

The terrestrial small mammals of the Parc National de Masoala, northeastern Madagascar

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The results of small mammal inventories at 11 sites ranging from sea level to 1000 m a.s.l. on the Masoala Peninsula in northeastern Madagascar are presented. The Rodentia and Lipotyphla (ex Insectivora) of this peninsula, that contain extensive areas of lowland rainforest and some montane habitat, were previously poorly known. Fifteen endemic (5 rodents and 10 tenrecs) and 2 introduced species [*Rattus rattus* (Linnaeus, 1758) and *Suncus murinus* (Linnaeus, 1766)] were recorded. Species diversity in the lowland forests was reduced as typically found in other lowland sites in the eastern humid forest, while that of the lower montane zone was notably low as compared with other nearby large forested areas to the interior of the peninsula. Several ideas are presented to explain this difference, including the peninsula effect.

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Introduction

Over the past 15 years a considerable number of field inventories have been conducted in the humid forests of eastern Madagascar and this zone is relatively well known for small mammals (Lipotyphla [ex Insectivora] and Rodentia) (see Goodman *et al.* 2003 for a review). More specifically the northeastern region of the island, which includes large tracts of forest from lowland to montane formations, has been the subject of small mammal surveys, particularly the massifs of Marojejy and Anjanaharibe-Sud (Goodman and Carleton 1998, Goodman and Jenkins 1998, 2000, Carleton and Goodman 2000, Soarimalala and Goodman 2003). Faunistic data from montane areas of this northern region indicate that it is biogeographically distinct from the central highlands and with notable levels of microendemism. This led Carleton and Goodman (1998) to separate this zone as a

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separate biogeographic unit from the central highlands further to the south and they proposed the name “northern highlands”. One of the last remaining large forest tracts in northeastern Madagascar for which few data exist on its terrestrial small mammal fauna is the Masoala Peninsula, which contains the Parc National (PN) de Masoala. The purpose of this paper is to present precise information on the small mammals of this region, which were studied at 11 different sites, and to evaluate these data in a biogeographic context with areas of the northern highlands. Further, information is presented on certain aspects of the ecology of the small mammal fauna of the Masoala region.

Study area

The Masoala Peninsula is the largest peninsular landmass on Madagascar (Fig. 1) and comprises 42 000 km², of which 230 000 ha includes the PN de Masoala (Kremen 2003) and the nearby island of Nosy Mangabe. This park was created in 1997 based on its notably intact and extensive forest and marine ecosystems and is the largest protected area on the island. The forests of the Masoala include lowland areas of littoral forests resting on sand, gallery forests along the margins of rivers, and lowland forests on lateritic and basaltic soils (below 800 m a.s.l.), as well as montane habitats on a steep central north-south aligned ridge running the length of the peninsula and reaching 1400 m a.s.l. This region of Madagascar receives considerable precipitation and the annual average rainfall at the Andranobe Field Station is 5.9 m. The months of January to March is the period of heaviest rainfall and September to November is the period of lowest rainfall. There are human pressures on the forests of this region, most notably in the form of slash-and-burn agriculture by subsistence farmers, and some commercial exploitation of forest trees.

Eleven sites were studied for small mammals on the Masoala Peninsula, including the Réserve Spéciale (RS) de Nosy Mangabe (Razafindrakoto 1995, Andrianjakarivelo 1997; Table 1). Of these sites all rest on basaltic or lateritic soils with the exceptions of Tampolo and Andranomainty which are littoral forests occurring on sand substrates. The Tampolo forest is the largest remaining littoral forest zone in the PN de Masoala, and this formation is continuous with the lowland forest on lateritic soils across an elevational range from sea level to 400 m a.s.l. Information has also been added in this paper on a few small mammal specimens collected by a herpetological group in 1998 in the Sahafary forest (15°18'S, 50°22'E).

