The non-primate and non-volant mammals of the Andrafiamena-Andavakoera protected area, northern Madagascar

Steven M. Goodman^{1,2} & Voahangy Soarimalala^{1,3}

¹ Field Museum of Natural History, Negaunee Integrative Research Center, 1400 South DuSable Shore Drive, Chicago, Illinois 60605, USA E-mail: sgoodman@fieldmuseum.org
² Association Vahatra, BP 3972, Antananarivo 101, Madagascar
E-mail: voahangysoarimalala@gmail.com
³ Institut des Sciences et Techniques de l'Environnement, Université de Fianarantsoa, BP 1624, Fianarantsoa 301, Madagascar

Abstract

We conducted an inventory of the small mammals at three sites in the Andrafiamena-Andavakoera protected area in November and early December 2023, which coincided with the transitional period between the dry and wet seasons. Two distinct habitats were surveyed - moist semi-deciduous and dry deciduous forests and two different trapping techniques were employed - pitfall traps intended for small terrestrial mammals including tenrecs (family Tenrecidae) and standard live traps principally for rodents (subfamily Nesomyinae and introduced family Muridae). Parallel techniques and trapping efforts were used at the different sites. In total, seven small mammal species were documented, of which four are Malagasy endemics (Microgale brevicaudata, Setifer nov. sp., Tenrec ecaudatus of the family Tenrecidae and *Eliurus carletoni* of the subfamily Nesomyinae) and three introduced (Suncus etruscus of the family Soricidae and Mus musculus and Rattus rattus of the family Muridae). Capture rates for both devices were low, but similar to the results of other regional sites with similar forest formations during the same season. From the biogeographic and conservation perspectives, two notable species occur at the site -Eliurus carletoni, described some 15 years ago from the neighboring protected area of Ankarana and known elsewhere in northern Madagascar, and a presumably a species of Setifer new to science and also a regional endemic. Not one of the endemic species documented is threatened based on IUCN Red List criteria, but the undescribed species of Setifer and E. carletoni are of conservation concern. Two species of the endemic Malagasy family Eupleridae (*Cryptoprocta ferox* and *Galidia elegans*) were documented in the protected area, and details are also presented for the local presence of another member of this family, *Eupleres goudoti*.

Keywords: Tenrecidae, Nesomyinae, Soricidae, Eupleridae, species inventory, Andrafiamena-Andavakoera

Résumé détaillé

Nous avons réalisé un inventaire des petits mammifères dans trois sites de l'aire protégée d'Andrafiamena-Andavakoera en novembre et début décembre 2023, période correspondant à la transition entre la saison sèche et la saison des pluies. Deux habitats distincts ont été étudiés, à savoir la forêt dense humide semi-décidue (sur les sites de Binara et Anjakely) et la forêt dense sèche caducifoliée avec des éléments de tsingy (sur le site d'Antsahabe). Deux techniques de piégeage différentes ont été employées dont les trou-pièges destinés aux petits mammifères terrestres, y compris les tenrecs (famille Tenrecidae), et les pièges vivants standard principalement destinés pour les rongeurs (sousfamille Nesomyinae et famille introduite Muridae). Des techniques et efforts de piégeage semblables ont été utilisés dans les différents sites.

Au total, sept espèces de petits mammifères ont été trouvées, dont quatre sont endémiques de Madagascar (Microgale brevicaudata, Setifer nov. sp., Tenrec ecaudatus de la famille Tenrecidae et Eliurus carletoni de la sous-famille Nesomvinae) et trois introduites (Suncus etruscus de la famille Soricidae ainsi que Mus musculus et Rattus rattus de la famille Muridae). A l'exception de Microgale brevicaudata (famille des Tenrecidae) qui n'a été trouvé que dans le site d'Anjakely, la richesse spécifique est similaire pour tous les trois sites explorés. En se basant sur les résultats obtenus, aucune différence remarquable n'a été constatée dans les trois sites inventoriés. Les taux de capture pour les deux types de pièges étaient faibles, mais comparables aux résultats d'autres sites régionaux présentant des formations forestières similaires à la même saison.

