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Habitat use and conservation of bats in rainforest and adjacent human-modified habitats in eastern Madagascar

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We used roost searches, mist netting and acoustic sampling to investigate the habitats used by bats in Parc National de Mantadia and the Réserve Spéciale d'Analamazaotra, eastern Madagascar. Four species were caught in relatively intact humid forest (*Myotis goudoti*, *Miniopterus manavi*, *Miniopterus majori* and *Emballonura atrata*) two in agricultural land, *Neoromicia matroka* and *Neoromicia melckorum*, and one, *Rousettus madagascariensis,* in *Eucalyptus* plantations. *Mormopterus jugularis*, *Chaerephon pumilus* and *Mops leucostigma* were found roosting in buildings ca. three km from the humid forest. Acoustic sampling revealed that *Neoromicia* spp. and molossids were ubiquitous and were recorded from intact and degraded humid forest, *Eucalyptus* plantations and agricultural land. *Myotis goudoti* showed the strongest association with intact humid forest. Taxon richness, determined by acoustic sampling, was highest in humid forest but activity was highest in plantations and agricultural land. Mixed-habitat landscapes that surround protected forests and consist of a mosaic of regenerating forest, agriculture, wetlands, villages and plantations are important for bats and promote chiropteran diversity because they provide roosting and foraging sites for species that rarely use intact forest. The humid forests of eastern Madagascar have lower bat diversity than the island's western deciduous karst forests.

Key words: acoustic, roosts, habitat, landscape, conservation, Madagascar

INTRODUCTION

Comprehensive species inventories have been made of rainforest amphibians, reptiles, small land mammals and primates in Madagascar and this information has been used to assess their conservation status (e.g., Raxworthy and Nussbaum, 2000), levels of forest dependency (e.g., Ganzhorn *et al*., 2003), biogeography (e.g., Goodman and Ganzhorn, 2004) and have contributed to macro-analyses to prioritise conservation efforts (e.g., Brooks *et al*., 2002). However as noted recently (Goodman and Benstead, 2005), many gaps remain in our knowledge of Madagascar's endemic species and there have been surprisingly few studies on the island's chiropteran fauna.

Since the late 1990s interest has grown in Malagasy bats and there have been a number of publications on taxonomy (e.g., Goodman and Cardiff, 2004; Goodman *et al*., 2006) and diet (e.g., Bollen and Van Elsacker, 2002; Razakarivony *et al*., 2005). Most Malagasy mammals receive some protection through their occurrence in forest formations that are included within the network of national parks and reserves. However, with questions being raised about the extent to which Malagasy bats are dependent on intact forest (Eger and Mitchell, 2003; Goodman *et al*., 2005) there is now a need to assess roost selection and habitat preference of bats in the eastern rainforests.

In this paper we systematically assess the habitat use of a chiropteran community using a combination of trapping and acoustic survey methods. We conducted the work in Parc National (PN) de Mantadia and the Réserve Spéciale (RS) d'Analamazaotra, in a landscape with both relatively intact humid forest and human-modified habitats (Dolch, 2003). Our specific objective was to determine the extent to which bats used human impacted landscapes or natural forest.

Materials and Methods

PN de Mantadia and RS d'Analamazaotra lie about 140 km east of the capital Antananarivo, between latitudes 18°24'47" and 18°57'11"S, and longitudes 48°16'39" and 48°24'21"E. Mean elevation of the study area is 900 m (range from 850 to 1,300 m). The climate is tropical with a hot and humid season from September to April and a cooler, drier season from May to August. Mean annual temperature is 18°C, with a mean minimum of 15°C in August and a mean maximum of 24°C in February. Mean annual rainfall is 1,700 mm (weather data 1984–1994, RS d'Analamazaotra, ANGAP). The vegetation of the reserves is medium altitude tropical moist forest with a canopy of *Weinmannia* spp., *Tambourissa* spp., *Symphonia* spp., *Dalbergia* spp. and *Veronia* spp. trees. The forest at PN de Mantadia is less disturbed than at RS d'Analamazaotra. Land use around the park edges consists mainly of *Eucalyptus* spp. plantations, regenerating secondary forest growths and agriculture (Fig. 1).