Material and methods

The target mammals during these surveys were members of the orders Rodentia and Lipotyphla. Two subfamilies of Muridae rodents occur in Madagascar – the introduced Murinae (the genera *Rattus* and *Mus*) and the endemic radiation of Nesomyinae (Jansa and Carleton 2003). Amongst the lipotyphlans there are two groups present on the island. The Soricidae is represented by 2 species of shrew, the introduced *Suncus murinus* (Linnaeus, 1766) (Hutterer and Tranier 1990) and the apparently endemic *Suncus madagascariensis* (Coquerel, 1848), and the endemic and diverse Tenrecidae, which comprises one of the most remarkable adaptive radiations of small mammals found in the world (Olson and Goodman 2003). In the eastern humid forests of Madagascar the Tenrecidae are represented by 2 different subfamilies: the spiny Tenrecinae and the smaller and smooth-furred Oryzoricinae. In general members of the Nesomyinae and Oryzoricinae are forest dwelling, while those of the Tenrecinae are less sensitive to forest disturbance and can be found in highly degraded forest habitats as well as open marshland and savannah areas. A number of new species and even two genera of Malagasy Rodentia and Lipotyphla from the humid forests have been described over the past 15 years (Goodman *et al.* 2003).

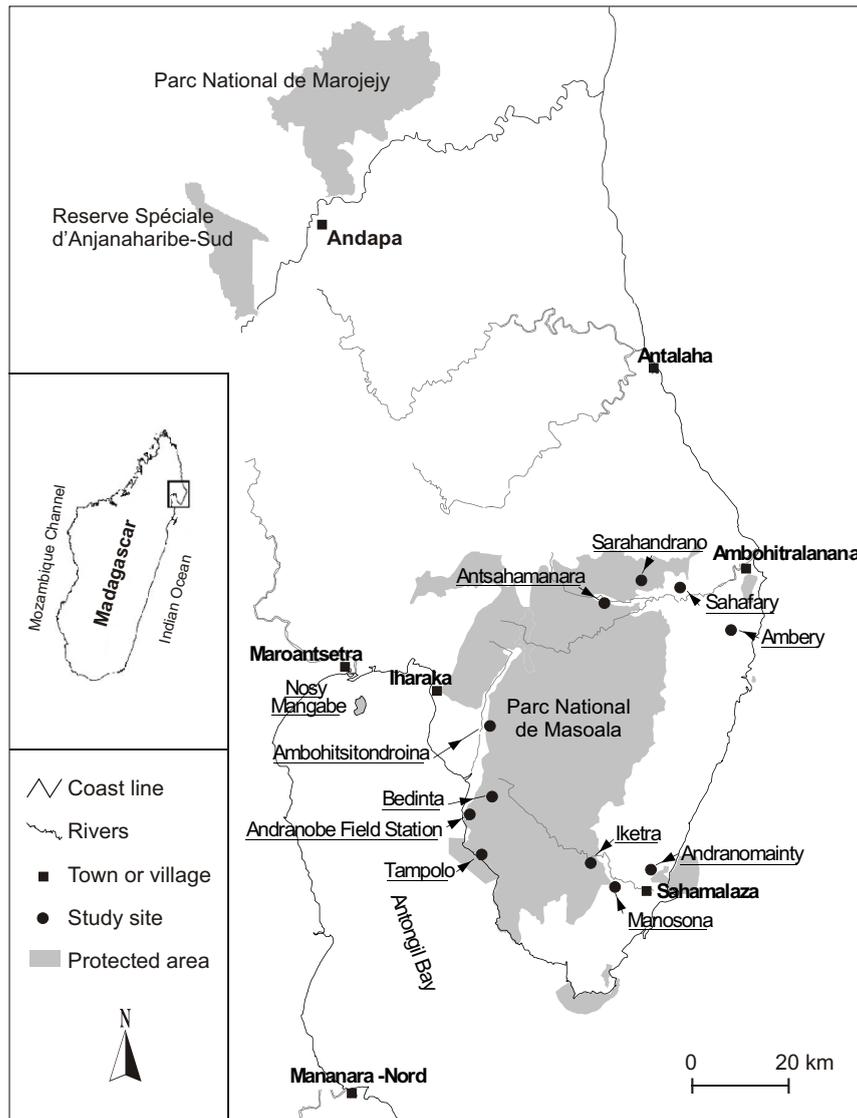


Fig. 1. Map of the general Masoala Peninsula region. Various localities and study sites mentioned in the text are illustrated. Study site names are underlined.

