The bats of the Parc National de Marojejy and surrounding areas

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Abstract

Herein we summarize information about the known bat fauna of northeastern Madagascar, specifically the Parc National de Marojejy, and immediate surrounding foothills. We present herein an annotated checklist and detailed species accounts for all of the species recorded on and around the Marojejy Massif. This zone has been the subject of several bat inventories over the course of more than three decades and since late 2019 intensive field studies on these animals have been conducted using mist nets and harp traps, as well as cave surveys. The recent studies included an elevational transect in late 2021 at five sites between 450 and 1880 m along the trail within the Parc National de Marojejy, starting in the Manantenina River valley and leading to the summit, which was a repeat of a parallel survey in 1996. Further, a large-scale project in the foothills of the massif and in forest just within the park was conducted to examine the role of human land use and habitat modification on the transmission of zoonotic diseases in wild and domestic mammals, including bats. In the context of this latter project, bat surveys were done at three different lowland areas surrounding the mountain (Antsahabe, Andatsakala, and Sarahandrano). The habitats sampled at these three sites included natural lowland forests (degraded in some cases), secondary forest, vanilla and fruit tree plantations (often referred to herein as agroforestry zones), rice and open agricultural areas, and village settings. Caves and rock shelters were present at Antsahabe and Andatsakala and bats were surveyed at these sites; no cave was located in the vicinity of Sarahandrano.

Cumulative trapping effort since late 2019 has been considerable and with more than 11,000 meter/hours of mist netting and over 1100 hours of harp trap capture. With these two devices, 470 individual bats were captured. Further, an additional 57 bats were trapped in nearby caves and rock shelters. Using bat trapping effort in the different sampled habitats, specifically the measure of total number of captures/the total number of accrued mist net meter/hours, with the greatest capture rates (in decreasing order) are: rice and open agriculture (0.06), agroforestry (0.04), secondary forest (0.04), intact forest (0.02), *savoka* (0.01), and villages (0.0).

On the basis of different bat inventories in and around the Marojejy National Park and using recent advances in taxonomy, 18 species have been documented over the more than three decades of field studies, 16 species (nearly 90%) of which are endemic to Madagascar. This is the highest level of bat species diversity known from any protected area in the moist evergreen forest region of the island. Two of these species are classified by IUCN as Vulnerable (*Pteropus rufus* and *Rousettus madagascariensis*), and the balance have non-threatened conservation statutes. Little serious human pressure is known on the local bat fauna, although some exploitation occurs for small insectivorous bats as dietary supplements; we have no evidence of fruit bats being locally exploited, as is the case in many areas of Madagascar. Further bat inventories of the massif are needed, including locating and surveying caves, to further complete what is known about these animals.

Keywords: bats, Marojejy, northeastern Madagascar, species diversity, ecology

Résumé détaillé

La connaissance sur la diversité de la faune chiroptérologique malgache s'améliore grâce aux

Goodman, S. M., Falimiarintsoa, D., Manana, C. M., Rafanomezanjanahary, J. M., Rasoanoro, M. & Todilahy, L. J. 2023. The bats of the Parc National de Marojejy and surrounding areas. In A floral and faunal inventory of the Parc National de Marojejy: Altitudinal gradient and temporal variation, eds. S. M. Goodman & M. J. Raherilalao. *Malagasy Nature*, 17: 229-248.

inventaires menés dans différents types d'endroits. Les informations sur la faune connue des chauves-souris dans le Nord-est, plus précisément dans le Parc National de Marojejy et les formations montagneuses environnantes sont compilées dans ce manuscrit. Cette zone a fait l'objet de plusieurs inventaires de chauves-souris au cours de plus de trois décennies et depuis la fin de l'année 2019, des études de terrain intensives de la faune chiroptérologique ont été menées en utilisant des filets japonais et des pièges harpes, installés à travers les territoires de chasse des chauves-souris. Pendant le jour, des prospections de gîtes diurnes, de grottes et d'abris sous-roches ont été faites. Vers la fin de l'année 2021, une étude récente dans cinq sites répartis entre 450 et 1880 m d'altitude a été menée. Elle a couvert un transect altitudinal à partir du village de Mandena jusqu'à la zone sommitale. De plus, un projet à grande échelle dans les versants avoisinants et à l'intérieur de la forêt a été entrepris pour examiner le rôle de l'exploitation des terres et la modification de l'habitat sur la transmission des maladies zoonotiques chez les mammifères sauvages et domestiques, y compris les chauves-souris. Dans le contexte de ce projet, un suivi de chauves-souris a été mené dans trois différentes plaines autour des montagnes (Antsahabe, Sarahandrano et Andatsakala). Les habitats échantillonnés dans ces trois sites comprennent la forêt naturelle de basse altitude (dégradées dans certains cas), les forêts secondaires, les plantations de vanille et d'arbres fruitiers (souvent appelées ici zones agroforesteries), les rizières et les zones agricoles ouvertes et près des habitations. Des grottes et des abris sous roche sont présents à Antsahabe et Andatsakala étant donnés que les chauves-souris ont été recensées sur ces sites ; aucune grotte n'a été localisée aux environs de Sarahandrano.

L'effort de capture cumulé depuis fin 2019 a été considérable et avec plus de 11 000 mètres/heures de filet japonais et plus de 1100 heures de capture au piège harpe. Au total, 470 individus ont été capturés. De plus, 57 chauves-souris ont été aussi capturées dans des grottes et des abris sous-roches à proximité. En utilisant la méthode de calcul de l'effort de capture des chauves-souris dans les habitats échantillonnés qui s'exprime par le nombre total de captures sur le nombre total de mètres de filet japonais cumulés par heure, les résultats montrent que les plus grands taux de capture (par ordre décroissant) sont dans les habitats suivants : rizière et agriculture ouverte (0,06), agroforesterie (0,04), forêt secondaire (0,04), forêt intacte (0,02), *savoka* (0,01) et villages (0,0).

Sur la base des différents inventaires de chauves-souris au sein du Parc National de Marojejy et ses environs et en utilisant les avancées récentes dans la taxonomie des chauves-souris malgaches, 18 espèces ont été documentées au cours de plus de trois décennies d'études sur le terrain, dont 16 espèces (près de 90 %) sont endémiques à Madagascar. Ce résultat montre une diversité des chauves-souris élevé parmi les forêts humides sempervirentes dans les aires protégées de la partie orientale de Madagascar. Parmi ces 18 espèces, seulement deux sont classées par l'UICN comme Vulnérables (*Pteropus rufus* et *Rousettus madagascariensis*) et les autres n'ont pas de statuts menacés. La faune locale de chauves-souris subit peu de pressions, mais bien qu'il y ait une certaine exploitation comme gibiers, aucune preuve d'exploitation locale des chauves-souris frugivores n'a été trouvée, comme c'est le cas dans de nombreuses régions de Madagascar. D'autres inventaires de chauves-souris à Marojejy seront encore nécessaires pour connaitre leur distribution et l'étude de ses habitats, pour compléter les informations sur ces animaux dans les zones sur et autour du massif.

Mots-clés : chauves-souris, Marojejy, Nord-est de Madagascar, diversité spécifique, écologie

Introduction

Well over 1400 species of bats are currently recognized, representing about 20% of the world's mammal fauna. Over the past decades different research projects have highlighted the importance of bats for ecosystem functioning, including pollination of forest trees and commercially grown fruit trees, dissemination of seeds, and a major motor in portions of the tropics for tree regeneration, as well as the control of insects, including those responsible for the transmission of different zoonotic diseases (Ramírez-Fráncel *et al*., 2022). These studies underline the importance of bats for the different services they provide and further knowledge on the distribution and ecology of these animals offers additional support on the important roles they play.

Over the past few decades, numerous field inventories have been conducted on Malagasy bats, which have provided the means for considerable advances in the understanding of the ecology and distribution of these animals on the island. Further,

on the basis of specimens and tissue samples collected during these surveys, new insights based on morphology and molecular genetic studies have progressed taxonomical work on Madagascar's bat fauna, including clearer definitions of species limits and measures of diversity (Goodman *et al*., 2022). To highlight this progress, 20 endemic species have been named as new to science since 2003. As of late 2022, the documented bat fauna of the island comprises 46 species, of which 36 species (78%) are endemic to the island.

To a large extent in the northern portion of Madagascar most of the fieldwork on bats has been conducted in areas with exposed limestone that include extensive cave systems and with dry deciduous forests, such as Ankarana and Montagne des Français (Goodman *et al*., 2005; Raherilalao *et al*., 2022), and areas of moist evergreen forest in the eastern portion of this region have not been intensively and systematically studied. One exception to this generalization is the Marojejy Massif, which has been the subject of different visits by bat researchers over the past 35 years and herein we summarize published and unpublished information on the bat fauna of the park and surrounding lowland areas. This protected area was formerly classified as a Réserve Naturelle Intégrale and the status was changed to a Parc National in May 1998 (Goodman *et al*., 2018).

