Animal Conservation (2005) **8**, 153–165 © 2005 The Zoological Society of London. Printed in the United Kingdom doi:10.1017/S136794300500199X

The distribution and conservation of bats in the dry regions of Madagascar

Steven M. Goodman[1,2,*], Daudet Andriafidison[3,4], Radosoa Andrianaivoarivelo[3,4], Scott G. Cardiff[5,6], Edina Ifticene[3], Richard K. B. Jenkins[4,7], Amyot Kofoky[4], Tsibara Mbohoahy[4,8], Daniel Rakotondravony[3], Julie Ranivo[2,3], Fanja Ratrimomanarivo[2,4], Julie Razafimanahaka[4,9] and Paul A. Racey[7]

[1] Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA
[2] WWF, B.P. 738, Antananarivo (101), Madagascar
[3] Département de Biologie Animale, Faculté des Sciences, Université d'Antananarivo, B.P. 906, Antananarivo (101), Madagascar
[4] Bat Conservation Madagascar, B.P. 5181, Antananarivo (101), Madagascar
[5] Columbia University, Department of Ecology, Evolution, and Environmental Biology, 1200 Amsterdam Avenue, New York, NY 10027
[6] Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History, Central Park West at 79th St., New York, NY 10024, USA
[7] School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, UK
[8] Département des Sciences Biologiques, Faculté des Sciences, Université de Toliara, Toliara (601), Madagascar
[9] Département des Eaux et Forêt, Ecole Supérieure des Sciences Agronomiques, Université d'Antananarivo, Antananarivo (101), Madagascar

(Received 15 July 2004; accepted 20 September 2004)

Abstract

We carried out extensive field surveys in the dry forest portions of Madagascar to document the species of bats occurring in these regions. These data combined with information in the literature and museum specimen records indicate that 28 species of Chiroptera occur in this region of the island, of which we documented 27 during our inventories. The community composition at sites occurring in areas of water-eroded sedimentary rock is notably different from sites on alluvial substrates. In contrast to the majority of native land mammal species on Madagascar, much of the microchiropteran fauna is not dependent on large tracts of intact forest and anthropogenic perturbations of forests may have less direct impact on their long-term survival. Conservation strategies for Chiroptera in the dry regions of the island should focus on reducing various types of human disturbance of cave environments.

INTRODUCTION

A recent evaluation of the native land mammals of Madagascar (Carnivora, Rodentia, Primates and Lipotyphla) found that 100% of the 101 described species are endemic to the island (Goodman, Ganzhorn & Rakotondravony, 2003). This level of endemism, which is unparalleled for any single country on Earth, has considerable implications for the implementation of conservation strategies for Malagasy land mammals, particularly when overlaid on patterns of micro-endemism and the continued anthropogenic degradation of the island's natural habitats. The past 15 years has seen a considerable increase in natural history data for a wide array of land mammals, including the description of species new to science. Conservation biologists are starting to understand sufficient aspects of Malagasy land mammal natural history, distribution and status to help take the necessary steps to ensure their long-term survival (e.g. Sommer, Toto Volahy & Seal, 2002). In contrast, little information is available on most of Madagascar's bat fauna and research on these animals, including taxonomic studies, measures of species richness and documentation of their distribution has lagged behind that of other mammals. Such details are necessary for the implementation of appropriate management activities and the lack thereof has hampered the defining of the conservation status of Malagasy bats (e.g. Hutson, Mickleburgh & Racey, 2001; CAMP, 2002).

The bats of Madagascar are the poorest known of the island's mammal groups and few publications provide precise details about their distribution and aspects of their natural history. The major exception to this is recent work on two of the three species of Malagasy Megachiroptera (*Pteropus rufus* and *Eidolon dupreanum*), which have been the subject of several field studies (e.g. Raheriharisena, 2000; Ranivo, 2001; Bollen & Van Elsacker, 2002; Long, 2002; Hutcheon, 2003; MacKinnon, Hawkins & Racey, 2003; Ratrimomanarivo, 2003; Razakarivony, 2003). Although other recent publications have appeared on the island's bats, most are associated with site surveys (e.g. Pont & Armstrong, 1990; Rasolozaka, 1994*a*;

*All correspondence to: S. M. Goodman.
E-mail: sgoodman@wwf.mg

Table 1. Sites surveyed for bats in western Madagascar divided by province

Location	Dates	Co-ordinates	Elevation	Habitat
Province d'Antsiranana				
RS d'Ankarana				
Campement des Anglais (Anilotra) and Grotte Tenan'Antsiroandoha	6, 7, 9 Apr 2002	12°54′S, 49°06′E	125 m	Dry deciduous forest and limestone karst
Grotte d'Ambahibe	13 Apr 2002, 9–11 May, 18–20 Jun 2003 & 6–8 Jun 2004	12°58′S, 49°07′E	80 m	Dry deciduous forest and limestone karst
Grotte des Chauves Souris	12 Apr 2002, 12–14 May & 21–23 Jun 2003	12°57′S, 49°07′E	120 m	Dry deciduous forest and limestone karst
Grotte du 3ième canyon, near Andôkotôkana River	15–17 May 2003	12°56′S, 49°03′E	50 m	Dry deciduous forest and limestone karst
Grotte d'Andrafiabe	22–27 Jan 2001 & 17–21, 25–27 May, 3–5 Jul & 30 Jun – 2 Jul 2003	12°55′S, 49°03′E	50 m	Dry deciduous forest and limestone karst
Grotte d'Antsirônandoha	11 Apr 2002, 8–10 Jun, 10–12 Jul 2003 & 7 Aug 2004	12°53′S, 49°05′E	100 m	Dry deciduous forest and limestone karst
Grotte d'Ambohimalaza	12–14 Jun, 13–15 Jul 2003 & 17, 19–20 Jun 2004	12°58′S, 49°05′E	130 m	Dry deciduous forest and limestone karst
Grotte Squelette	22–24 May, 7–9 Jul 2003	12°56′S, 49°03′E	80 m	Dry deciduous forest and limestone karst
Grotte Milaintety	9 Jul 2003, 23, 26 Jul 2004	12°57′S, 49°02′E	40 m	Dry deciduous forest and limestone karst
Grotte d'Andohankarano	16 Jun 2003	12°57′S, 49°03′E	40 m	Dry deciduous forest and limestone karst
Grotte d'Ampôsatôkana (1ière Rivière en Canyon Forestier)	9 Apr 2002	12°54′S, 49°07′E	120 m	Dry deciduous forest and limestone karst
Andavaka Ambitsôkotsôko	30 May 2004	12°49′S, 49°15′E	300 m	Dry deciduous forest and limestone karst
Andavaka Matsaborimalio	01 Jun 2004	12°48′S, 49°15′E	320 m	Dry deciduous forest and limestone karst
Grotte du Sentier Botanique	04 Jun 2004	12°52′S, 49°13′E	260 m	Dry deciduous forest and limestone karst
Perte de Rivière No. 2	10 Jun 2004	12°57′S, 49°08′E	100 m	Dry deciduous forest and limestone karst
Grotte Roland	12 Jun 2004	12°57′S, 49°09′E	170 m	Dry deciduous forest and limestone karst
Andavaka	21 Jun 2004	13°00′S, 49°06′E	100 m	Dry deciduous forest and limestone karst
Anabon'Ambatofomela 'Grotte Borikely'	25 Jun 2004	13°00′S, 49°00′E	20 m	Dry deciduous forest and limestone karst
Grotte Boribe	28 Jun, 03 Jul 2004	13°00′S, 49°00′E	20 m	Dry deciduous forest and limestone karst
Grotte d'Ambatoharanana (Grotte Crocodile)	08, 11,12 Jul 2004	12°59′S, 49°00′E	20 m	Dry deciduous forest and limestone karst
Grotte Ampandriampanihy (Andavakan' Andrehy)	16, 19 Jul 2004	12°58′S, 49°02′E	20 m	Dry deciduous forest and limestone karst
Grotte d'Ambiky (Ambitsky)	18 Jul 2004	12°58′S, 49°02′E	10 m	Dry deciduous forest and limestone karst
Andavaka Ankôhatra	11 Aug 2004	12°51′S, 49°07′E	140 m	Dry deciduous forest and limestone karst
RS d'Analamerana				
Grotte de Bazaribe	19 Jan 2004	12°42′S, 49°28′E	90 m	Dry deciduous forest and limestone karst
Province de Mahajanga				
Anjohibe region				
Anjohibe	20–23 May 2004	15°32′S, 46°53′E	100 m	Dry open palm savanna and limestone karst
Anjohikely	23 May 2004	15°33′S, 46°52′E	100 m	Dry open palm savanna and limestone karst
RNI de Namoroka				
Ambovonomby	7–13 Oct 2002	16°28′S, 45°20′E	200 m	Dry deciduous forest and limestone karst
source of Mandevy River	14–19 Oct 2002	16°22′S, 45°20′E	100 m	Dry deciduous forest and limestone karst
PN d'Ankarafantsika				
SF d'Ankarafantsika	17–22 Apr 2003 17 Mar – 8 Apr 2004	16°19′S, 46°48′E	160 m	Dry deciduous forest on sand
PN de Bemaraha				
Foret d'Andranogidro	14–20 Feb 2001	18°44′S, 44°42′E	120 m	Dry deciduous forest, limestone karst, and gallery forest
Grotte d'Anjohimbazimba	16 Feb 2001	18°41′S, 44°43′E	110 m	Dry deciduous forest and limestone karst
Region of Ankidrodroa	21–28 Nov 2001 & 17 Jul – 7 Aug & 9–30 Oct 2003	19°07′S, 44°48′E	100 m	Dry deciduous forest, limestone karst, and gallery forest

