

Roost selection and home range of an African insectivorous bat *Nycteris thebaica* (Chiroptera, Nycteridae)

Ara Monadjem^{1,*}, April Reside², Julien Cornut² and Mike R. Perrin³

¹ All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland, e-mail: ara@uniswacc.uniswa.sz

² All Out Africa Research Unit, P.O. Box 153, Lobamba, Swaziland

³ School of Biological and Conservation Sciences, Private Bag X01, University of KwaZulu-Natal, Scottsville, Pietermaritzburg, 3209 South Africa

*Corresponding author

Abstract

Roost site selection, daily movement patterns and home range area of African bats are poorly known. We used radio-telemetry to investigate these parameters in the African bat *Nycteris thebaica*. The bats predominantly used antbear *Orycteropus afer* burrows or culverts as night roosts. Day roost sites included caves and antbear burrows. Individuals travelled an average of 1.1 km between day roosts and foraging areas, a distance similar to that predicted from a comparative study of aspect ratios. Foraging (home) ranges were relatively small and averaged 12.9 ha. The foraging range of each bat overlapped on average with the ranges of 4.3 neighbouring bats, and the area of overlap covered 49% of its foraging range. For a bat with low wingloading, *N. thebaica* is capable of large travelling distances, suggesting that it is a strong flyer. We suggest that antbear burrows are not limiting; however, it is likely that these bats travel beyond the foraging area for more optimal roosts such as caves.

Keywords: Chiroptera; home range; *Nycteris thebaica*; radio-tracking; roost site.

Introduction

Bats show a high level of diversity on the African continent, with 282 extant species derived from 11 families (Van Cakenberghe and Seamark 2008). However, little is known about many aspects of their biology and ecology (Taylor 2000, Monadjem et al. in press), including patterns of movement across the landscape (Richter and Cumming 2008). The home ranges of insectivorous bat species have been studied more widely in Europe (Russo et al. 2002, Goiti et al. 2003, 2006, 2008, Rodrigues and Palmeirim 2008, Zahn et al. 2008), the Americas (Vonhof et al. 2004, Bonaccorso et al. 2007, Johnson et al. 2007, Trousdale et al. 2008), Asia (Gumal 2004), Australia (Tidemann et al. 1985, Law and Lean 1999, Law and Anderson 2000) and New Zealand (O'Donnell 2001, Griffiths

2007). Radio-tracking studies have, *inter alia*, elucidated roost site selection (Lausen and Barclay 2003, Russo et al. 2004), home range area (O'Donnell 2001, Bontadina et al. 2002) and movement patterns (Shiel et al. 1999, Barclay et al. 2000) in several bat species: information that is essential for the conservation of bats (Lumsden and Bennett 2005).

Telemetry work on bats in Africa have focused on fruit bats (Pteropodidae) resulting in improved understanding of large-scale movements (Jacobsen et al. 1986, Richter and Cumming 2008) and habitat utilisation (Thomas and Fenton 1978, Fenton et al. 1985). Radio-transmitters have determined roost selection by vesper bats (Vespertilionidae) in South Africa (Fenton et al. 1985), as well as foraging behaviour in *Nycteris grandis* in Zimbabwe (Fenton et al. 1987). However, sample sizes in these studies were very small and home range areas were not calculated.

The type and location of roost sites probably have a strong influence on the survival and reproductive success of a bat (Vonhof and Gwilliam 2007). Many bat species show high selectivity for roosts (Lumsden et al. 2002, Rodrigues and Palmeirim 2008) and these preferences change with season, sex and reproductive status (Kunz and Lumsden 2003). Males and non-breeding females often select cooler roost sites that allow them to enter torpor (Hamilton and Barclay 1994), whereas reproductive females select warmer or more thermally stable roosts to promote endothermy for facilitation of foetal development and lactation (Altringham 1996, Kunz and Lumsden 2003). Over 500 species of bats use plants as roosts, usually cavities, whereas others use rock crevices, caves and artificial structures (Kunz and Lumsden 2003). Caves, mines and rock crevices offer the advantages of thermal stability and protection from climatic extremes, whereas many roosts associated with vegetation are subject to environmental fluctuations but are more abundant (Kunz 1982).

Nycteris thebaica E. Geoffroy (Nycteridae) is widespread throughout much of Africa. It roosts in caves, burrows, culverts under the road and hollows in the trunks of large trees (Monadjem et al. in press). In Swaziland, this species commonly roosts in culverts but has rarely been observed roosting in other situations (Monadjem 2006a). At these culverts, females congregate in colonies of around 30–150 individuals prior to parturition in October, and give birth in early December (A. Monadjem, unpublished data). The adult sex ratio in these roosts is typically female biased by approximately 3:1, with a greater skew during the breeding season between July and December than post-weaning in February/March when the sex ratio approaches parity (Monadjem 2001, 2006a). By June the number of females present at the culverts has dropped significantly, but it is not known

whether these females leave the area on a regular migration or simply move locally to smaller, scattered roosts.