History of bat research in and around the Marojejy Massif

Over the course of more than three decades, bat surveys have been conducted in the Parc National de Marojejy and surrounding foothills. This work commenced with an inventory between 18 August and 23 October 1988 that involved a multidisciplinary field survey, focusing principally on the birds and land mammals of the massif (Safford & Duckworth, 1990). While the principal focus of the mammal work was on terrestrial species, some mist netting was conducted, and bats were captured.

The first in depth study of Marojejy's bat fauna was the following year (Pont & Armstrong, 1990). A group surveyed bats between 13 October and 22 November 1989 at a range of sites within and outside the protected area using mist nets and observations at roost sites. In total, close to 220 bats of about 11 species were captured in nets placed in relatively intact forest, secondary forest, and areas under different human land use. All of the sites they worked were below 800 m elevation. No specimens were collected and a few of the field identifications remain uncertain (Table 1 and species accounts below).

In 1996, as part of a transect of five separate elevational zones of the eastern slopes of Marojejy along the trail leading from Mandena to the summit, a range of different organisms were surveyed (Goodman, 2000). While bats were not regularly captured during the inventory, mist nets were erected at the different sites, at least in part to capture birds. Subsequently, the northwestern portion of the protected area was the subject of a multidisciplinary inventory at two sites, one at 810 m and the other at 1175 m, from 13 to 30 October 2002 (Goodman & Wilmé, 2003) and bats were the subject of capture with mist nets, but not in a systematic manner. During both the 1996 and 2002 surveys some of the captured bats were saved as voucher specimens with associated tissue samples. This material has been subsequently employed in different taxonomic and molecular studies and these different aspects are explained in the species accounts below.

The next phase of research on the bats of Marojejy was from 11 to 29 May 2016, when Mercia Rasoanoro captured bats in the zone to the east of the protected area between the village of Mandena and the principal tourist entry of the park, including around Antsahabe (Figure 1). Techniques employed included mist nets set in flight pathways and a hand net used in caves and rock shelters to capture roosting bats. Material from these collections was employed to study bat blood parasites (Rasoanoro, 2021).

In the context of a large-scale project in the foothills of the Marojejy Massif examining the role of human land use and habitat modification on the transmission of zoonotic diseases in wild and domestic animals, and humans (see Herrera *et al*., 2020, for some details), mammal surveys were conducted at three different lowland areas surrounding the mountain; these three sites, which we referred to herein as Antsahabe, Andatsakala, and Sarahandrano (Figure 1). Bats were among the different focal groups in this study and field techniques included mist nets and harp traps placed along flight pathways and some collections made in caves. The habitats sampled at these three sites included natural lowland forests, although in some cases notably disturbed, as well as secondary forest, vanilla and fruit tree plantations (often referred to herein as agroforestry zones), rice paddy, and riverine settings outside natural vegetation formations, and sites close to villages. Bat work near Antsahabe, along the path leading

Table 1. The documented bat fauna of the Marojejy Massif and surrounding areas. The IUCN Red List status is given after the scientific name. Those species endemic to Madagascar are preceded by an asterisk (*) and those given in **bold font** are known to, at least in part, use caves as day roost and/or breeding sites.

	Pont & Armstrong (1990)	Goodman *et al*. (2018)	Recent field studies[2]	Known bat fauna
**Pteropus rufus* (Vulnerable)	X	X	–	X
Rousettus madagascariensis (Vulnerable)	X	X	X	X
Macronycteris commersoni[3] (Near Threatened)	X	X	X	X
Triaenops menamena (Least Concern)	X	X	–	X
Paremballonura atrata (Least Concern)	X	X	X	X
Coleura kibomalandy (Data Deficient)	–	X	X	X
Taphozous mauritianus (Least Concern)	–	X	–	X
**Myzopoda aurita* (Least Concern)	X	X	X	X
**Chaerephon atsinanana* (Least Concern)	X	X	X	X
Mops leucostigma (Least Concern)	–	–	X	X
Myotis goudoti (Least Concern)	X	X	X	X
**Laephotis matroka* (Least Concern)	–	–	X	X
**Scotophilus robustus* (Least Concern)	X	X	–	X
Miniopterus aelleni (Least Concern)	–	–	X	X
Miniopterus ambohitrensis (Least Concern)	?[4]	X	X	X
Miniopterus brachytragos (Least Concern)	–	X	X	X
Miniopterus gleni (Least Concern)	X[5]	X	–	X
Miniopterus griveaudi (Data Deficient)	X[6]	–	X	X
Total number of species	**11**	**14**	**13**	**18**

[1] The information on the bats of Marojejy presented by Goodman *et al*. (2018) was based on a synthesis of previously unpublished records and museum specimens up to early 2018. See species accounts in main text for some further details.
[2] The information in this column is based on the recent field studies of Rafanomezanjanahary (2021), Rasoanoro (2021), Manana (2022), Falimiarintsoa (2022), and Todilahy and Goodman (unpublished data). See species accounts in main text for some further details.
[3] In the dry deciduous forests of the west this species often can be found in caves, although roosting sites have been found under vegetation. In contrast, in areas of moist evergreen forests of the east, it is known to roost in vegetation. See species account for further details.
[4] Pont and Armstrong (1990) reported a medium-size *Miniopterus* from the Marojejy Massif with a forearm of 44 to 45 mm that they identified as *M. inflatus*. The taxon in question might be *M. ambohitrensis*, but the published forearm length of this species is from 37 to 42 mm. Alternatively, *M. majori* has a forearm between 43 and 47 mm, but this species is not known from the northern portion of Madagascar.
[5] Pont and Armstrong (1990) reported a small *Miniopterus* from the Marojejy Massif with a forearm less than 40 mm that they identified as *M. minor*, a species group that was subsequently allocated to the *M. manavi* complex. In subsequent years, the small members of this genus in the Malagasy Region have been the subject of taxonomic studies and three different members of the *M. manavi* group are known from Marojejy (*M. aelleni*, *M. brachytragos*, and *M. griveaudi*). It is not possible to discern which of these species was captured by Pont and Armstrong (1990) and these records are most likely *M. griveaudi*, which based on capture records appears to be the most common species of the *manavi* group at Marojejy.
[6] Pont and Armstrong (1990) reported a large *Miniopterus* from the Marojejy Massif with a forearm ranging from 48 to 49 mm that they identified as *M. schreibersi*. The species in question is with little doubt *M. gleni*.

from Mandena to the park entry, was conducted by Johanna Rafanomezanjanahary from 28 September to 3 December 2019 (Rafanomezanjanahary, 2021); she worked in the above-named habitats and visited two caves just outside the park's limits (Bemanavy and Beamalona, also known as Antsahanisoavina). Along the southwestern slopes of the massif, near Marovato and more specifically the village of Sarahandrano and habitats above to the forest limit, bats were captured by Daniel Falimiarintsoa from 23 March to 13 May 2021 (Falimiarintsoa, 2022). He worked similar habitats to those mentioned above for

