY. 2005. The distribution and conservation of bats in the dry regions of Madagascar. *Animal Conservation*, 8: 153–165.
- KINGDON, J. 1974. *Mammals of Africa. An atlas of evolution in Africa*, Vol. IIA. Academic Press, London, 341 pp.
- KOFOKY, A., D. ANDRIAFIDISON, F. H. RATRIMOMANARIVO, J. H. RAZAFIMANAHAKA, D. RAKOTONDRAVONY, P. A. RACEY, and R. K. B. JENKINS. 2007. Habitat use, roost selection and conservation of bats in Tsingy de Bemaraha National Park, Madagascar. *Biodiversity and Conservation*, 16: 1039–1053.
- MUTERE, F. A. 1973. A comparative study of reproduction in two populations of the insectivorous bat, *Otomops martiensseni*, at latitudes 1°5'S and 2°30'S. *Journal of Zoology* (London), 171: 79–92.
- RAMAKRISHNA, R., M. S. PRADHAN, and S. THAKUR. 2003. Wroughton's free-tailed bat *Otomops wroughtoni* Thomas, 1913. Status Survey of Endangered Species, Zoological Survey of India, Kolkata, 16 pp.
- RYDELL, J., and D. W. YALDEN. 1997. The diets of two high-flying bats from Africa. *Journal of Zoology* (London), 242: 69–76.
- SCHOLTZ, C. H., and E. HOLM. 1989. *Insects of Southern Africa*. Butterworths, Johannesburg, 502 pp.
- WHITAKER, J. O., JR. 1988. Food habits analysis of insectivorous bats. Pp. 171–189, in *Ecological and behavioral methods for the study of bats* (T. H. KUNZ, ed.). Smithsonian Institution Press, Washington D.C., 533 pp.

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