The bats of the Andrafiamena-Andavakoera protected area, northern Madagascar

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Abstract

In late 2023 an inventory was conducted of the locally occurring bat species in the Andrafiamena-Andavakoera protected area of northern Madagascar, where only five bat species had been previously recorded. Our survey method was based for the most part on direct trapping of bats with mist nets and a harp trap, and to a lesser extent visiting cave roost sites and capturing them with a butterfly net. In total, 12 species were found to occur in the protected area, of which eight species are endemic to Madagascar and the balance only found in the Malagasy Region; one of these species, Paratriaenops auritus, is a microendemic to limestone areas of northern Madagascar and the Andrafiamena-Andavakoera protected area holds an important population. Of these 12 species, four (Eidolon dupreanum, Pteropus rufus, Rousettus madagascariensis, and Paratriaenops auritus) are considered Vulnerable based on the IUCN Red List. Local caves within the protected area form important day roost sites for bats and should be the subject of enhanced conservation programs.

Keywords: Chiroptera, inventory, ecology, reproduction, distribution, Andavakoera-Andrafiamena

Résumé détaillé

Un inventaire des chauves-souris a été entrepris dans la zone protégée d'Andrafiamena-Andavakoera pendant les mois de novembre et de décembre 2023, en vue de connaître la richesse chiroptérologique de cette zone située dans la partie nord de Madagascar et de faire progresser ainsi les connaissances sur la distribution des espèces malgaches. Cette zone est représentée par différentes formations forestières, notamment une forêt semi-décidue humide, une forêt sèche à feuille caduque et une forêt à feuilles caduques sur formation karstique connu sous le nom de « *tsingy* » en Malagasy ; ainsi qu'une géologie considérablement variée ; la partie nord est principalement composée de calcaire du Jurassique moyen, de calcaire argileux et de marne, tandis que dans la zone sud de l'aire protégée se trouvent d'autres formations géologiques qui ne sont généralement pas associées à la formation de passages souterraines.

La capture des chauves-souris a été effectuée à l'aide des filets japonais et un piège harpe dans cinq sites de l'aire protégée : 1) Forêt de Binara (13.101°S, 49.240°E) à 300 m d'altitude et à 5,4 km Est d'Ankatsaka ; 2) Forêt d'Antsahabe (12.894°S, 49.294°E) à 360 m d'altitude et la Grotte d'Antsahabe (12.8950°S, 49.2949°E) à 315 m localisée à 2,8 km Nord-ouest du village d'Anjakely ; 3) Forêt d'Anjakely (12.913°S, 49.328°E) à 1,3 km Sud-est du village d'Anjakely ; 4) Grotte d'Andavapanihy (12.844766°S, 49.348027°E) ; et 5) Grotte d'Antoby (12.884567°S, 49.302533°E) à 300 m d'altitude, près du village de Maroadabo.

Au total, 12 espèces de chauves-souris ont été trouvées lors de notre inventaire de la zone protégée Andrafiamena-Andavakoera dont trois espèces de Pteropodidae (Eidolon dupreanum, Pteropus rufus, Rousettus madagascariensis) ; une espèce de Hipposideridae (Macronycteris commersoni); deux espèces de Rhinonycteridae (Paratriaenops auritus, Triaenops menamena) ; une espèce de Emballonuridae (Paremballonura tiavato) ; deux espèces de Molossidae (Chaerephon leucogaster, Mops leucostigma) ; une espèce de Vespertilionidae (Myotis goudoti) et deux espèces de Miniopteridae (Miniopterus aelleni, M. griveaudi). Parmi ces 12 espèces, quatre (E. dupreanum, Pteropus rufus, Rousettus madagascariensis et Paratriaenops auritus) sont classées Vulnérable selon la Liste rouge de l'UICN. Après l'identification des chauvessouris, les mesures standards (en mm) et la masse corporelle (en g) ont été prises. Les données sur les organes reproducteurs ont été également notées. Afin d'étudier les aspects du régime alimentaire des chauves-souris insectivores locales, des excréments ont également été collectés.

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L'objectif de cet article est de présenter les résultats de l'inventaire des chauves-souris menés à Andrafiamena-Andavakoera à la fin de l'année 2023 dans le cadre d'un inventaire biologique, en se concentrant sur les espèces qui y sont présentes, leur distribution ainsi que leur écologie de reproduction. Davantage de recherches seraient néanmoins nécessaires pour approfondir les connaissances sur la biologie et l'écologie des chauves-souris de cette aire protégée.

