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ORIGINAL PAPER

Habitat use, roost selection and conservation of bats in Tsingy de Bemaraha National Park, Madagascar

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Abstract Although the land mammals of Madagascar have been the subject of many studies, the island's bats have yet to feature prominently on the research or conservation agenda. In this study we used mist nets, acoustic sampling and cave surveys to assess habitat use, seasonality and roost selection. Four microchiropteran species (*Triaenops rufus*, *T. furculus*, *Miniopterus manavi* and *Myotis goudoti*) appeared to be strongly associated with the forest interior based on trapping, but analysis of time-expanded echolocation recordings revealed that *T. rufus* and *M. manavi* were frequently recorded in forest edges and clearings. Bat activity was significantly lower inside the forest than at the interface between agricultural land and forest. The caves visited most often by tourists were low in bat abundance and species richness. Anjohikinakina Cave, which was visited infrequently by people, was used by five species and contained between 54% (winter) and 99% (summer) of bats counted in 16 caves and is a site of national importance for bat conservation. *Hipposideros commersoni* was only netted in our study area during October and may be a migrant to the site or present but inactive during the austral winter. The forest

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surrounding the caves is therefore important because it provides cover for emerging bats and a potential source of invertebrate prey whilst the forest edge is important to foraging bats.

Keywords Acoustic sampling · Caves · Chiroptera · Forest dependency · Karst · Roost

Introduction

Bats make a significant contribution to mammalian species richness and biomass in the tropics, but despite the extensive amount of previous research on Madagascar's vertebrates (Goodman and Benstead 2003) there have been few ecological studies on Malagasy Chiroptera (Eger and Mitchell 2003). Research biologists have traditionally focused on the island's endemic land mammals with lemurs, rodents and tenrecs being popular topics of study (e.g. Stephenson et al. 1994; Ramanamanjato and Ganzhorn 2001; Ganzhorn et al. 2003; Kappeler and Rasoloarison 2003).

Until recently the taxonomy of Malagasy bats was based mainly on a series of collections made in the 1970s (Peterson et al. 1995) and ecological information was almost completely lacking. Over the last few years, new information has helped to fill some of the gaps on species distribution (Goodman et al. 2005b) and have led to revisions of the existing bat taxonomy and the description of new species (e.g. Goodman and Cardiff 2004; Goodman and Ranivo 2004). Progress has also been made by other workers in describing the echolocation calls of Malagasy microchiropterans (Russ et al. 2003) and in assessing the conservation status (Eger and Mitchell 2003; MacKinnon et al. 2003) and diet of fruit bats (Bollen and Van Elsacker 2002; Hutcheon 2003). However, there has been little attempt to describe habitat requirements for bats in Madagascar with the result that the impact of large-scale habitat alteration or small-scale variation in habitat structure remains unknown.

Bats provide a unique set of challenges for conservation biologists because many species of conservation concern occur outside forests, in degraded or open habitats. Furthermore, as many species aggregate in conspicuous and accessible roosts that are often accessible to people, successful conservation measures should include the protection of roost sites, as well as foraging habitats (Hutson et al. 2001). Agricultural areas between forest fragments are used by some bat species and farmland is sometimes an important linking habitat between isolated forest fragments (Estrada et al. 1993). Likewise, other studies from South America have shown that non-forest habitats (e.g. farmland, savanna) constitute important habitats for bats (Bernard and Fenton 2003) and that certain forest-dependent species are reliable indicators of habitat disruption (Fenton et al. 1992). One of the first steps to address the conservation priorities of bats in Madagascar should therefore be to assess forest dependency and habitat requirements. Using presence and absence data from sites in the dry forests of Madagascar, Goodman et al. (2005b) report that few of the 25 bats species recorded from the region appear to be dependent on expanses of intact natural forest and they suggest that conservation of roosting sites, especially caves, is the most important goal for chiropteran conservation.

Here we aim to quantify habitat use by bats in a national park in western Madagascar which has a complex system of caves and is therefore likely to be an area of high bat abundance (Kunz 1982). We assessed bat species composition, abundance and activity in three distinct forest habitats (interior, clearings and edges) during the dry season and early wet season in Parc National Tsingy de Bemaraha. We also surveyed a selection of caves in areas subject to either high or low tourism pressure. Very little sustained research has been attempted in the park but inventory surveys have revealed high levels of vertebrate endemism to the reserve (Rasoloarison and Paquier 2003). As elsewhere in Madagascar, pressures from local people on the resources within the protected area remain high and research is now required to assess the impact of human activity (e.g. tourism, forest clearance) in and around the park.