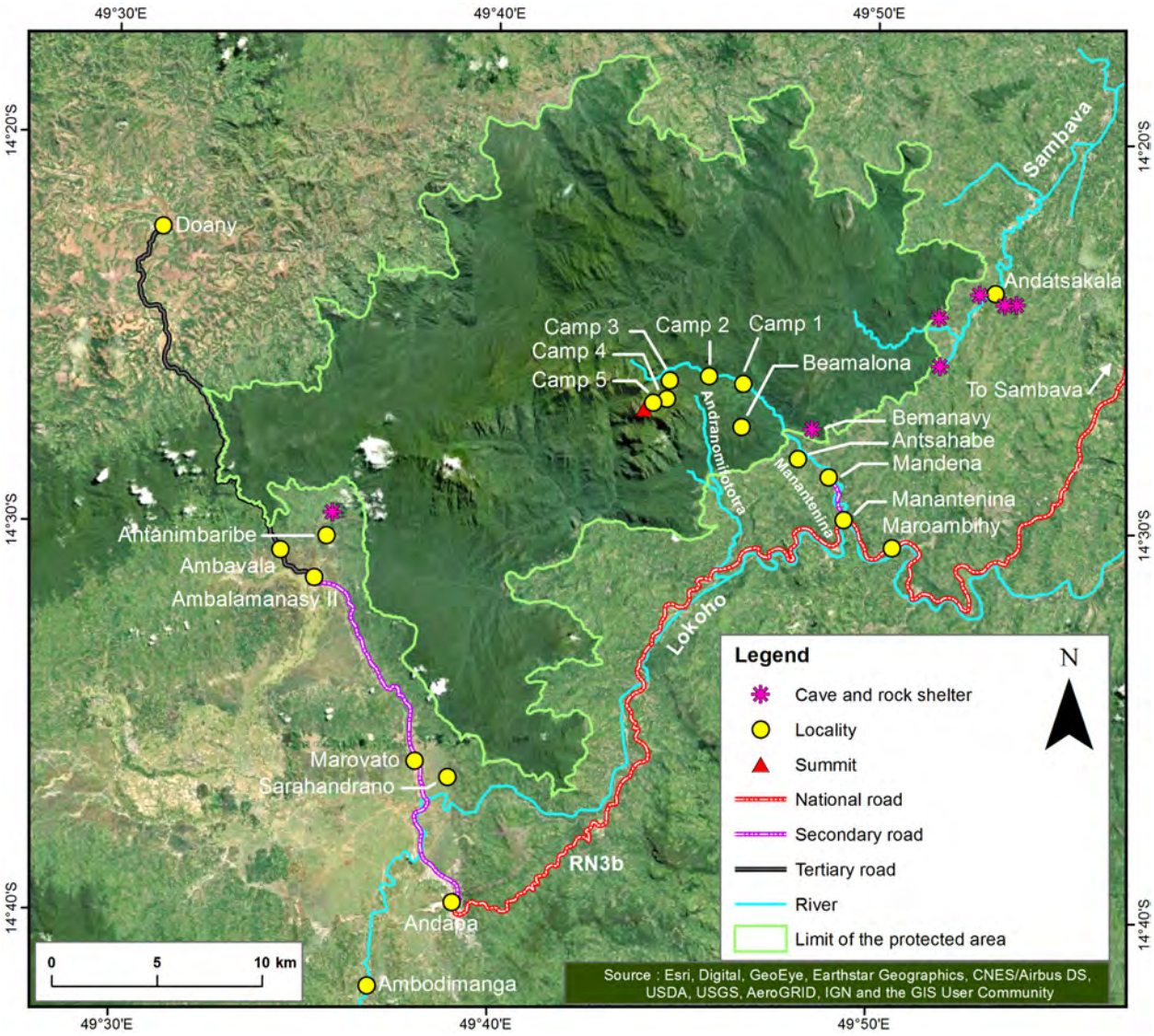

Figure 1. Map of the Parc National de Marojejy and surrounding areas where work has been conducted on the local bat fauna, including three separate study areas at the limit of the protected area: Antsahabe, Sarahandrano, and Andatsakala. Localities mentioned in the text and include towns and villages, as well as bat capture sites, are shown on the map. Irregular white patches on the map are patches of cloud cover.

Antsahabe, but no cave was located in this zone. The third site was on the northeastern side of the massif near the village of Andatsakala and was surveyed principally by Lomeris J. Todilahy between 5 March and 29 April 2022 (Todilahy & Goodman, unpublished data). The lower lying portions of this study area contained a considerable number of river drainages with shallow rock shelters.

From 2 October to 15 November 2021, an elevational transect was conducted within natural forest habitat in the eastern portion of the national park, along the trail from Mandena to the summital zone, and at five different sites. Installations included mist nets and a harp trap that were installed by Christian Manana and Steven M. Goodman at all five sites. The intent of this survey was to repeat a parallel transect conducted in 1996 and mentioned above (Goodman, 2000) of the biota occurring on the eastern slopes of the massif. The results from this transect are reported herein and also contained in Manana (2022).

In their monograph on the bats of Madagascar, Peterson *et al*. (1995), which was largely based on fieldwork in the late 1960s and subsequent review of material in different natural history museums around the world, made no reference to specimens from Marojejy; this underscores how poorly known the massif's chiropteran fauna was before the wave of studies starting in the late 1980s. One of the more recent tabulations of the bat fauna of Marojejy was published by Goodman *et al*. (2018) and included 14 species; however, since then, based on extensive fieldwork in and around the massif, an additional four

bat species have been added to the local list, which are presented herein.

Materials and methods

The Marojejy Massif has been the subject of numerous detailed plant and animal surveys over recent decades. For details on the ecological setting, including changing vegetation and flora, superimposed on an elevational range spanning from about 450 to the summit at 2132 m, see Goodman (2000), Goodman and Wilmé (2003), and other contributions in this monograph.

Over the course of the past nearly 35 years, since the first studies on the bat fauna of Marojejy by Safford and Duckworth (1990) and then by different research groups, a range of different techniques have been employed to capture bats. In all cases, mist nets of different styles were used and placed along bat flight pathways within or outside of natural forest settings, including a range of human-modified habitats. Further, as mentioned in the previous section, starting in late 2019 with a large-scale study of mammal zoonotic disease present on the massif and surrounding human-modified zones, work on bats commencing at the Andasibe site (Rafanomezanjanahary, 2019) and then several other sites, mist nets (style ATX, 36 mm mesh, 2.6 m high, 12 m long, four shelves and style GTX, 24 mm mesh, 2.4 m high, 6 m long, four shelves, Association of Field Ornithologists, Manomet, Massachusetts) and harp traps (Austbat, 2.6 x 1.0 m, Bat Conservation and Management, Carlisle, Pennsylvania) were employed, mostly along bat flight pathways. Finally, when appropriate, butterfly nets, often with extended telescoping handles, were used within caves and rock shelters to capture roosting bats. These same field techniques and equipment were used in the 2021 elevational transect of the massif.

For data presented herein on bat diet, feces from captured animals, starting with the late 2019 fieldwork, and preserved in 70% ethanol were used in analyses based on five (Falimiarintsoa, 2022) or six (Rafanomezanjanahary, 2021) pellets per individual, using measures of percent volume, and following the techniques of Shiel *et al*., 1997); these results are summarized within the species accounts below.

We also present data on the reproductive state of captured bats, often during different seasons, and based on information of the external anatomy of sexual organs, as well as internal anatomy of collected individuals. For females, these different parameters include the development of mammae (small, large and often without surrounding fur, and lactating, vagina (perforated or non-perforated), and presence of embryos detectable by external palpitation or measured during dissection. For males the principal characters were the position of the testes (abdominal or scrotal) and the condition of the epididymides (non-convoluted or convoluted).

During bat surveys conducted on the Marojejy Massif since 1996, specimens have been preserved and these collections are housed in the Département de Biologie Animale, Université d'Antananarivo (UADBA), Antananarivo, which is now named Mention Zoologie et Biologie Animale, and the Field Museum of Natural History (FMNH), Chicago. This material was employed in different taxonomic studies based on morphological variation in Malagasy bats (Goodman *et al*., 2015), as well as the phylogenetic and phylogeographic relations of a range of taxa based on molecular studies, and this work has been important in the understanding of species limits of the national bat fauna (Christidis *et al*., 2014; Goodman *et al*., 2015, 2022; Demos *et al*., 2020).

Taxonomy and other format aspects

Herein we follow the systematic order, taxonomy, and species' delineations given by Goodman *et al*. (2022), which includes the generic revision of pipistrelle-like bats by Monadjem *et al*. (2021). To reduce possible confusion, we refer to the survey sites of 1996 and 2021 along the elevational transect of the eastern slopes of Marojejy as "Camps", and all other sites as "camps". All of the "caves" visited in and around the park are technically best referred to as rock shelters, as they were not formed by the erosion of solid rock, but composed of zones of large boulders within which are relatively large dark spaces. For the terminology of natural vegetation types on Madagascar we use Gautier *et al*. (2018). All references in the text to elevation are meters above sea-level. Herein, the Malagasy Region refers to Madagascar and the surrounding archipelagos of the Comoros, Mascarenes, and Seychelles. In the species accounts presented below and for those taxa that have not been documented at Marojejy, the text is placed in brackets and these species are not included in the total number recorded at the site.

Results

Bats of the Marojejy Massif

Pteropodidae

[*Eidolon dupreanum* (Pollen, 1866)

Eidolon dupreanum, which is endemic to Madagascar, has not been documented on or around Marojejy, although with the different prominent rock crevasses that occur on the massif, many being largely inaccessible to humans, and its known distribution in northern Madagascar (Goodman & Ramasindrazana, 2013), it is possible that *Eidolon* has local day roost sites. During the 2021 elevational transect, the cliffs of Mount Ambatotsondrona were scanned with binoculars at dusk from a prominent look-out next to Camp 2 (Marojejya), particularly the different rock deep rock fissures, and this species was not observed.]

Pteropus rufus E. Geoffroy, 1803

Pteropus rufus is endemic to Madagascar. Safford and Duckworth (1990) reported this species feeding in a *Ficus* tree at Ambodimanga (450 m) in the northwestern portion of the massif. Pont and Armstrong (1990) found two *P. rufus* roost sites close to their camp 2, one being on an island in the Lokoho River and the second a short distance away and close to the Sambava-Andapa road; the latter colony was composed about 100 individuals. Subsequently, there are a few observations of this species in and around the protected area. For example, a group of four to seven individuals were observed near Antsahabe in late September 2019 feeding in a fruiting *Ficus* tree in an area of degraded natural forest (Goodman, unpublished data) and individuals were observed near Andatsakala in mid-March feeding on ripe mangos in a tree (Todilahy, unpublished data). We are not aware of any local hunting of this species for the bush meat trade in the Marojejy area, as known from many portions of Madagascar (Andrianaivoarivelo *et al*., 2022), but it is likely that such activities occur around the massif.