Mots-clés : Chiroptera, inventaire, écologie, reproduction, distribution, Andavakoera-Andrafiamena

Introduction

In general, for a tropical island of its size, the bat fauna of Madagascar can be considered as reasonably well known (Goodman, 2011). Chiropterological surveys conducted over the past decades, including the collection of specimens for taxonomic work and associated tissues for molecular studies, have resulted in numerous advancements with regards to insights into the natural history of locally occurring bats, their systematics, and distribution (Goodman & Ramasindrazana, 2013; Goodman *et al.*, 2022). One region of Madagascar that has been the focus of bat surveys and studies on the ecology and systematics of these animals is the sedimentary rock zones in the far north (Figure 1), areas with often karstic topography and different types of dry deciduous forests. The high bat species diversity of this region is associated with considerable cave formations in areas of exposed limestone providing day roost shelters with a range of microclimates (Cardiff, 2006).

The most extensively studied of these northern areas is Ankarana with 17 documented species of bats (Goodman *et al.*, 2018a), representing 37% of the 46 species on the island, and the subject of different bat inventories (Goodman *et al.*, 2005; Cardiff, 2006), studies on species level systematics (Goodman *et al.*, 2006, 2009, 2012), work on their ecology and conservation (Andrianiaina *et al.*, 2002; Cardiff *et al.*, 2009; Noroalintseheno Lalarivoniaina *et al.*, 2009; Vololona *et al.*, 2020), and zoonotic



Figure 1. Map of northern Madagascar showing the different official protected areas in proximity to Andrafiamena-Andavakoera.

diseases (Brook et al., 2019). Other protected areas in the same region, namely Analamerana and Montagne des Français, with 11 species at each site, have also been inventoried for bats, but less extensively than Ankarana (Goodman et al., 2005, 2018b; Raherilalao et al., 2022). One of the protected areas in the north that is poorly known for this group of mammals is Andrafiamena-Andavakoera, for which only five species have been previously reported (Goodman et al., 2018a). Much of this protected area is readily accessible by car or relatively short hikes and the lack of information on the bats is mostly associated with portions of the island not having been the subject of detailed biological inventories. The subject of this paper is to present the results of bat surveys conducted in Andrafiamena-Andavakoera in late 2023 in the context of a biotic inventory, concentrating on species present, distribution, and reproductive ecology.

Description of the site

The Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera was named as a new protected area in 2015. This area of 73,319 ha has different forest formations, including moist semi-deciduous forest, dry deciduous forest, dry deciduous forest on karstic limestone (*tsingy* in Malagasy) (Gautier *et al.*, 2018), of which in 2016 about 12,535 ha remain with natural forest (Goodman *et al.*, 2018a); for at least land vertebrates this protected area is not particularly well known (Goodman *et al.*, 2018b). Further, the underlying geological formations are notably complex (see below). More precise details on different aspects of the protected area are given by Tahinarivony & Goodman (2025, herein – intro chapter).

Methods

The main technique we employed to document the bats present in the Andrafiamena-Andavakoera protected area was capture with Japanese mist nets (6, 8 or 12 m long and 2.6 m height, with four pockets and mesh of 24 or 36 mm) placed across flight pathways. We also employed a harp trap (two-bank Austbat Harptrap, Faunatech, Rydalmere, Australia) installed at cave entrances and along trails that might serve as bat flyways, often placed in areas with constrictions in vegetation forming narrow passages. As bats are active from after sunset until 04h30 or 05h00, these different devices were installed before their evening exodus from day roost sites and disassembled after dawn. In some cases,

mist nets were closed from around 21h to 3h, periods of notably reduced bat activity. Some animals were captured within cave day roosts with butterfly nets and exiting building roost sites with mist nets. No echolocation recordings were made during this study.

Each trapping site was given a unique sequential number and a GPS (waypoint WGS84) was used to record the geographic coordinates and elevations. The principal study areas included (Figure 2):

- 1) Binara Forest Madagascar, ex-Province d'Antsiranana, Région DIANA, Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera, Binara-Andavakoera Forest. 5.4 km E Ankatsaka, 13.101°S, 49.240°E, 300 m. Much of the work took place in the vicinity of the camp site near the Ambaratra River and on the trails leading down to this area. This area was worked between 16 and 23 November 2023.
- 2) Antsahabe _ Madagascar, ex-Province d'Antsiranana. Région DIANA, Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera, Antsahabe Forest, 2.8 km NW Anjakely (village), 12.894°S, 49.294°E, about 360 m. Most of the bat capture took place in the Antsahabe Cave located at 12.8950°S, 49.2949°E, 315 m. This area was studied between 25 and 1 December 2023.
- Madagascar, 3) Anjakely _ ex-Province DIANA, d'Antsiranana, Région Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera, Anjakely Forest, 1.3 km SE Anjakely (village), 12.913°S, 49.328°E, about 420 m. Our efforts concentrated in the zone starting at the trail bifurcating from the road to Ampantsona and entering into the protected area and leading up to the Piscine Naturelle. This area was inventoried between 2 and 8 December 2023.
- 4) Andavapanihy Cave Madagascar, ex-Province d'Antsiranana, Région DIANA, Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera, 12.844766°S, 49.348027°E, 375 m. During of the reconnaissance trip for the inventory, the Andavapanihy Cave was briefly visited and some preliminary observations were made of bats occurring in this cavern and on the basis of photographs made by Rio Heriniaina some bats could be identified.
- 5) Antoby Cave Madagascar, ex-Province d'Antsiranana, Région DIANA, Paysage Harmonieux Protégé d'Andrafiamena-



