Chapter 12

The Rodents of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

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Abstract

In October and November 1994, rodents were studied on the slopes of the Réserve Spéciale d'Anjanaharibe-Sud in four elevational zones between 875 and 1950 m. Nine species belonging to the endemic subfamily Nesomyinae (*Brachytarsomys albicauda, Eliurus grandidieri, E. majori, E. minor, E. tanala, E. webbi, Gymnuromys roberti, Nesomys rufus,* and *Voalavo gymnocaudus*), as well as the introduced *Rattus rattus* (subfamily Murinae), were collected. We present information on distribution, measurements, ecology, and reproduction for each species.

The highest diversity and populations of indigenous rodents were encountered in montane forest at 1260 m (six species), but fewer occurred in lowland moist forest at 875 m (four species) and in sclerophyllous montane forest at 1950 m (three species) near the summit. Except for *Rattus rattus,* no species occurs across the complete elevational range sampled, although two, *Eliurus majori* and *Nesomys rufus,* were found at the three higher sites (1260–1950 m). Two rodent taxa are so far known only from the RS d'Anjanaharibe-Sud, *E. grandidieri* and *Voalavo gymnocaudus,* both newly discovered as part of the survey, and are described in Chapter 11.

Résumé

Au mois d'octobre et de novembre 1994, une enquête sur les rongeurs de quatre zones localisées sur un transect altitudinal réalisé entre 875 et 1950 m le long du versant oriental de la forêt humide sempervirente de la Réserve Spéciale (RS) d'Anjanaharibe-Sud a été réalisée. Neuf espèces de rongeurs appartenant à la sous-famille endémique des Nesomynae (*Brachytarsomys albicauda, Eliurus grandidieri, E. majori, E. minor, E. tanala, E. webbi, Gymnuromys roberti, Nesomys rufus,* et *Voalavo gymnocaudus*) ainsi que l'espèce introduite *Rattus rattus* (sous-famille des Murinae) ont été collectées. Les données relatives à la distribution, aux mesures morphométriques, à l'écologie et à la reproduction de chaque espèces sont présentées.

La plus grande diversité spécifique et les densités de populations les plus élevées ont été constatées dans la forêt d'altitude à 1260 m (six espèces), contre quatre espèces dans la forêt de basse altitude à 875 m et enfin trois dans la forêt sclérophylle proche du sommet à 1950 m d'altitude. A l'exception de *Rattus rattus,* aucune autre espèce ne se rencontre sur l'ensemble du transect altitudinal qui a fait l'objet de cet échantillonnage. Cependant deux espèces, *Eliurus majori* et *Nesomys rufus* ont été trouvées au niveau des trois sites les plus hauts en altitude (1260 à 1950 m). Deux genres de rongeurs étaient jusque là connus de la RS d'Anjanaharibe-Sud auxquels se rajoutent deux nouveaux, *E. grandidieri* et *Voalavo gymnocaudus* découverts au cours de cet inventaire.

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Introduction

The native rodents of Madagascar, as currently understood, comprise a group of 18 species that are classified in the Nesomyinae of a broadly defined Muridae (Carleton & Musser, 1984; Musser & Carleton, 1993; Carleton & Goodman, 1996; Chapter 11). In addition to uncertainty about the monophyly of the Nesomyinae (see discussions in Petter, 1972, 1990; Carleton & Musser, 1984; and Dubois et al., 1996), other major gaps still exist in our biological and systematic knowledge of these indigenous rodents. However, renewal of small-mammal field surveys over the past decade and study of the resulting collections are doing much to fill such voids. Recent investigations of Nesomyinae have covered many aspects of their natural history, geographic distribution and elevational range, and systematics (Nicoll et al., 1988; Carleton & Schmidt, 1990; Barden et al., 1991; Ryan et al., 1993; Stephenson, 1993; Carleton 1994; Goodman & Ganzhorn, 1994; Carleton & Goodman, 1996; Goodman & Carleton, 1996; Goodman & Rakotondravony, 1996; Chapter 11).

This chapter focuses on specimens and associated natural history information gathered during the 1994 inventory of rodents that inhabit slightly disturbed lowland moist forest and primary montane and sclerophyllous forests within the Réserve Spéciale (RS) d'Anjanaharibe-Sud. Special attention is devoted to species richness and relative population densities along the elevational gradient of the inventory, ranging from 875 to 1950 m. Finally, the data reported here are integrated with that from the Réserve Naturelle Intégrale (RNI) d'Andringitra (sampled from 720 to 2450 m), situated near the southern end of the Central High Plateau, and based on Goodman and Carleton (1996), Langrand and Goodman (1997), and Goodman (unpubl. data). Both sites form part of a series of inventories on the montane faunas of the island. The field methods and sampling protocols used in the two studies have been standardized, insofar as possible, to allow direct and more rigorous comparisons between rodents found in these widely distant, mountainous settings.