Rousettus madagascariensis G. Grandidier, 1928

This Malagasy endemic, which is known to make its day roosts in caves or rock shelters (Goodman, 2011), is one of the most commonly captured bats in mist nets within and just outside the protected area. We did not locate a cave roost of this species on the Marojejy Massif. During our field research, it was trapped in habitats ranging from intact forest to different human land use types, including within and near villages. During the inventories at the Sarahandrano site, 75% of the 70 individuals captured were near the village and netted near a fruiting litchi (*Litchi chinensis*) tree and the balance in a range of habitats, including largely intact and secondary forest, to different types of agricultural uses (Falimiarintsoa, 2022). Depending on the season, it was commonly captured near trees with ripe fruits, including native and introduced agricultural trees. We have no data on the diet of this species from around the Marojejy Massif, but information is available from the northern dry deciduous forests (Vololona *et al.,* 2020a, 2020b) and moist evergreen forests in the central east (Andrianaivoarivelo *et al*., 2011, 2012, 2022).

Data on the age and reproductive state of captured and in some cases collected individuals provides insights into the annual cycle of *R. madagascariensis* around the Marojejy Massif. Of the 59 *Rousettus* captured at Antsahabe in November 2019, 26 were adult females with embryos (crown-rump lengths ranging from 3 to 45 mm), 1 with placental scars in the uterine wall, two subadults (presumably born late during the last reproductive cycle of this species), and no neonates. This period coincided with when female *R. madagascariensis* where close to the end of pregnancy and about to give birth. Of the males captured at the site, 18 had scrotal testes and 12 non-scrotal testes. Of the 51 individuals of this species netted at Andatsakala in March and April 2022, 16 were adult females with large mammae, four adult females with embryos (crown-rump lengths ranging from 20 to 35 mm), eight lactating, and 10 subadults. Hence, this was a period falling between the first wave of females giving birth and having weaned their young and a second period of reproduction. Of the males captured at the site, 11 had scrotal testes, five non-scrotal testes, and two subadults. In total, 56 individuals were captured at Sarahandrano in April 2021, 21 were adult females with large mammae or placental scars, no individual was pregnant, one was lactating, and 17 were subadults. This was a period at the end of a reproductive cycle. Of the males captured at the site, four had scrotal testes and nine were subadults.

In general, the seasonality of reproduction at the sites around the Marojejy Massif follows a similar cycle to that found during a long-term study at Ankarana, a zone with dry deciduous forest (Ramanantsalama *et al*., 2023), with birthing taking place towards the end of the calendar year or early

in the new year, some subsequent reproduction a bit latter perhaps associated with females that lost their embryos/neonates or abundant food resources, and by April about half of the captured animals being subadults and recruited into the population during the last reproductive period.

Hipposideridae

***Macronycteris commersoni* (E. Geoffroy, 1803)**

This species is endemic to Madagascar. With some regularity, *Macronycteris commersoni*, formerly referred to as *Hipposideros commersoni* (Foley *et al*., 2017), was captured in mist nets and harp traps placed within natural forest settings, different types of human-modified land use types, as well as in close proximity to villages. It was not found roosting in any cave or rock shelter explored around the Marojejy Massif, settings it can be frequently be found elsewhere on the island (Goodman *et al.*, 2022), and no day roost sites were located in the area. Presumably, these occur in vegetation, specifically from thin branches, under the cover of leaves, and in areas with closed canopy forest, as known from other sites with moist evergreen forest in eastern Madagascar (Goodman *et al*., 2014; Razafimanahaka *et al*., 2016).

On the basis of fecal pellet analysis conducted by Rafanomezanjanahary (2021) for individuals of *M. commersoni* captured at the Antsahabe study site (n = 4), this species' diet was composed predominantly of Coleoptera (57%), followed by Diptera (29%), and Lepidoptera (14%). The contents of fecal pellets of an additional two individuals captured along the elevational transect, was also dominated by Coleoptera, and to a lesser extent by Hemiptera, Lepidoptera, and Ephemeroptera (Manana, 2022). The preponderance of beetles in the prey consumed by this species has been found in other dietary studies, both in dry deciduous forest and dry spiny thicket formations (Razakarivony *et al*., 2005; Rakotoarivelo *et al*., 2007, 2009; Ramasindrazana *et al*., 2012) and moist evergreen forest formations (Rasoanoro *et al*., 2015).

On the basis of captured individuals, some inferences can be made on the reproductive period for this species around the Marojejy Massif. Of five individuals captured at Antsahabe in early October to late November 2019, all females, three had embryos ranging in crown-rump length from 16 to 35 mm, and two were non-reproductive animals, presumably born during the last reproductive period. Of the three animals captured at Andatsakala in March 2022, two were non-breeding males and one a subadult female. This species was not captured in the April 2021 session at Sarahandrano. Hence, it would appear that females give birth towards the end of the calendar year, a period coinciding with the start of the rainy season and the presumed period of greatest beetle density.

Rhinonycteridae

***Triaenops menamena* Goodman and Ranivo, 2009**

Pont and Armstrong (1990) found one individual of this species, which they listed as *T. rufus*, in a cave near their camp 6 in the western portion of the protected area and directly north of Antanimbaribe. We are unaware of any subsequent records from the Marojejy Massif. Goodman and Ranivo (2009) found that the holotype of *T. rufus* reputed to be from Madagascar was morphologically similar to east African populations of this species and notably different from Malagasy populations, which was subsequently renamed *T. menamena.*

This widely distributed endemic species to Madagascar (Goodman & Ramasindrazana, 2013) shows little genetic variation, at least using mitochondrial markers (Russell *et al*., 2007), and based on associated inference it probably disperses widely across the island. There are a few sites where this species is rarely recorded and presumably associated with dispersal (Ramasindrazana & Goodman, 2014); perhaps its single recorded occurrence at Marojejy can be explained by such an event.

Emballonuridae

***Paremballonura atrata* (Peters, 1874)**

This endemic Malagasy species is not uncommon in the lowland portions of the Marojejy protected area and surrounding zones, within and outside of native forest formations. It occupies day roost sites in rock shelters and caves. Pont and Armstrong (1990), using the former name *Emballonura atrata*, found this species in drainage tunnels under the Sambava-Andapa road. At the Sarahandrano study site, this species was not captured in forest formations, but in *savoka* (regenerating secondary grassland) and vanilla plantations (Falimiarintsoa, 2022) and at the Antsahabe study site only in rock shelters (Rafanomezanjanahary, 2021). It was notably common in rock shelters at the Andatsakala study site (Todilahy & Goodman, unpublished data). Pont

and Armstrong (1990) also noted the presence of this species in rock shelters.

On the basis of fecal samples collected from 10 individuals of *P. atrata* netted at the Sarahandrano site, the following orders were consumed (Falimiarintsoa, 2022): Hymenoptera (36.4%), Diptera (21.0%), Lepidoptera (18.2%), Coleoptera (16.3%), and Hemiptera (8.1%). A few mites (Acaria) were also identified in the samples, and these were presumably secondarily consumed when an individual bat was grooming its fur. The work of Rasoanoro *et al*. (2015) on the diet of this species near Kianjavato, in the moist evergreen forest region of the southeast of the island, found similar results, but the order and representation of preferred prey was slightly different: Diptera (40.9%), Hymenoptera (31.3%), Coleoptera (26.7%), and Hemiptera (12.0%).

On the basis of individuals of this species captured at the principal study sites, some inferences can be made on its reproductive cycle. Of the three individuals captured at Antsahabe in mid to late October 2019, two were females, one with an embryo (measuring 12 mm in crown-rump length), and the other showing no signs of breeding, and the single male was non-reproductive. Fifty-one individuals were trapped at Andatsakala from early March to late April 2022, including 13 females, of which five were lactating and eight showed no signs of breeding, and 38 males, of which six had slightly enlarged testicles and convoluted epididymes and 32 were not in reproductive condition. At Sarahandrano in late March to early April 2021, 13 individuals were obtained, of which six were females, two with small embryos and four showing no signs of reproduction, and seven males, not one of which was in reproductive condition. Hence, it would appear that females give birth towards the end or early portion of the calendar year, a period coinciding with the start of the rainy season and presumably with high insect densities.