Flight in bats is linked to wing morphology (Norberg and Rayner 1987). Wing loading and aspect ratio provide useful measures of a bat's ecology, such as flight speed, aerodynamic efficiency of flight and manoeuvrability (Aldridge and Rautenbach 1987). *Nycteris thebaica* has short, rounded wings with low wing loading and low aspect ratio (Norberg and Rayner 1987), enabling it to forage in cluttered habitats (Aldridge and Rautenbach 1987). This seems to tie in with the species foraging strategy in which terrestrial arthropods, including orthopterans, arachnids and coleopterans (Bowie et al. 1999, Monadjem et al. in press), are gleaned off the ground. Jones et al. (1995) mathematically described the relationship between foraging range and aspect ratio for Microchiroptera.

We address some questions about the movement patterns of an insectivorous bat *Nycteris thebaica* in Africa. The primary objectives of this study were to determine: 1) the types of roosts selected during the day and at night, 2) the distance moved between roosting sites and foraging areas, and 3) the spatial overlap in home range areas of individual bats.

Material and methods

Study area

Field work was conducted at Mlawula Nature Reserve (26°14' S 32°00' E), north-eastern Swaziland, over a 16-month period between October 2005 and February 2007. The topography of the area is relatively flat with altitude varying between 150 and 250 m a.s.l. On the eastern border of the study area arise the Lubombo Mountains which extend to 500 m a.s.l. The climate is subtropical with hot, wet summers and dry, cool winters. Mean monthly temperatures for January and July are 26°C and 18°C, respectively, whereas mean annual rainfall ranges from 550 to 725 mm (Monadjem and Garcelon 2005). The subtropical climate at the study site can be divided into three seasons: a cool, dry season (May–August), a warm, dry season (September–October) and a warm, wet season (November–April). This can be related to the breeding cycle of *Nycteris thebaica* which mates in the cool, dry season, is pregnant during the warm, dry season, and gives birth and lactates during the warm, wet season. The dominant vegetation is classified as microphyllous (*Acacia*) savanna, but patches of riparian forest occur along rivers and major drainage lines (Roques et al. 2001). Characteristic tree species associated with the *Acacia* savanna are: *Acacia nigrescens*, *A. tortilis*, *Ziziphus mucronata*, *Sclerocarya birrea* and *Dichrostachys cinerea*; and large evergreen trees, such as *Ficus sycomorus* and *Schotia brachypetala*, are characteristic of the riparian forest (Monadjem 2005, Monadjem and Reside 2008).

Bat captures and telemetry

Bats were caught at a night roost in the Siphiso campsite ablution building by either placing a mist net across the

entrance to where the bats were roosting (under the thatch roof) or by positioning a three-bank harp trap [Faunatech, Bairnsdale, Vic, modified from Tidemann and Woodside (1978)] in front of the building. Bats generally began to use this night roost within a few hours after dusk. The building was only used as a day roost when inclement weather hit during the night, presumably preventing flight back to the usual day roost. Each individual *N. thebaica* caught was weighed, its forearm was measured, and age, sex and reproductive condition were assessed. All bats fitted with radio-transmitters in this study were adults following Monadjem (2001). Females were divided into three reproductive classes: pregnant (detected by palpation), post-lactating (nipples were still enlarged and bare, but no milk was being released) and non-reproductive (no sign of reproductive activity). Four bats were captured and tracked during the cool, dry season, five bats during the warm, dry season and nine bats during the warm, wet season.

A radio-transmitter (Biotrack PIP3, Biotrack, Dorset, UK) with mass 0.4 g, representing 3.5% of the bat's body mass was glued to the fur between the scapulae on the dorsal surface of the bat. Bats were released in under an hour of capture within 50 m of the night roost. They were followed using a radio-receiver (Alinco: Wide Band Receiver, Alinco, Osaka, Japan) and yagi antenna. The bat was followed on foot throughout the night and its location (latitude and longitude, using Garmin eTrex Global Positioning System, Garmin, Kansas City, USA) and signal strength recorded every 30 min. If the signal was lost and could not be regained for a few hours, wider searching from a vehicle was conducted. The signal was most commonly lost when the bat entered an underground roost (burrow or road culvert), as the signal could only be detected from within ca. 30 m of an underground roost. The day roost was found by tracking the bat back to its roost at dawn, or by searching in the direction of the first signal when the bat came into range at night. Once a day roost was located, it was checked daily to see how often it was occupied by the bat. For bats whose day roosts were not located, the last pre-dawn fix was used to approximate the position of the day roost. Because most of the bats left the foraging area in a direct line to the day roost, this approximation is conservative; day roosts would generally be further away from the foraging area than the last fix.