The work was conducted during two fieldwork periods between 16 October and 24 November 2002 (early rainy season) in PN de Mantadia and between 1 and 27 February 2003 (rainy season) in RS d'Analamazaotra. We assessed the use of both feeding habitats and roosts by bats using mist nets and harp traps. Assessments of habitat use consisted of trapping with 72 m of mist nets and two harp traps (1 m × 1 m) deployed from 18:00 h to 23:00 h on two nights in four different habitats at each reserve (see below). Mist nets were checked every 15 min throughout the trapping period; nets and traps were left open during rain. The traps were placed in potential flyways and feeding areas and were usually situated across trails, over streams or in forest gaps. This approach may have introduced some bias into the assessment of habitat use but is particularly justified in Malagasy eastern forests because capture rates are very low (S. M. Pont and J. D. Armstrong, unpubl. data; P. A. Racey, unpubl. data). Discussions with local people and searches of suitable areas were used to find roost sites and we sampled these by either placing mist nets at the roost entrance (e.g., buildings), placing nets as close as possible to where we thought the roost was located (e.g., in banana plantations) or by direct searching with head-lights (e.g., caves). We acknowledge that our roost searches probably under-represented bats using tree cavities or vegetation as these sites would be unknown to local people and very difficult for us to locate in forests.

We identified all bats caught using keys, notes and illustrations (Peterson *et al*., 1995; Russ *et al*., 2003) and released them at the site of capture. A maximum of two voucher specimens were collected per species that posed potential identification problems and these are deposited at the Département de Biologie Animale, Université d'Antananarivo.

We used two complimentary methods for our acoustic survey protocol. We listened to passing bats from point counts (100–200 m apart) in four different habitat types (relatively intact humid forest, degraded humid forest, *Eucalyptus* plantations and agriculture). Each point count lasted five minutes and one listener used a Pettersson D-980 bat detector (Pettersson Elektronik AB, Uppsala, Sweden) and the other used a Duet bat detector (Stag Electronics, UK). We conducted a preliminary survey in each habitat throughout the night over the course of four nights to determine the period of maximum of bat activity (F. Randrianandrianina, unpubl. data); all subsequent sampling was conducted between 18:00 and 21:00. Using the D-980 bat detector, the listener swept up and down the frequency range in heterodyne mode and all bat passes were recorded in time-expansion (×10) onto a Sony mini-disc player. Time-expanded recordings retain their structural integrity and have been used to identify sonograms to species and to genus in the case of *Neoromicia* (Russ *et al*., 2003). The second listener also detected passing bats in heterodyne mode and used this method to describe the frequency of the echolocation whilst also recording all activity in broadband (frequency division) onto a Sony mini-disk player. Bat activity was categorised as either 'bat passes' or 'feeding buzzes'; a 'bat pass' consisted of two or more pulses of all echolocation sounds and 'feeding buzzes' are the increased pulse rates in the approach phase to prey and represent foraging activity.