Du point de vue biogéographique, Andrafiamena-Andavakoera abrite deux espèces de petits mammifères endémigues, *M. brevicaudata* et *E.*

carletoni, qui sont caractéristiques de la formation végétale sèche malgache et aussi de la transition entre les forêts humide et sèche. Microgale brevicaudata se trouve même dans la forêt humide de basse altitude dans la région de Marojejy. Eliurus carletoni, décrit il y a environ 15 ans dans l'aire protégée voisine d'Ankarana et connu ailleurs dans le nord de Madagascar. En comparant avec les autres forêts sèches du Nord, la Réserve Spéciale d'Analamerana et la Réserve Spéciale d'Ankarana, Andrafiamena-Andavakoera présentent une richesse similaire. Par rapport aux forêts sèches caducifoliées plus au sud de Madagascar, cette région abrite moins d'espèce. Sur la base de données moléculaire, ainsi que de différences morphologiques, la population du nord de Madagascar, autrefois considérée comme S. setosus, est une nouvelle espèce pour la science et en cours de description. Setifer sp. nov. est communément capturée dans les trois sites visités et elle est endémique de la région.

En termes de conservation, aucune des espèces endémiques documentées n'est considérée comme menacée selon les critères de la Liste rouge de l'UICN. *Setifer* sp. nov. elle est bien connue de la population et également parmi les cibles de la chasse.

Quant au Carnivores, deux espèces de la famille endémique malgache Eupleridae (*Cryptoprocta ferox* et *Galidia elegans*) ont été recensées dans l'aire protégée, et des informations sont également présentées sur la présence locale d'un autre membre de cette famille, *Eupleres goudoti*. L'absence de *C*. *ferox* à Antsahabe pourrait être due à sa densité faible dans cette partie de l'aire protégée, particulièrement dans la forêt de *tsingy*. Aucun signe de présence de cette espèce comme les fèces n'a été trouvé à Antsahabe.

Mots clés : Tenrecidae, Nesomyinae, Soricidae, Eupleridae, inventaire des espèces, Andrafiamena-Andavakoera

Introduction

The last 35 years have seen major advances in available information on the terrestrial mammals of Madagascar. A number of books have been published on the island's land mammals in general (Mittermeier *et al.*, 2021; Garbutt, 2022), and guides are also available specifically on lemurs (Mittermeier *et al.*, 2023), bats (Goodman, 2011), carnivorans (Goodman, 2012), and small mammals (Soarimalala & Goodman, 2011); in all cases these different books

summarize details on the taxonomy, distribution, ecology, and conservation status of these different mammal groups (also see different contributions in Goodman, 2022). For primates, a remarkable number of new species to science have been named and numerous field studies on a wide range of aspects associated with the life history traits and conservation of these animals have been published (see details in Mittermeier et al., 2023; different contributions in Goodman, 2022). Herein we use the term "small mammals" to designate the endemic rodents of the subfamily Nesomvinae and tenrecs of the family Tenrecidae, as well as introduced rodents of the family Muridae and shrews of the family Soricidae. Within the results section we present details on the locally occurring members of the order Carnivora for which the native species belong to the endemic family Eupleridae.

For the small mammals of Madagascar, biological inventories have been conducted in numerous forest areas, some within and others outside of protected areas, and encompassing all of the different land vegetation types, from lowland and upland moist evergreen forests, summital zones of the highest mountains, semi-dry and dry deciduous forests to dry spiny bush. Between 1988 and 2022 a total of nine tenrecids and 11 nesomyines were described from Madagascar as new to science (Hoffman *et al.*, 2009; Goodman & Soarimalala, 2022).

northern portion of the island, In the morphological and molecular research based on specimens collected during survey work has led to the description of a new nesomyine species, Eliurus carletoni (Goodman et al., 2009) and molecular work on associated tissues provided insights into this species' evolutionary history (Rakotoarisoa et al., 2010, 2013a, 2013b). In what are now the DIANA and SAVA Regions, and previously placed in the Province d'Antsiranana before changes in the administrative structure of Madagascar, detailed small mammal surveys have been conducted in the protected areas of Montagne d'Ambre (Raxworthy & Nussbaum, 1994; Goodman et al., 1996, 1997), Ankarana (Goodman & Soarimalala, unpublished data), Montagne des Français (Raherilalao et al., 2022), Analamerana (Raheriarisena & Goodman, 2006), and Loky-Manambato (Raheriarisena & Goodman, 2006) (Figure 1).

One site that has not been adequately covered is the Andrafiamena-Andavakoera protected area (an area of 74,000 ha) and local work is limited to the Andavakoera Massif in close proximity to Betsiaka,



Figure 1. Map of northern Madagascar showing the regional protected area system overlaid on remaining forest cover, as well as the study sites within Andrafiamena-Andavakoera.

where one site was surveyed (Raheriarisena & Goodman, 2006). To date in this protected area, two species of nesomyine rodents (*E. carletoni* and *E. myoxinus*), one murid rodent (*Rattus rattus*), and two tenrecids (*Setifer* nov. sp and *Tenrec ecaudatus*) are documented (Goodman *et al.*, 2018a; Sgarlata *et al.*, 2024), which is fewer species than can be anticipated to occur at this site based on small mammal species diversity in neighboring areas.