Previous Work in the Region

To our knowledge nothing has previously been published on the rodents of the RS d'Anjanaharibe-Sud. The only list so far produced for the mammals of this reserve (Nicoll & Langrand, 1989) does not mention rodents. During the Mission Zoologique Franco-Anglo-Américaine (FAA), conducted between 1929 and 1931, a place "one day west of Andapa" was visited, and one specimen each of *Eliurus minor* and *Nesomys rufus* was collected in 1930 (Rand, 1932; Carleton & Schmidt, 1990). That locality was near or perhaps within the present-day boundaries of the RS d'Anjanaharibe-Sud, which was not designated as an official reserve until 1958; the coordinates for the site "one day west Andapa" were estimated by Jenkins (1987) as 14°39′S, 49°22′E. Rand (1936: p. 189) recorded the elevation as 1800 m and captured the majesty of the region:

> Here the country was beautiful. To the north a dark mountain rose; to the south, range after range of mountains stretched away, losing themselves in the bluish haze. . . . It was damp and rained nearly every day that we were there, but it was cool, even chilly at night. . . . There were traces of frost some mornings on the tobacco plants outside the tent. Our camp was situated in hilly country on the edge of a high plateau. Besides the low moss and lichen-draped trees and the forest of taller trees like those found on the forests at lower altitudes, we found open ground stretching away to the west. Each valley had a little swamp with grass or reeds growing in it, and the ridges were covered with low brush, bracken, and grass.

The Mission Zoologique FAA visited other places in the general region of the RS d'Anjanaharibe-Sud, where a few rodents were collected (Carleton & Schmidt, 1990; Carleton, 1994): *Eliurus minor,* 20 km SW of Maroantsetra; *E. webbi,* near Antalaha; *Nesomys audeberti,* 2 days NE of Maroantsetra; and *N. rufus,* on the Tsaratanana Massif to the west. Also, limited information is available for small mammals occurring in the RNI de Marojejy, a reserve located just across the Andapa basin from the RS d'Anjanaharibe-Sud (Duckworth & Rakotondraparany, 1990), but certain specific identifications are ambiguous for want of reference material.

Materials and Methods

This study is based on field work conducted between 16 October and 30 November 1994 by Goodman, who analyzed the trapping results and general ecological data. Carleton refined taxonomic determinations and undertook systematic comparisons.

Field Methods and Trapping Protocol

The general protocol follows that of Goodman and Carleton (1996). At four elevational levels (875, 1260, 1550, and 1950 m), trap lines were maintained for a minimum of 5 nights, and a minimum of 100 traps were installed within each zone (Table 12-1). Each trap line, numbered sequentially starting with the 875 m zone, consisted of Sherman live traps (9 × 3.5 × 3 in.) and National live traps (16 × 5 × 5 in.) in a ratio of 4:1. Traps were baited daily, generally between 15:00 and 17:00 hr, with finely ground peanut butter and ground maize freshly mixed in proportions to make a paste, and lines were inspected at least twice per day, once at dawn and again in late afternoon. Arrays of pitfall traps were also installed in each elevational zone, but these yielded few rodents in comparison to the numerous insectivores (see Chapter 10).

A trap-night is defined as one live trap in use for a 24-hour period (dawn to dawn). The total number of trap-nights accrued at each elevation varied slightly; consequently, the first 500 trap-nights in an elevational zone are considered the "standardized" trapping regimen to facilitate comparisons among the four sites. Standing biomass of a species is based on the total catch of individuals during a standardized trapping regimen multiplied by average body weight of the species (Table 12-2). Instead of an areal factor, population density is calculated as a linear estimate, that is, the number of individuals of a given species obtained per 100 m of trap line within an elevational zone.

The exclusive reliance on live traps during these small-mammal surveys, rather than on a combination of live and snap traps, stems from both the composition of the island's trappable small-mammal fauna and attendant permit restrictions. Significant in this regard is that small primates, such as mouse lemurs (*Microcebus*) and fat-tailed lemurs (*Cheirogaleus*), are relatively common at some sites and readily enter kill traps. The use of live traps allows release of any captured lemurs unharmed.

To quantify differences in spatial distribution of small-mammal captures, several trapping variables were systematically recorded for each trap installed: (1) type of trap, (2) total length of trap line, (3) distance between traps, and (4) specific placement of trap, including its substrate, surrounding forest structure, and position on or height above the ground. Categorization of microhabitat location (variable 4) was simplified from the overly detailed system presented by Goodman and Carleton (1996) as follows:

On ground: (1) In leaf litter, generally in area of open understory; (2) under decomposed downed trees or woody vegetation; (3) by tree root or trunk with or without cavity or hole; and (4) miscellaneous, including placement under exposed rocks or boulders, at base of rock face, in thick herbaceous vegetation, and on moss-covered rocks.

Above ground: (1) On liana, limb or trunk less than 10 cm in diameter in horizontal to vertical position; (2) on liana, limb or trunk greater than 10 cm in diameter in horizontal to vertical position; (3) on limbs or trunks suspended by lianas; and (4) miscellaneous, including placement on bamboo stalks, in small cavities at junctions of tree limbs, and on large moss-covered rocks.