Trapping techniques

Field surveys were largely based on the capture of small mammals with live traps. The techniques used at the 11 sites were not consistent, which precluded certain comparisons between sites. Nonetheless, the data from these surveys provides important insight into the small mammals occurring in this poorly known area of the island. Animals were captured at Andranobe, Ambohitsitondroina, Bedinta, Sarahandrano, Antsahamanara, Ambery, Andranomainty, Manosona,

Table 1. Site information and inventory effort for small mammals captured in metal traps and pitfall traps on the Masoala Peninsula and on Nosy Mangabe. The cumulative accrued number of trap-nights was 17 624 and bucket-nights 2892.

Site	Coordinates		Altitude (m a.s.l.)	State of preservation	Period of trapping	Trapping effort	
	Latitude (S)	Longitude (E)				Trap- nights	Bucket- nights
Andranobe	15°40'	49°57'	0–600	Largely intact	Feb–March 1993, Mar–Apr 1996	2472	480
Ambohitsi- tondroina	15°34'	50°0'	600–1000	Intact	Sep 1993, Feb–Mar 1996	2984	480
Bedinta	15°40'	49°59'	500–650	Largely intact	Oct 1993, Apr–May 1996	2472	480
Andranomainty	15°47'	50°17'	0–20	Disturbed	Jan 1994	672	–
Ambery	15°22'	50°25'	0–100	Disturbed	Nov 1993	672	–
Manosona	15°43'	50°10'	20–50	Largely intact	Feb 1994	672	–
Iketra	15°47'	50°1'	40–280	Largely intact	Feb 1994	672	–
Sarahandrano	15°16'	50°17'	50–430	Heavily disturbed	Oct 1993	672	–
Antsahamanara	15°18'	50°13'	50–470	Disturbed below 150 m	Nov 1993	672	–
Tampolo	15°44'	49°58'	10–300	Largely intact	Mar–Apr 1997	1824	1056
Nosy Mangabe	15°29'	49°46'	0–330	Disturbed	Mar–Apr 2001, Sep–Oct 2001	3840	396

and Iketra using a system of 4 different quadrats per site, each measuring 30 × 30 m, and with 16 traps placed 10 m apart. These 16 stations were placed on the ground and in different combinations of 4 different trap types: Havahart traps (80 × 18 × 18 cm and 44 × 13 × 13 cm) and Sherman traps (23.5 × 8 × 8 cm and 17 × 6.2 × 6.2 cm). In order to sample arboreal species 5 Sherman traps (33 × 8 × 8 cm) were placed up to 2 m off the ground on horizontal branches along a 50 m line at least 100 m from each quadrat. This protocol was used at all of these sites with the exception of Ambohitsitondroina where the trapping effort was doubled (32 stations in 8 quadrates of 16 × 16 m).

In 1996 the sites of Andranobe, Ambohitsitondroina, and Bedinta were revisited and pitfall traps (22 cm deep and 22 cm diameter at the upper rim and without drift fences) were used, in addition to metal traps. Three lines, each 1000 m in length (comprising 5 non-adjacent segments of 200 m), composed of Sherman (23.5 × 8 × 8 cm and 33 × 8 × 8 cm), Havahart (44 × 13 × 13 cm), Nationals (40 × 13 × 13 cm), and pitfalls were employed. These devices were placed in a consecutive order, 20 m apart, along each trap line along the 200 m segments. In addition to these 11 traps, 2 lots of 4 additional traps were also installed along each trap line, composed of 2 Sherman traps placed in arboreal positions and 1 National, and 1 pitfall positioned on the ground.