Study site

Parc National Tsingy de Bemaraha, Province de Mahajanga, lies approximately 200 km north of Morondava (18°12′–19°07′ S and 44°34′–44°56′ E) in western Madagascar. The climate has distinct wet and dry seasons which extend from November to April and May to October, respectively. Maximum monthly temperatures are recorded in October (max 41°C) and highest rainfall in February (456 mm; data from 1993 to 2000, Programme Bemaraha, Antsalova).

Situated within a limestone belt that stretches intermittently from the North West to the South West of the island, the area is famous for its water-eroded features, most notably its caves and 'tsingy' formations (sharp, needle-like limestone pinnacles). Since receiving its UNESCO World Heritage Site status in 1990 and being made a national park in 1997 the southern section of the Bemaraha plateau has become a major tourist attraction (Rasoloarison and Paquier 2003). Our study was conducted near Bekopaka village, on the northern bank of the Manambolo River. Land use outside of the park boundary is mainly rice cultivation and open pasture land and the improved access in recent years has led to increased immigration and growing levels of forest degradation on the fringes of the reserve.

Methods

The fieldwork was carried out over 9 weeks during 2003 from 12 July to 20 August in the austral winter and 7–30 October in the beginning of the austral summer. In most years the park is inaccessible by road from December until mid-May because of high water levels and our study periods were thus selected to represent a major seasonal contrast within the available time. Based on reconnaissance walks and conversations with park staff we selected three habitat types for the study (i) closed canopy deciduous forest, (ii) forest clearings of 'tsingy' rocks—a distinctive feature of the reserve and (iii) forest/agriculture edges containing a mixture of fruit trees, grazing pasture, rice fields, isolated large trees and patches of low shrubby vegetation.

Bat trapping

Bats were trapped in mist nets (6 or 9 m long) with the bottom pocket placed just above ground level. In intact forest, the nets were placed with the bottom shelf approximately 20 cm above the ground, across trails, small gaps and streams. We used five or six nets per night and the total length was either 36, 39 or 42 m, and varied in accordance with the size of the trap sites. Nets were open from 1800 h until 2200 h each night. During the first phase, 15 different netting sites, at least 500 m apart, were used each night. The nets were checked approximately every 5 min and bats were immediately extracted. Trapping was repeated at 14 of the same 15 sites during the second phase. Mist nets in the 'tsingy' clearings traversed the natural gaps, which were rarely larger than 200 × 100 m. Edge mist nets were placed either perpendicular to the forest edge or in vegetation gaps within the surrounding agricultural land and were always within 150 m of the forest edge.

After capture, bats were placed in cloth bags and retained for approximately 2 h for faeces collection (except bats caught within the first 15 min after sunset which were quickly identified and released). Species were identified using the keys and notes in Peterson et al. (1995) and Russ et al. (2003). For each individual bat the following information was recorded: time of capture, species, sex, age, reproductive condition, forearm length (mm) and weight (g). Voucher specimens were deposited at the Université d'Antananarivo.

Acoustic surveys

It is widely recognised that microchiropteran surveys should use both bat detectors and trapping devices to fully document the species composition or activity in a given area (Sedlock 2001). We assessed microchiropteran activity using 'Duet' bat detectors (Stag Electronics, UK) from point counts situated at approximately 300–400 m intervals. The closed-forest category was sub-divided into riparian (<50 m from water) and non-riparian (>50 m) habitats and bats were surveyed on trails and in the forest adjacent (c. 10 m) to trails. Listening with the 'Duet' detector in heterodyne mode, an observer swept through the frequency range until a bat was heard. Each 'bat pass' (defined as a sequence of at least two echolocation pulses of a passing bat) was counted and notes made on the maximum frequency and range of the pulse. We used the following system to classify bat passes heard in the field:

(i) <33 kHz—Molossidae and also *Taphozous mauritianus*
(ii) >33 kHz <60 kHz—Vespertilionidae
(iii) >60 kHz—Hipposideridae, but also includes *Myotis goudoti*

During each point count a second observer made simultaneous recordings with a Pettersson D980 bat detector in time-expansion mode (×10) which were recorded onto Sony mini-disks in the field for later analyses with Batsound Professional software (Pettersson Elektronik, Sweden). For trapped microchiropterans, we made reference recordings of flying individuals in a mesh-sided cage (3 × 3 × 3 m) and also recorded the bats as they were released. We identified species from recordings of their echolocation using notes and sonograms (Russ et al. 2003) and from comparisons with our own data. In Madagascar, the sonograms of Hipposideridae (*Triaenops rufus*, *T. furculus* and *Hipposideros commersoni*), *Myotis goudoti*, *Miniopterus manavi* and *Emballonura atrata* are straightforward to identify from field recordings (J. Russ *pers. comm.*; A. Kofoky unpubl. data). However, the echolocation calls of molossids, and the rarely caught *Scotophilus* spp., are less well described in Madagascar and cannot be used to identify free-flying bats from recorded echolocations. We calculated a frequency of occurrence for each species by the ratio of point counts with a species to total point counts for that habitat using determinations made from the time-expanded recordings.