Table 1. Continued.

Location Dates	Co-ordinates	Elevation	Habitat	
Grotte d'Anjohikinakina	8–13 Aug, 28–30 Oct 2003	19°00′S, 44°46′E	100 m	Dry deciduous forest and limestone karst
Region of Tombeau Vazimba	30 Nov – 6 Dec 2001	19°08′S, 44°49′E	100 m	Dry deciduous forest and limestone karst
Kirindy (CFPF)				
Kirindy River	5–6 Nov 2003	20°04′S, 44°40′E	30 m	Dry deciduous forest on sand
Piste de Conoco	7 Nov 2003	20°04′S, 44°39′E	35 m	Dry deciduous forest on sand
Province de Fianarantsoa				
PN de Zombitse-Vohibasia	6–25 Apr 1993	22°50′S, 44°42′E	870 m	Dry deciduous forest on sand
PN de l'Isalo				
Namaza	15–19 Apr 1999, 1–2 Dec 2002, 29–30 Mar 2003	22°32′S, 45°22′E	800 m	Degraded gallery forest in canyon
Canyon des Singes (Andranokova)	3–7 Dec 2002, 2 Apr 2003	22°29′S, 45°22′E	700 m	Degraded gallery forest in canyon
Analamanga	31 Mar – 1 Apr 2003	22°29′S, 45°23′E	800 m	Degraded gallery (mango) forest
Canyon des Rats (Andranohavo)	3–7 Dec 2002, 2 Apr 2003	22°28′S, 45°22′E	700 m	Degraded gallery forest in canyon
Sahanafa	9–12 Dec 2002	22°19′S, 45°17′E	550 m	Degraded gallery forest on sand
Bekapity	6 Apr 2003	22°37′S, 45°13′E	1000 m	Cave in degraded forest
Oasis campement	8–10 Apr 2003	22°37′S, 45°21′E	1000 m	Degraded gallery forest in canyon
Province de Toliara				
PN de Kirindy-Mitea				
13 km W Marofihitsa	9–14 Nov 2003	20°47′S, 44°08′E	30 m	Transitional dry deciduous forest and spiny bush on sand
10 km SE Marofihitsa	15–17 Nov 2003	20°53′S, 44°04′E	35 m	Degraded dry deciduous forest on sand
0.8 km SW Manahy	18 Nov 2003	20°52′S, 43°54′E	5 m	open salt pan at foot of dune and near freshwater pools
Forêt des Mikea				
9.5 km W Ankililoaka	14–19 Nov 2003	22°46′S, 43°31′E	80 m	Disturbed dry deciduous forest on sand
7.5 km NE Tsifota	20–26 Nov 2003	22°48′S, 43°26′E	60 m	Disturbed spiny bush with some dry deciduous forest elements on sand
16 km W Vorehy	2–5 Mar 2003	22°16′S, 43°28′E	80 m	Disturbed dry deciduous forest on sand
8.4 km SSE Befandefa	8–12 Mar 2003	22°13′S, 43°19′E	50 m	Disturbed dry deciduous forest on sand
Region of St. Augustin				
sea cave of Sarodrano	7 May 2002 14–25 Jun 2003, 5–28 Nov 2003, 10–29 Feb 2003	23°32′S, 43°44′E	sea-level	Disturbed spiny bush and limestone karst
Grotte de Mikea		23°28′S, 43°46′E	37 m	Disturbed spiny bush and limestone karst
Grotte de Bisihiko (Tanambao)	8 May 2002	23°32′S, 43°46′E	5 m	Disturbed spiny bush and limestone karst
RNI de Tsimanampetsotsa				
Grotte de Mitoho area	28 Feb – 6 Mar 2003	24°03′S, 43°45′E	50 m	Disturbed spiny bush and limestone karst

Protected areas are designated as: PN, Parc National, RNI, Réserve Naturelle Intégrale, RS, Réserve Spéciale, SF, Station Forestière.

Göpfert *et al*., 1995; Yoshiyuki, 1995; Goodman, 1998, 1999; Russ & Bennett, 1999; Bennett & Russ, 2001) or popular accounts (Hutcheon, 1994, 1997), and details presented in several taxonomic studies are out of date (e.g. Dorst, 1947*a*, *b*; Hill, 1993).

Peterson, Eger & Mitchell (1995) published a monograph on the island's bat fauna largely using data from field research conducted in the 1970s. More recently, Eger & Mitchell (2003) reviewed published information on the Malagasy Microchiroptera, and, based on their summary, the drier western formations have a higher species richness than the more humid eastern portion of the island. While these two reviews provide important overviews of the island's bat fauna, considerable regions remained unexplored. Over the course of the past few years we have been conducting bat surveys in the dry forests of Madagascar. This field research has helped to provide faunal information for several unknown or poorly known sites in dry areas of the island, mostly in the west, and herein we present this information and associated biogeographical and conservation status analyses.

METHODS AND MATERIALS

We surveyed 13 sites between January 2001 and August 2004. From north to south we visited the following locations as part of our bat surveys: Analamerana, Ankarana, Anjohibe, Ankarafantsika, Namoroka, Bemaraha, Kirindy (CFPF), Kirindy-Mitea, Zombitse-Vohibasia, Isalo, Mikea, St. Augustin and Tsimanampetsotsa (Table 1; Fig. 1). Nine of these sites are within reserves and parks and four are outside of any existing protected area. We