Some details are available about the Carnivora occurring in the Andrafiamena-Andavakoera protected area, including species of the endemic family Eupleridae, or introduced species of the families Canidae, Felidae, and Viverridae. In a recent tabulation of the vertebrates known from the site (Goodman *et al.*, 2018a), two endemic species (*Cryptoprocta ferox* and *Galidia elegans*) were listed, as well as the introduced *Viverricula indica*.

The purpose of this contribution is to report on the small mammals captured during a biological

inventory of Andrafiamena-Andavakoera conducted in late 2023 in different types of forested habitats within the protected area. Herein we describe the species found, their habitat specificities, relative measures of density, conservation status, and some general natural history observations. Data were also gathered on the Carnivora of the site, which are also presented herein.

Methods

Sites

Three sites were inventoried for small mammals in the Andrafiamena-Andavakoera protected area and these are presented in detail in the introductory contribution to this monograph (Tahinarivony & Goodman, 2025, herein). The three sites include (see Figure 1 for further details):

 Binara Forest : Madagascar, ex-Province d'Antsiranana, Région DIANA, Paysage Harmonieux Protégé d'AndrafiamenaAndavakoera, Binara-Andavakoera Forest, 5.4 km E Ankatsaka, 13.101°S, 49.240°E, 300 m. Much of the trapping took place in moist semi-deciduous forests from the camp site near the Ambaratra River and to the west on the trail leading towards the village of Ankatsaka and before the Binara Forest crest. This area was surveyed 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. All of the small mammal trapping took place in tsingy dry deciduous forest on the lower slopes or on the nearly flat portion of the Antsahabe plateau. This area was studied between 25 and 1 December 2023.
- 3) Anjakely: Madagascar, ex-Province d'Antsiranana, Région DIANA, Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera, Anjakely Forest, 1.3 km SE Anjakely (village), 12.913°S, 49.328°E, about 420 m. Traps were installed exclusively in the zone of moist semi-deciduous forest starting at the trail bifurcating from the old 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.

Trapping techniques

Two trapping techniques (pitfall and live standard traps) were employed to capture small mammals at each of the three sites. These devices were left in place for six consecutive nights and installed in an assortment of settings to evaluate possible microhabitat differences between species.

Standard traps were composed of two different types: Sherman (22.5 x 8.6 x 7.4 cm) and National (39.2 x 12.3 x 12.3 cm). A total of 100 standard traps are set up at each site to capture alive small mammals, mainly intended for rodents, with a ratio of four Sherman traps to one National trap. During a given session, each trap had a fixed position and with a unique serial order number marked on an adjacent colored flag. Trap lines included different microhabitats to increase the probability of capturing species with specific niche requirements and for each trap placement notes were made on the habitat and specific post. About 20% of the traps were placed above ground level, on tree trunks and branches or on vines, and the balance were located on the

ground, such as below a leaning tree trunk, along a fallen tree trunk or at the base of a tree in front of a seemingly active burrow. Traps were baited with unsalted peanut butter, which was renewed daily in the late afternoon. We checked all of the traps twice a day: at dawn and in the late afternoon. A trap night is defined as a standard trap open for 24 hours (from dawn to dawn next day).

Pitfall traps was a technique shared with the amphibian and reptile group (see Rakotoarimalala et al., 2025, herein for details on the associated trap captures). Each line of this device employs 11 buckets (12 I in capacity and measuring 275 mm internal depth and 220 mm internal lower diameter) placed on a narrow trail of about 0.5 m wide that had been cleared of vegetation and fallen vegetation debris. The buckets were buried with the rim level flush with the ground and spaced 10 m apart. A plastic drift fence, approximately 110 m long and 0.8 m wide, was erected from the start to finish of each line and bisected the central portion of each bucket. The plastic fence was stapled in a vertical position to wooden stakes. The lower part of the plastic, approximately 10 cm, overlapped the ground and was covered with forest debris or soil litter to prevent animals from slipping underneath and also serving as a guide to direct animals to the buckets. The bottom of each bucket was pierced with small holes to allow rainwater to drain. No bait was placed in the buckets. At the sites of Binara and Anjakely, three pitfall trap lines were installed in different microhabitats (ridge, slope, valley), while at Antsahabe, all three lines were on a limestone plateau. A bucket in place for 24 hours is considered a pitfall trap night.