Calibration of signal strength of (and distance to) the transmitter was repeated throughout the study. If the signal was at full strength, the transmitter was within 30 m. When the bat was not underground, the detection range was up to 500–600 m.

Additional bats were captured in culverts under the road at Mlawula Nature Reserve (Monadjem 2001, 2006a). Digital photographs of the outstretched wings of 42 adult *N. thebaica* (17 males and 25 females) were taken to allow the calculation of wing loading and aspect ratio. Each individual was laid ventral-surface down on graph paper and its wings were gently opened until fully extended, without being overstretched, and lightly held onto the board while the bat's body was held securely (Norberg and Rayner 1987). The dorsal image was taken using a digital camera on a tripod 60 cm above the bat. This process took less than 30 s for each individual.

Wing measurements were taken from the photographs using Sigmascan software (Sigmascan, San Jose, USA). These were wingspan (the distance between the two furthest tips of the wings when outstretched) and wing area (the area of both wings, tail and body, excluding the head). The photographs contained graph paper with squares of 1×1 (mm) for calibration of the area measurements. These measurements were used to calculate wing loading (total body mass/wing area) and aspect ratio (wingspan²/wing area).

The radio-tracked fixes were mapped using ArcView 3.1 (ArcView, California, USA), and home range area calculated using the Home Range Extension (Rogers and Carr 1998). Prior to calculation of home range areas, the locations of all fixes were corrected using the extension “Bearing & Distance 1.1”. All home ranges were calculated by the 95% minimum convex polygon method (MCP). The bats generally used day roosts situated some distance from where they spent the nights. The day roosts of 13 bats were either physically located (n=6) or could be approximated from pre-dawn and sunset fixes (n=7). The area where the bat spent the night while foraging we refer to as the foraging home range. Invariably, the night roost was located within this foraging area. Bats generally flew out of the day roost shortly after sunset and headed for the night home range. These flights were usually direct and rapid. Once within the foraging range, distances between fixes were shorter and the bats rarely moved very far until the pre-dawn flight back to the day roost. To convey this spatially, we measured and averaged the distance from the day roost to the centre of the foraging home range. We tested for differences between reproductive and non-reproductive females using the Mann-Whitney rank test, as the data were not normally distributed. We used the Student t-test to test for differences between the wing loading and aspect ratio of males and females, as these data were normally distributed.

The expected distance travelled between day roost and foraging area was calculated using the equation provided by Jones et al. (1995) where foraging range = $0.12 \times 10^{0.18(\text{aspect ratio})}$.

Results

A total of 20 bats were fitted with radio-transmitters, but two individuals disappeared shortly after their release and were removed from the analysis. Thus, 18 individuals were tracked for a mean of 7.1 days and 45.2 fixes (Table 1). Bats were tracked over a 9–11 day period (i.e., tracking of the same individual was not necessarily on consecutive nights), which was the general duration of the battery, whereas two bats were tracked over 13 days. The sample included four pregnant, four post-lactating and eight non-reproductive females, and just two adult males. Owing to the small sample size of males, they are not included in the analyses. There was no difference in the number of days reproductive and non-reproductive females were tracked (U=85.0, df=14, p=0.081). Also, there was not a significant correlation between number

Table 1 Sampling effort, foraging home range (95% MCP), daily travel distance between day roost and the centre of the foraging area, and the proportion of overlap in foraging home range (95% MCP) between neighbouring individuals of 18 *Nycteris thebaica* radio-tracked at Mlawula Nature Reserve, Swaziland.

	Mean number of days tracked (±SD, n)	Mean number of fixes (±SD, n)	Foraging home range ha ±SD (n)	Daily travel distance m, range (n)	Mean number of individuals overlapping±SD (range, n)	Proportion of individuals (range, n)
Adult female						
Pregnant	5.8 (±2.1, 4)	34.8 (±18.1, 4)	14.3±9.7 (4)	830, 0–1660 (2)	7.5±3.7 (3–12, 4)	0.86±0.28 (0.43–1.00, 4)
Post-lactating	5.5 (±5.1, 4)	29.8 (±27.8, 4)	12.0±6.1 (4)	753, 300–1350 (3)	2.5±3.1 (0–7, 4)	0.30±0.48 (0–1.00, 4)
Non-reproductive	8.1 (±2.5, 8)	57.1 (±17.0, 8)	14.5±11.8 (8)	1223, 0–2450 (6)	4.0±2.8 (0–7, 8)	0.39±0.35 (0–1.00, 8)
Adult male	8.5 (±3.5, 2)	49.5 (±17.7, 2)	5.6 (2)	1530, 440–2620 (2)	3.0 (0–6, 2)	0.50 (0–1.00, 2)
Total	7.1 (±3.2, 18)	45.2 (±22.0, 18)	12.9±9.4 (18)	1101, 0–2620 (13)	4.3±3.4 (0–12, 18)	0.49±0.42 (0–1.00, 18)

of fixes and foraging home range area (95% MCP) ($r=-0.226$, $df=16$, $p=0.370$).