In 1997, 4 different trapping techniques were used at 6 different sites in the Tampolo forest – 3 sites in the littoral forest and another 3 in the lowland forest. The first trapping methodology consisted of a 30 × 30 m quadrat that utilized 16 traps of 3 types (Sherman 23.5 × 8 × 8 cm, National 40 × 13 × 13 cm, and Havahart 44 × 13 × 13 cm). The second technique included 22 traps (Sherman 23.5 × 8 × 8 cm and National 40 × 13 × 13 cm), which were placed along 2 trap lines each 100 m in length, and the distance between traps was 10 m. The third technique utilized was 1 pitfall line (22 cm deep and 22 cm diameter at the upper rim), with a vertical 50 cm high dark plastic drift fence, along a distance of 100 m and with the buckets placed every 10 m. The fourth technique was identical to the third, with the exception that drift fences were not employed.

During the inventories of the RS de Nosy Mangabe, only Sherman (23.5 × 8 × 8 cm) traps were employed during the first trapping session. Three different quadrats, each 30 × 30 m, were installed with 2 traps placed every 10 m, 1 on the ground and another in an arboreal position up to 2 m off the ground. Four stations were censused with this methodology. During the second session Sherman traps were combined with pitfall traps at 2 different stations. The Sherman traps were placed along 3 different trap lines of 150 m in length, with 1 trap every 10 m on the ground and another in an arboreal position up to 2 m off the ground. The pitfall lines, each 100 m long and without drift fences, were composed of 11 buckets (22 cm deep and 22 cm diameter at the upper rim), and 10 m apart.

At all of the surveyed sites traps were left in place during 8 consecutive nights, but on Nosy Mangabe traps were installed for 7 consecutive nights during the first session and for 6 nights during the second session. The Sherman, Havahart, and National traps were baited with peanut butter, fresh banana or dried fish and no clear order was followed. At sites along steep elevational gradients, traps were placed in different zones along continuous slopes.

Captured animals and specimens

A considerable proportion of the trapped animals were released at the site of capture after being marked with ear tags. Given the rarity of retrapping marked individuals, these animals are not included in the trap capture figures. At each site a collection of reference specimens was made, which were preserved in formalin and subsequently transferred to 70% ethanol. These specimens are housed and catalogued in the Département de Biologie Animale, Université d'Antananarivo, Antananarivo, Madagascar. Skulls were subsequently removed and cleaned. The majority of collected specimens were compared by SMG to an extensive reference collection of Malagasy terrestrial small mammals housed at the Field Museum of Natural History, Chicago, for the final species identifications based on external measurements and pelage, cranial, and dental characters. Dr. M. Carleton at the Smithsonian Institution, Washington, D.C, also identified certain rodent specimens. Released animals were assigned to morphospecies that were associated with reference specimens.

Results

An accrued total of 2892 bucket-nights (pitfall) and 17 624 trap-nights (Sherman, Havahart, and National) at 11 different sites resulted in the capture of 14 endemic and 2 introduced small mammal species (Table 2). The endemics comprise 5 rodent and 9 tenrec species. The introduced species included the murid rodent *Rattus rattus* (Linnaeus, 1758) and the shrew *Suncus murinus*, and their trap capture rate was notably high in the disturbed habitat of the RS de Nosy Mangabe (Table 2). Three other sites also harboured introduced small mammal species, Ambohitsitondroina and Andranobe with *R. rattus* and Tampolo with *S. murinus*. A group of herpetologists captured by means of pitfalls an additional endemic tenrec, *Microgale brevicaudata* Grandidier, 1899, at Sahafary. Thus, in total 15 endemic and 2 introduced small mammal species are known from the peninsula (Table 2).