Figure 2. Map of the different bat study sites included in the Andrafiamena-Andavakoera protected area in the context of the present study.

Andavakoera, near village of Maroadabo, 12.884567°S, 49.302533°E, 300 m. This cave was briefly visited on 4 December 2023 and bats were captured with a butterfly net.

For captured bats that were not released after identification, standard external measurements were taken in millimeters (Mitchell-Jones & McLeish, 2004): total length, tail length, hind foot length (not including claws), tragus length (certain species), ear length, and forearm length. We also recorded body mass in grams with Pesola scales of the appropriate size to maximize the measurement precision. For collected individuals, data were obtained on the condition of reproductive organs and include for males the width and length of testes and the development of the epididymis and for females the size of the mammae and in pregnant individuals the number of embryos and their crown-rump length measured from the head to the buttocks. To study aspects of the dietary regime of the local insectivorous bats, scats were collected. Voucher specimens are housed in the Mention Zoologie et Biodivesité Animale, Université d'Antananarivo (formerly Université d'Antananarivo, Département de Biologie Animale or UADBA) and the Field Museum of Natural History (FMNH), Chicago. We define the Malagasy Region as Madagascar, and its nearshore islands, and the archipelagos of the Seychelles, Comoros, and Mascarenes (La Réunion and Mauritius).

Geological setting and relation to the occurrence of caves

The exposed geology of the Andrafiamena-Andavakoera protected area is variable (Crowley & Sparks, 2018a). The northern portion is composed largely of Middle Jurassic limestone, clayeylimestone, and marl. This is the section with karst topography and associated caves and limestone pinnacles known as tsingy in Malagasy. Further south in the protected area are different geological formations, which are not generally associated with the formation of underground passages. In contrast, in the neighboring protected areas of Analamerana and Ankarana, the principal formations are Middle Jurassic limestone (Crowley & Sparks, 2018b, 2018c), but in Ankarana the cave formations are distinctly more extensive. Montagne des Français in contrast is largely composed of Upper Cretaceous sandstone (Crowley & Sparks, 2018d) and containing some caves and rock shelters and generally shallow.

Results General aspects

In total, 12 species of bats were found during our inventory of the Andrafiamena-Andavakoera protected area. Of these, seven had not been previously recorded at the site (Goodman *et al.*, 2018a). With the exception of four species, which have a broader distribution in the Malagasy Region (*Mops leucogaster, Mops leucostigma, Miniopterus aelleni*, and *M. griveaudi*), the balance is endemic to the island. Below we present an annotated checklist on the 12 species found during the inventory. Species endemic to Madagascar are preceded by an asterisk.

Family Pteropodidae

Eidolon dupreanum* (Pollen, 1866) **English: Madagascar Straw-colored Fruit Bat **French:** Roussette paillée de Madagascar **IUCN Redlist status:** Vulnerable (VU) **Locality found during inventory**: Observed roosting in the Andavapanihy Cave near Ambery. No other records.

*Pteropus rufus E. Geoffroy, 1803
English: Madagascar Flying Fox
French: Renard volant de Madagascar
IUCN Redlist status: Vulnerable (VU)
Locality found during inventory: This species was observed on two occasions flying over the Anjakely

Table 1. Bat species recorded by site during the Andrafiamena-Andavakoera biological inventory in November and December 2023. Species preceded by an asterisk (*) are endemic to Madagascar and those that are <u>underlined</u> not previously documented in the protected area. See Methods section for details on the sites.

	Binara	Antsahabe	Anjakely	Andavapanihy Cave (Ambery)
Pteropodidae				
* <u>Eidolon dupreanum</u>				+
* <u>Pteropus rufus</u>			+	
* <u>Rousettus madagascariensis</u>			+	+
Hipposideridae				
*Macronycteris commersoni	+	+	+	
Rhinonycteridae				
*Paratriaenops auritus	+	+	+	
* <u>Triaenops menamena</u>	+		+	
Emballonuridae				
*Paremballonura tiavato		+	+	
Molossidae				
Chaerephon leucogaster			+	
Mops leucostigma			+	
Vespertilionidae				
*Myotis goudoti	+	+	+	+
Miniopteridae				
Miniopterus aelleni		+		+
Miniopterus griveaudi		+		+
Number of bat species	4	6	9	5

Forest, once after dusk and the other before sunrise. Presumably there is a day roost site relatively close to the Anjakely area.