Specimens and Measurements

Captured animals were prepared as either standard museum skins with associated skulls and partial skeletons, fluid-preserved carcasses, or full skeletons. Whole carcasses were wrapped in fine cheesecloth before immersion in formalin to prevent loss or mixing of ectoparasites between their specific hosts (see Chapter 6). A large proportion of captured rodents were preserved as vouchers during the survey of the RS d'Anjanaharibe-Sud. This material is housed in the Field Museum of Natural History (FMNH), Chicago, and a representative series has been returned to the Départment de Biologie Animale, Université d'Antananarivo (UA). Specimens deposited immediately after the survey in the latter institution have not yet been catalogued and are individually referenced by the collector's field numbers (UA-SMG). To confirm taxonomic identifications, nesomyine holdings in other museums (see Appendix in Goodman & Carleton, 1996) were also consulted, and one or both authors have examined the holotypes of all described forms of Nesomyinae, except for Peters's (1870) *Nesomys rufus.*

Six measurements, in millimeters (mm) or grams (g), were taken by Goodman for each specimen in the flesh; their abbreviations and definitions are given below:

TOTL = total length of body and tail, measured from the tip of the nose to the end of

TABLE 12-1. Summary of trap lines in the RS d'Anjanaharibe-Sud.*

Elevation	No. of traps	Length of line (m)	Mean distance between traps (m)	Mean height above ground (m)
875 m (17–29 October)				
Line 1	100	730	7.6 ± 5.80 (1–30)	1.4 ± 0.59 (0.25–2.5), n = 40
Line 2	50	345	7.1 ± 5.24 (1–24)	1.5 ± 0.76 (0.25–3.0), n = 22
1260 m (4–10 November)				
Line 3	100	520	5.2 ± 3.61 (0.5–23)	1.6 ± 0.55 (0.5–3.0), n = 43
1550 m (17–22 November)				
Line 4	100	396	4.0 ± 1.14 (1–10)	1.5 ± 0.46 (0.25–2.0), n = 39
1950 m (24–29 November)				
Line 5	100	423	4.3 ± 2.29 (0.25–12)	1.9 ± 0.62 (0.5–3.0), n = 32

* Descriptive statistics presented as mean ± SD (range). Each line consisted of National and Sherman live traps in a ratio of 4:1 (see page 203).

the last caudal vertebra (not including terminal hair tuft)

HBL = head and body length, measured from the tip of the nose to the distalmost point of the body (at base of tail)

TL = tail length, measured from the base of the tail (held at right angles to the body) to the end of the last caudal vertebra (not including terminal hair tuft)

HFL = hindfoot length, measured from the

TABLE 12-2. External measurements and sample statistics of adult Nesomyinae rodents from the RS d'Anjanaharibe-Sud.*

Species	TOTL	HBL	TL	HFL	EL	WT
Brachytarsomys albicauda	459	210	240	35	17	205
Eliurus grandidieri	293.4	129.8	161.7	27.7	20.0	52.8
	13.4	12.8	12.3	0.8	1.1	5.5
	275–324	118–185	141–186	26–29	18–22	44.5–67.5
	(n = 19)	(n = 23)	(n = 19)	(n = 23)	(n = 23)	(n = 22)
Eliurus majori	354.4	158.7	186.6	29.3	18.8	94.2
	11.4	3.4	8.9	1.1	0.9	10.5
	330–370	155–165	170–202	27–31	18–20	78–109
	(n = 11)	(n = 11)	(n = 11)	(n = 11)	(n = 11)	(n = 10)
Eliurus minor	244.0	110.4	127.8	22.1	16.9	36.9
	17.0	4.4	14.6	0.8	1.0	4.1
	205–260	105–116	94–139	21–23	15–18	31.0–43.5
	(n = 8)	(n = 7)	(n = 8)	(n = 8)	(n = 8)	(n = 7)
Eliurus tanala	361.5	167.8	187.2	33.3	23.2	105.9
	16.1	4.3	17.3	0.5	0.8	12.0
	342–381	163–174	158–203	33–34	22–24	96.5–120
	(n = 4)	(n = 5)	(n = 5)	(n = 4)	(n = 5)	(n = 5)
Eliurus webbi	309.7	142.0	163.5	27.7	23.0	71.9
	14.4	4.8	10.1	1.5	1.6	5.9
	294–332	138–149	153–179	26–29	20–25	63.5–78.5
	(n = 6)	(n = 4)	(n = 6)	(n = 6)	(n = 7)	(n = 6)
Gymnuromys roberti	402, 402	177, 186	210, 212	38, 39	21, 22	141, 170
Nesomys rufus	348.7	183.4	161.3	44.3	26.6	160.8
	9.0	6.1	6.1	1.5	1.1	17.3
	334–361	169–191	154–174	41–46	24–28	128–190
	(n = 12)	(n = 12)	(n = 12)	(n = 12)	(n = 12)	(n = 12)
Voalavo gymnocaudus	212.7	87.7	119.3	20.7	15.0	22.0
	1.2	2.1	0.6	0.6	0.0	1.5
	212–214	86–90	119–120	20–21	15–15	20.5–23.5
	(n = 3)	(n = 3)	(n = 3)	(n = 3)	(n = 3)	(n = 3)

*Values presented are mean, SD, range, and number. See text (pp. 203–205) for definitions of measurement abbreviations.

heel to the tip of the longest toe (not including claw)

EL = ear length, from the basal notch to the distalmost tip of the pinna.

WT = weight, measured in grams with Pesola spring scales to within ±0.5 g for animals less than 100 g and to within ±1.0 g for those between 101 and 300 g.