Of the native rodents, *Eliurus webbi* Ellerman, 1949 was most commonly encountered in the PN de Masoala and in a variety of forest types. This species was recorded at 6 of the 11 sites and was commonly captured in the metal rodent traps. The vast majority of individuals were in undisturbed dense humid forest on granitic soils and in arboreal trap sets (Table 3). The next most common native rodents were *Eliurus minor* Major, 1896 and *Eliurus tanala* Major, 1896, of which

12 individuals were captured. *E. minor* was found at Ambohitsitondroina, Ambery, and Bedinta across a broad range of elevational zones, but never in littoral forest and its capture-rate was notably higher in the mid-elevational zone at Ambohitsitondroina. Further, this species showed a marked preference for

Table 2. Inventory results for small mammals captured in metal traps and pitfall traps on the Masoala Peninsula and on Nosy Mangabe. Sight records without associated voucher specimens are denoted by "s". Recaptured animals are not included in these figures. Figures in standard font are from the metal traps and those in italics from the pitfall traps. * – introduced species, ** – the specimen record of *Microgale brevicaudata* is from Sahafary, a site that was not part of the systematic inventories reported here

Site	Andranobe	Ambohitsitondroina	Bedinta	Andranomainty	Ambery	Manosona	Iketra	Sarahandrano	Antsahamanara	Tampolo	Nosy Mangabe
Rodentia											
Muridae											
<i>Eliurus minor</i>		3	7		1			1			
<i>E. tanala</i>		12									
<i>E. webbi</i>	9	16	30	1				1		1	
<i>Nesomys audeberti</i>		6	2								
<i>N. rufus</i>			2				1				
<i>Nesomys</i> sp.	s				s	s	s				
<i>Rattus rattus</i> *											37
Lipotyphla											
Tenrecidae											
<i>Microgale cowani</i>		2									
<i>M. dobsoni</i>			1	1							
<i>M. parvula</i>		13									
<i>M. taiva</i>		19									
<i>M. talazaci</i>	1	18/7	1/2					1	1		
<i>M. brevicaudata</i> **											
<i>Oryzoricetes hova</i>											6
<i>Hemicentetes semispinosus</i>										8	
<i>Setifer setosus</i>	6/4	1/1	1/2	1						3/3	1
<i>Tenrec ecaudatus</i>	s		s								
Soricidae											
<i>Suncus murinus</i> *										1	13
Total species captured											
in live/pitfalls traps	3/1	6/5	6/3	3	1	0	1	3	1	2/3	2/2
Total endemic species captured											
in live/pitfall traps	3/1	6/5	6/3	3	1	0	1	3	1	2/2	0/2
Total endemic species	5	9	8	3	2	1	1	3	1	3	2

undisturbed dense humid forest on granitic soils and all individuals were in arboreal trap sets (Table 3). *E. tanala* was captured only at Ambohitsitondroina in undisturbed dense humid forest on granitic soils and in all cases in traps placed off the ground. *Nesomys audeberti* (Jentink, 1879) was also relatively common, but at 4 sites (Andranobe, Manosona, Iketra, and Ambery) the local presence of members of this genus were based on direct observations of animals in the forest and not captured individuals. These sight records are assigned only to *Nesomys* sp. *Nesomys rufus* (Peters, 1870) was captured at Iketra and Bedinta. All records of members of this genus are from undisturbed dense humid forest on granitic soils and they are exclusively terrestrial (Table 3). No native rodent was found on Nosy Mangabe.

Amongst native Lipotyphla captured or observed at the 11 surveyed sites, the Tenrecinae are represented by 3 species and the Oryzorictinae by 7 species (Table 2). All 3 species of Tenrecinae recorded occur widely across the park, particularly *Setifer setosus* (Schreber, 1777). *Tenrec ecaudatus* (Schreber, 1777) was observed at Bedinta and Andranobe, but never captured. Six species of Oryzorictinae were recorded during these surveys. *Microgale cowani* Thomas, 1882, *Microgale parvula* Grandidier, 1934, and *Microgale taiva* Major, 1896 were only found at Ambohitsitondroina. *M. talazaci* Major, 1896 was the most common member of the genus, having been recorded at 5 sites and their capture rate was notably high at Ambohitsitondroina. *Microgale dobsoni* Thomas, 1884 was the only species of *Microgale* found in the littoral forest. *Oryzorictes hova* Grandidier, 1870 was captured only on Nosy Mangabe. Members of the genus *Microgale* showed a very

Table 3. Ecology of the more common small mammal species known from the Parc National de Masoala. Data by species are presented as the number of individuals captured in the different habitats or positions. DHF – dense humid forest, *n* – total number of captured individuals.