In total, 74% of the fixes were taken at full signal strength, so the bat was within 30 m of the recorder, whereas 82% of the fixes were recorded within 50 m of the bat. The location of the bat was estimated for 26% of fixes where the bat was >30 m away.

The bats used a variety of day roosts. Four used antbear (*Orycteropus afer*) burrows, one used a cave (situated in the Lubombo mountains) and the sixth individual alternated between a cave and an antbear burrow. The day roosts of the remaining 12 bats were not found (although day roosts of seven of these could be approximated, see Material and methods section), mostly owing to the loss of signal underground. Day roost fidelity was not investigated owing to the small sample size; however, one individual spent six consecutive days in a burrow, and another spent three consecutive days in a cave.

Of a total of 13 day roosts found or approximated, three day roosts were situated within the foraging home range, whereas the remaining day roosts were situated up to 2.6 km away (Table 1). There were no differences in the distance travelled from the day roost to the foraging area between reproductive and non-reproductive females ($U=39.5$, $df=9$, $p=0.580$). Emergence times (\pm SD) were calculated for 12 bats; the bats left their day roosts 38 min (± 8 min) after sunset. The last fix for 10 bats returning to their day roost was 55 min (± 20 min) before sunrise.

Night roosts of 13 individuals were located and included culverts under roads and railway tracks, antbear burrows, the ablution building (Siphiso campsite), the underside of a low bridge (over a dry stream) and a bird hide. The night roosts of the remaining five individuals were not found. In total, 13 individuals had a mean of 1.8 different night roosts each (range: 1 to 5). On average, 20.5% of fixes per bat were taken when a bat was in a night roost and did not differ between reproductive and non-reproductive females ($U=35.0$, $df=9$, $p=0.927$).

The foraging home ranges (95% MCP) of the 18 *N. thebaica* radio-tracked at Mlawula are shown in Figure 1. The mean foraging home range area was 13.7 ha and there was no difference between the ranges of reproductive and non-reproductive females ($U=67.0$, $df=14$, $p=0.958$). Of the 18 home range areas, 14 overlapped with at least one neighbouring individual. The average (\pm SD) number of home ranges that an individual overlapped with was 4.3 (Table 1). There was no difference in the proportion of home range overlapping with neighbouring bats between reproductive and non-reproductive females ($U=59.0$, $df=14$, $p=0.372$).

There were no differences in the wing loadings ($t=18$, $df=40$, $p=0.861$) or aspect ratios ($t=1.04$, $df=40$, $p=0.305$) of male and female *N. thebaica* (Table 2) so all data were pooled. Using the equation provided by Jones et al. (1995), *N. thebaica* is expected to forage 1.2 km from their day roost.

Discussion

Owing to the difficulty in detecting the radio-transmitter when the bats were inside a burrow or cave, only limited

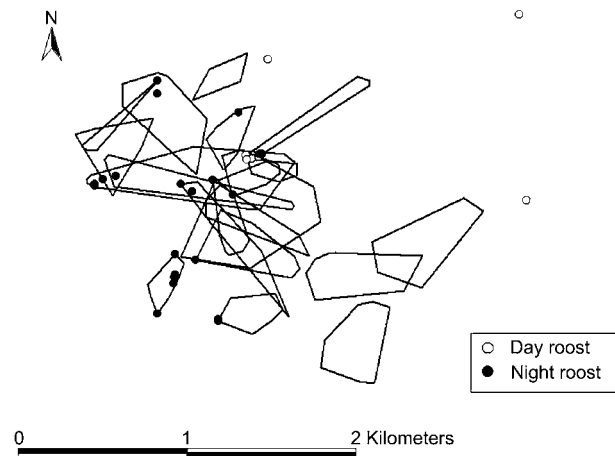


Figure 1 Foraging home ranges, day roosts and night roosts of 18 *Nycteris thebaica* radio-tracked at Mlawula Nature Reserve, Swaziland.

Table 2 Wing loading and aspect ratio of 17 male and 25 female *Nycteris thebaica* measured at Mlawula, Swaziland.