Sixteen cranial and two dental dimensions were measured by Carleton to the nearest 0.1 mm using handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations, follow the anatomical landmarks defined and illustrated in Carleton (1994):

BBC = breadth of the braincase
BIF = breadth of incisive foramina
BM1s = breadth of the bony palate across the first upper molars
BOC = breadth across the occipital condyles
BR = breadth of rostrum
BZP = breadth of the zygomatic plate
DAB = depth of the auditory bulla
IOB = interorbital breadth
LBP = length of bony palate
LD = length of diastema
LIF = length of the incisive foramina
LM1-3 = coronal length of maxillary tooth row
LR = length of rostrum
ONL = occipitonasal length
PPB = posterior breadth of the bony palate
PPL = postpalatal length
WM1 = width of the first upper molar
ZB = zygomatic breadth

Standard descriptive statistics (mean, range, and SD) were derived for adult specimens in each species sample. We define "adult" as those animals that lack the finer, juvenile pelage and that possess fully erupted, although sometimes unworn, third molars. Where sample sizes permitted, two-sample *t* tests and one-way analyses of variance were applied to the mensural variables, with sex as the categorical variable. Analytical routines were carried out using Systat (version 6.01, 1996). Mammae formulae are presented as the number of paired postaxial, abdominal, or inguinal teats.

Species Accounts

Within each account, field observations and natural history data are presented under the subheadings "Distribution," "Ecology and Reproduction," "Comments" (as necessary), and "Specimens Examined." For identification criteria and taxonomic discussion, see Carleton (1994), Goodman and Carleton (1996), and Chapter 11. External measurements and weights, however, are provided for the 10 species, both as a practical key and as background reference to the size and mass differentials that characterize the rodent guild of the RS d'Anjanaharibe-Sud.

Family Muridae: Subfamily Murinae

Rattus rattus (Linnaeus, 1758)

DISTRIBUTION—The black rat was captured in all elevational zones sampled throughout the reserve. Elsewhere on the island, wherever surveyed, it seems to occur in remaining stands of pristine eastern humid forest (Goodman, 1995; Goodman & Carleton, 1996).

ECOLOGY AND REPRODUCTION—*Rattus* was most common at 1550 m, where 15 individuals were captured in 500 trap-nights, as compared with the 875, 1260, and 1950 m zones, where only one or two individuals were obtained during each 500 trap-nights of effort (Fig. 12-1). The Andringitra transect, conducted between 720 and 2450 m, within habitats ranging from lowland to sclerophyllous forests (tree line at about 2000 m) through high mountain meadows and the open rocky summital zone (Goodman & Carleton, 1996; Langrand & Goodman, 1997; Goodman, unpubl. data), found a parallel midelevational increase in *R. rattus* densities as in the RS d'Anjanaharibe-Sud (Fig. 12-1). At Andringitra, more *R. rattus* were captured in the 1210 and 1625 m zones than in areas of the mountain above or below this zone.

The 875 m camp was a few kilometers from several small settlements and cleared areas of *tavy*. Such human activities would presumably attract *Rattus rattus* as a commensal animal, yet only one individual was captured in 1,000 trap-nights at this transect. *Rattus* does not appear to be more common in disturbed forest close to human habitation in the RS d'Anjanaharibe-Sud, contrary to the situation in some other Old World tropical countries (Musser, 1987; Heaney et al., 1989).

Seventeen of 19 (89%) *Rattus rattus* captured within the RS d'Anjanaharibe-Sud were trapped on the ground, particularly by roots and trunks (Table 12-3). The other two individuals were

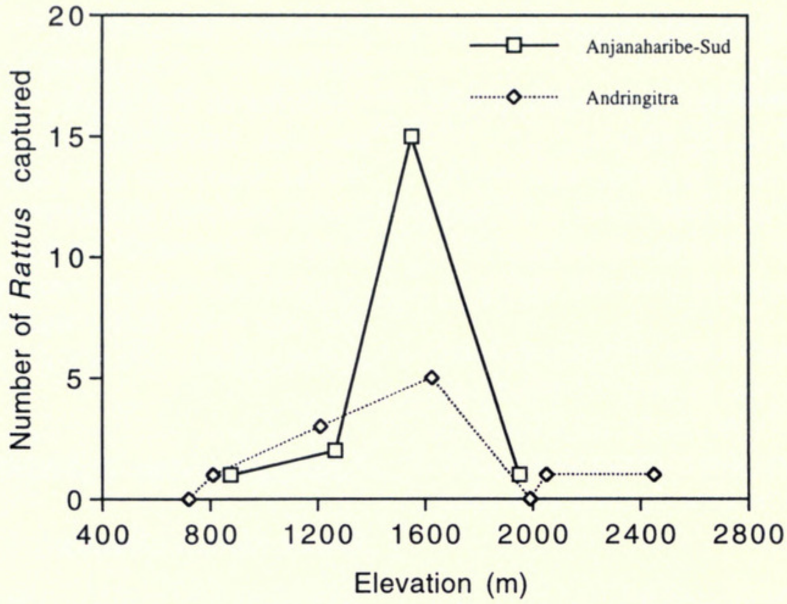

FIG. 12-1. Number of *Rattus rattus* captured at different elevational zones in the RS d'Anjanaharibe-Sud (squares) and the RNI d'Andringitra (diamonds) using similar trapping regimens. The trap success within each elevational zone is standardized at 500 accrued trap-nights. The Andringitra data are based on Goodman and Carleton (1996), Langrand and Goodman (1997), and Goodman (unpubl. data).

taken in sets placed above ground, on limbs and tree trunks at least 10 cm in diameter. The predominantly terrestrial sphere of *Rattus* activity conforms to results obtained in the RNI d'Andringitra, where 64% of black rats were captured in traps set on the ground.