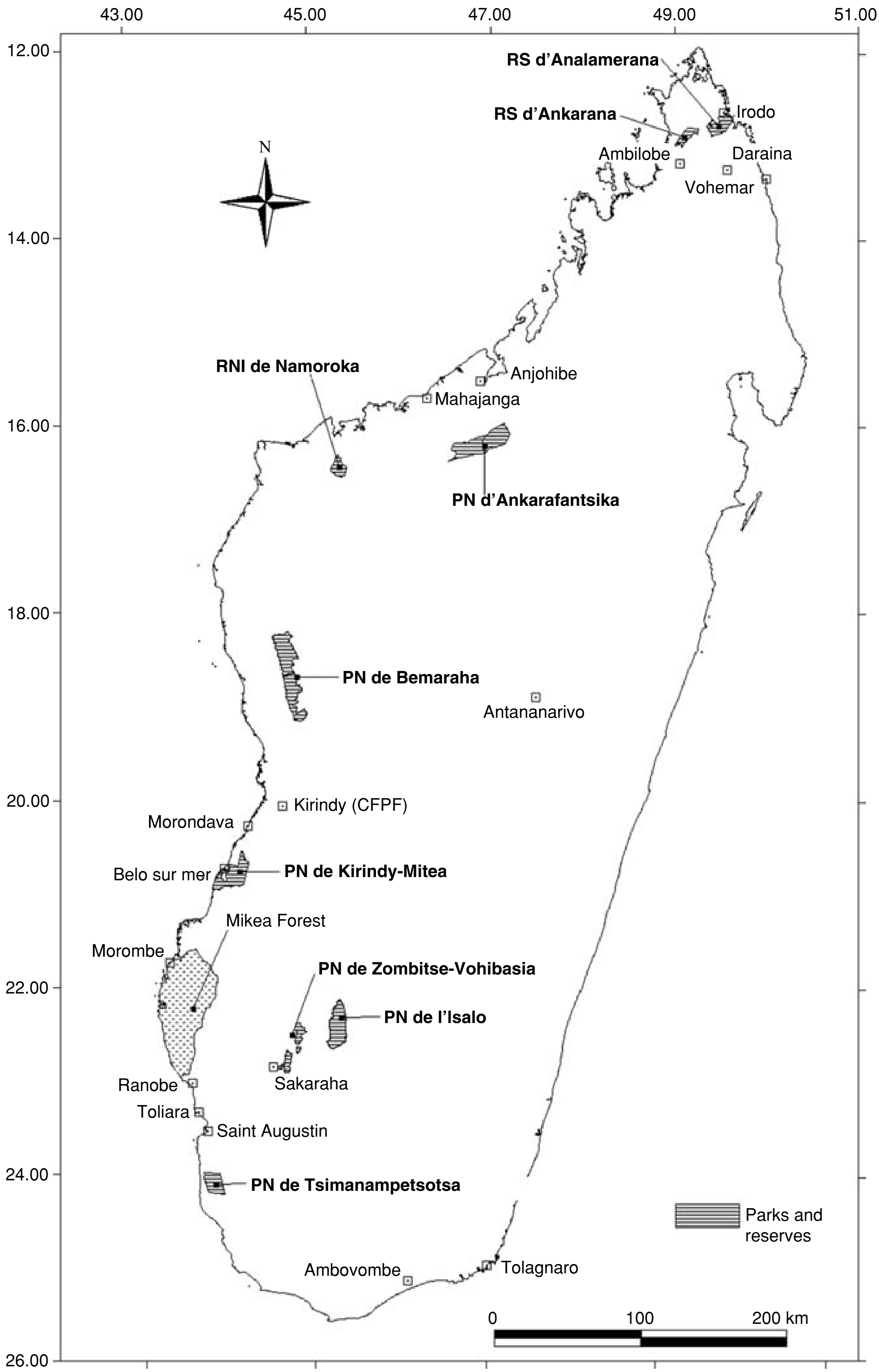

Fig. 1. Map showing the study localities and other sites mentioned in the text.

have assembled bat species lists for these sites based on our field surveys, specimens housed in natural history museums and some published records.

The original vegetation of large portions of western Madagascar consists of dry forest formations that show a cline of increased aridity from north to south. Levels of annual precipitation vary from 1858 mm at Ambilobe, 1503 mm at Mahajanga, 780 mm at Morondava, 496 at Morombe and 390 at Toliara (Chaperon, Danloux & Ferry, 1993). Associated with this meteorological cline is a transition in natural forest formations. In the north and northwest, the natural formation is dry deciduous forest. Further south a longer, more pronounced annual dry season occurs. In the region between Belo-sur-Mer and Toliara there is a shift to spiny bush habitat and in this transitional area the remaining natural forested areas in the coastal zone are spiny bush and, on higher ground away from the sea, dry deciduous forest. In the northern portion of the west, dry deciduous forest also extends towards the east, particularly in the area between Ambilobe and Vohemar, passing through the Daraina region (Gautier & Goodman, 2003). Throughout the dry regions of the island, but more pronounced in the drier central west and south, gallery forest grows along the margins of rivers.

One of the principal exposed geological strata of western Madagascar is limestone that has been heavily eroded in numerous areas by water action into karst formations. These deposits are divided into two distinct geological periods: (1) Mesozoic – dating to the Jurassic and early Cretaceous (about 195–100 million years ago) that are associated with the sites of Ankarana, Bemaraha and Namoroka and those of the middle Jurassic (172–162 million years ago) found in the Analamerana region and (2) Cenozoic – dating from the Eocene (54–38 million years ago) found in the areas around Mahajanga and along the Mahafaly Plateau in the extreme southwest (Besaire & Collignon, 1972). These karstic areas often contain a myriad of caves and deep canyons that provide ideal roosting sites for bats. For example, in the Réserve Spéciale (RS) d'Ankarana, an area of 18 225 ha, at least 70 caves have been discovered comprising over 110 km of underground passageways (Wilson, 1987; Cardiff & Befourouack, 2003; J. Radofilao, pers. comm.).

A substantial proportion of the survey sites reported on in this paper are associated with this limestone habitat. The Isalo Massif, in the southwestern central portion of the island, is a vast expanse of exposed soft sandstone, which in numerous areas, particularly along ancient or active river margins, has been heavily eroded and is notably ruiniform. The balance of sites reported here occur on alluvial deposits and are not associated with significant areas of exposed sedimentary rock outcrops (Kirindy (CFPF), Kirindy Mitea, Zombitse-Vohibasia and Mikea).

We used a combination of harp traps and mist nets (the majority of sets placed at ground-level) to capture bats. We placed these devices along trails, over water and at entrances to caves. Trap type, placement and effort varied between sites. Our intent was to capture as many bats in as wide a variety of microhabitats as possible in order to have the best estimate of local species richness based on presence–absence data. In some caves we used long-handled sweep nets or bucket traps to catch bats roosting on the ceiling. We also obtained information on bat species living synanthropically in local villages close to the study areas. Voucher specimens were saved at most sites and are housed at the Field Museum of Natural History (FMNH), Chicago and the Université d'Antananarivo, Département de Biologie Animale (UADBA), Antananarivo. We also examined specimens held in The Natural History Museum (BMNH), London; The Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA; the Muséum National d'Histoire Naturelle (MNHN), Paris; Royal Ontario Museum (ROM), Toronto; The National Museum of Natural History (USNM), Washington, DC; The University of Wisconsin Zoological Museum, Madison, WN (UWZM); and Yale Peabody Museum (YPM), New Haven, CT.

Given that some species of Malagasy bats are difficult to identify in the hand and the taxonomy of several genera is in a state of flux, we have relied extensively on verified specimen records. The Pteropodidae, which can be identified in flight and easily in the hand, are the exception. A few microchiropteran species have been cited in the literature or in unpublished reports as occurring at the sites we review but were not documented at these localities during our surveys. In such cases, when specimen or photographic documentation is unknown to us, these taxa are not presented in our site tabulations. We have followed the higher-level and generic classification of Simmons (2005) and, for species, that of Peterson *et al.* (1995). To this latter work we have added information from Goodman & Cardiff (2004), Goodman & Ranivo (in press) and Goodman, Ranivo & Cardiff (unpublished results).

In order to compare the faunal similarity of bats between each pair of surveyed sites, we used Jaccard's coefficients, which were then analyzed using the SYSTAT cluster programme (linkage, complete; distance, Euclidean). Jaccard coefficients of similarity represent relatively reliable estimates of community similarity although they may present some bias (Real & Vargas, 1996). To address certain conservation issues, we present a basic GAP analysis to examine which species are not occurring or are poorly represented within the current protected areas system. For the purpose of describing patterns of occurrence, we define forest-dependent species as those animals that require largely intact-forested habitats at any point during their life cycle.