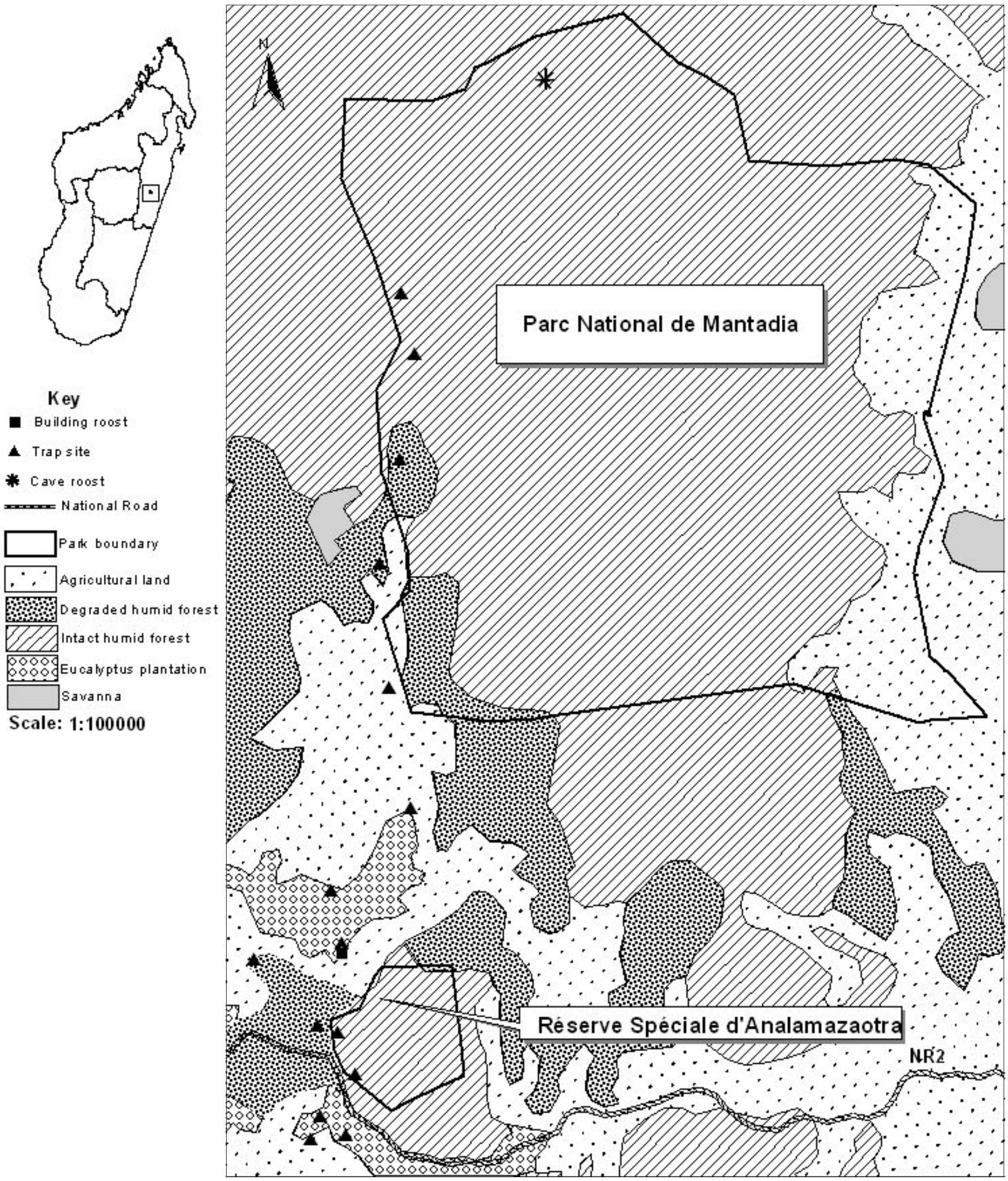

FIG. 1. Map of Madagascar showing the location of our study site (inset) and a more detailed depiction of major habitat types, bat roosts and trap sites from in and around PN de Mantadia and RS d'Analamazaotra

Results

We netted six bats in 126 hours of standard trapping and further 107 bats during emergence from roosts. We captured nine microchiropteran and one megachiropteran species. Ninety percent of the bats were trapped near roost sites in buildings, with only 2% at caves, 5% in the forest and 3% in an agricultural setting. The six bats caught in forest habitat (four *Rousettus madagascariensis* and individual *Miniopterus manavi* and *Myotis goudoti*) were the only captures from the standardised trapping protocol. All *R. madagascariensis* individuals were trapped in mist nets set across trails in mature *Eucalyptus* plantations. *Miniopterus manavi* and *M. goudoti* were captured in a harp trap and mist net, respectively, inside relatively intact humid forest. *Emballonura atrata* and *Miniopterus majori* were also found inside relatively intact humid forest but were collected from a small riverside cave. Two *Neoromicia melckorum* and a single *Neoromicia matroka* were mist netted together near a small group of banana plants at dusk approximately 1 km from the edge of intact forest in PN de Mantadia. The three molossid species were trapped as they emerged from buildings, about 0.5 km from *Eucalyptus* plantations and 3 km from the edge of the intact forest, included *Mormopterus jugularis* ($n = 42$), *Chaerephon pumilus* ($n = 35$) and *Mops leucostigma* ($n = 26$).