Coleura kibomalandy Goodman, Puechmaille, Weyeneth, Gerlach, Ruedi, Schoeman, Stanley, and Teeling, 2012

This genus was first recorded in Madagascar by Goodman *et al*. (2008) and tentatively identified as *C. afra*, a species known from sub-Saharan Africa and the Arabian Peninsula (Monadjem *et al*., 2020). Subsequent work based on morphology and molecular characters found that the Malagasy population was specifically distinct from that on Africa, as well as *C. seychellensis* in the Seychelles, and was described as a species endemic to Madagascar, *C. kibomalandy* (Goodman *et al*., 2012). In the north of Madagascar, this species was previously only known from the Ankarana protected area until its discovery in Bemanavy Cave to the west of Mandena and outside the Parc National de Marojejy. All records of this species from near the protected area are from this rock shelter and it has not been captured during other sessions in mist nets or harp traps, presumably an attestation to its high foraging height. Sébastien Puechmaille, now at the University of Montpellier, sequenced tissues from several individuals captured at Marojejy, and found that they fell within the genetic variation of *C. kibomalandy* from elsewhere on the island (Puechmaille, unpublished data).

In total, 11 individuals of this species were captured in the Bemanavy Cave. Ten of these animals were captured on 21 May 2016 and one on 3 Nov. 2019 and comprised six females and five males and not one showed signs of breeding activity.

Taphozous mauritianus (E. Geoffroy, 1818)

Safford and Duckworth (1990) observed one individual of this species at Ambalamanasy II (300 m) in the southwestern foothills of the Marojejy Massif, which, after emerging from the day roost site, flew towards the rice fields in the Andapa basin. This is the only record we are aware of for this broadly distributed African and Malagasy Region species in or around Parc National de Marojejy.

Myzopodidae

Myzopoda aurita Milne-Edwards & A. Grandidier, 1878

There are several records of this species, a member of an endemic family, in the Marojejy protected area and surroundings. Safford and Duckworth (1988) captured an individual in 1988 in the southwestern portion of Marojejy in a mist net placed over a small stream. Further, two individuals were captured in close proximity to the protected area boundary by Pont and Armstrong (1990): 1) at their camp 1 (about 500 m) on 14 October 1989 in a mist net placed in an open vanilla plantation that was a “parous” female, and 2) at their camp 4 (elevation not given) on 5 November 1989 and close to a stream in a sparsely forested area that was an immature male. The descriptions and images available of these three individuals fit with *M. aurita*, the member of this genus known from the eastern moist evergreen forest (Goodman *et al*., 2007; Russell *et al*., 2008). *Myzopoda aurita* tends to be relatively common in

eastern lowland areas with dense stands of *Ravenala madagascariensis* (Ralisata *et al*., 2022), which were not present near our different study sites on the massif and surrounding areas, perhaps explaining its lack of subsequent documentation on the massif and is known to local people residing in Mandena based on interviews conducted by S. M. Goodman (October, 2021).

Molossidae

***Chaerephon atsinanana* Goodman, Buccas, Naidoo, Ratrimomanarivo, Taylor & Lamb, 2010**

Chaerephon atsinanana is largely known from synanthropic day roost sites and is often found as a human commensal. Until recently, the Madagascar population of this species was considered part of a widespread African species, *C*. *pumilus*. Based on morphological and molecular characters the Malagasy animals were named as an endemic species, *C*. *atsinanana* (Goodman *et al*., 2010a). Pont and Armstrong (1990) reported capturing this species from a roosting colony in the attic of a building at Ambavala. Further, in 2021 a colony was located in a school at Sarahandrano (Falimiarintsoa, 2022).

On the basis of an analysis of fecal pellets from 21 individuals captured at Sarahandrano, the following invertebrate groups were identified (Falimiarintsoa, 2022): Odonata (24.6%), Hemiptera (19.0%), Coleoptera (18.4%), Lepidoptera (15.3%), Diptera (10.7%), Hymenoptera (9.3%), and Ephemeroptera (2.7%). Some remains of Acaria and Siphonaptera were identified in the fecal remains and these were presumably ingested by the individual bats during grooming. The occurrence of such a considerable number of Odonata in the diet of this species is exceptional, and not known from any African member of this genus (Monadjem *et al.*, 2020), but is presumably associated with local differences in seasonal prey availability and individual preferences, as found for Central American and Asian members of the family (e.g. Fenton *et al.,* 1998; Leelapaibul *et al*., 2005). Among the Hymenoptera in the Sarahandrano fecal samples, seven individuals of the ant genus *Pheidole* were identified, not one of the ant specimens showed signs of having wings, and were presumably gleaned off vegetation by this bat. The work of Rasoanoro *et al*. (2015) on the diet of *C*. *atsinanana* near Kianjavato, in the moist evergreen forest region of eastern Madagascar, found notably different results with respect to dietary composition: Coleoptera (44.0%), Lepidoptera (25.4%), Homoptera (19.0%), and Diptera (8.3%).

On the basis of the 25 individuals of this species trapped at Sarahandrano between 30 April and 2 May 2021, some inferences can be made concerning their reproduction. In total, 14 females were captured, of which 11 did not show signs of recent or active breeding and three had large mammae, and of the 11 males, nine had abdominal testes with non-convoluted epididymides and two had slightly descended testes and partially convoluted epididymides.

[***Chaerephon leucogaster* A. Grandidier, 1870**

This non-endemic species is widely distributed in portions of Madagascar, including the north (Ratrimomanarivo *et al*., 2009a; Goodman & Ramasindrazana, 2013), often associated with anthropogenic settings. Presumably it occurs in buildings and other structures in villages around the Marojejy Massif.]

***Mops leucostigma* G. M. Allen, 1918**

This endemic species to the Malagasy Region is widely distributed in portions of Madagascar, including the north (Ratrimomanarivo *et al*., 2008; Goodman & Ramasindrazana, 2013), often associated with anthropogenic settings. At the Sarahandrano study site, this species was not captured in the different surveyed natural and human-generated habitats, and only found at a roost site in the village (Falimiarintsoa, 2022).

On the basis of fecal pellets of a single individual captured near the village of Sarahandrano and calculated as percent volume, the principal invertebrate group consumed include Coleoptera (close to 85%), followed by Diptera (slightly more than 10%) (Falimiarintsoa, 2022). On the basis of a few *M*. *leucostigma* fecal samples from the central east lowlands near Betampona, Rabarison (2016) found that it feeds predominantly on Coleoptera (67.0%), and then in descending order of importance Hemiptera, Hymenoptera, Lepidoptera, Diptera, Ephemeroptera, and Trichoptera. At another site in the central eastern, on the basis of fecal analysis, and a large number of individuals (n = 129), Todilahy *et al*. (2022) established that the diet of this species includes (in order of importance) Coleoptera (Scarabeidae, Carabidae, Staphilinidae, Nitudilidae, and Chrysomelidae), Hymenoptera (Formicidae), Lepidoptera, Hemiptera, and Diptera;

notable differences were found in the diet of the different age and sex classes. Near Moramanga, in the inland central east and in close proximity to moist evergreen forest, Raharinjatovo Ny (2012) found that Coleoptera of the families Scarabaeidae, Coccinelidae, Dermestidae, Hydrophilidae, and Chrysomelidae were dominant prey, followed by Hemiptera and Diptera (Culicidae, Tipulidae).

On the basis of the six individuals captured at Sarahandrano on 6 May 2021, some details can be presented on their reproductive state. Of the five females, three had large mammae, one was lactating (also possessing a single placental scar), and the last individual had small mammae. The single male captured had enlarged testicles and with convoluted epididymes.

[***Mops midas*** **(Sundevall, 1843)**

This non-endemic species is widely distributed in portions of Madagascar (Goodman & Ramasindrazana, 2013), often associated with disturbed habitats, and can be found roosting in different types of building. It presumably occurs in village settings close to the Marojejy Massif.].

[***Mormopterus jugularis*** **(Peters, 1865)**

This endemic species, which is often found in synanthropic settings, including roost and breeding sites, has not been recorded in the immediate vicinity of Marojejy. It has been documented near Andapa, in relatively close proximity (Ratrimomanarivo *et al*., 2009b) and presumably occurs in villages around the massif.]

Vespertilionidae

Laephotis matroka **(Thomas & Schwann, 1905)**

This widespread endemic Malagasy species, particularly the east (Goodman & Ramasindrazana, 2013), is known from a single record from the Marojejy Massif. This species was previously referred to as *Eptesicus matroka* or *Neoromicia matroka.* An individual was captured in a vanilla plantation above the village of Sarahandrano (Falimiarintsoa, 2022). This animal was a female and showed no sign of recent or ongoing breeding activity.

On the basis of fecal pellets of the single captured individual, the principal insect group consumed are Coleoptera (close to 75%), followed by Diptera and Lepidoptera (each slightly more than 10%). This general dietary regime is similar to that found for this species based on a larger sample size in the moist evergreen forest area of Anjozorobe-Angavo, in the Central Highlands (Rakotondramanana *et al*., 2015).