Species	Altitude (m a.s.l.)	<i>n</i>	Habitat type			Habitat condition		Trap position	
			DHF on granitic soil	Coastal forest on basaltic soil	Littoral forest	Undis- turbed forest	Dis- turbed forest	Arboreal	Terres- trial
Rodentia									
<i>Eliurus minor</i>	0–1000	12	11	1	–	10	2	12	–
<i>E. tanala</i>	600–1000	12	12	–	–	12	–	12	–
<i>E. webbi</i>	0–1000	58	56	–	2	56	2	56	2
<i>Rattus rattus</i>	0–330	37	37	–	–	–	37	15	22
Lipotyphla									
<i>Microgale parvula</i>	900–1000	13	13	–	–	13	–	–	13
<i>M. taiva</i>	900–1000	19	19	–	–	19	–	–	19
<i>M. talazaci</i>	0–1000	31	31	–	–	29	2	3	28
<i>Setifer setosus</i>	0–1000	23	16	–	–	21	2	–	23
<i>Suncus murinus</i>	0–350	14	14	–	–	1	13	–	14

clear preference for undisturbed habitats in dense humid forest on granitic soils (Table 3). The exceptions being captures of *M. talazaci* and *M. dobsoni* in disturbed habitat. Further, all captures of members of this genus were on the ground, with the exception of 10% of the *M. talazaci* that were captured in arboreal trap sets. In contrast, all of the six *O. hova* captured were in disturbed habitat. Amongst the Tenrecinae, *Hemicentetes semispinosus* was restricted to intact littoral forest and *Setifer setosus* occurred in a variety of forest types and levels of disturbance.

Species richness

Ambohitsitondroina, between 600 and 1000 m, has the highest small mammal species richness of any of the sites surveyed with nine species, of which *Eliurus tanala*, *Microgale cowani*, *M. parvula*, and *M. taiva* were not encountered at any other site (Table 2). Eight species were identified at Bedinta and five species at Andranobe. All three of these sites are within the watershed of the Ambanizana River. At all of the other sites small mammal species richness was not higher than three species. This includes the littoral forest of Tampolo, the most extensively surveyed portion of the Masoala Peninsula for small mammals. Even though the RS de Nosy Mangabe was surveyed on two separate occasions and with considerable trapping effort, only four species of small mammals are known from the island – two introduced (*R. rattus* and *S. murinus*) and two endemic (*O. hova* and *S. setosus*).

Discussion

Before this series of small mammal surveys on the Masoala Peninsula some previous fieldwork had been conducted in the area. Earlier collected specimens include *N. audeberti*, *E. webbi* and *E. minor* from several different sites on the peninsula (Carleton and Schmidt 1990), and specimens of *M. cowani* and *M. talazaci* from Hiaraka [= Iharaka] (MacPhee 1987). Further, the holotype of *Eliurus ellermani* Carleton, 1994 was collected at Hiaraka (Carleton 1994). The validity of this taxon has been called into question and it may be a junior synonym of *E. tanala* (Carleton and Goodman 1998). Thus, to our knowledge no species of small mammal has been previously recorded on the Masoala Peninsula that was not documented during the survey work reported here.

The small mammal inventories conducted in 1993 and 1994 on the Masoala Peninsula were the first large scale efforts for these animals in this area. The second round of inventories in 1996 clearly demonstrated that the techniques used during the earlier surveys were incomplete, as an additional three species of Oryzoricinae were captured with the employment of pitfall traps. This technique is now known to be highly efficient to survey species of Oryzoricinae, particularly when a drift fence is employed.