We completed 418 point counts, 111 in *Eucalyptus* forest, 128 in relatively intact forest, 96 in degraded forest and 83 in agricultural land. Bat activity was significantly lower in PN de Mantadia during the pre-wet season than in RS d'Analamazaotra during the wet season (Mann-Whitney $U = 13{,}80$, $d.f. = 1$, $P < 0.001$) so we present the analyses separately.

Bat passes in PN de Mantadia were significantly different between habitat types (Kruskal-Wallis $H = 29.9$, $d.f. = 3$, $P < 0.001$) and were highest in *Eucalyptus* forest and lowest in relatively intact forest (Fig. 2A), although there was no such significant difference for feeding buzzes (Kruskal-Wallis $H = 3.3$, $d.f. = 3$, $P > 0.05$). In RS d'Analamazaotra, there also were significant differences in bat passes between habitat types (Kruskal-Wallis $H = 10.0$, $d.f. = 3$, $P < 0.02$) and highest activity was recorded in agricultural land. Feeding buzzes were also significant differences between habitat types in this area (Kruskal-Wallis $H = 10.7$, $d.f. = 3$, $P < 0.01$) and were highest in degraded forest and lowest in relatively intact forest (Fig. 2B).

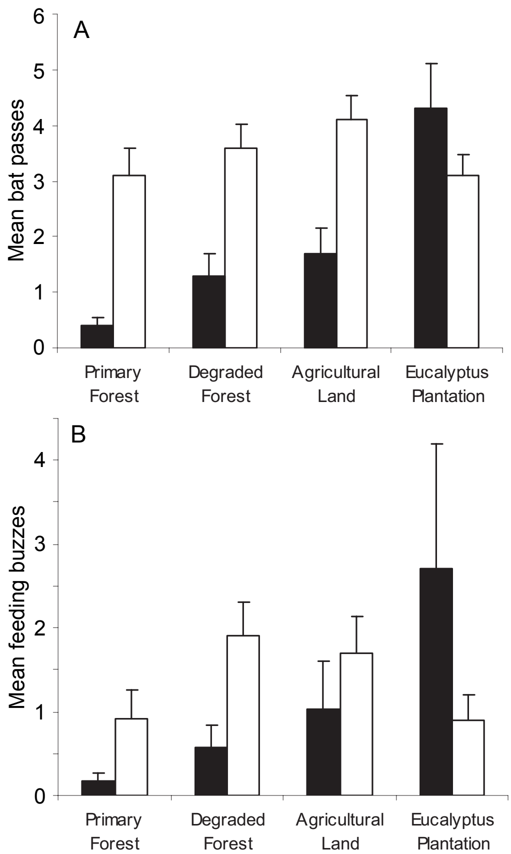

FIG. 2. Mean (+ 1 SE) microchiropteran activity in four different habitats in Parc National de Mantadia (black) during November 2002, and Reserve Spéciale d'Analamazaotra Forest (white) during February 2003

We recognised five different bat taxa based on echolocation recordings (Table 1). As we detected molossids in all habitats but were unable to ascribe the echolocation recordings to individual species, the actual taxon richness in each habitat may be two species higher than estimated. Three [to five] taxa were recorded in *Eucalyptus* plantations, with molossids and *Neoromicia* spp. predominating. Highest species richness of 5–7 was found in relatively intact humid forest where *Miniopterus* cf. *majori* and *M. goudoti* were the most frequently recorded. *Myotis goudoti* appears to have the strongest association with relatively intact humid forest (Table 1).