Rousettus madagascariensis* G. Grandidier, 1928 **English: Madagascar Rousette

French: Roussette de Madagascar

IUCN Redlist status: Vulnerable (VU)

Locality found during inventory: Observed roosting in the Andavapanihy Cave near Ambery. Two individuals were observed at night in the Anjakely Forest feeding on *Schizolaena viscosa* (Sarcolaenaceae) in a tree near the forest edge.

Family Hipposideridae

Macronycteris commersoni* (E. Geoffroy, 1803) **English: Commerson's Leaf-nosed Bat **French:** Phyllorhine de Commerson

IUCN Redlist status: Near threatened (NT)

Systematics: This species was previously placed in the genus *Hipposideros* and based mostly on molecular characters has been transferred with the other large-bodied members of the Afro-Malagasy *commersoni*-group to the genus *Macronycteris* (Foley *et al.*, 2017).

Localities found during inventory: Over the course of six nights, nine individuals, all males, were netted over largely calm water pools associated with the Ambaratra River and in close proximity of the Binara Forest camp. One individual was captured in a harp trap while exiting the Antsahabe Cave and another with the same device along a trail in the Anjakely Forest.

Morphological characters: There was considerable size difference between the male *M*. *commersoni* captured during the inventory (Table 2) and all except for one did not appear to be in a reproductive state. No females were captured during the inventory and this seemingly biased sex-ratio may be related to differential seasonal movements (see below).

Reproduction: Of the 11 male *M. commersoni* captured during the inventory, 10 had small abdominal testes, not notably developed epididymides, and did not appear to be reproductively active. In the one case of an animal in reproductive condition, the testes measured 4 x 7 mm and the epididymis were notably convoluted. Further, this individual had a well-developed white crown tuft in the folds of the frontal sac (Figure 3).

In a closely related species of southern Africa, *M. vittatus*, females roosting in a Zimbabwean

cave showed notable seasonality in their presence and males remained faithful to the site (Cotterill & Fergusson, 1999). In another closely related species, M. gigas, from Kenya, pregnant females left their roosts after copulation and returned approximately eight weeks later to give birth (McWilliam, 1982). The observation that no female was captured in the Andrafiamena-Andavakoera protected area during the months of November and December 2023 may also be related to energetic demands during pregnancy and these individuals may have moved to other areas with more abundant or more easy to catch food resources. Larger scale movements may also explain the pattern, as found for this species in the Kirindy Forest, north of Morondava, where it showed a highly seasonal presence, with males returning before females in the period between mid-November and mid-December (Rakotondramanana, 2011).

Family Rhinonycteridae

Paratriaenops auritus* (G. Grandidier, 1912) **English: Golden Trident Bat **French:** Triénope doré

IUCN Redlist status: Vulnerable (VU)

Systematics: This species was previously considered a member of the genus *Triaenops* and on the basis of morphological and molecular data has been transferred with *T. furculus* to the genus *Paratriaenops* (Benda & Vallo, 2009). Molecular work on Malagasy members of what would become *P*.



Figure 3. The individual illustrated here is an adult male *Macronycteris commersoni*, which on the basis of its sexual organs was in breeding condition and had a notably developed white crown tuft in the folds of the frontal sac. (Photo by Voahangy Soarimalala.)