RESULTS

In total 27 species of bats were recorded during these surveys at 13 sites, 24 Microchiroptera and three Megachiroptera (Table 2). Amongst the Molossidae we found a few species occurring in human dwellings. The two sites with the highest species richness are Ankarana in the north and St. Augustin in the southwest with 14 species

Table 2. Bat species recorded within and outside of protected areas in the dry forest regions of Madagascar

Site	Ankarana[1]	Analamerana	Anjohibe	Ankara-fantsika[2]	Namoroka	Bemaraha	Kirindy (CFPF)	Kirindy Mitea	Zombitse-Vohibasia	Isalo	Mikea[3]	St. Augustin[4]	Tsimanam-petsotsa	Number of protected areas
Protected status[5]	**RS**	**RS**	**None**	**PN**	**RS**	**PN**	**None**	**PN**	**PN**	**PN**	**None**	**None**	**RS**	
Latitude (S)	12°53′	12°42′	15°33′E	16°19′	16°24′	18°50′	20°04′	20°50′	22°50′	22°20′	22°30′	23°33′	24°03′	
Limestone cave systems	Yes	Yes	Yes	No	Yes	Yes	No	No	No	No[6]	No	Yes	Yes	
Pteropodidae														
Pteropus rufus	S	+	S[7]	S	S	S	S	S	–	–	S	S[8]	–	6
**Eidolon dupreanum*	+	S	+[9]	+[10]	+	+[11]	–	–	+	S	–	–	+	8
**Rousettus madagascariensis*	+	+	+	+	+	+	–	–	–	+	–	–	–	6
Hipposideridae														
**Hipposideros commersoni*	+	+	+	+	+	+	+	+	+[12]	+	+	+	+	9
**Triaenops auritus*	+	+	–	–	–	–	–	–	–	–	–	–	–	2
**T. furculus*	–	–	+	–	+	+	–	+	–	–	+	+	+	4
**T. rufus*	+	+	+	+	+	+	+	+	–	+	–	+	+	8
Emballonuridae														
**Emballonura* nov. sp.	+	+	–	–	–	+	–	–	–	–	–	–[13]	–	3
Coleura sp.[14]	+	–	–	–	–	–	–	–	–	–	–	–	–	1
Taphozous mauritianus	–[15]	–	–	+	–	S	–	–	+	–	–	+	–	2
Myzopodidae														
Myzopoda aurita	–	–	–	+	–	–	–	–	–	–	–	–	–	1
Molossidae														
**Mormopterus jugularis*	+	–	–	–	–	–	–	–	+	+	–	+	–[16]	2
**Chaerephon leucogaster*	–[17]	–	–	x[18]	–	+[19]	+[20]	x	+	–	x	x	–	4
**C. jobimena*	+	–	–	–	–	–	–	–	+	+	–	–	–	3
**Mops leucostigma*	–[21]	–	–	x	–[22]	x	+	–	+	–	x[23]	x	–	3
M. midas miarensis	–	–	–	–	–	–	–	–	+	–	–	–	–	1
**Otomops madagascariensis*	+	+	+	–	+[24]	+	–	–	–	+	–	+	–	5
[*]*Tadarida fulminans*	–	–	–	–	–	–	–	–	–	+	–	–	–	1
Vespertilionidae														
Scotophilus cf. *borbonicus*	–	–	–	–	–	–	–	–	–	–	–	+[25]	–	0
S. nov. sp.	–	–	–	–	–	x[26]	+[27]	–	–	–	–	+[28]	–	1
S. robustus	–	–	–	–	–	+	+[29]	–	+	–	–	–	–	1
Pipistrellus sp. 1[30]	–	–	–	–	–[31]	–	+	–	–	–	+	–[32]	–	0
P. sp. 2 cf. *kuhlii*	–	–	–	–	–	–	+[33]	+	+	–	–	–	–	2
Neoromicia malagasyensis	–	–	–	–	–	–	–	–	–	+	–	–	–	1
**Myotis goudoti*	+	+	+	–	+	+	–[34]	+	–	+	+	+	–	6
**Miniopterus gleni*	+[35]	+	+	–	+	+	–[36]	–	–	+	+	+[37]	–	5
**M. manavi*	+	+	+	–	+	+	–	+	–	+	+	+	+	7
Total number of species	14	11	10	9	10	16	9	8	10	12	9	14	5	
Total number of species excluding commensals	14	11	10	7	10	14	9	7	10	12	7	12	5	

Documented records based on specimens or captured individuals are denoted with '+'. 'S' indicates sight record, which includes flying, feeding and roosting individuals. In several cases commensal species were found in a nearby village but not in the study area and these records are denoted as 'x'. Species known or presumed to inhabit caves or rock shelters are preceded by an * or [*], respectively. Species expected at a given site based on the designations of Eger & Mitchell (2003) are not included.

[1] Garbutt (1999) reported *Nycteris madagascariensis* as occurring in the Ankarana. This species was named by Grandidier (1937) based on two specimens collected in the Irodo area, which is north of Analamerana and not within the Ankarana. Recent fieldwork (2004) at Analamerana and near Ambery (between Ankarana and Analamerana) did not find this species and we have not included it in the species tally for this site.

[2] Includes records from the Station Forestière d'Ampijoroa.

[3] Based on Goodman & Razakarivony (2004).

[4] This includes animals from the Sarodrano region.

[5] None, not within a protected area; PN, Parc National; RS, Réserve Spéciale.

[6] Limestone caves do not occur in this region, but rather water cut sandstone cliffs with numerous sites for bat roost sites.

[7] This species occurs in the mangroves of the Baie de Mahajamba a few kilometers from the cave.

[8] Several colonies occur in the mangroves to the south of St. Augustin.

[9] Bone remains of this species are dispersed in various portions of Anjohibe. No living individuals were found in the cave during a May 2004 visit. Based on discussions with local people *Eidolon* has not occurred in the cave for several decades. Record included in site tabulation.

[10] Specimen collected at Ampijoroa (MNHN).

[11] This species has been observed in rocky overhangs in the Grand Tsingy and collected just outside of the reserve near Tsiandro (BMNH).

[12] Specimen in YPM.

[13] Specimen in MCZ obtained at 'Tuléar' [= Toliara] is not included here because the exact provenance is unclear.

[14] The specific status of this animal is currently under study.

[15] Garbutt (1999) noted that this species occurs in the Ankarana but we are unaware of specimen documentation to support these records. The photo presented of this species in an Ankarana cave by Garbutt (1999, figure 27) is incorrect and the illustrated species is *Rousettus madagascariensis*.

[16] A specimen was collected in the village of Efoetse (FMNH), just outside the reserve limit.

[17] Although not documented by a specimen, this species may roost within the large colony of *Mormopterus jugularis* in the Cathedral Cave in the Andrafiabe complex. We have not included this bat in the list of the species for this reserve.

[18] Record based on Peterson *et al*. (1995), but uncertain if captured in a non-commensal setting.

[19] This species was captured in the Grande Tsingy.

[20] We have specimens of this species from Kirindy (CFPF). The '*Tadarida pumila*' reported for this site by Rasolozaka (1994*b*) could be *C. leucogaster*, while his records of '*Chaerephon chapini*' might be *C. pumilus* – his specimens have not been available for study.

[21] This species was probably observed exiting the Cathedral Cave roost amongst large numbers of *Mormopterus jugularis*. A colony was found occupying an abandoned bus 1.5 km outside the reserve boundary. However, given that no voucher specimen is available for Ankarana we have not included it in the list of documented species for this reserve.

[22] This species was obtained outside of the park in the vicinity of Belo-sur-Mer.

[23] Specimen in MNHN collected near Lac Ihotry. Unknown if obtained in a commensal situation. Also collected in the local villages of Ankiloaka and Tsifota. (FMNH).

[24] We did not capture this species at Namoroka. The holotype (MNHN) was collected by the late R. Paulian in this reserve.

[25] Specimens collected near the Grotte de Sarodrano (MNHN). See Goodman & Jenkins (unpublished results) for details on this specimen.

[26] Captured just outside the park near the village of Andadoany and potentially a commensal species (Goodman & Jenkins, unpublished results).

[27] An individual captured Kirindy (CFPF) was identified as *Scotophilus borbonicus* (Ganzhorn *et al*., 1996), but based on more recent taxonomic work it was almost certainly referable to *Scotophilus* nov. sp. (Goodman & Jenkins, unpublished results).

[28] Specimens collected near the Grotte de Sarodrano (MNHN).

[29] Reported to occur at this site by Ganzhorn *et al*. (1996), based on unpublished information from M.C. Göpfert *et al*.

[30] The specific status of the two *Pipistrellus* spp. reported here is unclear and they may represent new taxa to science.

[31] Nicoll & Langrand (1989) reported *Pipistrellus nanus* from this reserve. This record is presumably based on the capture of a member of this genus at Cape St. Vincent, some distance from Namoroka.

[32] Bennett & Russ (2001) reported the presence of *Eptesicus*/*Pipistrellus*. This record is not entered into the species total for this site.

[33] Ganzhorn *et al*. (1996) reported two species of *Pipistrellus* for this site – one of the *kuhlii*-group and the other potentially new to science, which we presume, is our morpho-species 1. Eger & Mitchell (2003) also reported *P. nanus* from this site.

[34] Eger & Mitchell (2003) reported this species at Kirindy (CFPF). We are unaware of any supporting specimen evidence.