Discussion

Chiropteran Diversity

Although Madagascar's forests are famous for exceptional levels of endemism in groups such as primates and insectivores (Ganzhorn *et al*., 1997; Goodman and Rasolonandrasana, 2001; Jenkins, 2003), the chiropteran fauna of these forests (ca. 11 species) appears rather low. We found a total of ten bat species during our study, although only four were recorded from inside the protected areas. The only previous bat survey at RS d'Analamazaotra trapped 14 individuals of seven species (Russ *et al*., 2003). All species captured by Russ *et al*. (2003) were also found during our study, with the notable exception of *Myzopoda aurita,* which was only detected during their acoustic survey. The echolocation calls of *M. aurita* are distinctive (Göpfert and Wasserthal, 1995; Russ *et al*., 2003) and are unlikely to be overlooked in an acoustic survey. *Myzopoda aurita* may therefore be a rare or transient species in the area we surveyed and this could be related to seasonality. The two previous records of this species near RS d'Analamazaotra were in July/August (Russ *et al*., 2003) and September (F. Ratrimomanarivo, unpubl. data) and our survey was in February. A recent taxonomic assessment of the voucher specimens from our study revealed the first record of *N. melckorum* in Madagascar (Bates *et al.,* 2006). This species is otherwise known from South Africa, Zimbabwe, Zambia, Mozambique, Kenya and Tanzania (Simmons, 2005). The capture of *N. melckorum* in the same small banana plantation as *N. matroka* illustrates, not only that non-forested zones surrounding protected areas augment chiropteran diversity at the landscape level, but also how little is known about the ecology of Madagascar's bats in areas that have been comprehensively surveyed for other mammal species.

Table 1. Acoustic sampling at point counts in four habitats in Parc National de Mantadia and Réserve Spéciale d'Analamazaotra Madagascar. Values are the percentage of detections from time-expanded sonograms for five taxa in each habitat. Totals are not 100 because more than one species was heard on a single point count and some point counts yielded no recordings (*n* = number of point counts). *Miniopterus majori* and *M. fraterculus* are morphologically similar (Petersen *et al*., 1995); our recordings resembled those of *M. majori*. Sonograms of the *Neoromicia* verspertilionids were distinctive but we were unable to assign them to species because of a lack of reference material

Taxon	*Eucalyptus* plantation *n* = 80	Primary forest *n* = 64	Degraded forest *n* = 77	Agriculture *n* = 56
Miniopterus manavi	0	2	0	2
M. cf. *majori*	0	8	1	0
Neoromicia spp.	11	4	8	9
Myotis goudoti	1	22	0	0
Molossidae spp.	39	13	23	52

Previous chiropteran surveys in and around other eastern humid forests found 11 species in the Masoala Peninsula (Russ *et al.*, 2003), eight in RS d'Analamazaotra forest (Russ *et al.*, 2003), 11 from PN de Marojejy (S. M. Pont and J. D. Armstrong, unpubl. data) and seven from Makira forest (J. Bayliss and B. Hayes, unpubl. data). Other surveys in the humid forests that incorporated non-intensive bat trapping as part of more general vertebrate surveys found fewer spe-cies, with only four bats known from PN d'Andringitra (Goodman, 1996), three from RS d'Anjanaharibe-Sud (Goodman, 1998) and four from PN d'Andohahela (Goodman, 1999). Although species tallies for the latter surveys may have been higher had the teams also included roost sites at the edge of the reserves (e.g., buildings), the humid forests consistently have a lower chiropteran diversity than the dry, deciduous forests of Madagascar (Goodman *et al.*, 2005). Bat surveys of protected areas in western Madagascar, using similar methods to our study reported here, found 14–16 species (Goodman *et al.*, 2005).

In western Madagascar, Goodman *et al.* (2005) noted a higher species richness of bats in forests on a karst substratum than those without exposed surface rock deposits and attributed this difference to the greater availability of roosting sites. Synanthropic species, such as the molossids found in our survey, are less constrained by roost site availability and are able to use buildings as well as natural roosts (Goodman and Cardiff, 2004). Bat species diversity and abundance may therefore be relatively low in the eastern rainforests because of a scarcity of cave roost sites and this may explain the absence of obligate cave roosting species such as *Miniopterus gleni* during our survey.

The traditional model of mammal conservation in Madagascar has been to protect large expanses of intact forest because forest-dependency is a common trait of threatened, endemic vertebrates on the island. Our results show that bats use a wider variety of habitat types than most endemic Malagasy mammals and that bat activity is highest in human-modified areas outside of relatively intact forest. A clear message from our study is that the conservation of Madagascar's endemic, volant mammals requires new strategies that identify roost sites, whether inside or outside of protected areas, and recognises the importance of non-forest habitats for bats.