presented separately and as	ssociated t-st	atistics given.							
Species	Sex	Total length	Tail length	Hindfoot length (minus claws)	Tragus length	Ear length	Forearm length	Mass	Mass of pregnant females
Hipposideridae									
Macronycteris commersoni ¹	50 70	147.7 ± 4.71, 136-150, n = 11	35.6 ± 2.88, 32- 42, n = 11	17.1 ± 1.64, 15- 21, n = 11	-	28.8 ± 1.83, 25- 31, n = 11	94.6 ± 2.61, 91- 100, n = 11	52.8 ± 4.20, 44.3- 58.9, n = 11	1
Rhinonycteridae									
Paratriaenops auritus	PQ	75.2 ± 2.39, 71- 79. n = 9	21.3 ± 1.80, 17- 23. n = 9	6.6 ± 0.52, 6-7, n = 8	1	17.2 ± 0.44, 17- 18. n = 9	44.9 ± 0.93, 44- 47 n = 9	6.3 ± 0.55, 5.5- 7.5, n = 9	
	0+ 0+	77.6 ± 2.32, 73-	23.6 ± 1.53, 21-	7.0 ± 0.38, 6-8,		18.0 ± 0.73, 17-	48.1 ± 1.32, 45-	6.4, n = 1	9.2 ± 0.58, 8.1-
		84, n = 22	26, n = 22	n = 21		19, n = 22	51, n = 22		10.3, n = 21
		t = 2.57, P = 0.01,	t = 3.37, P = 0.000	n.s.		t = 3.44, P =	t = 7.77, P <	t = 13.1, <i>P</i> =	
		df = 15	0.003, df = 13			0.001, df = 24	0.001, df = 21	0.0001, df = 16 ²	
Triaenops menamena ³	0+ 0+	93.7 ± 3.05, 91-	$31.3 \pm 1.16, 30-$	$7.0 \pm 1.00, 6-8,$	1	14.3 ± 0.58, 14-	$51.0 \pm 1.00, 50-$		12.0 ± 0.83, 11.1-
Emballonuridae		<i>ai</i> , = - 0	0e, II - 0			-0,	<u>7</u> , 11 - 3		12.1, 11 - 0
Paremballonura tiavato	Combined	59.3 ± 2.35, 58-	15.6 ± 1.24, 13-	6.1 ± 0.60, 5-7,	5.7 ± 0.50, 5-6,	12.3 ± 0.71, 11-	<u>37.7</u> ± 1.19, 36-	3.8 ± 0.39, 3.2-	4.4 ± 0.21, 4.1-
		65, n = 9	17, n = 9	n = 9	n = 9	13, n = 8	39, n = 9	4.2, n = 5	4.6, n = 4
Molossidae									
Chaerephon leucogaster	Combined	91.9 ± 2.43, 88- 06 n = 12	29.1 ± 2.47, 27- 34 n = 12	$6.2 \pm 0.44, 6-7, 0.5 \pm 13$	1	17.1 ± 0.49, 16- 18 n = 13	34.4 ± 0.96, 33- 36 n = 13	8.9 ± 0.45, 8.2- 0 3 n = 5	11.1 ± 0.97, 9.1- 12 5 n = 8
Mops leucostigma	60	<u>113, n = 1</u>	44, n = 1	9, n = 1		18, n = 1	45, n = 1	24.7, n = 1	2
Vespertilionidae									
Myotis goudoti	Combined	$90.5 \pm 5.69, 84-$	41.5 ± 2.64 , $38-$	$6.8 \pm 0.50, 6-7, n = 4$	$7.5 \pm 0.58, 7-8, n = 4$	13.3 ± 0.96, 12- 14 n = 4	$37.5 \pm 1.91, 36-$	4.8, 4.3-5.2, n = 2	7.0, 7.0-7.0, n = 2
Miniopteridae					+				
Miniopterus aelleni	Combined	$90.3 \pm 0.58, 90-$	41.0 ± 1.73, 39- 42 n = 3	6.7 ± 0.58, 6-7, n = 3	5, 5-5, n = 3	10, 10-10, n = 3	36.3 ± 1.15, 35- 37 n = 3	5.1 ± 0.06, 5.0- 5.1 n = 3	
Miniopterus griveaudi	Combined	84.6 ± 2.70, 81- 88, n = 5	<u>39.6 ± 2.07, 39-</u> 40, n = 5	5.8 ± 0.45, 5-6, n = 5	5.6 ± 0.55, 5-6, n = 5	9.6 ± 0.89, 8-10, n = 5	36.4 ± 0.89, 35- 37, n = 5	5.1 ± 0.25, 4.9- 5.4, n = 3	6.5, 6.0-6.9, n = 2

Table 2. External measurements in millimeters and body mass in grams for different bat species captured in the Andrafiamena-Andavakoera protected area. Data are presented as mean ± standard deviation, minimum-maximum measurements, n = number of specimens. When no sexual dimorphism was found, sexes combined and when present the sexes are

auritus and *P. furculus* provided the needed details on the delineation of their distribution, with *P. auritus* being endemic to northern Madagascar, particularly in areas with exposed limestone, with the south limit being between Ambilobe and Ambanja (Russell *et al.*, 2007, 2008).

Localities found during inventory: *Paratriaenops auritus*, listed as Vulnerable on the IUCN Red List, is a cave roosting species limited to northern Madagascar. This species was found at all three of the inventoried sites (Figure 4), including a considerable number trapped entering and exiting the Antsahabe Cave. Information on the diet of this species in the Andrafiamena-Andavakoera area is present by Razafindranosy *et al.* (2025, herein).