	Wing loading \pm SD (N m ⁻²)	Aspect ratio \pm SD
Adult female	8.3 \pm 0.72	5.5 \pm 0.25
Adult male	8.3 \pm 0.59	5.6 \pm 0.39
Mean	8.3 \pm 0.66	5.5 \pm 0.31

data on the roost use and fidelity was obtained. However, the findings show that an individual used a burrow for up to six consecutive days and that individuals switched between burrows and caves. A review of bat roosting showed that roost fidelity is positively correlated with roost permanency and inversely correlated with roost availability, and that individuals alter their fidelity depending on the type of roost (Lewis 1995).

Nycteris thebaica was found to use a variety of roosts in this study, selecting different roosts for day and night shelter. Antbear burrows within the bats' foraging ranges were frequently used as night roosts but less frequently as day roosts. Bats often used more than one antbear burrow; it appeared that these burrows were not limiting as they were ubiquitous at Mlawula Nature Reserve (we estimated over a hundred burrows in the study area). Despite the availability of burrows, the bats travel beyond their foraging area (low-lying savanna) to the caves within the Lubombo mountain range approximately 1 km to the east of the capture site (Siphiso campsite). These mountains harbour a few small caves which are absent in the foraging area. We suggest that antbear burrows do not constitute optimal day roosts for *N. thebaica* at Mlawula and that caves might be the preferred roost owing to the advantages of relative stable microclimates (Kunz and Lumsden 2003).

Night roosts were used frequently by *N. thebaica*. We observed individual *N. thebaica* feeding on invertebrates while stationary inside a night roost (April Reside personal observation), which were presumably caught on the wing. Night roosts serve a range of purposes for bats, as resting places between foraging bouts, promoting ingestion, digestion and energy conservation, a retreat from predators and inclement weather, and places that pro-

mote social interactions and information transfer (Kunz 1982, Kunz and Lumsden 2003). *Nycteris thebaica* forages both by continuous flight and by flights from perches (Fenton 1990), the latter a strategy common amongst species with low wing loadings and aspect ratios (Kunz and Lumsden 2003). In addition to the different flight modes used while foraging (Fenton 1990), which presumably consist of low speed and high manoeuvrability (Aldridge and Rautenbach 1987), it is possible that a third mode for commuting (Lumsden et al. 1994, Arlettaz 1999) is employed by *N. thebaica*. Banding records show that individuals are capable of covering large distances, in excess of 100 km (Monadjem 2006b); however, it is likely that such movements are rare.

In our study *Nycteris thebaica* individuals generally travelled the expected distances, given the aspect ratio, between day roost and foraging area (1.1 km). However, three individuals travelled less than expected, with the day roosts located within the foraging area, a pattern also found for the congeneric *N. grandis* (Fenton et al. 1987), and one female travelled over twice the expected distance. *Rhinolophus hipposideros*, a cave-roosting species smaller than *N. thebaica*, travelled a comparable distance of 1.2 km from roosting caves to feeding areas (Bontadina et al. 2002). In contrast, the similar-sized *Rhinolophus euryale* travelled a mean maximum distance of 2.2 km per night (Russo et al. 2002), almost double that of *N. thebaica*. In a different study, *R. euryale* travelled a mean of between 1.3 and 4.6 km, depending on sex and breeding condition (Goiti et al. 2006), again significantly further than *N. thebaica* in this study. However, a tree cavity-roosting species with a similar aspect ratio to *Nycteris thebaica* (5.9 compared to 5.5), *Nyctophilus geoffroyi*, regularly commuted up to 12 km between day roosts and foraging areas (Lumsden et al. 2002). Long commuting distances between day roosts and foraging area are typical where roosts are limiting (Lumsden et al. 2002). That *N. thebaica* generally moved distances expected according to its aspect ratio provides further weight to the hypothesis that roosts were not limiting for this species.

A potential source of error in estimating home range area was unequal sampling effort, with the possibility of more fixes being correlated with larger home ranges. However, in this study there was no correlation between the number of fixes and home range area, validating a comparison of the home ranges of the various radio-tracked individuals.

The foraging home ranges presented here are rather small by comparison with ranges of similar-sized bats with low wing loading. For example, in one study *R. euryale*, with a mass of approximately 11 g, had a mean foraging range of 415 ha (Russo et al. 2002), 30 times that of *N. thebaica*, whereas in another study its mean home range varied between 37 and 272 ha (Goiti et al. 2006), again significantly larger than *N. thebaica* in this study. However, in yet another study, the mean home range of *R. euryale* varied between 1.3 and 10.7 ha (Goiti et al. 2008), and was slightly smaller than that of *N. thebaica*. These studies illustrate the point that home range, even within a species, is flexible and might differ radically between habitats. A species perhaps more similar to *N.*

thebaica in foraging strategy could be *Plecotus auritus*, which also gleans terrestrial arthropods on the wing (Swift and Racey 1983). Interestingly, home ranges are also very small in *P. auritus*, mostly less than 10 ha (Swift 1998). However, comparable African studies are limited. *Nycteris grandis* has an estimated foraging area of at least 50 ha in extent, based on a sketch map of the foraging areas produced by a radio-tracking study (Fenton et al. 1987). A smaller foraging range area than expected could be an indicator of high food availability; however, prey densities were not measured in this study.