For small mammals, some specimens were collected for certain species and these serve as a reference collection for the taxa occurring in the protected areas and associated samples will be employed in different taxonomic and zoonotic disease research projects. For those taken as specimens, information was recorded on the reproductive state of each, as well as different external measurements. Tissue samples were also preserved in EDTA for molecular studies. The associated specimens have been deposited in the Collection Room of the Mention Zoologie et Biodiversité Animale (formerly the Département de Biologie Animale or UADBA), Université d'Antananarivo and the Field Museum of Natural History, Chicago.

Carnivorans

During our inventory of the Andrafiamena-Andavakoera protected area in November and December 2023, we were able to obtain additional information on the local Carnivora, including direct observations and interviews with local people, which are presented herein, as well as information from different field workers. None of these results presented herein on this group are based on trapping data.

Results

Small mammals

At the three surveyed sites in the Andrafiamena-Andavakoera protected area, a total of seven small mammal species were documented, four being Malagasy endemics and three being introduced species (Table 1). At each of the sites, species diversity ranged from a maximum of six (Binara and Anjakely) to five (Antsahabe), which included up to two introduced species.

The number of small mammal species captured in the pitfall traps at the three sites was few (Table 2) and in total four species were obtained, three endemic and one introduced, in a total 198 pitfall trap nights per site. The number of individuals captured in the pitfall traps at the surveyed sites varied from five in total at Anjakely to three at Antsahabe. The most frequent form was *Setifer*, for which five animals were obtained in a total of 594 pitfall trap nights.

Table 1. List of species of small mammals found during the late 2023 survey of the Andrafiamena-Andavakoera protected area and based on animals captured in standard live traps and pitfall traps. Species preceded by an asterisk are introduced to Madagascar and the balance are endemic to the island. Codes for IUCN Red List status: LC = Least Concerned, NA = not assessed.

Species	IUCN Red List status	Binara (site 1)	Antsahabe (site 2)	Anjakely (site 3)
Tenrecidae				
Microgale brevicaudata	LC	-	-	+
Setifer nov. sp.	NA	+	+	+
Tenrec ecaudatus	LC	+	+	+
Soricidae				
*Suncus etruscus	_	+	+	+
Nesomyinae				
Eliurus carletoni	LC	+	+	+
Muridae				
*Mus musculus	_	+	-	-
*Rattus rattus	_	+	+	+
Total number of small mammal species		6	5	6
Total number of endemic small		4	3	4
mammal species				

Table 2. The total number of small mammal captured in the pitfall traps during the late 2023 inventory of the Andrafiamena-Andavakoera protected area. The total number of pitfall trap nights per site was 198. Species preceded by an asterisk are introduced to Madagascar and the balance are endemic to the island.

Species	Binara (Site 1)	Antsahabe (Site 2)	Anjakely (Site 3)
Tenrecidae			
Microgale brevicaudata	-	-	2
Setifer nov. sp.	2	1	2
Tenrec ecaudatus	-	-	1
Soricidae			
*Suncus etruscus	2	2	-
Total number of animals	4	3	5
captured			
Total number of small	2	2	3
mammal species			
Total number of endemic small mammal species	1	1	3

Table 3. The total number of small mammal captured in the standard live traps during the late 2023 inventory of the Andrafiamena-Andavakoera protected area. The total number of trap nights per site is 600. Species preceded by an asterisk are introduced to Madagascar and the balance are endemic to the island.

Species	Binara (Site 1)	Antsahabe (Site 2)	Anjakely (Site 3)
Nesomyinae			
Eliurus carletoni	3	3	1
Muridae			
*Mus musculus	1	-	-
*Rattus rattus	3	1	1
Total number of animals	7	4	2
captured			
Total number of small	3	2	2
mammal species			
Total number of endemic	1	1	1
small mammal species			

Table 4. Comparative capture rates of small mammals at different sites in northern Madagascar with different types of dry deciduous forest and during approximately the same season.

Site	Dates and source of	Forest type	Pitfa	ll traps	Standard live traps	
	information					
			Number of pitfall trap nights - capture rate	Species & number individuals (number endemic / number introduced)	Number of trap nights - capture rate	Species & number individuals (number endemic / number introduced)
Andrafiamena-						
Andavakoera						
Binara	16 to 23 November 2023, herein	Moist semi- deciduous forests.	198 trap nights - capture rate of 2%.	2 species (2/2)	600 trap nights capture rate of 1.2%.	3 species (3/4)
Antsahabe	25 to 1 December 2023, herein	<i>Tsingy</i> dry deciduous forest.	198 trap nights - capture rate of 1.5%.	2 species (1/3)	600 trap nights capture rate of 0.6%.	2 species (3/1)
Anjakely	2 to 8 December 2023, herein	Moist semi- deciduous forests.	198 trap nights - capture rate of 2.5%.	3 species (5/0)	600 trap nights - capture rate of 0.3%.	2 species (1/1)
Ankarana						
Campement des Princes ¹	3 to 8 December 2019, (Goodman & Soarimalala, unpublished)	Moist semi- deciduous forests.	198 trap nights - capture rate of 2.5%.	2 species (4/5)	600 trap nights - capture rate of 1.5%.	2 species (2/7)
Analamerana						
Bobakindro ²	17 to 22 January 2004 (Raheriarisena & Goodman, 2006)	Dry deciduous forest.	165 trap nights - capture rate of 1.8%.	2 species (2/1)	500 trap nights - capture rate of 0.6%.	2 species (4/1)
Ankavanana ³	23 to 29 January 2004 (Raheriarisena & Goodman, 2006)	Moist semi- deciduous forests.	198 trap nights - capture rate of 2.5%.	2 species (4/1)	600 trap nights - capture rate of 2.7%.	2 species (6/10)