Morphological characters: This species shows sexual size dimorphism in external measurements, with females being on average larger than males (Table 2). Pregnant females with well advanced embryo development weighed about 30% heavier than females not actively reproducing. **Reproduction:** Of the 16 female specimens collected from the Antsahabe Cave between 27 and 30 November with single embryos, the average crown-rump length was 19.3 mm (range 17-21) and of the five females obtained at Binara between 19 and 22 November the average crown-rump measure was 17.6 mm (range 17-18). Given the differences in the periods the two sites were inventoried and presumed embryo growth, it can be surmised that at a regional scale the breeding of this species is notably synchronized. Without exception, all of the 28 pregnant females captured during the inventory had auxiliary pubic nipples (nipples located on the ventral abdominal body wall, Figure 5), for which the function remains unclear, but at the very least probably act as holdfasts for neonates (Simmons, 1993), and not one of the three non-pregnant females had auxiliary pubic nipples. This indicates that these structures in females are associated with breeding and appear to retract during periods an individual is not reproducing.



Figure 4. One of the most beautiful endemic bats of Madagascar is *Paratriaenops auritus*, known in English as the Golden Trident Bat and in French as Triénope doré, which is restricted to the north. During our survey of the Andrafiamena-Andavakoera protected area, a considerable number of individuals of this species were captured and this zone is an important area for this regional endemic. (Photo by Voahangy Soarimalala.)



Figure 5. In certain groups of bats, auxiliary pubic nipples have been documented (Simmons, 1993), although the precise function of these remains unclear, but is clearly associated with reproduction and perhaps as additional holdfasts for neonates. In all of the 28 individuals of *Paratriaenops auritus* captured that were pregnant, all had these auxiliary nipples and three non-pregnant females lacked these structures. (Photo by Voahangy Soarimalala.)

In contrast to the advance breeding state of females, of the six males collected, not one showed active signs of reproduction. In all cases the testes were reduced in size and the epididymides not convoluted. In the closely related African species, *Triaenops afer* in Tanzania, spermatogenesis is active from June to October and by November has all but ceased (Mainoya, 1979). Hence, for *P. auritus* a parallel seasonality in male reproduction seems to be in place.

**Triaenops menamena* Goodman & Ranivo, 2009

- English: Rufous Trident Bat
- French: Triénope roussâtre

IUCN Redlist status: Least Concerned (LC)

Systematics: The type series of *T. rufus* is composed of individuals not collected on Madagascar but mainland Africa and are referable to *T. afer*, hence, the Malagasy species was renamed as *T. menamena* (Goodman & Ranivo, 2009).

Localities found during inventory: This species was trapped in harp traps at the Binara and Anjakely sites.

Reproduction: Of the three females captured, all were pregnant with single embryos. One from Binara on 22 November 2023 had an embryo measuring 11 mm crown-rump length and two from Anjakely on 6 December 2023 had both embryos 23 mm crown-rump length. Given the time period separating these dates and associated fetus growth, it would appear that reproduction in this species at the regional scale is somewhat synchronized. All three females had well developed auxiliary pubic nipples (nipples located on the ventral abdominal body wall), for which the function remains unclear, but at the very least act as holdfasts for neonates (Simmons, 1993).

Family Emballonuridae

**Paremballonura tiavato* (Goodman, Cardiff, Ranivo, Russell & Yoder, 2006)

English: Rock-dwelling Sheath-tailed Bat

French: Emballonure rupestre

IUCN Redlist status: Least Concern (LC)

Systematics: The sheath-tailed bats of Madagascar were formerly placed in the widespread Old World genus *Emballonura*. Based on molecular data, this genus was found to be paraphyletic and the two Malagasy species placed in the new genus *Paremballonura* (Goodman *et al.*, 2012). *Paremballonura tiavato* was described recently from material from western Madagascar (Goodman *et al.*, 2006) and has a broad distribution from Loky-

Manambato and Analamerana to the northwest coast and south to at least Bemaraha.

Localities found during inventory: *Paremballonura tiavato* was captured in harp traps at the entrance of Antsahabe Cave and in the Anjakely Forest.

Morphological characters: This species did not show any statistical differences between the sexes in external measurements (Table 2). Pregnant females were about 15% heavier than females not carrying any embryos.

Reproduction: On the basis of individuals of this species trapped and collected during a period of nine days, there was considerable individual variation in their reproductive state. Of the two examined males, both had small testes with undeveloped epididymides. Of the five pregnant females, the average crownrump length of embryos was 13.0 mm (range 10 to 18 mm); two other females showed no sign of carrying embryos. One female had already given birth and was lactating. These different aspects taken together can be interpreted as this species showing seasonality in breeding, but not highly synchronized.