Cave surveys

Diurnal surveys were made in 16 caves to assess bat species composition and abundance in caves visited by tourists and to look for species not trapped during the mist netting inventories. All but one of the caves were located near Bekopaka, with Anjohikinakina cave located approximately 20 km from the other caves in the area known as 'Grande Tsingy'. Using advice from park staff we selected seven caves that are frequented (perhaps daily between July and September) by tourists and a further nine that are less frequently visited by tourists. Direct counts were made of roosting bats using torches fitted with red filters. When bats were found in large groups we counted the number in a known area and extrapolated based on the total estimated area of the colony. In each cave chamber with bats we measured the relative humidity (Hygros H100 Hygrometer), temperature (Hanna Mini-therm HI8753 probe) and light levels (Testo 245 Lux meter) at breast height at number of points on a transect running along the chamber axis. The same measurements were taken for each group of roosting bats (defined as one or more individuals with clear spatial separation from other bats) to investigate the microclimate at each roost position.

Statistical analysis

Bat captures were standardised according to the length of mist net used each night (range 36–42 m) and values given are means and SE. Chi-square was used to test for differences in capture frequency between seasons. Counts of bat passes resulted in non-parametric data and we therefore used Mann–Whitney and Kruskal–Wallis to test for differences between habitat and season. Relative humidity (%) was arcsine transformed before analysis. ANOVA and Kruskal–Wallis were used to compare roost microclimate of the two bat species with transect points.

Results

Community composition

Mist netting resulted in the capture of 10 species over the two seasons (Table 1). The small fruit bat *Rousettus madagascariensis* was the most frequently netted species and made up 33% of all captures. Four vespertilionid species made up a further 38% of captures with *M. manavi* the most common. Three hipposiderid species contributed 28% (Table 1) with *Triaenops rufus* the most common. Two species, *Scotophilus tandrefana* and *Emballonura* sp. nov., were represented by singletons.

Our cave surveys revealed the presence of two large microchiropteran bats that were not trapped in mist nets, *Miniopterus gleni* and *Otomops madagascariensis*. Three other bat species, *Pteropus rufus*, *Eidolon dupreanum* and *T. mauritianus*, were neither trapped, detected acoustically nor observed in caves. *Pteropus rufus* and *E. dupreanum* were observed feeding on kapok trees *Ceiba pentandra* near Andadoany village. Two *E. dupreanum* roosts were found, located high up in rock faces. We also discovered a small roost (<20 animals visible in the day) of *T. mauritianus* in a rocky fissure in a gorge along the Manambolo River.

Table 1 Species composition of Chiroptera in Parc National Tsingy de Bemaraha caught with mist nets during two different seasons in 2003

Taxa	July	October
*R. madagascariensis***	114	37
Emballonura nov. sp.	1	0
*T. furculus***	19	5
*T. rufus**	52	16
Hipposideros commersoni	0	37
*M. manavi**	85	49
*Myotis goudoti**	30	7
S. robustus	0	3
S. tandrefana	1	0
Chaerephon leucogaster	4	0
Total	308	155
Species richness	8	7

Significance levels are based on chi-squared statistics (*<0.05, **<0.01) for between season comparisons

Our time-expanded recordings of echolocation calls revealed six microchiropteran species and we also identified a sonogram similar to that of *Miniopterus majori*, but since that species was not trapped we have excluded it from our results. A medium-sized *Miniopterus* sp., which may have been *M. majori* or *M. fraterculus* was also observed during the cave surveys but was not trapped.

Seasonality

For the species caught in large numbers, all were significantly more abundant in July than October, with the notable exception of *Hipposideros commersoni* (Table 1). *H. commersoni* was not trapped or detected during July but made up 24% of captures and was detected on 3% of point counts in October (Table 1, Fig. 1). It is noteworthy however that a spot-survey conducted 25 km north of the Bekopaka site trapped two adult *H. commersoni* in July. Species richness was similar in both seasons, but visits made only in July would have missed three species and a further two different species