¹ GPS coordinates and elevation of site locality: 12.9601°S, 49.1199°E, 130 m

² GPS coordinates and elevation of site locality: 12.7500°S, 49.4933°E, 40 m

³ GPS coordinates and elevation of site locality: 12.7950°S, 49.3683°E, 200 m

In the case of the standard live traps at the three sites, the number of captured species was also limited and comprised three species, one endemic and two introduced (Table 3). The number of individuals trapped varied from seven at Binara to two at Anjakely. On the basis of 1800 cumulative trap nights (600 per site), the most frequently captured species was *Eliurus carletoni* and seven were trapped. While these capture rates for both the pitfalls and standard live traps were seemingly low, they are comparable to other regional inventoried dry deciduous forest sites at about the same time of year, including two sites in Analamerana and one site in Ankarana (Table 4).

Carnivora

Below we present an annotated listing of the Carnivora known from the Andrafiamena-Andavakoera protected area.

Family Eupleridae

Subfamily Euplerinae Cryptoprocta ferox English name: Fossa French name: Cryptoprocte Local Malagasy name: Fosa IUCN Red List status: Vulnerable

Details from Andrafiamena-Andavakoera and surrounding areas: During the period after arriving in the Binara Forest (site 1) on 16 November until 19 November 2023, a *C. ferox* mating site about 15 m up in a *Canarium* tree (family Burseraceae) was in use (Figure 2). The tree was in close proximity to the camp and just above an occupied tent. During the course of this period, the female, which was distinctly thin and with a cut on the left ear, copulated with at least three different males. These activities took place mostly during the night, with lots of harsh calling and presumably aggressive activity, but copulatory activities also occurred just after dawn and before dusk. During this period, the female and different males could be observed along the main trail connecting the camp with the Binara crest. Individuals were observed drinking from the water pools along the Ambaratra River just below the Site 1 camp.

One local guide mentioned that *C. ferox* enters into villages located 1 or 2 km from the forest edge and predates on chickens. This is more common during the rainy season. On occasion this species is killed during raids on village chickens.

Eupleres goudotii

English name: Slender Fanalouc French name: Euplère de Goudot Local Malagasy name: *Ridarida* IUCN Red List status: Vulnerable

Details from Andrafiamena-Andavakoera and surrounding areas: We found no evidence of this species during the late 2023 inventory. Based



Figure 2. While in the Binara Forest (Site 1) in mid-November and in close proximity to the camp, a *Cryptoprocta ferox* mating tree was found and often occupied by copulating pairs. (Photo by Carlos G. Boluda.)

on discussions with a guide from Ananjaka, who described its physical features with precision, he mentioned that it is mostly forest-dwelling, but can be found close to villages, specifically in areas with marsh habitat. The ecological monitoring team from Fanamby found animals they referred to this species at three different localities in the protected area: 1) at Andohan'ny Barabanjabe (12.91118°S, 49.32110°E) on 20 September 2019 at 06h00; 2) at Analambaliha (12.91140°S, 49.32474°E) on 10 June 2022 at 09h30; and 3) Lalagna Andrevokely (12.91486°S, 49.31796°E) on 15 October 2022 at 12h15.

Subfamily Galidinae *Galidia elegans*

English name: Ring-tailed Vontsira French name: Vontsira à queue annelée Local Malagasy name: *Vontsira mena* IUCN Red List status: Least Concerned

Details from Andrafiamena-Andavakoera and surrounding areas: During the late 2023 inventory, this species was only seen in the Anjakely Forest (Site 3) and at two different sites: in close proximity to the Piscine Naturelle (Figure 3) and near one of the small mammal trap lines about 500 m away from the Piscine Naturelle (A. P. Raselimanana & F. Rakotoarimalala, unpublished data). During the day it hunted in the vicinity of the Piscine Naturelle pools and on one occasion was observed to dive into water and fed on some type of prey, perhaps a frog.