The vast majority of *Rattus rattus* collected were adults. Of the 14 specimens preserved, eight (57%) were scrotal males, one was a male with abdominal testes, three were adult females with large mammae, and two were subadult females with small mammae and imperforated vaginas. The mammae formulae varied among the four females (3-0-1, 1-2-2, 1-2-1, and 2-1-2).

COMMENTS—The history of the introduction and subsequent colonization of Madagascar by *Rattus rattus* is poorly known. As currently documented, the earliest presence of commensal rats on the island dates from 11th to 14th century middens excavated at the Islamic site of Mahilaka, near Ambanja (Rakotozafy, 1996; Radimilahy, 1997). Presumably, rats were transported to Madagascar by Arab traders during this period.

By the close of the 19th century, *Rattus* was already found in numerous remote sites in the eastern humid forest. In 1895 and 1896, Forsyth Major collected *R. rattus* at Ampitambe (BM(NH) 97.9.1.156) and Vinanitelo (BM(NH) 97.9.1.157 and 97.9.1.158), although he made no mention of these captures in his expedition summary (Major 1896a). In the forest in and around the RS d'Analamazaotra, the earliest vouchered record of *R. rattus* is a specimen obtained in May 1916 (MNHN 1983.941); by 1939, *Rattus* had colonized the reserve and surrounding forest and "multiplied at an alarming rate," according to Webb (1954: p. 256).

Recent field work has revealed that *Rattus rattus* is a common to abundant member of the small-mammal community and is broadly distributed, geographically and altitudinally, in secondary to pristine humid forest throughout the island (Goodman, 1995; Goodman & Carleton, 1996). The overwhelming abundance of *R. rattus* at certain sites far exceeds the native nesomyines (Goodman et al., in press) and raises concerns that introduced rats are displacing the indigenous small mammals of Madagascar.

No *Rattus norvegicus* were found within the reserve, but a dead individual was discovered in the nearby village of Befingitra.

SPECIMENS EXAMINED—6.5 km SSW of Befingitra, 875 m (UA-SMG 6864); 9.2 km WSW of Befingitra, 1260 m (FMNH 154275; UA-SMG 6983); 11.0 km WSW of Befingitra, 1550 m (FMNH 154039, 154278, 154279, 154280, 154281, 154282, 154283, 154284; UA-SMG 7043); 12.2 km WSW of Befingitra, 1950 m (FMNH 154293).

Family Muridae: Subfamily Nesomyinae

Brachytarsomys albicauda Günther, 1875

DISTRIBUTION—*Brachytarsomys albicauda* is recorded from various localities broadly scattered

TABLE 12-3. Microhabitat occurrences of rodent species by elevation in the RS d'Anjanaharibe-Sud.

		Trap position		Ground location*				Above-ground location			
Elevation and species	No. taken	On ground	Above ground	Leaf litter	Under rotten wood	By roots, trunks	Misc.	Vine, limb, or trunk <10 cm	Limbs, trunks >10 cm	Suspended trunks	Misc.
875 m											
Trap distribution†		60	40	11	12	36	1	22	13	3	2
Rattus rattus	1	1				1					
Eliurus minor	1		1					1			
Eliurus webbi	4		4					2	2		
1260 m											
Trap distribution		61	39	7	12	35	7	23	16		
Rattus rattus	2	1	1			1			1		
Eliurus grandidieri	23	19	4	2	3	11	3	1	3		
Eliurus majori	6	1	5	1				2	3		
Eliurus minor	6	1	5			1		2	3		
Eliurus tanala	6	5	1			1	4				1
Gymnuromys roberti	1	1				1					
Nesomys rufus	8	8			2	6					
1550 m											
Trap distribution		60	40	8	13	36	3	21	10	1	8
Rattus rattus	15	14	1		1	13			1		
Eliurus grandidieri	1	1			1						
Eliurus majori	2		2					1	1		
Nesomys rufus	3	3				3					
1950 m											
Trap distribution		66	34	7	7	49	3	12	16		6
Rattus rattus	1	1			1						
Eliurus majori	4		4					1	3		
Nesomys rufus	4	4				3	1				
Voalavo gymnocaudus	3	2	1		1	1			1		
Totals (875–1950 m)											
Trap distribution		247	153	33	44	156	14	78	55	4	16
Rattus rattus	19	17	2		2	15			2		
Eliurus grandidieri	24	20	4	2	4	11	3	1	3		
Eliurus majori	12	1	11	1				4	7		
Eliurus minor	7	1	6			1		3	3		
Eliurus tanala	6	5	1			1	4				1
Eliurus webbi	4		4					2	2		
Gymnuromys roberti	1	1				1					
Nesomys rufus	15	15			2	12	1				
Voalavo gymnocaudus	3	2	1		1	1			1		
Total	89	60	29	3	9	42	6	10	18		1

* See page 203 for habitat definitions.
† Restricted to first 500 trap-nights of line 1.

across the eastern humid forest of the island, over an elevational range of 450–1300 m, from the Sihanaka Forest around the Lac Alaotra region to as far south as Vinanitelo in the vicinity of Fianarantsoa (Carleton & Schmidt, 1990). The record of this species within the RS d'Anjanaharibe-Sud thus extends its known range about 320 km farther north.