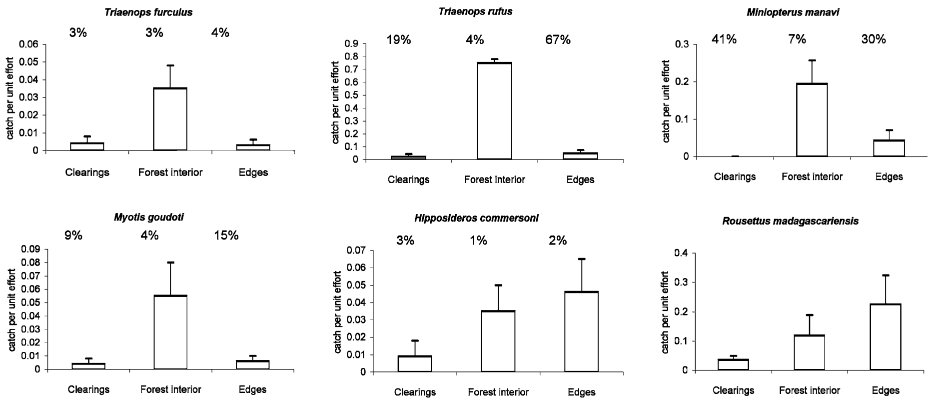

Fig. 1 Mean catch per unit effort (+1 SE) of bats in three forest habitats in Parc National Tsingy de Bemaraha. Also shown, above each bar for the microchiropterans, is the percentage frequency of occurrence of each species determined acoustically from point counts

were only recorded in October (Table 1). The mean number of bat passes was not significantly different between seasons (Mann–Whitney $U = 12{,}711$, ns).

Habitat use

The capture frequency of six species differed between habitats (Fig. 1) but the comparison was only statistically significant for *M. manavi* (Kruskal–Wallis $H = 9.07$, $P < 0.01$). Based on capture data alone, four species were caught most often in the forest—*Triaenops rufus* (71% of captures in the forest interior), *T. furculus* (92%), *M. manavi* (90%) and *Myotis goudoti* (92%). *Rousettus madagascariensis* and *H. commersoni* were caught less frequently in clearings but used edges and forest interior to a similar degree. All four individuals of *Chaerephon leucogaster* were caught in tsingy clearings. *S. robustus* was trapped in clearings and the forest edge, whilst the single *S. tandrefana* and *Emballonura* nov. sp. individuals were caught on the forest/agriculture interface.

A total of 320 point counts were made, 161 in July and 159 during October. Most point counts (184) were in the forest interior, with a further 104 in forest edge and 32 in clearings. Total bat activity was significantly different between habitats (Kruskal–Wallis H=29.6, $P < 0.01$). We detected highest activity along the forest/agriculture interface (mean = 15.7 ± 1.6 bat passes), lower activity in clearings (13.1 ± 3.7 bat passes) and the least activity inside the forest (7.5 ± 0.9 bat passes). Using bat passes classified into frequency categories there was also a significant difference between habitats (Fig. 2) for all groups (>60 kHz: $H = 19.0$, $P < 0.001$; 33–60 kHz: $H = 17.5$, $P < 0.01$; <33 kHz: $H = 7.5$, $P < 0.05$) and activity was consistently lower on forest-trails. Bat passes attributed to vespertilionids (33–60 kHz) were most commonly heard along the forest/agriculture interface, whilst the hipposiderids and *M. goudoti* (>60 kHz) used both edges and clearings.

Activity was significantly higher in riparian areas than non-riparian areas (Fig. 2) for >60 kHz passes (Mann–Whitney $U = 5{,}842$, $P < 0.001$) and 33–60 kHz passes (Mann–Whitney $U = 4{,}347$, $P < 0.001$) but not for the lower frequency <33 kHz

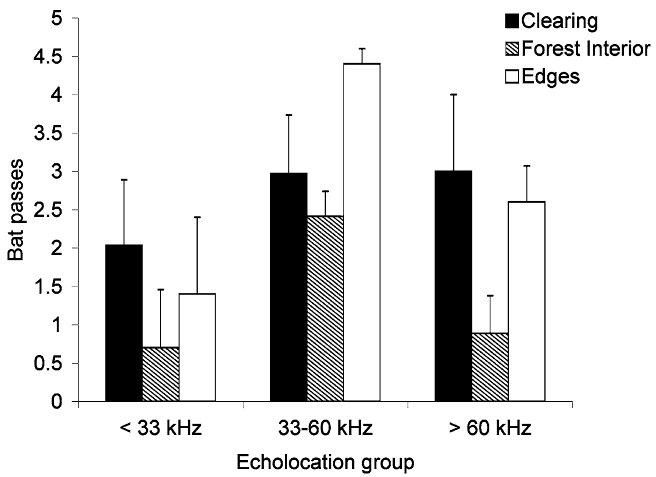

Fig. 2 Mean activity (+1 SE) of bats in three echolocation groupings in Parc National Tsingy de Bemaraha during July, August and October 2003 in three types of forest habitat

passes (Mann–Whitney U = 6,987, ns; Fig. 3a). A comparison of mist net captures in these habitats found significantly more microchiropterans in non-riparian habitats (Chi-squared = 65, P< 0.01) whilst megachiropterans were caught most often netted in the drier parts of the forest (Fig. 3b).