Myotis goudoti **(A. Smith, 1834)**

This endemic species is widely distributed across Madagascar (Goodman & Ramasindrazana, 2013) and shows little genetic variation across the island based on mitochondrial markers (Weyeneth *et al*., 2011); this is presumably associated with patterns of widespread dispersal. It was notably common at the principal study sites on and around the Marojejy Massif and was found in a variety of habitats (Table 3). For example, at the Antsahabe study site, 108 individuals were captured, with 53% in *savoka* (regenerating secondary grassland), 23% in relatively intact forest, 18% in secondary forest, and the balance in a variety of agroforestry habitats and rice fields (Rafanomezanjanahary, 2021). Elsewhere on the island, this species tends to make its day roost sites in caves or rock shelters (Goodman *et al*., 2022). During the course of exploration of caves and rock shelters in and around Marojejy, it was not found roosting at any site. Presumably, this species' day roost sites are in small caves and crevices, or perhaps hollow trees, and upon exiting after dusk they have a relatively large home range that encompasses a variety of habitats.

On the basis of an analysis of fecal pellets from 28 individuals captured at the Sarahandrano study site, the following groups of invertebrates were identified (Falimiarintsoa, 2022): Coleoptera (55.6%), Diptera (20.4%), Lepidoptera (17.7%), and less than 3% of Hemiptera and Hymenoptera. The diet of this species at the Antsahabe study site and based on the analysis of 54 individuals was much more varied than at Sarahandrano and consisted of Coleoptera (44%), Lepidoptera (22%), Diptera (14%), Orthoptera (5%), and Araneae, Blattoptera, Ephemeroptera, Hemiptera, and Hymenoptera (each less than 4%) (Rafanomezanjanahary, 2021). The fecal pellets of 45 individuals captured along the elevational transect of the eastern slopes of the massif were analyzed and 13 different groups of invertebrates were identified, with the principal ones in decreasing order of representation being Coleoptera, Lepidoptera, Homoptera, and Hymenoptera (Manana, 2022). The work of Rasoanoro *et al*. (2015) on the diet of this species near Kianjavato, a zone of moist evergreen forest in the southeast of the island, found notably different results based on a sample size of two individuals: Coleoptera (43.7%), Araneae (40.7%), and Hymenoptera (8.4%). Hence, the diet of this

species around Marojejy, as well as sites in similar habitats, appears to be notably variable.

Using information from captured individuals of *M*. *goudoti*, some inference can be made on its breeding ecology. Of 109 individuals captured at Antsahabe in late September to late November 2019, 55 were females, all adults and three had no fur around the mammae (an indication that they had nursed young in the previous breeding period), but no individual had discernable embryos, and of the 52 males, 34 had testes descended into the uropatagium and 18 had abdominal testes. Of the 36 individuals captured at Sarahandrano between late March and late April 2021, 21 were females, including 11 adults, not one with discernable embryos, and 10 subadults. Of the 15 males from the site, all excluding one had descended testes in the uropatagium. At Andatsakala three individuals of this species were trapped, including one adult and one subadult females and a male with non-descended testes. Remarkably little has been published on the breeding ecology of this species and the data from Marojejy does not help to provide more precise information.

Scotophilus robustus Milne-Edwards, 1881

Pont and Armstrong (1990) reported capturing this endemic species outside natural forest vegetation and near a river. This is the only record we are aware of for the Marojejy area, although it is known from different sites in the eastern portion of the island (Goodman & Ramasindrazana, 2013). No subsequent records from the massif and surrounding lowland areas.

Miniopteridae

Since 2007, members of the genus *Miniopterus* on Madagascar and the Comoro islands have been the subject of different taxonomic and molecular studies, which resulted in the description of eight new species to science (Goodman *et al*., 2022). The associated phylogenetic work has brought new insights into the evolutionary and colonization history of the genus in the Malagasy Region (Christidis *et al*., 2014; Demos *et al*., 2020). At least five named species occur within and around the Marojejy protected area, as well as one belonging to an apparently unnamed clade (P3, after Christidis *et al*., 2014). In the expedition report of Pont and Armstrong (1990), the following species are tentatively listed for Marojejy: *M*. *minor*, *M*. *inflatus*, and *M*. *schreibersii*, following the taxonomy of Hill (1993). These three species based on more modern systematics do not occur on Madagascar and the inferred identity of these forms are discuss below in the different species accounts.

Miniopterus aelleni Goodman, Maminirina, Weyeneth, Bradman, Christidis, Ruedi & Appleton, 2009

This species, only known from Madagascar and the Comoros, occurs at scattered localities in central western and northern Madagascar (Goodman & Ramasindrazana, 2013; Goodman *et al*., 2015). During the elevational transect of Marojejy in 2021, a single individual was capture at Camp 1 (480 m) in a mist net traversing the Manantenina River. The other record from the area is an individual at the Andatsakala study site found in degraded forest near the Sambava River at 290 m. Neither of these animals showed indications of recent or on-going breeding activity.

Miniopterus ambohitrensis Goodman, Ramasindrazana, Naughton & Appleton, 2015

This endemic species was described as new to science within the past decade and the holotype comes from the extreme north of the island (Montagne d'Ambre), as well as part of the type series from the northwestern portion of Marojejy (Goodman *et al*., 2015). On the basis of information provided in the species description, it tends to occur at higher elevations.

Pont and Armstrong (1990) reported a medium-size *Miniopterus* from Marojejy with a forearm of 44 to 45 mm, which they identified as *M*. *inflatus*, a species that based on more recent taxonomic work is restricted to sub-Saharan Africa and does not occur on Madagascar (Monadjem *et al*., 2020). The individuals captured by Pont and Armstrong (1990) might be best referred to *M*. *ambohitrensis*, but the published forearm length of which ranges from 37 to 42 mm. Another possibility is that the animals are best referred to *M*. *majori*, which has a forearm length between 43 and 47 mm (Goodman, 2011), but this species is not known from the northern portion of Madagascar (Goodman & Ramasindrazana, 2013).

Since the description of *M*. *ambohitrensis*, it has been found at different sites on the Marojejy Massif, where it has a broad elevational distribution from 230 to 1880 m. A series was obtained in Bemanavy Cave in May 2016 and a single individual in a rock shelter near Antanimbaribe on 29 May 2016. The animal captured at 1880 m was in a mist net set for birds and

in a zone of montane ericoid thicket above forest line composed.

Details are available on the diet of this species based on the fecal pellets of two individuals captured along the elevational transect (Manana, 2022). The principal insect groups consumed are Coleoptera (45.7%), Hymenoptera (24.8%), and Lepidoptera (24.4%). These data are to our knowledge the first information on the diet of this species.

Miniopterus brachytragos Goodman, Maminirina, Bradman, Christidis & Appleton, 2009

This Malagasy endemic is known from several different localities across the island, but the number of records are limited (Goodman & Ramasindrazana, 2013). At Marojejy, specifically near the Antsahabe study site, two individuals were found roosting in Bemanavy Cave and a single animal captured in a rice field near Mandena (Rafanomezanjanahary, 2021). At Andatsakala, a single individual was captured in an agroforestry area at 330 m (Todilahy & Goodman, unpublished data). The different animals handled showed no clear sign of past or on-going breeding activity.

Miniopterus gleni Peterson, Eger & Mitchell, 1995

This species is broadly distributed across much of Madagascar (Goodman & Ramasindrazana, 2013) and at least based on mitochondrial markers shows little genetic variation across its range (Goodman *et al*., 2010b). *Miniopterus gleni* tends to be more common in areas with limestone exposed geological formations and uses caves for breeding and day roost sites.

Pont and Armstrong (1990) reported a large *Miniopterus* from the Marojejy Massif with a forearm of 48 to 49 mm that they identified as *M*. *schreibersii*, a species based on more recent taxonomy does not occur on Madagascar (Goodman *et al*., 2022) or sub-Saharan Africa (Monadjem *et al*., 2020). The species they handled is with little doubt *M*. *gleni*.

Miniopterus gleni has been found at several different places on the Marojejy Massif. At the Sarahandrano site a single non-reproductive male was captured in a vanilla plantation (Falimiarintsoa, 2022). In the vicinity of Andasibe, specifically in the Bemanavy Cave, a day roost was found on 21 May 2016, and also in a rock shelter near Antanimbaribe on 29 May 2016. A visit to the Bemanavy Cave on 3 and 25 October 2019 did not result in the capture of this species. Whether it has natural local movements and occupies different roost sites, accounting for its presence in the cave during certain periods, or abandoned the site associated with human pressures, for example, is unclear. However, during the October 2019 visit to the site, it was mentioned by a local person from Mandena that children capture bats in the cave as dietary supplements, particularly during periods of food shortages (Rafanomezanjanahary, 2021).

One the basis of fecal pellets from a single individual of this species captured in a vanilla plantation above Sarahandrano, the diet is composed principally of Diptera and to a much less extent Coleoptera (Falimiarintsoa, 2022).