ECOLOGY AND REPRODUCTION—People from villages neighboring the reserve mentioned that a large nocturnal and arboreal rodent lives in the forest. They recounted its unusual mode of locomotion, how it inhabits tree hollows, and how, when disturbed, particularly during the day, it sticks its head outside the cavity and utters a chattering sound. Their careful description undoubtedly fits the behavior and form of *Brachytarsomys albicauda,* a single specimen of which was captured in the 875 m zone.

The individual had entered a National trap baited with dried coconut and set apart from the standardized small-mammal trap line. The trap was placed on a horizontal portion of a canopy vine, about 3 cm in diameter and 1.5 m above the ground. The vine made a complete loop from an entanglement near midcanopy, down to within 1.5 m of ground, and then back up. The animal was an adult female with large mammae (1-0-2) and was carrying embryos (four in the left uterine horn and two in the right); the crown–rump length was about 21 mm. Lactation tissue had started to form. During specimen preparation it was striking how thick and durable the skin was in comparison with other nesomyine rodents and how much connective tissue was attached to the inner surface of the skin.

When moving about vines and branches of the subcanopy, this arboreal and nocturnal rodent, with its slow-climbing locomotion, is reminiscent of fat-tailed lemurs (*Cheirogaleus*). Furthermore, it is reported to feed mainly on fruits (Petter, 1972). At 875 m on the Anjanaharibe-Sud Massif, *Brachytarsomys albicauda* coexists with a variety of arboreal nocturnal lemurs, including *C. major, Microcebus rufus, Allocebus trichotis, Avahi laniger, Lepilemur mustelinus,* and *Daubentonia madagascariensis* (see Chapter 14). It would be fascinating to investigate aspects of food resources and nesting sites commonly used by *Brachytarsomys* and nocturnal lemurs.

Specimens Examined—6.5 km SSW of Befingitra, 875 m (FMNH 154055).

Eliurus grandidieri Carleton and Goodman, 1998

Distribution—This newly described species (see Chapter 11) is so far known only from middle to upper montane slopes (1260 and 1550 m) in the RS d'Anjanaharibe-Sud. In view of its elevational occurrence in the reserve, it may be expected to occur on the nearby Tsaratanana and Marojejy massifs.

Ecology and Reproduction—At 1260 m, *Eliurus grandidieri* was the most common species of mammal captured, accounting for 23 (47%) of the 49 rodents found in the standardized trap lines. The majority (19 of 23) were taken on the ground; of these, most (11 of 19) were captured near tree roots or trunks, and the remainder were captured in a variety of microhabitats, such as under rotten and fallen tree trunks (three), in areas of open understory with relatively thick leaf litter (two), and at openings under large boulders (three). The dispositions of the arboreal sets that yielded four *E. grandidieri* were as follows: 0.5 m off the ground on the base of an inclined tree trunk (20 cm diameter, 40° slope); at 2 m height, on an arched tree trunk (25 cm diameter); 0.5 m up a moss-covered vine (3 cm diameter) that reached from the ground to lower canopy and back down; and on a horizontal moss-covered tree trunk (14 cm diameter), 1.5 m above the ground. The single individual from the 1260 m zone was trapped on the ground, at the opening of a large hole passing under a tree root and covered with debris.

Animals from the 1260 m zone varied considerably in breeding condition, with four males having scrotal testes and six having abdominal or partially descended testes and with nine females possessing enlarged mammae (one individual lactating) and seven having undeveloped mammae. The single individual from 1550 m was adult, its mammae large, with single embryos (10 mm crown–rump length) present in both the left and right arms of the uterus. The mammae formula, as counted in 16 females, was uniformly 1-0-2.

Specimens Examined—9.2 km WSW of Befingitra, 1260 m (FMNH 154046, 154047, 154253–154257, 154259–154265, 154288, 154290, 154291, 154292; UA-SMG 6913, 6936, 6937, 6944-6946, 7002, 7006); 11.0 km WSW of Befingitra, 1550 m (FMNH 154048).

Eliurus majori Thomas, 1895

Distribution—The elevational range of this species within the reserve is 1260–1950 m, a middle to upper montane setting in accordance with the altitudinal transect performed in the RNI d'Andringitra (Goodman & Carleton, 1996).

As of only a few years ago, *Eliurus majori* was known from only four specimens from three widely separated places: Montagne d'Ambre (1000 m), an isolated peak at the northernmost end of Madagascar; Ambohimitombo (1200 m), the type locality on the eastern edge of the Central High Plateau; and Anjavadilava (2000 m), a place on the Andringitra Massif at the southern end of the Central High Plateau (Carleton, 1994). The relatively common status of *E. majori* in the RS d'Anjanaharibe-Sud indicates that the species may be more generally distributed than previously thought and that it should be sought in other suitable highland regions of eastern Madagascar.