A comparison of bat activity between point counts on the forest-trails and in the forest-interior revealed significantly higher mean bat passes on the former (mean = 5.0 ± 0.6) than the latter (mean = 2.97 ± 0.8; Mann–Whitney U = 2,915, P < 0.001).

Our time-expanded recordings of free-flying bats show slightly different results to the capture data (Fig. 1). Most notable is that *Miniopterus manavi* was recorded in 41% of the point counts made in clearings but was not trapped in this habitat (Fig. 2). A high proportion of the recordings made during point counts from edges revealed the presence of *Triaenops rufus* and *M. manavi*, whereas trapping data suggested low use of edges by both species. *Emballonura* nov. sp., which was trapped only once, was most frequently recorded (11%) using the forest/edge interface.

We divided the capture and bat pass data into two categories (inside and outside the forest) for each 15-min period to investigate whether proximity to the cave roosts, which were located inside the forest, influenced temporal patterns of activity. Inside the forest, mist nets captures peaked between 1800 and 1814 h whilst captures outside the forest peaked between 1815 and 1829 h (Fig. 4a). Bat

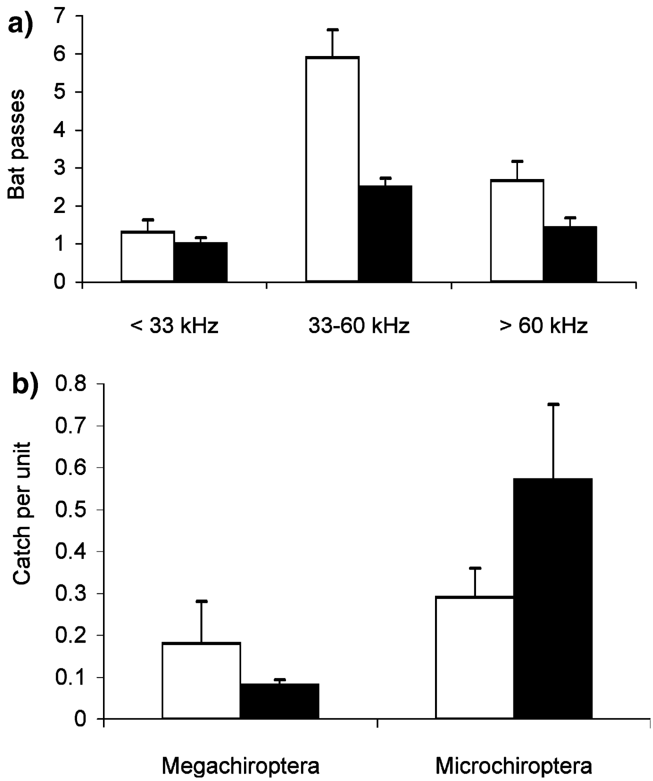

Fig. 3 (**a**) Mean activity of bats in three echolocation groupings and (**b**) catch per unit effort (+1 SE) for Megachiroptera and Microchiroptera in riparian (white) and non-riparian forest (black) in Parc National Tsingy de Bemaraha during July, August and October 2003

Table 2 Bat species composition and abundance in 16 caves, Parc National Tsingy de Bemaraha, frequented regularly or rarely by tourists

Cave name	Abundance		Species
	July	October	
Higher tourism			
Anjohifipetrahana	0	0	–
Anjohimanapaka	16	6	Em, Mm
Anjohimanitsikoa	1	4	Mm, My
Anjohimanitsy	38	9	Mg, Mm, My
Anjohimboro	0	0	–
Anjohitantely	31	19	Em
Gorge II	18	5	Mm
Lower or no tourism			
Anjohiatsimo I	24	0	Mm
Anjohiatsimo II	0	7	Em, Mm
Anjohiatsimo-nord	12	22	Mg, Mm
Anjohibemoka	50	–	Mm, My
Anjohikinakina	1,712	9,174	Mg, Mm, Ot, Ro, Tr
Anjohisiramamy I	9	6	Em, Mm
Anjohisiramamy II	12	–	Mm
Anjohitrombastimo	0	0	–
Gouffre cave	151	20	Mg, Mm, My

– not visited in October

Species abbreviations: *Miniopterus manavi* (Mm), *M. gleni* (Mg), *Myotis goudoti* (My), *Emballanura* nov. sp. (Em), *Rousettus madagascariensis* (Ro), *Otomops madagascariensis* (Ot), *Triaenops rufus* (Tr)

activity peaked between 1845 and 1859 h inside and outside the forest, although activity at the forest edge only exceeded that of forest-trails after 1815 h (Fig. 4b).