Miniopterus griveaudi Harrison, 1959

This species is known from central western and northern Madagascar (Goodman & Ramasindrazana, 2013). It appears to be broadly distributed on the Marojejy Massif and surrounding areas and known to occur from 100 to 750 m elevation. In the southwestern sector of the area, at the Sarahandrano site, it was trapped in relatively intact forest, presumably exiting a cave or rock shelter roost site(s) to forage in more open and lower areas; it was not found in any of the agroforestry and agricultural areas or in the vicinity of the village (Falimiarintsoa, 2022). In contrast, at the Antsahabe study site, it was captured in a variety of habitats, ranging from secondary forests, *savoka* (regenerating secondary grassland), agroforestry areas, rice fields, and near the village of Mandena; it was also found roosting in the Bemanavy Cave (Rafanomezanjanahary, 2021). At the Andatsakala site, single individuals were captured, one in the Andaimpotsy rock shelter, one over a rice field, and one in degraded forest (Todilahy & Goodman, unpublished data). During the 2021 elevational transect of the eastern slopes of the massif, it was found at Camp 1 (450 m) and Camp 2 (780 m) (Manana, 2022).

On the basis of an analysis of fecal pellets from four individuals captured at the Sarahandrano study site, the following groups of invertebrates were identified (Falimiarintsoa, 2022): Coleoptera (54.0%), Diptera (35.0%), and Lepidoptera (9.5%). At the Antsahabe study site and based on fecal pellets of 10 individuals, the diet was similar to that near Sarahandrano (Rafanomezanjanahary, 2021): Coleoptera (50%), Lepidoptera (33%), and Diptera (11%). On the basis of fecal pellets of five

individuals collected along the elevational transect of the eastern slopes of the park, the diet is dominated by Coleoptera (42.4%), Lepidoptera (37.2%), and Hymenoptera (25.4%) (Manana, 2022). Thus, based on these data, there seems to be some variation in the dietary preferences of this species.

On the basis of individuals of *M*. *griveaudi* handled at the principal study sites in and around the Marojejy Massif, some insights can be inferred on their breeding ecology, specifically seasonality. At Antsahabe between 29 September and 19 November 2019, 20 individuals were captured, including eight females of which three had small mammae, four with single embryos (ranging from 4 to 18 mm crown-rump length), and one with large mammae, and 12 males of which seven had abdominal testes with not convoluted epididymides and five abdominal testes with partially convoluted epididymides. Further three individuals of this species captured at Sarahandrano on 25 and 26 April, including one male and three females, showed no sign of breeding activity. An additional three individuals were trapped at Andratsakala between 6 March and 25 April 2022, which included two subadult females and one male with convoluted epididymides. Hence, it would appear that females give birth towards the end of the calendar year, a period coinciding with the start of the rainy season and the presumed period of greatest insect densities.

[***Miniopterus manavi* Thomas, 1906**

Pont and Armstrong (1990) captured members of the genus *Miniopterus* on Marojejy with a forearm length less than 40 mm and referred them to *M*. *minor*. On the basis of different lines of inference and more recent taxonomic research, these animals are presumably referable to members of the *M*. *manavi* group (*sensu lato*). These include a range of taxa that have been subsequently found on and around Marojejy: *M*. *aelleni*, *M*. *brachytragos*, and *M*. *griveaudi* (see species accounts above). In their molecular phylogeny of Malagasy *Miniopterus*, Christidis *et al*. (2014) found a clade (P3 clade) that could not be assigned to a named species and was part of the *manavi* species group (*sensu lato*), which included a bat obtain in the northwestern sector of Marojejy.]

Discussion

On the basis of the information presented herein, synthesizing a range of different published and unpublished data on the bats occurring in and around the Parc National de Marojejy, a total of 18 bat species has been documented. An additional four species, including one Pteropodidae (*Eidolon dupreanum*) and three Molossidae (*Chaerephon leucogaster*, *Mops midas*, and *Mormopterus jugularis*), are anticipated to occur in the immediate area, but require further documentation. There are numerous areas of the massif that have yet to be the subject of relatively intensive bat surveys and it is almost certain that such work will document additional species in and around the park.

Cumulative trapping effort since late 2019 has been considerable and at the sites of Sarahandrano and Andatsakala with about 10,900 meter/hours of mist netting and over 1076 hours of harp trap capture. (Such data are not available for Antsahabe.) With these two devices, 470 individual bats were captured at all three sites. Further, an additional 57 bats were trapped in nearby caves and rock shelters.

Use of caves and rock shelters

The geological formation of Marojejy is primarily granitic (Goodman *et al*., 2018) and lacks areas of sedimentary rock typical of western Madagascar, particularly limestone with karst habitat and extensive erosion and underground cave systems. During the bat surveys in and around the Marojejy Massif, a total of six species were found roosting in caves or rock shelters (Table 2). In certain cases, the difference between these two types of underground structures is ambiguous. In general, the sites were shallow, a maximum of 5 m high and 10 m deep, and largely dark spaces under large, eroded boulders, sometimes partially covered by soil, and with entrances sufficiently large for small insectivorous bats to exploit. In fact, based on the definitions presented in the methods section all of the “caves” visited during our work are best referred to as rock shelters. In certain cases, the sites were along river and stream banks, and after heavy rains would at least be partially flooded. Hence, in general, one limiting factor that can be suggested for the bats of the Marojejy Massif is the lack of cave systems and several species known from the area and generally cave-dwelling were not found in these underground formations.

The dominant bat occurring in these caves and rock shelters was *Paremballonura atrata*, and in many cases the only species found in a given structure. In the watershed below the Andatsakala study site, there are numerous drainages leading to

Table 2. The bats known from caves and rock shelters in and around the Parc National de Marojejy. The different sites in their respective sector maps are indicated on Figure 1. All of these sites are best considered as rock shelters based on the definition given herein.

Antsahabe area
1. Antanimbaribe rock shelter, 14.49519°S, 49.59583°E (based on fieldwork of Rasoanoro in May 2016)
Miniopterus ambohitrensis
M. gleni
2. Beamalona or Antsahanisoavina rock shelter, 14.45670°S, 49.80622°E (based on fieldwork of Rafanomezanjanahary in October 2019)
Paremballonura atrata
3. Bemanavy, 14.45946°S, 49.80271°E (based on fieldwork of Rasoanoro in May 2016, and Rafanomezanjanahary in October 2019)
Paremballonura atrata
Coleura kibomalandy
Miniopterus ambohitrensis
M. brachytragos
M. gleni
M. griveaudi

Andatsakala area
1. Ambodivohitra rock shelter, 14.43893°S, 49.86213°E (based on fieldwork of Todilahy in March and April 2022)
Paremballonura atrata
2. Andaimpotsy rock shelter, 14.40235°S, 49.89531°E (based on fieldwork of Todilahy in March and April 2022)
Paremballonura atrata
3. Antsahafoaka rock shelter, 14.39810°S, 49.87908°E (based on fieldwork of Todilahy in March and April 2022)
Paremballonura atrata
4. Antsahambary 1 rock shelter, 14.40262°S, 49.89025°E (based on fieldwork of Todilahy in March and April 2022)
Paremballonura atrata
5. Antsahambary 2, rock shelter 14.41276°S; 49.89163°E (based on fieldwork of Todilahy in March and April 2022)
Paremballonura atrata
5. Bemanasy rock shelter, 14.40806°S, 49.86142°E (based on fieldwork of Todilahy in March and April 2022)
Paremballonura atrata

the Sambava River, often with rock shelters under large partially exposed boulders, and at such sites small populations of *P*. *atrata* occurred. The one such site, Bemanavy near Antsahabe, with a relatively tall ceiling rising to 5 m, had the greatest diversity of bat species.

Eleven of the 18 bat species documented from the Marojejy area are known elsewhere on the island to occupy caves for day roost and breeding sites (Table 1). *Triaenops menamena* is only known from the Marojejy area based on an individual found in a cave by Pont and Armstrong (1990). Of these 11 taxa, six were found in the Marojejy area in caves and rock shelters during our intensive surveys starting in late 2019 (Tables 2 & 3). Excluding the case of *T*. *menamena*, those not found in caves during our work in and around the massif include *Rousettus madagascariensis*, *Macronycteris commersoni*, *Myotis goudoti*, and *Miniopterus aelleni*. Two of the most commonly captured bats during the recent surveys and absent from cave roosts were *R*. *madagascariensis* and *Myotis goudoti*; Pont and Armstrong (1990) did find a few *M*. *goudoti* occupying caves. The fact that these two species have notably large populations at our three principal study sites and were not found occupying caves, indicates that other unexplored cave systems or rock shelters occur on the massif. It is our impression that cave roosting sites might be a limiting factor for the local bat populations and for certain species they roost higher up on the massif and descend each dusk to forage.