Table 4. Species occurring on the Masoala Peninsula, Marojejy and Anjanaharibe-Sud. In all cases the surveys were conducted on the eastern and western sides of each of these massifs. Data for Masoala based on information presented in this paper; for Marojejy on Carleton and Goodman (2000), Goodman and Jenkins (2000), Soarimalala and Goodman (2003); and for Anjanaharibe-Sud on Goodman and Carleton (1998), Goodman and Jenkins (1998), Soarimalala and Goodman (2003) and includes the Betaolana Forest (800–1200 m).

Species	Region		
	Masoala (0–1000 masl)	Marojejy (450–1175 masl)	Anjanaharibe-Sud (875–1200 masl)
Rodentia			
Muridae			
<i>Brachytarsomys albicauda</i>		s	+
<i>B. villosa</i>			+
<i>Eliurus grandidieri</i>		+	+
<i>E. majori</i>			+
<i>E. minor</i>	+	+	+
<i>E. myoxinus</i>		+	
<i>E. tanala</i>	+	+	+
<i>E. webbi</i>	+	+	+
<i>Gymnuromys roberti</i>		+	+
<i>Nesomys audeberti</i>	+		
<i>N. rufus</i>	+	+	+
<i>Rattus rattus</i> (introduced)	+	+	+
Lipotyphla			
Tenrecidae			
<i>Microgale brevicaudata</i>	+	+	
<i>M. cowani</i>	+	+	+
<i>M. dobsoni</i>	+	+	+
<i>M. fotsifotsy</i>		+	+
<i>M. gracilis</i>		+	+
<i>M. gymnoryhncia</i>		+	+
<i>M. longicaudata</i>		+	+
<i>M. parvula</i>	+	+	+
<i>M. principula</i>			+
<i>M. soricoides</i>		+	+
<i>M. taiva</i>	+	+	+
<i>M. talazaci</i>	+	+	+
<i>Oryzoryctes hova</i>	+	+	+
<i>Hemicentetes semispinosus</i>	+	+	
<i>Setifer setosus</i>	+	+	+
<i>Tenrec ecaudatus</i>	+	+	+
Soricidae			
<i>Suncus murinus</i> (introduced)	+		
Total species richness of endemics	15	23	23
Total species richness	17	24	24

The extensive small mammal inventories conducted on the mountains of Anjanaharibe-Sud and Marojejy, to the northwest of the Masoala Peninsula (Fig. 1), provides a good comparison with the fauna occurring in the PN de Masoala (Table 4). This is for several reasons: (1) at all of these sites both the western and eastern slopes have been inventoried, (2) the same general trap types were employed and trap efforts are comparable (see below), and (3) other potential sites in the eastern humid forest that could be used lack montane habitat which would preclude certain assessments. When restricting comparisons to the same general elevational zone, the small mammal faunas of the Anjanaharibe-Sud and Marojejy massifs are notably greater in species richness, and for endemics there are 23 species occurring at these 2 sites as compared with 15 on the Masoala Peninsula. The trapping effort in the mountains of Anjanaharibe-Sud and Marojejy for Sherman and National traps was a cumulative total of 8190 trap-nights and for pitfall traps 2629 trap-nights, which is less than for the Masoala Peninsula (17 624 and 2892, respectively). Thus, the differences in these inland and peninsular sites are not simply related to trapping effort.

Several reasons can be provided to explain the difference in species richness between these sites. The Anjanaharibe-Sud and Marojejy massifs rise to around 2000 m a.s.l. and there is considerable montane habitat with a particular and speciose small mammal community. Several of the small mammals occurring in this zone descend to the lower limit of montane forest on these massifs (*Eliurus grandidieri* Carleton and Goodman, 1998, *E. majori* Thomas, 1895, *Microgale gracilis* Major, 1896, *M. gymnoryncha* Jenkins, Goodman and Raxworthy, 1996) and thus are recorded within the elevational zone we have compared with the Masoala Peninsula, which does not have extensive areas of this habitat. Another explanation is that the Masoala Peninsula has a lower small mammal species richness as compared with other inland areas of the island associated with what is known as the "peninsula effect" (Brown and Lomolino 1998). This phenomenon is characterized by a decrease in biotic species richness associated with the extension and constriction of landmasses in the form of a peninsula. This decrease may be a result of lower surface contact area between the base of the peninsular region and attached landmass due to reduced number of biotopes or lower dispersion rates. Several examples of this effect have been proposed elsewhere in the world (Taylor and Regal 1978, Brown 1987, Means and Simberloff 1987). Further evidence of this effect with regards to the Masoala Peninsula include the presence of the poorly known *Microgale dryas* Jenkins, 1992 in the Makira Forest at the base of the Masoala Peninsula (V. Andrianjakarivelo *et al.*, unpubl.), and although similar habitats and elevations were surveyed in the nearby Masoala forest this species has not been recorded.