The home ranges of radio-tracked bats overlapped greatly in this study, which is consistent with results for the congeneric *N. grandis* (Fenton et al. 1987). Although there was great variability in overlap (from 0% to 100%), overlap was greater in the core area in the vicinity of the capture site (the Siphiso campsite) than along the periphery (Figure 1). This might be an artefact of an increasing perimeter at incremental distances away from a point locality. Hence, the amount of home range overlap on the periphery of the study area was probably significantly underestimated. Moreover, it must be noted that this study was conducted over a relatively long time period and the spatial overlap could have been as a result of different bats using the same area at different times. The overlapping home ranges, in conjunction with the large congregational roosts in road culverts (Monadjem 2001, 2006a), suggest that *N. thebaica* does not defend a territory. Some insectivorous bats seem to have extensively overlapping foraging areas and high intra-specific tolerance without exclusive territories (Lumsden 2004, Rodrigues and Palmeirim 2008), whereas other species do not (Kerth et al. 2001).

Our study has begun to show patterns of how a micro-bat species uses the landscape. To better understand the resource requirements of *N. thebaica* it would be worth investigating in more detail how roost use, foraging area and home range changes seasonally, and according to sex and reproductive status. Further investigation might show patterns in roost fidelity and how conditions might alter roost choice. This study shows that individual bats use low-lying savanna for foraging and the Lubombo mountain range for valuable roosting sites, highlighting the need for protection of the entire landscape to ensure the persistence of this species.

Acknowledgements

This is the 12th communication of the All Out Africa Research Unit (www.alloutafrica.org). Ngwane Dlamini, Senior Warden of Mlawula Nature Reserve, is thanked for permitting us to work at Mlawula. Christian Busch, Maria Rasmussen, Emily Rathey, Florian Dessimoz, Mduduzi Ngwenya and Andy Bamford spent many a sleepless night chasing tagged bats. For their efforts we are extremely grateful. Lindy Lumsden not only generously assisted with the tracking but provided much valuable advice on methodology and experimental design. Jen Parsons, Lisa Evans and two anonymous reviewers made valuable comments on an earlier draft of this paper.