Cave surveys

Over 2,000 bats were observed in the 16 caves in July and over 9,000 in October (Table 2). *Triaenops rufus* was the most abundant, making up 54% (n = 1,127) of observations in July and 90% (n = 8,306) in October. *Rousettus madagascariensis* made up 19% (n = 400) and 6% (n = 620) of total observations in July and October respectively. *M. manavi* was the most widespread species and was found in 75% of the caves, but *O. madagascariensis*, *R. madagascariensis* and *T. rufus* were found only in Anjohikinakina. Extraction of *O. madagascariensis* from holes in the ceiling at this site accounted for 88 and 114 individuals in July and October, respectively. This cave contained 83% of all bats counted in July and 99% in October. Numbers of *R. madagascariensis* and *T. rufus* were higher in October than in July, but the opposite was observed for *M. gleni*.

Three caves contained no bats (including two that are frequently visited by tourists) in either season and another cave only contained *Emballonura* nov. sp. during October. In terms of species richness and number of individuals, Anjohikinakina Cave is the most important for bat conservation (Table 2).

Roost site selection

In many caves, the bats used small, round, vertical holes in the ceiling, and in Anjohikinakina *O. madagascariensis* was only observed in these features.

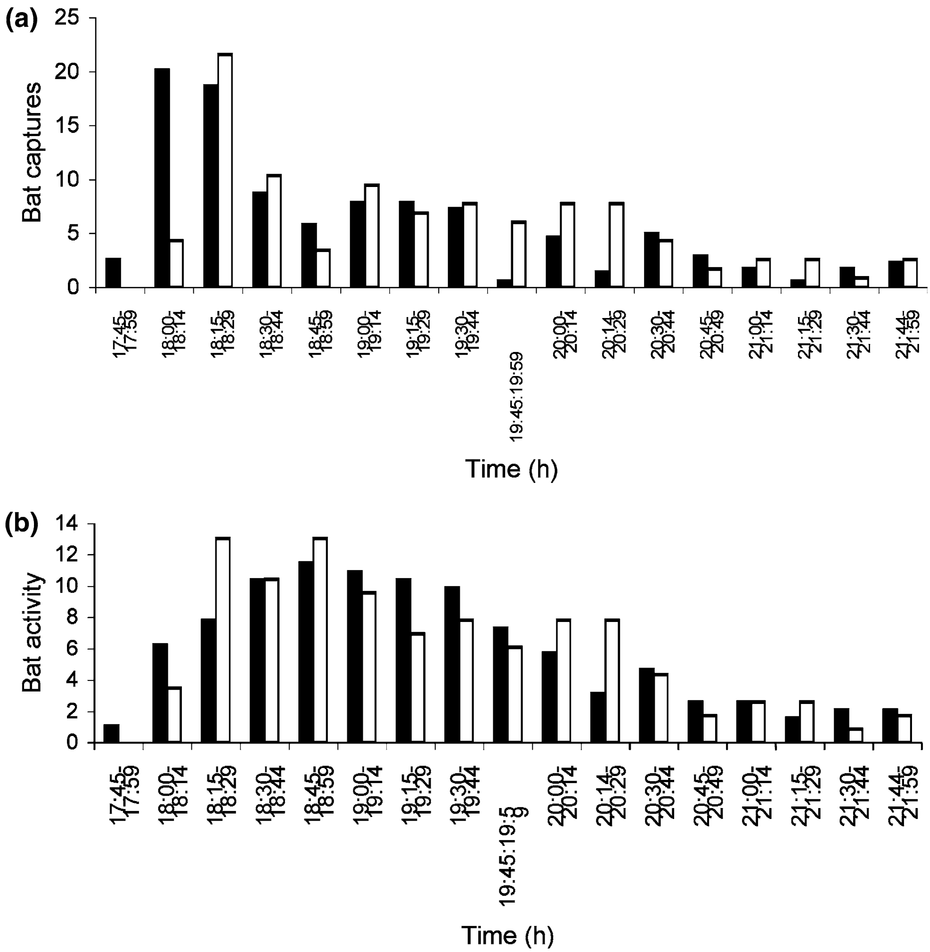

Fig. 4 (**a**) Bat captures and (**b**) activity in 15 min time periods from sunset to 22:00 in Bemaraha National Park during July, August and October 2003 from inside (black) and outside (white) the forest

Miniopterus manavi also sometimes used these holes, but were also observed suspended from over-hanging cave walls. *R. madagascariensis* and *Triaenops rufus* roosted in single, large colonies in Anjohikinakina. *Myotis goudoti* frequently roosted alone and was sometimes seen hanging from long roots dangling from the cave ceilings.