Family Canidae

Canis lupus - Introduced English name: Domestic dog French name: Chien domestique Local Malagasy name: *Amboa*

Details from Andrafiamena-Andavakoera and surrounding areas: During our time in the Andrafiamena-Andavakoera forest, whether during the day or at night, we only observed dogs that were accompanying people. Hence, we have no evidence of feral populations of dogs at any of the three sites. Many local people gathering items in the forest, working as porters for the team, or other activities, regularly traveled with their pet dogs.

Family Felidae

Felis silvestris - Introduced English name: Wild Cat French name: Chat sauvage Local Malagasy name: *Rabosy dia*

Details from Andrafiamena-Andavakoera and surrounding areas: Only one observation was made



Figure 3. One species of the endemic family Eupleridae that is widespread in forest formations around the island is *Galidia elegans*. During our survey of three sites in the Andrafiamena-Andavakoera protected area, this species was only observed at two sites in the Anjakely (Site 3) forest block. (Photo by Voahangy Soarimalala.)

of a feral cat during the inventory. This is an individual that was heard calling and observed on the bank of the Ambaratra River tributary just below the Binara (Site 1) camp. According to a local guide, *Felis* observed in the forest are domestic cats that have gone feral.

Family Viverridae

Viverricula indica - Introduced English name: Indian Civet French name: Civette Indienne Local Malagasy name: *Kari*

Details from Andrafiamena-Andavakoera and surrounding areas: According to a local guide and based on a good description of the morphology and coloration of this species, they do not occur in forest settings, but rather in open habitat, including around villages. During our work in the protected area, one was observed at dawn in close proximity to the Antsahabe Massif and another along the trail leading from Anjakely to the village of Ampantsona and in an area before the start of the secondary forest.

Discussion

Species and faunistics of small mammals

Among the endemic species of small mammals found in the Andrafiamena-Andavakoera protected area, two are regional endemics. Eliurus carletoni was originally described from Ankarana and subsequently identified from Loky-Manambato, Analamerana, Andavakoera, and sites further south with the Fanambana River forming the apparent southern limit (Raheriarisena & Goodman, 2006; Rakotoarisoa et al., 2013b; Sgarlata et al., 2024). During small mammal surveys, this species can be abundant, such as in the Loky-Manambato area where capture rates of this species reached 44 individuals in 600 trap nights in late November 2003 (Raheriarisena & Goodman, 2006), but during our mid-November to early December surveys of the Andrafiamena-Andavakoera protected area a total of five individuals were captured in 594 pitfall trap nights (Table 2).

Recent phylogeographic and morphometric studies across the extensive nearly island-wide distribution of *Setifer setosus* (Goodman *et al.*, 2013) found that the northern population is genetically distinct and adults are smaller in body size than areas further to the south (Olson *et al.*, unpublished data). These results lead to the populations occurring in Montagne des Français, Analamerana, and Ankarana

being listed in Goodman *et al.* (2018a) as *Setifer* nov. sp. Adult animals of this genus from Andrafiamena-Andavakoera are indeed small and we are awaiting the results of genetic work and this population is tentatively assigned to *Setifer* nov. sp.

Habitats and biogeography of small mammals

In comparison to other sites of different types of moist semi-deciduous and dry deciduous forests in northern Madagascar, all being official protected areas (Figure 1), that were surveyed during the same seasonal period as our work presented herein (Table 5), the results indicate that the Andrafiamena-Andavakoera protected area does not have a particularly rich or unique small mammal fauna. There is considerable similarity between the forest sites of Montagne des Français, Analamerana, Andrafiamena-Andavakoera, and Ankarana that have an endemic small fauna ranging from four to seven species and these sites also have several introduced shrews and rodents. The notable exceptions in northern Madagascar to the aspect of high species diversity are Loky-Manambato and Montagne d'Ambre, which have 12 and 13 endemic small mammal species, respectively.

The natural forest vegetation of the Loky-Manambato protected area is notably heterogeneous, ranging from medium altitude moist evergreen, moist semi-deciduous, and dry deciduous forests (Ranirison et al., 2018). The pattern and distribution of different vegetation types is related to distance from the sea, soil types, and topography, with several prominent local massifs having medium altitude moist evergreen formations at higher elevations (Gautier et al., 2006). While Montagne d'Ambre has the same vegetation types as Loky-Manambato, they are arranged from dry to moist with increasing elevation on the massif and the upper reaches received considerable precipitation associated with an orographic effect (Gautier & Wohlhauser, 2018). Hence, these two areas, although not connected today by mesic forests, show similar small mammal faunas, and given the moist evergreen forest requirements of some of forest-dwelling mammals, it can be hypothesized that the two sites in the recent geological past were connected by a moist forest corridor.