References

- Aldridge, H.D.J.N. and I.L. Rautenbach. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* 56: 763–778.
- Altringham, J.D. 1996. *Bats. Biology and behaviour.* Oxford University Press, Oxford. pp. 262.
- Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *J. Anim. Ecol.* 68: 460–471.
- Barclay, R.M.R., B.J. Chruszcz and M. Rhodes. 2000. Foraging behaviour of the large-footed myotis, *Myotis moluccarum* (Chiroptera: Vespertilionidae) in south-eastern Queensland. *Aust. J. Zool.* 48: 385–392.
- Bonaccorso, F.J., J.R. Winkelmann, D. Shin, C.I. Agrawal, N. Aslami, C. Bonney, A. Hsu, P.E. Jekielek, A.K. Knox, S.J. Kopach, T.D. Jennings, J.R. Lasky, S.A. Menesale, J.H. Richards, J.A. Rutland, A.K. Sessa, L. Zhaurova and T.H. Kunz. 2007. Evidence for exploitative competition: comparative foraging behavior and roosting ecology of short-tailed fruit bats (Phyllostomidae). *Biotropica* 39: 249–256.
- Bontadina, F., H. Schofield and B. Naef-Daenzer. 2002. Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. *J. Zool. Lond.* 258: 281–290.
- Bowie, R.C.K., D.S. Jacobs and P.J. Taylor. 1999. Resource use by two morphologically similar insectivorous bats (*Nycteris thebaica* and *Hipposideros caffer*). *S. Afr. J. Zool.* 34: 27–33.
- Fenton, M.B. 1990. The foraging behaviour and ecology of animal-eating bats. *Can. J. Zool.* 68: 411–422.
- Fenton, M.B., R.M. Brigham, A.M. Mills and I.L. Rautenbach. 1985. The roosting and foraging areas of *Epomophorus wahlbergi* (Pteropodidae) and *Scotophilus viridis* (Vespertilionidae) in Kruger National Park, South Africa. *J. Mammal.* 66: 461–468.
- Fenton, M.B., D.H.M. Cumming, J.H. Hutton and C.M. Swanepoel. 1987. Foraging and habitat use by *Nycteris grandis* (Chiroptera: Nycteridae) in Zimbabwe. *J. Zool. Lond.* 211: 709–716.
- Goiti, U., J.R. Aihartza, I. Garin and J. Zabala. 2003. Influence of habitat on the foraging behaviour of the Mediterranean horseshoe bat, *Rhinolophus euryale*. *Acta Chiropterol.* 5: 75–84.
- Goiti, U., J.R. Aihartza, D. Almenar, E. Salsamendi and I. Garin. 2006. Seasonal foraging by *Rhinolophus euryale* (Rhinolophidae) in an Atlantic rural landscape in northern Iberian Peninsula. *Acta Chiropterol.* 8: 141–155.
- Goiti, U., I. Garin, D. Almenar, E. Salsamendi and J.R. Aihartza. 2008. Foraging by Mediterranean horseshoe bats (*Rhinolophus euryale*) in relation to prey distribution and edge habitat. *J. Mammal.* 89: 493–502.
- Griffiths, R.W. 2007. Activity patterns of long-tailed bats (*Chalinolobus tuberculatus*) in a rural landscape, South Canterbury, New Zealand. *N. Z. J. Zool.* 34: 247–258.
- Gumal, M.T. 2004. Diurnal home range and roosting trees of a maternity colony of *Pteropus vampyrus natunae* (Chiroptera: Pteropodidae) in Sedilus, Sarawak. *J. Trop. Ecol.* 20: 247–258.
- Hamilton, I.M. and R.M.R. Barclay. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). *Can. J. Zool.* 72: 744–749.
- Jacobsen, N.H.G., P.C. Viljoen and W. Ferguson. 1986. Radio tracking of problem fruit bats (*Rousettus aegyptiacus*) in the Transvaal with notes on flight and energetics. *Z. Säugetierkd.* 51: 205–208.
- Johnson, J.S., M.J. Lacki and M.D. Baker. 2007. Foraging ecology of long-legged myotis (*Myotis volans*) in north-central Idaho. *J. Mammal.* 88: 1261–1270.
- Jones, G., P.L. Duvergé and R.D. Ransome. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. *Symp. Zool. Soc. Lond.* 67: 309–324.
- Kerth, G.K., M. Wagner and B. König. 2001. Roosting together, foraging apart: information transfer about food is unlikely to explain sociality in female Bechstein's bats (*Myotis bechsteinii*). *Behav. Ecol. Sociobiol.* 50: 283–291.
- Kunz, T.H. 1982. *Roosting ecology of bats.* In: (T.H. Kunz, ed) *Ecology of bats.* Plenum Press, New York. pp. 1–55.
- Kunz, T.H. and L. Lumsden. 2003. *Ecology of cavity and foliage roosting bats.* In: (T.H. Kunz and M.B. Fenton, eds) *Bat ecology.* The University of Chicago Press, Chicago, IL. pp. 3–89.
- Lausen, C.L. and R.M.R. Barclay. 2003. Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices. *J. Zool. Lond.* 260: 235–244.
- Law, B.S. and M. Lean. 1999. Common blossom bats (*Syconycteris australia*) as pollinators in fragmented Australian tropical rainforest. *Biol. Conserv.* 91: 201–212.
- Law, B.S. and J. Anderson. 2000. Roost preferences and foraging ranges of the eastern forest bat *Vespadelus pumilus* under two disturbance histories in northern New South Wales, Australia. *Austral Ecol.* 25: 352–367.
- Lewis, S.E. 1995. Roost fidelity of bats: a review. *J. Mammal.* 76: 481–496.
- Lumsden, L.F. 2004. *The ecology and conservation of insectivorous bats in rural landscapes.* Deakin University, Melbourne. pp. 281.
- Lumsden, L.F. and A.F. Bennett. 2005. Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia. *Biol. Conserv.* 122: 205–222.
- Lumsden, L.F., A.F. Bennett, J.E. Silins and S.P. Krasna. 1994. *Fauna in a remnant vegetation-farmland mosaic: movements, roosts and foraging ecology of bats* In: Report to the Australian Nature Conservation Agency “Save the Bush” Program. Department of Conservation and Natural Resources, Melbourne. pp. 60–72.
- Lumsden, L.F., A.F. Bennett and J.E. Silins. 2002. Location of roosts of the lesser long-eared bat *Nyctophilus geoffroyi* and Gould's wattled bat *Chalinolobus gouldii* in fragmented landscape in south-eastern Australia. *Biol. Conserv.* 106: 237–249.
- Monadjem, A. 2001. Sexual dimorphism, sex ratio and preliminary recapture rates of *Nycteris thebaica* (Nycteridae: Chiroptera) in Swaziland. *Durban Mus. Novit.* 26: 49–52.
- Monadjem, A. 2005. Association between avian communities and vegetation structure in a low-lying woodland-savanna ecosystem in Swaziland. *Ostrich* 76: 45–55.
- Monadjem, A. 2006a. Survival and roost-site selection in the African bat *Nycteris thebaica* (Chiroptera: Nycteridae) in Swaziland. *Belg. J. Zool.* 135: 101–105.
- Monadjem, A. 2006b. Longevity and movement of the common slit-faced bat *Nycteris thebaica*. *Afr. Bat Conserv. News* 9: 7.
- Monadjem, A. and D.K. Garcelon. 2005. Nesting distribution of vultures in relation to land use in Swaziland. *Biodiv. Conserv.* 14: 2079–2093.
- Monadjem, A. and A. Reside. 2008. The influence of riparian vegetation on the distribution and abundance of bats in an African savanna. *Acta Chiropterol.* 10: 339–348.
- Monadjem, A., P. Taylor, F.P.D. Cotterill and M.C. Schoeman. in press. *Bats of Southern Africa: a biogeographic and taxonomic synthesis.* University of Witwatersrand Press, Johannesburg. In press.
- Norberg, U.M. and J.M.V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. Lond. B* 316: 335–427.
- O'Donnell, C.F.J. 2001. Home range and use of space by *Chalinolobus tuberculatus*, a temperate rainforest bat from New Zealand. *J. Zool. Lond.* 253: 253–264.