[35] The records of *Miniopterus inflatus* from this site (McHale 1987; Hill, 1993; Hutcheon 1997) are incorrect and the associated voucher specimens in the BMNH and UWZM have been examined and are referable to *M. gleni*.

[36] This species was cited by Eger & Mitchell (2003) as occurring at Kirindy (CFPF). We are unaware of the supporting documentation for this record.

[37] Peterson *et al*. (1995) reported *Miniopterus majori* from this site. It is almost certain that these individuals are referable to *M. gleni*.

Table 3. Jaccard's coefficients among 13 sites in the dry regions of Madagascar

	ANK	ANAL	ANJ	ANKA	NAM	BEM	KIR	KIRM	ZOMB	ISAL	MIK	AUG	TSIM
Ankarana (ANK)	1												
Analamerana (ANAL)	0.786	1											
Anjohibe (ANJ)	0.600	0.750	1										
Ankarafantsika (ANKA)	0.313	0.385	0.417	1									
Namoroka (NAM)	0.600	0.750	1.000	0.417	1								
Bemaraha (BEM)	0.526	0.625	0.667	0.375	0.667	1							
Kirindy (CFPF) (KIR)	0.150	0.176	0.188	0.231	0.188	0.333	1						
Kirindy Mitea (KIRM)	0.313	0.385	0.545	0.273	0.545	0.375	0.333	1					
Zombitse (ZOMB)	0.200	0.105	0.111	0.214	0.111	0.250	0.357	0.133	1				
Isalo (ISAL)	0.625	0.533	0.571	0.267	0.571	0.421	0.105	0.267	0.222	1			
Mikea (MIK)	0.313	0.385	0.545	0.167	0.545	0.375	0.231	0.556	0.063	0.267	1		
St. Augustin (AUG)	0.444	0.438	0.571	0.267	0.571	0.588	0.235	0.462	0.158	0.412	0.462	1	
Tsimanampetsotsa (TSIM)	0.267	0.333	0.500	0.333	0.500	0.333	0.167	0.500	0.154	0.308	0.333	0.308	1

Data based on non-commensal species occurring at these sites (see Table 2).

and Bemaraha in the central west with 16 species. At St. Augustin two species (*Chaerephon leucogaster* and *Mops leucostigma*) occurred in human-dwellings and at Bemaraha one species (*M. leucostigma*) was found only as a synanthropic and one other (*Scotophilus* sp. nov.) was documented outside the protected area limit. The lowest species richness was five at the southern-most surveyed site of Tsimanampetsotsa, in the heart of the dry spiny bush.

For the majority of sites surveyed, the number of bat species known to occur locally was augmented considerably as compared to earlier literature. For example, Nicoll & Langrand (1989) list one species of bat, a Megachiroptera, for the Parc National de l'Isalo, while we documented 12 species of bats there, including one new to science (*Chaerephon jobimena*) and another previously known only from the holotype (*Tadarida f. fulminans*). At least 34 bat species are currently documented to occur on Madagascar (Eger & Mitchell, 2003; Goodman & Cardiff, 2004; Goodman *et al*., unpublished results) and the bat fauna of the dry forests represent about three-quarters of that known on the island.

Several species occur across most of the surveyed zone (Table 2), a distance of 1300 km from the northern to southern-most sites. These include, for example, *Eidolon dupreanum*, *Hipposideros commersoni*, *Triaenops rufus* and *Miniopterus manavi*. Other species have broad distributions but do not reach Tsimanampetsotsa, the southern limit of the surveyed area (i.e. *Pteropus rufus*, *Myotis goudoti*, *Miniopterus gleni* and *Otomops madagascariensis*). Another suite of species, that have patchy distributions, occur at a few sites as synanthropics and at other sites in natural situations; these consist of members of the Molossidae (*Mormopterus jugularis*, *Chaerephon leucogaster* and *Mops leucostigma*).

On the basis of the biogeographical analysis with the Jaccard's coefficient (Table 3), there are differences in the taxonomic composition of bat communities occurring in areas of limestone, sandstone and alluvium (Figure 2). Most notable in this regard are non-coastal sites resting on alluvial soils, several of which form a separate cluster within the analysis (Ankarafantsika, Kirindy (CFPF) and Zombitse-Vohibasia). The other two sites occurring on alluvium, both close to the coastal zone, are Mikea and Kirindy-Mitea. In this case these study areas cluster with those on sedimentary rock, but as a subgroup with the species-poor site of Tsimanamanpetsotsa. The balance of the sites on limestone completes the second cluster (Ankarana, Analamerana, Namoroka, Anjohibe, Bemaraha and St. Augustin), while the sandstone site of Isalo forms the outlier to the sub-cluster of Ankarana and Analamerana.

DISCUSSION

Given the difficulty in capturing certain groups of free-living bats and the different techniques and efforts used to inventory the various sites reported on in this paper, there are potential problems in comparing measured levels of species richness between sites. On the basis of the capture techniques used outside of cave settings, canopy foragers may be under-represented amongst the captured species and most notable in this regard are molossid bats. At the dry forest sites resting on alluvial soils, we used nets and harp traps erected in forest or open habitats and capture rates were notably lower than those associated with sedimentary rock sites. At several of the limestone areas bat capture was entirely or largely restricted to cave entrances (i.e. Ankarana, Anjohibe, St. Augustin, Tsimanampetsotsa), while at several other sites a proportion of capture effort was within the forest, along river and stream margins, or in open areas (i.e. Analamerana, Namoroka, Bemaraha, Isalo). A comparison at the sites where bats were trapped both at cave entrances and away from such roost sites and in forest shows few differences in the species captured. For example, in Analamerana species trapped in free-flying situations are a subset of those captured at cave entrances. In Bemaraha several species were documented in open areas close to a village (*Scotophilus robustus, Scotophilus* sp. nov., *Chaerephon leucogaster* and *Mops leucostigma*), but *C. leucogaster*

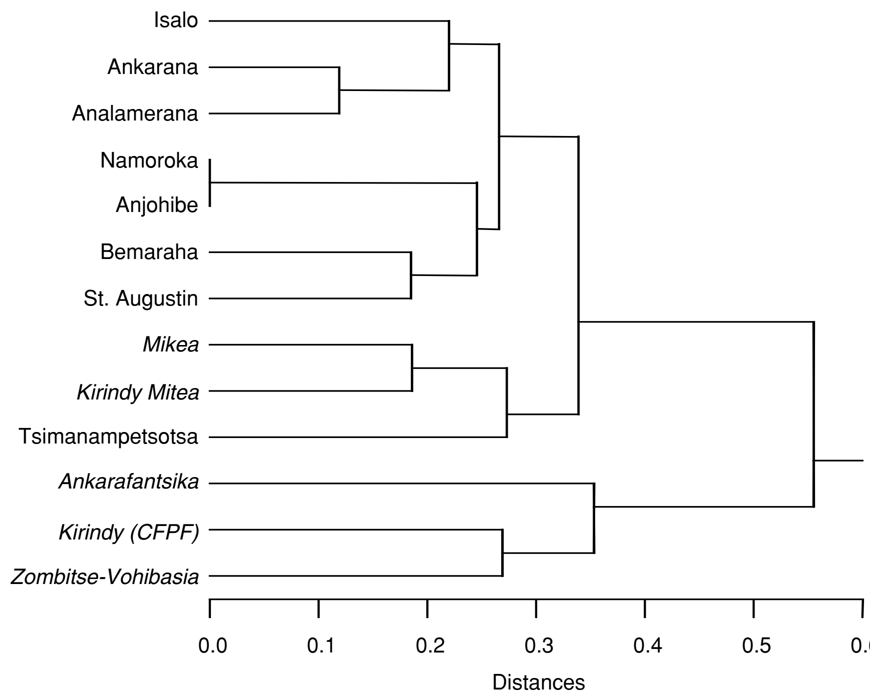

Fig. 2. Cluster analysis of biogeographical relationships of 27 species of bats in the dry portions of Madagascar. Data derived from Table 2 were used to calculate Jaccard's coefficients, which are presented in Table 3, and exclude known or presumed records of synanthropic species. Sites in italics are those resting on alluvium and those in non-italics rest on sedimentary rock (limestone and sandstone). Distances are Euclidian distance coefficients.

and *S. robustus* were also captured within the park. On the basis of these comparisons and since only one bat species known from the dry areas of Madagascar was not captured during these surveys (see below), it would appear that our measures for establishing local species richness at the different sites is largely complete. Given that our surveys were conducted at different times of the calendar year and that nothing is known about migratory movements and hibernation of Malagasy bats, it is difficult to interpret what affect seasonality might have on our measures of species richness at the various sites.