Forest Dependency and Habitat Use

Bat communities in other Old World rainforests possess closed canopy specialists, with low aspect ratios and wing loadings that are considered forest specialists (e.g., Crome and Richards, 1988). Other studies in Africa have demonstrated a close relationship between habitat use and wing morphology (e.g., Fenton and Rautenbach, 1986; McDonald *et al.*, 1990). By contrast, surveys and research in Madagascar have yet to identify bat species that are reliant on large expanses of intact forest (Goodman *et al.*, 2005). Our results from trapping and acoustic surveys showed that *M. goudoti* predominantly used relatively intact humid forest, suggesting that it maybe a forest-species. By contrast, Goodman *et al*. (2005) observed *M. goudoti* in two caves with no discernable intact forest in the vicinity. Its short, round wings and frequency modulated echolocation indicate adaptations to feeding in and around cluttered vegetation and an ability to also fly in open habitats. These observations suggest therefore that this species may either travel significant distances from its roost to foraging sites or has very small minimum requirements for intact vegetation (certainly smaller than other endemic mammals). Additional research on foraging and commuting behaviour are now needed to resolve this fundamental question.

No other species was strongly associated with intact forest although both *E. atrata* and *M. majori* were found roosting in a small cave well inside the intact forest. We cannot easily explain the absence of *E. atrata* during the acoustic surveys but this may have been because it occurs at very low densities inside the forest and the probability of detection is therefore low or because it forages in zones that were not thoroughly sampled during the current study (e.g., canopy).

It is clear from our acoustic surveys that degraded forests, plantations and agriculture provide suitable habitats for many bats and that the use of relatively intact forest for these species is limited by comparison. Clutter levels were high in humid forest and *Eucalyptus* plantations (away from the roads) and low in agricultural land. Many bats adjust their echolocation according to clutter and acoustic characteristics therefore vary according to the habitat or vegetation (Siemers, 2002). Species that are active across clutter gradients use calls with lower frequencies, longer durations and narrower bandwidths in open habitats (Jacobs, 1999). Although some notes have been made on the influence of clutter on the acoustic characteristics of Malagasy microchiropterans (Russ *et al.*, 2003) there is insufficient data for a complete assessment. Our study would have benefited from a greater understanding of the influence of clutter but our comparisons between molossids, *Neoromicia, Miniopterus* and *Myotis* are robust because of the major differences in echolocation between these groups. Assessments of *Miniopterus manavi* and *M.* cf. *majori* may however have been more sensitive to the influence of clutter.

Captures of the small fruit bat *R. madagascariensis* were restricted to wide trails in *Eucalyptus* forest. Notwithstanding a caveat of small sample sizes, this suggests that at least during November and February, *Rousettus* use *Eucalyptus* plantations and spend little or no time in the other forest areas sampled during the survey. The wide trails inside the *Eucalyptus* forest may be acting as conduits of movement between foraging sites, or the bats maybe feeding in the plantation. The nearest known roost is ca. five km from the plantation, well within the known nightly flight range of *Rousettus* (Jacobsen *et al.*, 1986).

Roost Conservation

Roost protection is a priority for bat conservation in Madagascar (Goodman *et al.*, 2005). The wide variety of different sites used by roosting bats, including caves, buildings and vegetation, need to be included in conservation plans in Madagascar. Molossids that roost synanthropically are subject to persecution by local people and conservation awareness campaigns designed to protect endemic Malagasy mammals should be extended beyond reserve boundaries to include buildings with important bat roosts. The use of vegetation or tree holes by roosting bats in Madagascar is not well understood (Andriafidison *et al.,* 2006) and future studies should search all potential roost sites. *Rousettus madagascariensis* is a species potentially vulnerable to human disturbance because it is dependent on caves for roosting (MacKinnon *et al.*, 2003) and is hunted for food (C. Golden, personal comm.) and known roost sites should be included within conservation plans and periodically monitored.

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