- Richter, H.V. and G.S. Cumming. 2008. First application of satellite telemetry to track African straw-coloured fruit bat migration. *J. Zool. Lond.* 275: 172–176.
- Rodrigues, L. and J.M. Palmeirim. 2008. Migratory behaviour of the Schreiber's bat: when, where and why do cave bats migrate in a Mediterranean region? *J. Zool. Lond.* 274: 116–125.
- Rogers, A.R. and A.P. Carr. 1998. HRE: the home range extension for ArcView™. Ontario Ministry of Natural Resources, Thunder Bay.
- Roques, K.G., T.G. O'Connor and A.R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J. Appl. Ecol.* 38: 268–280.
- Russo, D., G. Jones and A. Migliozi. 2002. Habitat selection by the Mediterranean horseshoe bat, *Rhinolophus euryale* (Chiroptera: Rhinolophidae) in a rural area of southern Italy and implications for conservation. *Biol. Conserv.* 107: 71–81.
- Russo, D., L. Cistrone, G. Jones and S. Mazzoleni. 2004. Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. *Biol. Conserv.* 117: 73–81.
- Shiel, C.B., R.E. Shiel and J.S. Fairley. 1999. Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. *J. Zool. Lond.* 249: 347–358.
- Swift, S.M. 1998. Long-eared bats. Poyser Natural History, London. pp. 182.
- Swift, S.M. and P.A. Racey. 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool. Lond.* 200: 249–259.
- Taylor, P.J. 2000. Bats of southern Africa. Guide to biology, identification, and conservation. University of Natal Press, Pietermaritzburg. pp. 206.
- Thomas, D.W. and M.B. Fenton. 1978. Notes on the dry season roosting and foraging behaviour of *Epomophorus gambianus* and *Rousettus aegyptiacus* (Chiroptera: Pteropodidae). *J. Zool. Lond.* 186: 403–406.
- Tidemann, C.R. and D.P. Woodside. 1978. A collapsible bat-trap and a comparison of results obtained with the trap and with mist-nets. *Aust. Wildl. Res.* 5: 355–362.
- Tidemann, C.R., D.M. Priddel, J.E. Nelson and J.D. Pettigrew. 1985. Foraging behaviour of the Australian ghost bat, *Macroderma gigas* (Microchiroptera: Megadermatidae). *Aust. J. Zool.* 33: 705–713.
- Trousdale, A.W., D.C. Beckett and S.L. Hammond. 2008. Short-term roost fidelity of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) varies with habitat. *J. Mammal.* 89: 477–484.
- Van Cakenberghe, V. and E.C. Seemark (eds). 2008. African Chiroptera report. In: African Chiroptera project 2008, Pretoria. pp. 1867.
- Vonhof, M.J. and J.C. Gwilliam. 2007. Intra- and interspecific patterns of day roost selection by three species of forest-dwelling bats in Southern British Columbia. *For. Ecol. Manage.* 252: 165–175.
- Vonhof, M.J., H. Whitehead and M.B. Fenton. 2004. Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. *Anim. Behav.* 68: 507–521.
- Zahn, A., J. Holzhaider, E. Kriner, A. Maier and A. Kayikcioglu. 2008. Foraging activity of *Rhinolophus hipposideros* on the Island of Herrenchiemsee, Upper Bavaria. *Mamm. Biol.* 73: 222–229.