Family Molossidae

Chaerephon leucogaster A. Grandidier, 1870 English: Grandidier's Lesser Free-tailed Bat French: Molosse de Grandidier

IUCN Redlist status: Least Concerned (LC)

Locality found during inventory: This species was captured in mist nets placed next to the school in Anjakely (village) that had the distinct smell of Molossidae bats. The open internal portion of the building was without a separation of an attic space and the bats probably roosted in spaces at the base of roof rafters.

Morphological characters: This species did not show any significant differences between the sexes in external measurements (Table 2). Pregnant females were about 20% heavier than females not carrying any embryos.

Reproduction: The individuals discussed here were captured the same night. Of the two collected males, both had scrotal testes of enlarged size and well developed epididymides. Of the nine females, all were pregnant with single embryos, averaging 21.5 mm in crown-rump length (range 15-23 mm). On the basis of embryo size, there was a highly synchronized breeding season and the females were close to giving birth.

Mops leucostigma G. M. Allen, 1918

English: Malagasy Large White-bellied Free-tailed Bat

French: Grand Molosse malgache

IUCN Redlist status: Least Concerned (LC)

Locality found during inventory: One individual of this species was trapped in a mist net outside the Anjakely (village) school, where it occupied a day roost site. (See previous account for further details.) **Reproduction:** The single captured male had abdominal testes measuring 6 x 4 mm, partially convoluted epididymides.

Family Vespertilionidae

*Myotis goudoti (A. Smith, 1834)

English: Malagasy Mouse-eared Bat

French: Murin de Madagascar

IUCN Redlist status: Least Concerned (LC)

Localities found during inventory: This species was found at all three of the inventoried sites, including one captured in a harp trap at the Antsahabe Cave entrance.

Morphological characters: This species did not show any statistical differences between the sexes in external measurements (Table 2). Pregnant females were about 30% heavier than females not carrying any embryos.

Reproduction: Of the two males captured during the inventory, one had abdominal testes and the other slightly enlarged testes that had descended to the uropatagium. Of the two females captured in the Binara Forest, both had single embryos, one 17 mm and the other 20 mm crown-rump length; the latter when the mammae were compressed exuded milk, an indication that birth was imminent.

Family Miniopteridae

Miniopterus aelleni Goodman, Maminirina, Weyeneth, Bradman, Christidis, Ruedi & Appleton, 2009 **English:** Aellen's Long-fingered Bat **French:** Minioptère d'Aellen

IUCN Redlist status: Least Concerned (LC)

Systematics: This species was recently described from northern Madagascar and occurs in the area around Ankarana and Montagne d'Ambre and then south along the west coast to at least Bemaraha (Goodman *et al.*, 2009). It is also known from Anjouan in the Union of the Comoros.

Localities found during inventory: This species was captured while exiting the Antsahabe Cave, where it was distinctly less common than *M. griveaudi*, and also on the basis of photographs

was found roosting in the Andavapanihy Cave near Ambery.

Morphological characters: This species did not show any significant differences between the sexes in external measurements (Table 2).

Reproduction: Of the three individuals collected from the Antsahabe Cave, one male had enlarged $(5 \times 3 \text{ mm})$ and convoluted epididymides, another with slightly enlarged testes $(3 \times 2 \text{ mm})$ and intermediate developed epididymides, and the single female showed no signs of reproduction.

Miniopterus griveaudi Harrison, 1959 English: Griveaud's Long-fingered Bat French: Minioptère de Griveaud

IUCN Redlist status: Data Deficient (DD)

Localities found during inventory: This species was only captured exiting day roost sites in the Antsahabe and Antomby Caves. In the former, based on captures, it was distinctly more common than *M. aelleni* by more than a 10-fold. *Miniopterus griveaudi* has a broad distribution in northern Madagascar and along the western coast to at least the Tsiribihina River (Goodman & Ramasindrazana, 2013) and is also known to occur on Grande Comore and Anjouan in the Comoros Archipelago.

Morphological characters: This species did not show any significant differences between the sexes in external measurements (Table 2). Pregnant females were about 20% heavier than females not carrying any embryos.

Reproduction: Of the three collected males, not one showed signs of enlarged testes and epididymides. In total, 39 different females were handled and 31 of these were pregnant. Two pregnant females collected from the Antsahabe Cave had single embryos that measured 18 and 19 mm crown-rump length and it would appear that the reproductive season is synchronized.

Discussion

On the basis of an inventory made from 17 November to 8 December 2023 of different sites in the Andrafiamena-Andavakoera protected area in northern Madagascar, a total of 12 species of bats were documented. Field survey techniques employed mostly direct capture with mist nets or a harp trap, as well as some cave visits and observations on the locally occurring inhabitants. Of these 12 species, eight (67%) are endemic to Madagascar, of which one, *Paratriaenops auritus*, is restricted to the far north of the island. The remaining four occur in other areas of the Malagasy Region, specifically the Comoros Archipelago, and these include *Chaerephon leucogaster* (also Pemba Island off Tanzania), *Mops leucostigma*, *Miniopterus aelleni*, and *M. griveaudi*. Hence, not a single species occurs on the African continent and the fauna is 100% regionally endemic.