Bat species habitat use and capture rates

A number of intensive bat surveys have been conducted since late 2019 at three different sites around the park (Figure 1), which included work within relatively intact forest, secondary forest, *savoka* (regenerating secondary grasslands), a range of different agroforestry areas (most with some closure to the over story), rice fields, and village settings. A synthesis of where the different bat species were captured across this habitat matrix provides some insights into their utilization or passage in these different zones (Table 3). The abundance of bats in these different habitats showed a statistically significant trend ($\chi 2 = 1996$; degree of freedom = 3942; $P = < 0.0001$). Different bat species do not consistently occur in the habitats between the forest to village settings and show ecological preferences.

Table 3. Habitat utilization of the documented bat fauna of Marojejy based on captured individuals during inventory studies starting in late 2019 at the sites of Antsahabe, Andatsakala, and Sarahandrano. This data set includes 13 of the 18 species documented from the massif and the balance are only known from pre-2019 records. Species endemic to Madagascar are preceded by an asterisk.

	Relatively intact forest[1]	Secondary forest	*Savoka*[2]	Agroforestry habitat[3]	Rice fields	Village settings	Caves and rock shelters
**Rousettus madagascariensis*	X	X	X	X	X	X	–
**Macronycteris commersoni*	X	X	–	X	–	X	–
**Paremballonura atrata*	X	X	–	–	–	–	X
**Coleura kibomalandy*	–	–	–	–	–	–	X
**Chaerephon atsinanana*	–	–	–	–	–	X	–
Mops leucostigma	–	–	–	–	–	X	–
**Myotis goudoti*	X	X	X	X	X	X	–
**Laephotis matroka*	–	–	–	X	–	–	–
Miniopterus aelleni	X	X	–	–	–	–	–
**Miniopterus ambohitrensis*	X	X	–	X	–	–	–
**Miniopterus brachytragos*	–	–	–	–	–	–	X
**Miniopterus gleni*	–	–	–	X	–	–	X
**Miniopterus griveaudi*	X	–	X	X	X	X	X

[1] Includes riverine forest within the protected area.
[2] Regenerating secondary grasslands.
[3] Different sorts of plantations generally, but not exclusively, under some canopy cover and including vanilla, coffee, litchis, pineapples, and banana.

Table 4. Trapping effort and number of captures at the sites of Andatsakala (Todilahy & Goodman, unpublished data) and Sarahandrano (Falimiarintsoa, 2022), as well as the elevational transect (Manana, 2022), across different sampled habitats, excluding caves and rock shelters[1].

	Relatively intact forest	Secondary forest	*Savoka*[2]	Agroforestry habitat[3]	Rice and open agriculture	Village settings
Cumulative number of harp trap hours[3]	440	144	132	132	144	84
Cumulative number of mist net meter/hours[4]	5663	654	1047	1284	1107	1154
Combined harp trap and mist netting effort	6103	798	1179	1316	1251	1238
Captures by species						
Rousettus madagascariensis	1	23	4	41	41	0
Macronycteris commersoni	5	2	0	1	0	0
Paremballonura atrata	3	0	4	9	0	0
Chaerephon atsinanana	0	0	0	0	25	0
Mops leucostigma	0	0	0	0	6	0
Myotis goudoti	73	5	1	2	4	0
Laephotis matroka	0	0	0	1	0	0
Miniopterus aelleni	3	0	0	0	0	0
Miniopterus ambohitrensis	2	0	0	0	0	0
Miniopterus brachytragos	0	0	0	1	0	0
Miniopterus gleni	0	0	0	1	0	0
Miniopterus griveaudi	10	0	0	1	1	0
Total number of captures	**97**	**30**	**9**	**57**	**77**	**0**
Ratio of effort/captures	**0.02**	**0.04**	**0.01**	**0.04**	**0.06**	**0.0**

[1] Data from the site of Antsahabe are not included herein and hence measures of efforts were greater than presented in this table.
[2] Regenerating secondary grasslands.
[3] At all of the sites in and around Marojejy inventoried since the latter portion of 2019, the same style harp trap has been employed (see Methods). The figures reported here are the cumulative number of hours the trap was functioning in each habitat.
[4] Calculated as the cumulative number of meter/hours mist nets were employed in a given habitat. For example, two nets of 12 m in place for three hours tabulates to 72 meter/hours.

Although trapping effort with mist nets and harp traps was not equal in the different habitats (Table 4) capture rates were highest and in decreasing order: rice and open agriculture, agroforestry, secondary forest, intact forest, *savoka*, and villages. The number of captures in natural lowland forest, albeit in some cases degraded, was about half of the agroforestry and secondary forest habitats. No species was captured exclusively in relatively intact forest formations. These results emphasize that the bat fauna of the Marojejy area is not forest-dependent *per se*. However, presumably areas with natural

forest hold include day roost sites either in hollows of large trees or caves and rock shelters.

Conservation and future work

The Parc National de Marojejy, which in 1996 had an estimated forest cover of 50,412 ha, has been the subject of deforestation over the past decades, with slightly more than a 600 ha reduction in forest cover between 1996 and 2006 and 240 ha between 2006 and 2016 (Goodman *et al*., 2018). It is important to mention that these figures are derived from LANDSAT 5, 7, and 8 images and at a relatively course scale at the level of a single pixel (30 x 30 m). Hence, finer level disturbances, such as selective logging of hardwoods or other forms of exploitation, would not be picked up by these analyses. For example, the lowland forests, particularly in the eastern and northeastern portions of the protected area, have been the subject of illegal exploitation of rosewood of the genus *Dalbergia* (Patel, 2007). Maintaining forest integrity of the Parc National de Marojejy is critical for the continued existence of its unique biota, which includes a considerable number of local microendemics and forms one of the pearls of Madagascar's terrestrial protected area system.

With regards to bats, Marojejy has a local fauna of 18 documented species, which is the highest for any eastern moist evergreen forest known to date (Goodman *et al.*, 2018). This is certainly related to the proportionately intensive effort that has been devoted to studying Marojejy's vertebrate fauna, including bats, superimposed on the ecological and elevational variation of the site. It is easy to imagine that other large protected areas, such as Masoala and Makira with additional survey efforts and associated systematic research, would also yield important levels of diversity. The bat fauna of Marojejy does not contain any Critically Endangered or Endangered species, and two species, *Pteropus rufus* and *Rousettus madagascariensis*, are classified as Vulnerable; the balance of species fall within non-threatened categories (Table 1). Further, no bat species in this protected area can be considered strictly forest dependent.

Some pressures do exist at a local scale. Bat species making their day roosts in caves or rock shelters in the surrounding foothills of the massif are subject to at least occasional exploitation for bush meat. In late 2019, a local guide mentioned that the Bemanavy Cave close to Antsahabe, was visited by young people from neighboring villages to capture insectivorous bats for dietary protein supplement. Further, a similar form of exploitation occurs in the rock shelters near Andatsakala, where small insectivorous species are exploited during periods of food shortage (Todilahy, unpublished data). This is presumably a problem in and around other portions of the massif where bat roosts are accessible. We have no direct information on the exploitation of fruit bats of the family Pteropodidae in and around Marojejy, a group that is widely hunted across portions of the island for food (Andrianaivoarivelo *et al*., 2022). Another pressure near Andatsakala mentioned by local people associated with insectivorous bats in areas with vanilla plantations is that certain people are afraid of the bats roosting in such sites and send others into day roost sites to kill the animals (Todilahy, unpublished data).

While the Marojejy Massif has a notably rich bat fauna, it is almost certain with further efforts to explore poorly known areas of the park and surrounding areas, measures of species diversity will increase. Further, particular emphasis should be given to finding and inventorying caves, crevices, and rock shelters for bats, which will certainly result in an augmentation of what is known about the protected area's chiropteran fauna.

Acknowledgements

We are grateful to the Malagasy Government and Madagascar National Parks for permission to conduct research in the Parc National de Marojejy and surrounding areas (N°280/19/MEDD/SG/DGEF/DGRNE, N°57/20/MEDD/SG/DGEF/DGRNE, N°191/20/MEDD/SG/DGGE/DAPRNE/SCBE. Re, N°048/22/MEDD/SG/DGGE/DAPRNE/SCBE. Re). A number of local people helped with the bat surveys and we are grateful for their assistance, including Philibert Belazaina of Sarahandrano, Edouard Mahazandry of Manantenina, and Frédéric Rahamavita of Andatsakala. The work at Antsahabe, Sarahandrano, and Andatsakala was financed by a NIH-NSF NIFA Ecology and Evolution of Infectious Disease Award grant (1R01-TW011493-01) awarded to Charles Nunn from Duke University as principal investigator. Field research associated with the elevational transect of Marojejy was financed by a grant from Korea International Cooperation Agency (KOICA) to UNESCO Madagascar, Madagascar National Parks, and Association Vahatra. We are grateful to Sébastien Puechmaille for sequencing tissue samples of the Marojejy population of *Coleura kibomalandy*. For comments on an earlier version

of the manuscript, which notably improved its presentation, we are grateful to Ara Monadjem.

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