None of the small mammal taxa thought to be restricted to the northern highlands were captured on the Masoala Peninsula (eg *Microgale monticola* Goodman and Jenkins, 1998 or *Voalavo gymnocaudus* Carleton and Goodman, 1998). In most cases these are species that occur in montane forest, a habitat not

extensively represented on the Masoala Peninsula. Our biogeographic conclusion is that the small mammal fauna of the Masoala Peninsula does not show any clear affinities to the northern highlands.

Research conducted in littoral and lowland forests elsewhere in eastern Madagascar indicate that these habitats have distinctly lower species richness for small mammals than montane habitats (Stephenson 1995, Rakotondravony *et al.* 1998, Ganzhorn *et al.* 2000). The littoral and lowland forests of the Masoala Peninsula follow this same pattern, and this is presumably related to differences in habitat productivity along elevation gradients (*sensu* Rosenweig 1995) and an associated annual dry season that is more pronounced at lower elevations. Further, it is the lowland humid forest formations in the eastern portion of the island that have been the most severely impacted by human activities of deforestation and the associated invasion of non-native biota.

Nosy Mangabe has a notably low number of mammal species: two endemic Lipotyphla and two abundant introduced species (one shrew and one murid rodent). No native rodent is known from this island. Even though the island has a broad expanse of native forest, it has been the subject of extensive anthropogenic habitat modification. On the basis of radiocarbon dating of archaeological remains the island was extensively deforested starting in the 8th century, and the natural habitats were able to regenerate by the time Dutch pirates installed on the island on the 17th century (Wright and Rakotoarisoa 1997). Thus, Nosy Mangabe has had a long history of anthropogenic modification and invasion of introduced species. It is interesting to note that the two native small mammal species recorded from this island, *S. setosus* and *O. hova*, can be found outside forested zones.

Other littoral forests along the eastern coast of Madagascar and south of the Masoala Peninsula have been surveyed for small mammals, which include the Mandena and Manafiafy forests near Tolagnaro (Ganzhorn *et al.* 2000) and the Tampolo forest near Fénériver-Est (Rakotondravony *et al.* 1998). Consistently across these sites, including the littoral forests of Masoala, the only nesomyine rodent captured was *E. webbi*. No oryzorictine is known to occur in the two different Tampolo forests (Masoala and Fénériver-Est) and only *Microgale pusilla* Major, 1896 has been recorded in the Tolagnaro littoral forests. The presence of *M. dobsoni* in the Andranomainty littoral forest is an exceptional record of this species that is normally only present in forests resting on lateritic soils.

It has been proposed that the colonization of *Rattus rattus* into natural forested habitats on Madagascar has created a potential problem for the native rodents associated with the introduction of disease vectors or direct competition (Goodman 1995). In the case of the PN de Masoala, the impact of this introduced rodent does not seem to be notable, at least for the time being. In 1993 *R. rattus* was captured at Ambohitsitondroina and Andranobe and subsequent surveys of these sites in 1996 did not find this species. We interpret these results to show that there was not a notable increase in this rodent in the region and that it is not

a dominant member of the local mammals community. In 2000 the Masoala Peninsula was hit with a massive cyclone that toppled a considerable number of trees, resulting in the opening of the forest, which in turn might provide ideal conditions for a large-scale increase in the number of *Rattus* in this forest. Further monitoring of this situation is needed.

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