The species diversity of Andrafiamena-Andavakoera is similar to three neighboring protected areas, Montagne des Français, Analamerana, and Loky-Manambato, which both have not been extensively surveyed for bats, and less than the 17 species known from the notably surveyed protected area of Ankarana (Table 3). In general, the bat fauna of these different areas of northern Madagascar is largely homogeneous and at least in part this can be explained by the local bioclimatic and habitat conditions and a good proportion of the species occupy caves and exposed rock shelters for day roost sites. For all of these sites, the percentage of endemic species varied from 67% to 91%, and the fauna at all of these sites is 100% endemic to the Malagasy Region. This aspect underlines a general uniqueness for the island's bat fauna, which is particularly the case for the species composition in the north, and highlighting the importance of conservation in general and protecting bat roosts occurring in caves.

The period of the inventory of Andrafiamena-Andavakoera coincided with the reproductive season of several species of insectivorous bats, including *P. auritus*, *Triaenops menamena*, *Paremballonura atrata*, *Chaerephon leucogaster*, *Myotis goudoti*,

Table 3. The known bat fauna of protected areas in northern Madagascar with sedimentary rock exposures and associated caves. The scientific names of species preceded by an asterisk are endemic to Madagascar. Data sources: 1 = Raherilalao *et al.* (2022), 2 = Goodman *et al.* (2018a), 3 = Goodman *et al.* (unpublished data). Level of completeness: ranging from 0 = unknown to 5 = very well known. Codes for IUCN Redlist status: DD = Data Deficient, LC = Least Concerned, NT = Near Threatened, and VU = Vulnerable. All of the listed species are endemic to the Malagasy Region.

Species	IUCN Red List status	Montagne des Français	Analamerana	Loky-Manambato	Andrafiamena- Andavakoera	Ankarana
Data sources		1	2	2, 3	Herein	2
Level of completeness of		3	2	2	3	4
surveys						
Pteropodidae						
*Eidolon dupreanum	VU	+	+	+	+	+
*Pteropus rufus	VU	+	+	+	+	+
*Rousettus	VU	+	+	+	+	+
madagascariensis						
Hipposideridae						
*Macronycteris commersoni	NT	+	+	+	+	+
Rhinonycteridae						
*Paratriaenops auritus	VU	+	+	+	+	+
*Triaenops menamena	LC	+	+	+	+	+
Emballonuridae						
*Coleura kibomalandy	DD	-	-	-	-	+
*Paremballonura tiavato	LC	+	+	+	+	+
Molossidae						
*Chaerephon jobimena	LC	-	-	-	-	+
Chaerephon leucogaster	LC	-	-	-	+	+
Mops leucostigma	LC	-	-	-	+	+
*Mormopterus jugularis	LC	-	-	+	-	+
*Otomops madagascariensis	LC	-	+	-	-	+
Vespertilionidae						
*Myotis goudoti	LC	+	+	+	+	+
Miniopteridae						
Miniopterus aelleni	LC	+	-		+	+
*Miniopterus brachytragos	LC	-	-	+	-	
*Miniopterus gleni	LC	+	+	-	-	+
Miniopterus griveaudi	DD	+	+	+	+	+
Total number of species		11	11	11	12	17
Number of species		9 (82%)	10 (91%)	10 (91%)	8 (67%)	13 (77%)
endemic to Madagascar						

and *Miniopterus griveaudi*, for which many females were reaching the final stages of pregnancy. The timing of the birthing season coincides with the start of the rainy season and the period of higher insect abundance.

Of these 12 species of bats recorded in the Andrafiamena-Andavakoera protected area, four (Eidolon dupreanum, Pteropus rufus, Rousettus madagascariensis, and Paratriaenops auritus) are considered Vulnerable based on the IUCN Red List. Within Andrafiamena-Andavakoera, we found no clear evidence of the exploitation of bats near any of our three study sites, as compared to other nearby protected areas, such as Ankarana (Cardiff et al., 2009), where people are known to hunt in caves insectivorous bats for bush meat. Further, we found no evidence in the caves visited for the exploitation of bat guano as fertilizer. We suggest that among the insectivorous species found in Andrafiamena-Andavakoera, this is the one that should be monitored for fluctuations in the local population. While a number of areas of the protected area were visited and surveyed for bats, it is almost certain with more extensive surveys additional species will be found previously unknown from the site.

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