Ecology and Reproduction—As in the RNI d'Andringitra, the majority of *Eliurus majori* captured in the RS d'Anjanaharibe-Sud were taken off the ground (Table 12-3). Eleven of 12 individuals captured during the standardized trapping regime were found in sets affixed to vines, limbs, and trunks, all within 3 m of the ground. Of these 11, four had entered traps placed on substrates less than 10 cm in diameter, and seven had entered traps placed on substrates greater than 10 cm in diameter. The single individual trapped on the ground was at the base of a massive tree with a hollow base.

Among the 14 *Eliurus majori* collected were five adult males with scrotal testes, four males with abdominal testes, four adult females with enlarged mammae, and one adult female with small mammae. A lactating female contained three placental scars, but no other females with large mammae showed signs of lactation. The mammae formula was consistently 1-0-2 (n = 4).

Specimens Examined—9.2 km WSW of Befingitra, 1260 m (FMNH 154052, 154241, 154242, 154243, 154258, 154266; UA-SMG 6981, 6998); 11 km WSW of Befingitra, 1550 m (FMNH 154053, 154244); 12.2 km WSW of Befingitra, 1950 m (FMNH 154054, 154245, 154289; UA-SMG 7090).

Eliurus minor Major, 1896b

Distribution—*Eliurus minor* has been previously collected at a site "1 day W of Andapa" (Carleton, 1994), which is in or around the RS d'Anjanaharibe-Sud. *Eliurus minor* was found only in the two lower elevational zones at 875 and 1260 m, and information on relative trap success indicates that it was more common in the latter zone. On other mountains in the eastern humid forest, this species has a broad elevational range within the forested zone. For example, in the RNI d'Andringitra, it occurred from 720 to 1625 m, although more individuals were trapped at lower elevations (Goodman & Carleton, 1996).

Ecology and Reproduction—Of seven *Eliurus minor* captured in the standardized small-mammal trap lines, one was on the ground, and the remainder were in trap sets placed off the ground. The six arboreal captures were equally split between sets on vines and branches less than 10 cm in diameter and those greater than 10 cm in diameter.

The reproductive state of the nine total specimens collected in the reserve was as follows: four scrotal adult males, two young males with abdominal testes, and three females with enlarged mammae (none lactating). The females possessed a mammary complement typical of *Eliurus* (1-0-2).

Specimens Examined—6.5 km SSW of Befingitra, 875 m (FMNH 154042; UA-SMG 6880); 9.2 km WSW of Befingitra, 1260 m (FMNH 154043, 154045, 154246, 154247, 154248; UA-SMG 6974, 6980).

Eliurus tanala Major, 1896b

Distribution—Seven individuals of this handsome species, with its cream-colored venter and white caudal plume set against dark gray upperparts, were collected at 875 and 1260 m in the RS d'Anjanaharibe-Sud. As argued in Chapter 11, we tentatively assign these specimens to *Eliurus tanala* until the status and morphological limits of *E. ellermani* are evaluated.

Ecology and Reproduction—Trapping results indicate that this species is largely terrestrial. Four of six individuals captured at 1260 m were taken in the same trap set placed on the ground. The ground was wet in the vicinity of the trap, set within 5 m of a stream and by an opening under a large boulder. A fifth individual was obtained a few meters away in another ground set this one under a clump of root material and next to the river. The only *Eliurus tanala* taken in an arboreal set was located in a tangle of vines and broken branches, 1 m above ground.

One evening, about 19:00 hr, a rodent was observed in the kitchen area of the 875 m camp, clambering over a makeshift table and feeding on rice. After a fumbled attempt was made to grab it, the animal awkwardly scrambled up the vertical trunk (15 cm diameter) of a *Pandanus* next to the table and remained motionless on the tree's bole until it was captured by hand. The animal, the lone example of *Eliurus tanala* obtained at 875 m, mounted the vertical trunk with considerable difficulty.

Four of seven specimens collected, three males and one female, were clearly young and reproductively immature. The other male was an adult with scrotal testes; the mammae (1-0-2) of two adult females were conspicuously large, but neither contained embryos or discernable placental scars.

SPECIMENS EXAMINED—6.5 km SSW of Befingitra, 875 m (FMNH 154049); 9.2 km WSW of Befingitra, 1260 m (FMNH 154050, 154051, 154249, 154250; UA-SMG 6977, 6979).

Eliurus webbi Ellerman, 1949

DISTRIBUTION—In the RS d'Anjanaharibe-Sud, *Eliurus webbi* was captured only in the 875 m zone. A parallel elevational distribution was found in the RNI d'Andringitra, where this species was trapped at 720 m and 810 m but not at higher elevations (Goodman & Carleton, 1996). Elsewhere in Madagascar, its distribution is predominantly lowland moist forest, although it has been recorded as high as 1525 m (Carleton & Schmidt, 1990; Carleton, 1994).

ECOLOGY AND REPRODUCTION—All four *Eliurus webbi* obtained in the standardized trap lines were trapped on limbs and vines, two each on those less than 10 cm in diameter and those greater than 10 cm in diameter. Another four individuals captured at 875 m were equally split between terrestrial and arboreal sets.