Using the accounts of the Malagasy chiropteran fauna of Madagascar presented in Peterson *et al*. (1995) and some other works, we did not document the occurrence of one bat species, *Nycteris madagascariensis* (family Nycteridae) that reportedly occurs in dry portions of Madagascar. This species is only known from two specimens, which were obtained in the 'Vallée de la Rodo' (Grandidier, 1937), which is presumed to be the Irodo River valley. This site is close to, or at the edge of, the Réserve Spéciale d'Analamerana, which is one of our study sites. Thus, of the 28 bat species known from dry areas of Madagascar, based on previously published information or the records presented herein, 27 were recorded from our survey sites (Table 2).

On the basis of our field research and previous specimen records a few other bat species are apparently uncommon in the dry portions of the island. These include *Mops midas miarensis*, which has been collected in the Parc National de Zombitse-Vohibasia (Rasolozaka, 1994*a*) and the Toliara region (Peterson *et al*., 1995). This species has recently been found in the Ranobe area north of Toliara (Goodman & Cardiff, 2004), within 20 km of one of our Mikea Forest sites, and also as a synanthropic at Ambovombe in the south (Goodman, unpublished results).

A few dry region species are known only from a small number of sites that are widely dispersed across this region (e.g. *Chaerephon jobimena* and *Otomops madagascariensis*), while others have been recorded from only a few localities in the west, but are known from the east (e.g. *Scotophilus robustus*). However, within the dry region bat fauna there are a few species that are rather localised. *Triaenops auritus* is only known from the northern end of the island from the sites of Ankarana and Analamerana (Ranivo & Goodman, unpublished results). It has an apparently non-overlapping range with its sister taxa, *T. furculus*, which occurs to the south. The distibution of *Mops midas* is described above. Other than the holotype collected in the central highlands near Fianarantsoa, *Tadarida fulminans* is known only from the Isalo region (Goodman & Cardiff, 2004), which is the same area from which *Neoromicia malagasyensis* was first described and subsequently recollected (Goodman & Ranivo, 2004). The only known site for *Coleura* sp. on the island is one cave in Ankarana, but this species may occur rather locally in the northern region. Finally, *Scotophilus* sp. nov. is known from a few specimens from Bemaraha south to near Sarodrano and *S. cf. borbonicus* from a single specimen obtained at Sarodrano (Goodman *et al*., in press).

The sucker-footed bat, *Myzopoda aurita*, is considered to be an eastern humid forest species but Schliemann &

Goodman (2003) had previously reported its occurrence from the Mahajanga area based on an older specimen record. In April 2003 we captured this species at the edge of a marsh in the Parc National d'Ankarafantsika. This is the only case of this bat being found at one of our western bat survey sites reported on in this paper. What appears to be an undescribed species of *Pipistrellus*-like vespertilionid has been collected only in the Kirindy (CFPF) forest.

Two general patterns emerge from the bat survey data with respect to species distribution and community structure. First, there is no clear evidence of a north–south cline in species richness and in the southwestern dry spiny bush area, here represented by Tsimanampetsotsa, there is a drastic reduction in species richness ($n = 5$) compared to more northern sites. At Tsimanampetsotsa, which receives less than 400 mm on average annual rainfall, fruits for Megachiroptera or flying insects for Microchiroptera may show steep cycles in abundance and food availability may be rather limited during a significant portion of the year. However, the site of St. Augustin, which is in the same climatic regime as Tsimanampetsotsa, has 14 documented bat species and it is clear that simple models based on rainfall cannot explain biogeographical patterns associated with species richness of bats in western Madagascar.

The second general pattern is that zones with karst limestone formations have higher species richness than those in other geological formations. The caves, fissures and faults of these areas provide excellent sites for a variety of bat species to rest and breed. This aspect is clear when sites at the same general latitude are compared. For example, Bemaraha is part of an extensive limestone region and 14 species (excluding those species found just outside the reserve) have been recorded locally while that of Kirindy (CFPF) resting on alluvium has nine species. Another example is that of two coastal sites, St. Augustin, composed of limestone caves and containing 12 species (excluding synanthropic species), and the northern Mikea forest, resting on alluvium and containing nine species. However, in contrast to this pattern, two inland sites, Isalo and Zombitse-Vohibasia, are not in areas with exposed limestone but have relatively high measures of bat species diversity. Isalo rests on a vast zone of exposed soft sandstone, which in numerous areas, particularly along ancient or active river margins, has been heavily eroded and is notably ruiniform. In Isalo there are numerous rock overhangs and fissures for bats to roost in and this area, thus, show parallels to the limestone sites. In contrast, the Zombitse-Vohibasia forest is on the eroded alluvial deposits of the Isalo sandstone. To our knowledge, there is no exposed sedimentary rock deposit within this forest block. Presumably bats living in the area use vegetation in various forms for their daily resting sites. For example, large standing baobabs (*Adansonia*) with hollow sections might serve as roosts. Further, the vegetation of this forest shows some transitional elements from eastern humid forests (Gautier & Goodman, 2003) and seasonal variation may be less pronounced here than in sites further to the west, thus accounting for a slightly higher measure of species richness than in more western sites. Areas with greater sedimentary rock and cave availability, therefore, appear to indeed have greater bat species richness.

The emergence of improved models of Malagasy bioclimatic regions will allow more intricate GAP analyses using programmes such as GARP or other biogeographical analyses for bats in Madagascar. Biologists have successfully conducted such analyses for bats in Israel (Yom-Tov & Kadmon, 1998) and South Africa (Gelderblom *et al*., 1995). If combined with additional bat surveys, such analyses could further refine our understanding of bat distribution and conservation on Madagascar.

CONSERVATION

The patterns of occurrence of bats in the dry regions of Madagascar observed through our work have important consequences for conservation of Malagasy bats. The patterns suggest that northern sites with sedimentary rock may have more species and further inventories might find more species in such areas. The notable exception to this is St. Augustin, a limestone area, which has 12 species of non-synanthropic bat species. In addition, the patterns suggest which protected areas have more important bat species richness and to what extent Malagasy bats of the dry regions are adequately represented in the current protected area network.

Several species occurring in western Madagascar are also known from sites in the humid regions of the east, including several reserves and parks, and may receive additional protection in those areas. These include the non-synanthropic species *Pteropus rufus*, *Eidolon dupreanum, Rousettus madagascariensis, Hipposideros commersoni, Myzopoda aurita, Myotis goudoti, Scotophilus robustus* and *Miniopterus manavi* (Peterson *et al*., 1995; Eger & Mitchell, 2003; Goodman & Cardiff, 2004; unpublished results). Furthermore, several species recorded in the west also occur in the east and are generally synanthropic – these include *Mormopterus jugularis* and *Mops leucostigma*.

Only two of the 27 bat species documented in the dry areas of Madagascar in the context of this project do not occur in a protected area. This first species '*Pipistrellus*' sp. 1 is known only from the Kirindy (CFPF) forest to the north of Morondava. This site, which is composed of dry deciduous forest, is a logging concession of nearly 120 km^2 that is part of a much larger forested area known as the Menabe. The only current protected area within the Menabe is the RS d'Andranomena, just to the south of the Kirindy (CFPF) concession, which was not amongst the sites we surveyed in the context of this project. It is assumed that '*Pipistrellus*' sp. 1 has a broader range than currently known in the central deciduous forests of western Madagascar. The second species, *Scotophilus* cf. *borbonicus*, is only known from a single specimen collected by A. Grandidier near Sarodrano in 1868. Given that this site has been extensively surveyed over the past few years and no further evidence of this species was found, it has been proposed that this individual may have been a vagrant to Madagascar (Goodman & Jenkins, unpublished results).