Microclimate measurements at the roost sites of *M. manavi* and *Emballonura* nov. sp. were significantly different from each other, and different to the transect (Table 3). No other species was common enough to allow statistical validation of roost site selection. *Emballonura* nov. sp. roost sites were significantly warmer than both the random points and *M. manavi* roosts. Both bat species roosted in areas of similar humidity levels, which were significantly lower than the levels recorded on the random points. High light values for the transect points reflect the starting points at cave entrances. However, *Emballonura* nov. sp. roosts were in localities that received significantly more sunlight at the time of the surveys.

Table 3 Roost site selection in caves by two Malagasy microchiropterans in Parc National Tsingy de Bemaraha

	Light (lux)	Temperature (°C)	Humidity (%RH)
Roosts			
Emballonura nov. sp.	1.8 ± 0.5	23.7 ± 0.3	80.9 ± 1.1
M. manavi	0.06 ± 0.1	20.5 ± 0.3	79.2 ± 1.2
Transect points	8.8 ± 2.33	21.8 ± 0.1	83.3 ± 0.6
Statistic	$H = 22.9$	$F = 36.2$	$H = 17.7$
P value	<0.001	<0.001	<0.05

The data are combined for two seasons and from 12 caves

Discussion

These results emphasize the important contribution that bats make to the island's endemic mammal fauna. Parc National Tsingy de Bemaraha has the highest chiropteran species richness of any known site in Madagascar (Goodman et al. 2005a, b) and must therefore be considered as a site of national importance for mammal conservation. Failure to incorporate bats into surveys of important conservation sites in Madagascar is therefore likely to significantly underestimate the true mammalian species richness.

Bat habitat use

Surveys to establish inventories of bat species for important wildlife areas traditionally involve either assessments of roosting populations in caves and buildings (e.g. Petit 1996) or intensive mist netting programs in conjunction with harp traps (e.g. Clarke and Downie 2001). Although some surveys incorporate trapping and the use of bat detectors (e.g. Bernard and Fenton 2002) many biologists rely solely on mist net captures to study habitat use by bats (e.g. Angelici et al. 2000). Harps traps are routinely employed in bat surveys in Madagascar (Goodman et al. 2005a, b) but would need to be deployed in prohibitively large quantity to provide information on habitat use. Foraging height, flight speed, type of echolocation and body size are amongst the many factors that can influence the capture rate of a given species in a mist net. The majority of studies from South and Central America use only mist nets because the chiropteran fauna of these regions are dominated by phyllostomid bats that have quiet echolocations which render them difficult to detect with bat detectors (Fenton et al. 1992). By contrast Madagascar's bat community is made up mostly of vespertilionid species and recent progress in the description of the echolocation of this family, as well as Hipposideridae, Myzopodidae and Emballonuridae (Russ et al. 2003) is good reason to begin to incorporate acoustic sampling into bat surveys in Madagascar.

Interpretation of either trapping or echolocation results alone would have resulted in markedly different conclusions from our study. For example, results from the bat detector surveys showed lowest microchiropteran activity in the forest interior, but trapping revealed the opposite result with four species caught most often inside the forest. Mist nets in the forest traversed trails and streams and were probably more efficient at intercepting passing bats than nets placed in the more open areas of the edge and clearings. Another important factor was that the rocks and crevices in the study area were mainly located in the forest, resulting in a large numbers of bats emerging around sunset in the forest and flying along the trails. This point is supported by our analysis of temporal patterns in bat activity that showed the first peak in the forest, followed 30 min later by a peak outside of the forest. Mist nets have been used in Madagascar to establish inventories of bats in the eastern rainforests (e.g. Pont and Armstrong 1990; Bayliss and Hayes 1999; Goodman 1999) but few attempts have been made to assess their habitat preferences. Our results demonstrate the important influence that roost location can have on bat surveys and further emphasizes the inherent biases in using ground level mist nets. We recommend that bat surveys report results for roost and foraging site captures/observations separately.

Assessments of activity using bat detectors are less susceptible than mist nets to variation from habitat features and we would not expect a significant bias between trails, edge or clearings using acoustic survey methods. We are therefore confident that the lower activity, measured as 'bat passes', detected inside the forest compared to edges and clearings is representative of habitat use by microchiropterans.