(2022), B = Goodman *et al.* (2018a), C = Raheriarisena and Goodman (2006). Measures of the level of knowledge of the local small mammal fauna: ranging from 0 = unknown to 5 = very well-known and based on Goodman *et al.* (2018b). Codes for IUCN Red List statutes: DD = Data Deficient, LC = Least Concerned, and NA = not assessed. All of the listed species are endemic to Madagascar with the exception of non-native taxa marked in the IUCN Red List column as I = introduced. The occurrence of site records for species presented in brackets is Table 5. The known small mammal fauna of protected areas in northern Madagascar with dry deciduous and moist semi-dry deciduous forests. Data sources: A = Raherilalao et al. based on interviews with local people.

Species	IUCN Red List status or	Montagne des Français	Analamerana	Loky-Manambato	Andrafiamena- Andavakoera	Ankarana	Montagne d'Ambre
Data sources	introduced (I)		ď	c a	Horein B	ď	ď
Level of knowledge of the local mammal fauna as of 2018		2	0 0)] m		n m	n n
Forest type ¹		Moist semi-deciduous forest.	Moist semi-deciduous and dry deciduous forests.	Moist semi-deciduous, moist evergreen humid, and dry deciduous forests.	Moist semi-deciduous and dry deciduous forests.	Moist semi-deciduous and dry deciduous forests.	Moist evergreen humid, moist semi- deciduous, and dry deciduous forests.
Tenrecidae							
Tenrecinae							
Setifer sp. nov. ²	NA	+	+	[±	[+]	+	+
Tenrec ecaudatus	LC	+	+	+	+	+	+
Oryzorictinae							
Microgale brevicaudata	LC	+	+	+	+	+	+
Microgale drouhardi	LC		1	+		I	+
Microgale fotsifotsy	C	1	1	+		ı	+
Microgale longicaudata ³	ГC		-	+	-		+
Microgale parvula	LC	-	-	+			+
Nesogale dobsoni	ГC	+4			+5		+
Nesogale talazaci	LC	+4		+	+5	ı	+
				_			
Soricidae							
Suncus etruscus		+	+	+	+	+	
Suncus murinus			1	I			+
Nesomyidae				_			
Nesomyinae							
Eliurus carletoni	ГC	+	+	+	+	+6	
Eliurus ellermani	DD	1	1	+	-	I	+
Eliurus majori	LC	-	-	-	-		+
Eliurus minor	ГC		'	+			+
Eliurus myoxinus	ГC	1	-	+	+	I	
Eliurus webbi	ГC	+		ı			+

Table 5. (continued)

Species	IUCN Red List status or introduced (I)	Montagne des Français	Analamerana	Loky-Manambato	Andrafiamena- Andavakoera	Ankarana	Montagne d'Ambre
Data sources		A,B	В	B,C	Herein, B	В	В
Level of knowledge of the		2	2	3	1	3	3
local mammal fauna as of							
Forest type ¹		Moist semi-deciduous	Moist semi-deciduous	Moist semi-deciduous,	Moist semi-deciduous	Moist semi-deciduous	Moist evergreen
		forest.	and dry deciduous	moist evergreen	and dry deciduous	and dry deciduous	humid, moist semi-
			forests.	humid, and dry	forests.	forests.	deciduous, and dry
				deciduous forests.			deciduous forests.
Muridae							
Mus musculus	_	+	+		+	-	
Rattus rattus	_	+	+	+	+	+	+
Total number of species		10	6	14	6	6	15
Number of species		7	9	12	9	4	13
endemic to Madagascar							

¹ The forest type classification follows Gautier et al. (2018).

³ It has previously been proposed by Soarimalala & Goodman (2011) that the species of long-tailed Microgale occurring in the north, including the moist evergreen forest of Montagne d'Ambre and different ² Preliminary data are presented in Goodman et al. (2018c) that based on molecular and secondarily morphometric analyses that the species of Setific occurring in Montagne des Français, Analamerana. Ankarana, and Montagne d'Ambre is an undescribed diminutive species that is different than the widespread S. setosus; this new taxon is in the process of being described (Olson et al., unpublished data). On the basis of the external measurements of adults of this genus from Andrafiamena-Andavakoera, which are notably small, they are presumed to represent the undescribed species.

dry forest sites is M. prolixacaudata, a species originally described by Grandidier (1937) from the "province zoologique de Diego-Suarez" (Antsiranana). This taxon was provisionally synonymized with M. longicaudata (Olson et al., 2004) and until some DNA can be obtained from the type material of M. prolixacaudata, we follow this suggestion.