An additional seven species have only been recorded from a single protected area. In a few cases we presume that these taxa are widespread in various portions of the island and simply in low density or difficult to capture (*Tadarida fulminans*, *Mops midas* and *Scotophilus robustus*), while in other cases certain species may have limited geographical distributions within the dry portions of Madagascar (*Coleura* sp., *Myzopoda aurita*, *Scotophilus* sp. nov. and *Neoromicia malagasyensis*). Four other taxa are known only to occur within their dry forest distribution in two protected areas and two of these are only known to occur in western Madagascar: *Triaenops auritus* is confined to the northern portion of Madagascar and appears to be broadly distributed in karstic regions of the Antsiranana Province; we know relatively little about the distribution of *Pipistrellus* sp. 2 *cf. kuhlii*. The other two species, *Mormopterus jugularis* and *Taphozous mauritianus*, are known to have broad distributions. Fifteen out of the 27 dry region species documented in the context of our research are known from three or more protected areas. The three species of Pteropodidae occurring on Madagascar, two of which are considered of conservation concern (MacKinnon *et al*., 2003), are well represented in dry region protected areas.

Our studies suggest that many species of bats in the dry regions of Madagascar may not rely on forest cover for roosting and foraging. Several of the sites we studied are not within relatively intact-forested zones. For example, the caves of Anjohibe are at least 30 km from degraded forest and those of St. Augustin are within a short distance of heavily degraded spiny bush coastal habitat. Thus, based on current information, the assumption that the species do not seasonally migrate between forested and non-forested areas, and the definition presented above, bat species occurring in these caves are not forest-dependent. Of the 27 bat species known to occur across the dry portion of Madagascar, 17 (*Pteropus rufus, Eidolon dupreanum, Rousettus madagascariensis, Hipposideros commersoni, Triaenops furculus, T. rufus, Taphozous mauritianus, Mormopterus jugularis, Chaerephon leucogaster, Mops leucostigma, M. midas, Otomops madagascariensis*, *Scotophilus* sp. nov., *Scotophilus* cf. *borbonicus*, *Myotis goudoti*, *Miniopterus gleni* and *M. manavi*) were recorded at these two sites. Of the remaining 10 species, five species can be removed from the list of possible forest-dependent species because of the habitats in which they have been captured at other sites; these include *Myzopoda aurita* in marshy habitat dominated by *Ravenala*, *Chaerephon jobimena* recorded in a zone of heavily degraded spiny bush forest, *Tadarida fulminans* occurring in non-forested canyons, *Pipistrellus* sp. 1 in open palm savanna and sand dune habitat and *Neoromicia malagasyensis* in palm savanna and non-native gallery forest. On the basis of current information, five species are possibly forest-dependent (*Triaenops auritus, Emballonura* sp. nov., *Coleura* sp., *Scotophilus robustus* and *Pipistrellus* sp. 2). These data, combined with ongoing field studies of dry forest bat ecology, indicate that the chiropteran community occurring in the dry regions of Madagascar is largely not forest-dependent and that disturbance of bats at cave roosts and hunting may present a greater threat than forest loss for many of these animals. This is in stark contrast to native Malagasy land mammal species that are for the most part forest-dependent and considerably affected by human habitat degradation, specifically forest clearing for agricultural purposes and various other types of exploitation. Further work on habitat use of these bat species will help reveal the importance of forest to their conservation.

Caves are amongst the most vulnerable ecosystems in the world (Watson *et al*., 1997) and are not necessarily covered in standard protected area networks (Redford *et al*., 2003). Human use of caves has a wide variety of impacts, which can have a cumulative negative impact on local animal populations. Throughout the dry regions of Madagascar, both in protected areas and non-protected areas, cave roosting bats are subjected to various forms of human perturbation ranging from mineral and guano exploitation, uncontrolled tourist visit to collection for bush meat. In addition, climate change may render cave-roosting bats more vulnerable to human disturbance of their habitat (Scheel, Vincent & Cameron, 1996). On the basis of current information we conclude that the greatest threat to Madagascar's bat species occurring in the dry regions of the island is human utilisation of caves and conservationists ought to give additional consideration to the protection of such sites for these animals, particularly those species that are dependent on caves during different portions of their life-cycles.

Acknowledgements

It is with pleasure that we acknowledge the assistance of the Association pour le Gestion des Aires Protégées (ANGAP) and the Direction des Eaux et Forêts for issuing permits to conduct this research. We are grateful to Madame Olga Ramilijaona for her help with administrative details. A portion of this fieldwork associated with WWF was undertaken with the financial aid of Bat Conservation International, the Ellen T. Smith and Marshall Field funds of the Field Museum of Natural History, National Geographic Society (6637–99 and 7402–03), National Speleological Society and Volkswagen Foundation and conducted under the *protocol de collaboration* between the Université d'Antananarivo, WWF-Madagascar and the Field Museum of Natural History. This material is based upon work also supported under a National Science Foundation Graduate Research Fellowship. Bat Conservation Madagascar work was conducted under the *protocol de collaboration* between the University of Aberdeen, the Université d'Antananarivo and the Université de Toliara. Research grants were kindly awarded by Bat Conservation International, British Ecological Society, the British Government's Darwin Initiative, Fauna and Flora International, National Geographic Society (C23-02) and Rufford Foundation. Figure 1 was kindly prepared by Lucienne Wilmé.

For access to specimens in their care we are grateful to the curators of the following institutions for access to material (acronyms defined in the text): BMNH, Paulina Jenkins; MCZ, Judy Chupasko; MNHN, Michel Trainer and Jean-Marc Pons; ROM, Judith Eger; USNM, Michael D. Carleton; UWZM, Paula Holahan; YPM, Anne Yoder.

REFERENCES

Bennett, D. & Russ, J. (Eds.). (2001). *The bats of Madagascar: A field guide with descriptions of echolocation calls.* Glossup, UK: Viper Press.

Besaire, H. & Collignon, M. (1972). Géologie de Madagascar; I. Les terrains sédimentaires. *Annal. Géol. Madagascar* **35**: 1–463.

Bollen, A. & Van Elsacker, L. (2002). Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar. *Acta Chiropterol.* **4**: 33–47.

CAMP (2002). *Evaluation et plans de gestion pour la conservation (CAMP) de la faune de Madagascar: Autres mammifères*. Apple Valley, MA: IUCN/SSC Conservation Breeding Specialist Group.

Cardiff, S. & Befourouack, J. (2003). The Réserve Spéciale d'Ankarana. In *The natural history of Madagascar*: 1501–1507. Goodman, S. M. & Benstead, J. P. (Eds). Chicago: The University of Chicago Press.

Chaperon, P., Danloux, J. & Ferry, L. (1993). *Fleuves et rivières de Madagascar.* Paris: Editions ORSTOM.

Dorst, J. (1947*a*). Les chauves-souris de la faune Malgache. *Bull. Mus. Nat. d'Hist. Nat., Paris (2)* **19**: 306–313.

Dorst, J. (1947*b*). Essai d'une clef de détermination des chauves-souris malgaches. *Mémoir. l'Institut Sci. Madagascar, sér. A,* **1**: 81–88.

Eger, J. L. & Mitchell, L. (2003). Chiroptera, bats. In *The natural history of Madagascar*: 1287–1298. Goodman, S. M. & Benstead, J. P. (Eds). Chicago: The University of Chicago Press.

Ganzhorn, J. U., Sommer, S., Abraham, J.-P., Ade, M., Raharivololona, B. M., Rakotovao, E. R., Rakotondrasoa, C. & Randriamarosoa, R. (1996). Mammals of the Kirindy Forest with special emphasis on *Hypogeomys antimena* and the effects of logging on the small mammal fauna. In *Ecology and economy of a tropical dry forest in Madagascar.* Ganzhorn, J. U. & Sorg, J.-P. (eds.). *Primate Rep*. **46-1**: 215–232.

Garbutt, N. (1999). *Mammals of Madagascar*. New Haven: Yale University Press.

Gautier, L. & Goodman, S. M. (2003). Introduction to the flora of Madagascar. In *The natural history of Madagascar*: 229–250. Goodman, S. M. & Benstead, J. P. (Eds). Chicago: The University of Chicago Press.

Gelderblum, C. M., Bronner, G. N., Lombard, A. T. & Taylor, P. J. (1995). Patterns of distribution and current protection status of the Carnivora, Chiroptera, and Insectivora in South Africa. *S. Afr. J. Zool.* **30**: 103–114.

Goodman, S. M. (1998). Notes on the bats of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. In *A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: with reference to elevational variation.* Goodman, S. M. (Ed.). *Fieldiana: Zool., new ser*. **90**: 223–226.