Eger and Mitchell (2003) suggested that both *T. rufus* and *T. furculus* have similar requirements for forest habitats and this is supported by our results. *Myotis goudoti* and *M. manavi* are both distributed widely across Madagascar and are found in forests near suitable cave roosting sites (Eger and Mitchell 2003). Both species were caught most frequently in the forest but detected most frequently in edges and clearings. Of the four individuals of *Scotophilus* captured, representing two different species, two were at the agriculture/forest interface and two were in the tsingy clearings. Given the success of our nets at catching other vespertilionid species inside the forest, this suggests that *Scotophilus* is not strongly associated with either forests or caves. Information on this genus of bats is particularly lacking in Madagascar, and the discovery of a new species during this survey (Goodman et al. 2005a) should provide an incentive for further comprehensive bat surveys in Tsingy de Bemaraha and other protected areas in western Madagascar.

The high capture rates of four small bat species in the forest appears to be explained by the presence of cave roost sites in the forest and the efficiency of nets across narrow trails at catching hungry, emerging bats at sunset. Many studies on habitat use of bats have demonstrated a close link between bat activity and linear or aquatic habitat features (Verboom and Spoelstra 1999; Law and Chidel 2002; Russ and Montgomery 2002). Forest trails in the park appear to be used mainly by bats as thoroughfares to access the edge habitats where foraging occurs; the forest maybe an important source of insect prey in these areas. Riparian habitats were used mainly by vespertilionids, but overall microchiropteran activity was higher away from water, possibly reflecting the importance of the edges to foraging bats.

Although many of Madagascar's small land mammals are forest dependent (Ganzhorn et al. 2003) and successful conservation is closely linked with the preservation of intact forest, bat conservation may demand a change in approach to recognize the value of non-pristine habitats adjacent to the forest. Estrada et al. (1993) found that agricultural habitats contained a high bat species richness and abundance and they suggested that areas of mixed plantation and isolated forest trees are important habitat to bats because they reduce the distance between blocks of remaining rainforests. Similarly, Bernard and Fenton (2002) recorded most species and highest capture rates in savanna habitats located in a mosaic of rainforest fragments in Brazil. Similar studies in Africa are rare, but Angelici et al. (2000)

found a higher species richness and abundance of bats in secondary forest than either bush or primary forest habitats. Although the change in microclimate associated with forest edges is often detrimental to forest species (Lethinen et al. 2003), we show in this study that forest edges are important for habitats foraging bats. Associations between bats and the forest are less clear, and although they appear to be mainly associated with the presence of suitable roosts, the forest vegetation is likely to be an important source of insect food and to provide the structural formations (e.g. tree-lined edges) necessary for bats with short, wide-wings to forage alongside. A preference for forest edges over the forest interior may make bats less susceptible to the detrimental effects from forest fragmentation, although this area of research clearly requires further work.

Cave conservation in Tsingy de Bemaraha

Although caves are key habitats for bats, our survey revealed that most of the potential cave roosts in Bemaraha contained small populations of the common and abundant *M. manavi* and *M. goudoti*. The capture of obligate caves species such as *T. furculus* with mist nets, but their absence from the 16 caves studied demonstrates that other bat roost caves remain undiscovered.

Tourism at its current levels is unlikely to be presenting a significant threat to bat populations in Bemaraha, especially as the park is closed to visitors from December to April when water levels are high, and which coincides with the period of chiropteran parturition and lactation. However, we propose some conservation recommendations for both the management of caves and the monitoring of species. Anjohikinakina is clearly a cave of national importance to bats in Madagascar because it contains relatively large roosting colonies of five species. Although *R. madagascariensis* has a wide distribution in Madagascar only a small number of roost sites are known from the protected area network (MacKinnon et al. 2003). *O. madagascariensis* is associated with Madagascar's limestone and sandstone deposits and has been recorded from sites across the dry portions of the island (Goodman et al. 2005b); however only a handful of roost sites have been identified.

Anjohikinakina Cave is off the main tourist circuit and although it receives some visits by intrepid groups from July until September, current visitation rates are unlikely to threaten the bats. Complacency in this respect should be avoided we recommend that the cave is excluded from any future expansion of the tourist circuits. Occasional monitoring by park staff is, however, recommended to deter potential hunters.

Goodman et al. (2005b) list *Emballonura* nov. sp. as one of only five bat species that are possibly dependent on intact forest. We frequently observed the species roosting near cave entrances and it readily took to flight when approached. Other studies have shown that tour group visits to caves can have a detrimental impact on roosting bats by provoking increased levels of activity and flight during the day (Lacki 2000), presumably leading to increased demands on the energy budget. The roost site preference and behaviour of this species therefore appear to make it vulnerable to disturbance by tour group visits to caves and we strongly recommend that the frequency of such visits are at least monitored, and preferably limited, to manage noise, light levels and human behaviour (Mann et al. 2002).

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