⁴ This species was reported by Raherilalao et al. (2022) as occurring in this protected area based on specimen material. The definitive species identification is awaiting molecular verification

⁶ Material from owl pellets collected at Ankarana and identified before the description of *E. carletoni* (Goodman *et al.*, 2009) were incorrectly assigned by Cardiff and Goodman (2008) as *E. antsingy*. ⁵ This species is reported herein as occurring in this protected area based on specimen material. The definitive species identification is awaiting molecular verification.

Forest habitat change in recent geological time and biogeographical inferences

There is good evidence from the paleontological record dating from the Late Pleistocene and Holocene that the north of the island, specifically in areas in close proximity to the Andrafiamena-Andavakoera protected area, have undergone notable change in vegetation cover (Goodman & Jungers, 2014). The question arises if these vicissitudes were associated with natural climate change or human modifications of the forest environments (Crowley et al., 2017). Data coming from subfossil animal bones excavated mostly from cave deposits indicate that several lemur species that based on osteological characters and inferred locomotion styles were largely or completely arboreal and lived in forested habitats with vegetation more mesic than today, including closed canopy forest. Several of these species are now extinct or in some cases extant and have experienced reduction in their geographical distributions. In the extinct species group are several sloth lemurs (family Palaeopropithecidae), including three genera, one of which (Babakotia) was named from Ankarana (Simons et al., 1992, 1995), as well as extant species, Indri indri and Hapalemur simus, that now occur much further to the south in moist evergreen forests (Godfrey & Vuillaume-Randriamanantena, 1986; Jungers et al., 1995; Goodman & Jungers, 2014). Extinct sloth lemurs have been identified from archaeological deposits at Montagne des Français, indicating that these animals temporally overlapped locally with human populations (Douglass et al., 2019). Further, given that it is well documented that people using stone tools were present in northern Madagascar several millennia ago (Dewar et al., 2013), human colonization of the north is much older than previously considered and the long-term impact on the natural forest habitats and its constituent species may have been considerable. Such paleontological and archeological investigations need to be conducted in cave deposits in Andrafiamena-Andavakoera, but based on information from adjacent zones, the same anthropogenic aspects almost certainly impacted this protected area.

What these insights tell us on the changes that have taken place in the forested habitats of the north and the role of natural change versus human actions needs some finer level information. Such data might be found in the form of stable isotope studies of the subfossils themselves overlaid on the former habitat signature, as Crowley and Samonds (2013) have done in the northwest. With all of the limestone cave formations in the north, another source of detailed information on precise ecological change and associated causes would be from spleothems, as Faina *et al.* (2021) and his colleagues have demonstrated for other areas of Madagascar.

Now turning back to small mammals of forested areas of northern Madagascar, several of the species occurring at Loky-Manambato and Montagne d'Ambre are only found in moist evergreen forest, such as Microgale drouhardi, M. fotsifotsy, and M. parvula (Table 5), which underlines that this portion of the island in the recent geological past had distinctly more mesic forest conditions and habitat linking corridors. Presumably moist evergreen forest habitat occurred from the Marojejy and Sorata forest areas north to Montagne d'Ambre, passing through the Loky-Manambato region, which retains in the summital areas of certain massifs remnants of this connection. Detailed genetic analyses are available for *M. fotsifotsy* (Everson et al., 2020), which shows that the populations of this species in the Loky-Manambato area, specifically the mesic forest on the upper slopes of the Binara Massif, form a clade with the Montagne d'Ambre animals, and this clade is in turn separate from populations further to the south. Hence, a clear biogeographic connection exists between the moist evergreen forest habitats of Montagne d'Ambre and certain peaks in the Loky-Manambato area, separated by about 65 km and today other vegetation types, supporting the notion of linking forested corridors in the recent past that today are not present.

Conservation of small mammals

Although the small mammals of the Andrafiamena-Andavakoera protected area do not contain any species unique to the site, two taxa are of conservation concern occur at the site and restricted to the north of the island. The first is an undescribed species of the endemic genus *Setifer* that is known from several protected areas, including Montagne d'Ambre, Montagne des Français, Analamerana, Ankarana, and presumed to present in Andrafiamena-Andavakoera. The second is a recently described endemic rodent species, *Eliurus carletoni*, which was named from Ankarana and subsequently found in other areas of the north of the island, including Andrafiamena-Andavakoera. In both of these cases, the remaining forested areas of this region and existing habitat corridors are crucial for the long-term existence of these species.

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