Goodman, S. M. (1999). Notes on the bats of the Réserve Naturelle Intégrale d'Andohahela and surrounding areas of southeastern Madagascar. In *A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: with reference to elevational variation.* Goodman, S. M. (Ed.). *Fieldiana: Zool., new ser* **94**: 251–257.

Goodman, S. M. & Cardiff, S. G. (2004). A new species of *Chaerephon* (Molossidae) from Madagascar with notes on other members of the family. *Acta Chiropterol.* **6**: 227–248.

Goodman, S. M. & Ranivo, J. (2004). The taxonomic status of *Neoromicia somalicus malagasyensis. Mamm. Biol.* **69**: 434–438.

Goodman, S. M. & Razakarivony, V. (2004). Chiroptères de la forêt de Mikea. In *Inventaire floristique et faunistique de la forêt de Mikea: paysage écologique et diversité biologique d'une préoccupation majeure pour la conservation.* Raselimanana, A. P. & Goodman, S. M. (Eds). *Recherches pour le développement, Sér. Sci. Biol.* **21**: 81–85.

Goodman, S. M., Ganzhorn, J. U. & Rakotondravony, D. (2003). Introduction to the mammals. In *Natural History of Madagascar*: 1159–1186. Goodman, S. M. & Benstead, J. P. (Eds). Chicago: The University of Chicago Press.

Goodman, S. M., Jenkins, R. K. B. & Ratrimomanarivo, F. H. (In press). A review of the genus *Scotophilus* (Chiroptera: Vespertilionidae) on Madagascar, with the description of a new species. *Zoosystema*.

Göpfert, M. C., Heller, K.-G., Volleth, M. & Wasserthal, L. T. (1995). Madagascar Microchiropteran bats: New records including new species. *Bat Res. News* **36**: 68–69.

Grandidier, G. (1937). Mammifères nouveaux de la région de Diego-Suarez (Madagascar). *Bull. Mus. Nat. d'Hist. Nat., Paris* **9**: 347–353.

Hill, J. E. (1993). Long-fingered bats of the genus *Miniopterus* (Chiroptera: Vespertilionidae) from Madagascar. *Mammalia* **57**: 401–405.

Hutcheon, J. M. (1994). The great red island: A future for its bats? *Bats* **12**: 10–13.

Hutcheon, J. M. (1997). Tracking bats at Ankarana. *Bats* **15**: 14–15.

Hutcheon, J. M. (2003). Frugivory by Malagasy bats. In *The natural history of Madagascar*: 1205–1207. Goodman, S. M. & Benstead, J. P. (Eds). Chicago: The University of Chicago Press.

Hutson, A. M., Mickleburgh, S. P. & Racey, P. A. (2001). *Microchiropteran bats – Global status survey and conservation action plan.* Gland: IUCN/SSC Chiroptera Specialist Group.

Long, E. (2002). *The feeding ecology of* ***Pteropus rufus*** *in a remnant gallery forest surrounded by sisal plantations in south-east Madagascar.* PhD Thesis: University of Aberdeen.

McHale, M. (1987). Bats. In *The Crocodile Caves of Ankarana: expedition to northern Madagascar, 1986*. Wilson, J. (Ed.). *Cave Sci., Trans. Brit. Cave Res. Assoc.* **14**: 107–119.

MacKinnon, J. L., Hawkins, C. E. & Racey, P. A. (2003). Pteropodidae. In *The natural history of Madagascar*: 1299–1302. Goodman, S. M. & Benstead, J. P. (Eds). Chicago: The University of Chicago Press.

Nicoll, M. E. & Langrand, O. (1989). *Madagascar: revue de la conservation et des aires protégées.* Gland: WWF.

Peterson, R. L., Eger, J. L. & Mitchell, L. (1995). *Chiroptères. Faune de Madagascar, vol. 84.* Paris: Muséum National d'Histoire Naturelle.

Pont, S. M. & Armstrong, J. D. (1990). *A study of the bat fauna of the Reserve Naturelle Integral de Marojejy in north-east Madagascar. Report of the Aberdeen University expedition to Madagascar 1989*. Aberdeen: University of Aberdeen.

Raheriharisena, M. (2000). *Contribution à l'étude bio-écologique de la colonie de* ***Pteropus rufus*** *(Tiedeman, 1808), et de son rôle dans le maintien et la régénération forestière dans la réserve privée de Berenty et de ses alentours.* Mémoire D.E.A., Faculté des Sciences, Département de Biologie Animale, Université d'Antananarivo.

Ranivo, J. C. (2001). *Contribution à l'étude de la Biologie et de l'effet de la prédation humaine sur la roussette:* ***Eidolon dupreanum***. Mémoire D.E.A., Faculté des Sciences, Département de Biologie Animale, Université d'Antananarivo.

Ratrimomanarivo, H. F. (2003). *Etude du régime alimentaire de Mégachiroptéres:* ***Eidolon dupreanum*** *(Pollen, 1866) dans les Hautes-Terres Centrales Malgaches et son rôle potentiel sur la dispersion des graines de plantes dans l'écosystème modifié par l'homme.* Mémoire D.E.A., Faculté des Sciences, Département de Biologie Animale, Université d'Antananarivo.

Rasolozaka, I. N. (1994*a*). Les micro-chiroptères. In *Inventaire biologique foret de Zombitse*: 64–67. Goodman, S. M. & Langrand, O. (Eds.). *Recherches pour le développement, Sér. Sci. Biol. No. Spécial*.

Rasolozaka, I. N. (1994*b*). *Contribution á l'Anatomie descriptive, comparative et fonction des microchiroptéres de la région de Morondava*. Mémoire D.E.A., Faculté des Sciences, Service de Paléontologie, Université d'Antananarivo.

Razakarivony, H. V. (2003). *Etude d'Impact de la prédation humaine sur la roussette* ***Pteropus rufus*** *[Tiedemann, 1808] dans la région de Morondava.* Mémoire D.E.A., Faculté des Sciences, Département de Biologie Animale, Université d'Antananarivo.

Real, R. & Vargas, J. M. (1996). The probabilistic basis of Jaccard's index of similarity. *Syst. Biol.* **45**: 380–385.

Redford, K. H., Coppolillo, P., Sanderson, E. W., Da Fonseca, G. A. B., Dinerstein, E., Groves, C., Mace, G., Maginnis, S., Mittermeier, R. A., Noss, R., Olson, D., Robinson, J. G., Vedder, A. & Wright, M. (2003). Mapping the conservation landscape. *Conserv. Biol.* **17**: 116–131.

Russ, J. & Bennett, D. (Eds). (1999). *The bats of the Masoala Peninsular, Madagascar and the use of time expansion ultrasound detectors in surveying Microchiropteran communities.* Glossup, UK: Viper Press.

Scheele, D., Vincent, T. L. S. & Cameron, G. N. (1996). Global warming and the species richness of bats in Texas. *Conserv. Biol.* **10**: 452–464.

Schliemann, H. & Goodman, S. M. (2003). *Myzopoda aurita*. In *The natural history of Madagascar*: 1303–1306. Goodman, S. M. & Benstead, J. P. (Eds). Chicago: The University of Chicago Press.

Simmons, N. B. (2005). Order Chiroptera. In *Mammal species of the world: a taxonomic and geographical article reference.* 3rd edition. Wilson, D. E. & Reeder, D. M. (Eds.). Washington, DC: Smithsonian Institution Press.

Sommer, S., Toto Volahy, A. & Seal, U. S. (2002). A population and habitat variability assessment for the highly endangered giant jumping rat (*Hypogeomys antimena*), the largest extant endemic rodent of Madagascar. *Anim. Conserv.* **5**: 263–273.

Watson, J., Hamilton-Smith, E., Gillieson, D. & Kiernan, K. (Eds). (1997). *Guidelines for cave and karst protection.* Gland and Cambridge: IUCN.

Wilson, J. M. (1987). The crocodile caves of Ankarana: expedition to northern Madagascar, 1986. *Cave Sci.* **14**: 107–119.

Yom-Tov, Y. & Kadmon, R. (1998). Analysis of the distribution of insectivorous bats in Israel. *Div. Distrib.* **4**: 63–70.

Yoshiyuki, M. (1995). Two rare species of the bats, *Triaenops rufus* and *Mormopterus jugularis* (Mammalia, Chiroptera) from Madagascar. *Bull. Nat. Sci. Mus., Tokyo, Ser. A* **21**: 119–126.