Evidence of ongoing reproduction was apparent among the eight *Eliurus webbi* collected. Two adult males possessed scrotal testes, and one adult female was lactating. Another three females had large mammae, and two of these each retained two placental scars. A younger male and female, presumably immature, showed no signs of reproduction. Mammae formulae varied from 1-0-2 (n = 4) to 1-0-1 (n = 1).

The high level of reproductive activity contrasts with the condition found in the sample of *Eliurus webbi* collected in November and December 1993 in the RNI d'Andringitra. There, only one of 16 males was a fully scrotal adult, and just two of seven females had enlarged mammae (Goodman & Carleton, 1996). Nor did any female dissected possess fetuses or placental scars. The great distance between the RS d'Anjanaharibe-Sud (14°45′S) and the RNI d'Andringitra (22°13′S), situated almost at the northern and southern extremes of Madagascar's eastern highlands, suggests geographic or seasonal variation in the breeding cycle of this species.

SPECIMENS EXAMINED—6.5 km SSW of Befingitra, 875 m (FMNH 154035, 154036, 154037, 154038, 154044, 154251, 154252; UA-SMG 6860).

Gymnuromys roberti Major, 1896c

DISTRIBUTION—Although known from relatively few sites, *Gymnuromys roberti* appears to be broadly distributed in humid forest found along the eastern versant of Madagascar. Based on specimens then available, Carleton and Schmidt (1990) noted its occurrence from the vicinity of Vondrozo (ca. 22°48′S) north to Périnet (or RS d'Analamazaotra, ca. 19°S). The documentation of *G. roberti* in the RS d'Anjanaharibe-Sud extends its known distribution 480 km to the north (ca. 14°45′S), still within the limits of the eastern humid forest domain.

Only three individuals of *Gymnuromys roberti* were trapped during the 1994 survey, all at 1260 m. In the RNI d'Andringitra, this species was similarly captured in small numbers but at all four elevational zones between 710 and 1625 m (Goodman & Carleton, 1996).

ECOLOGY AND REPRODUCTION—*Gymnuromys roberti* appears to be an exclusively terrestrial rat. One specimen was taken on the ground at the opening of a small hole leading under rocks and small roots, and the other two were captured in buckets, one in a pitfall line following bottomland along a river and the other in a line on a moderately sloping hillside. The buckets contained water from overnight rains, which probably hindered escape by jumping. Of the three individuals collected, two were adults, a male with testes partially descended and a female with slightly enlarged mammae (1-0-2), and the third was a juvenile female.

SPECIMENS EXAMINED—9.2 km WSW of Befingitra, 1260 m (FMNH 154056, 154057, 154268).

Nesomys rufus Peters, 1870

DISTRIBUTION—The presence of this comparatively large (Table 12-2), brightly colored rodent in the RS d'Anjanaharibe-Sud was expected based on previous records of its occurrence on the western and eastern slopes of the Tsaratanana Massif and its widespread distribution in eastern forest (Carleton & Schmidt, 1990). The species was captured in the higher zones of the RS d'Anjanaharibe-Sud (1260, 1550, and 1950 m), occupying a middle to upper montane belt like that documented on the Andringitra Massif (Goodman & Carleton, 1996).

ECOLOGY AND REPRODUCTION—As found in previous field studies, *Nesomys rufus* is wholly terrestrial and seems to prefer forest with an uncluttered understory and relatively thick mat of leaf litter (Ryan et al., 1993; Goodman & Carleton, 1996). Fourteen of 15 individuals were trapped in close proximity to tree roots and trunks, the 15th in a passageway under a shrubby thicket. In view of its preference for relatively open understory, this diurnal or crepuscular species could be seen moving about the forest floor, often in areas near large trees with partially exposed and extensive root systems, in which they locate their burrows. The species was usually observed to forage in the early morning and late afternoon, but on occasion it was active during the middle of the day.

The reproductive condition of the 15 *Nesomys rufus* varied but indicated active breeding. Six of eight males possessed fully scrotal testes with generally highly convoluted epididymides; the other two males had abdominal testes. Three of seven females were lactating, one with four fresh placental scars, but none with embryos in utero. The remaining females had small, inconspicuous mammae, and two of those, by their size, appeared to be recently weaned subadults. A high incidence of reproductive activity was also evident among the *N. rufus* captured in the RNI d'Andringitra during a survey undertaken in November and December 1993 (Goodman & Carleton, 1996).

SPECIMENS EXAMINED—9.2 km WSW of Befingitra, 1260 m (FMNH 154058–154061, 154269, 154270, 154274; UA-SMG 6996); 11 km WSW of Befingitra, 1550 m (FMNH 154062, 154063; UA-SMG 7028); 12.2 km WSW of Befingitra, 1950 m (FMNH 154271–154273; UA-SMG 7099).

Voalavo gymnocaudus Carleton and Goodman, 1998

DISTRIBUTION—During the 1994 inventory, three individuals of this small nesomyine (Table 12-2) were captured, all at 1950 m just below the summit. From 4 to 12 February 1996, Franco Andreone, Museo Regionale di Scienze Naturali, Torino, conducted a herpetological survey of the western slopes of the RS d'Anjanaharibe, between 1200 and 1600 m, and captured two more individuals of *Voalavo gymnocaudus* in pitfall buckets. The altitude of their collection is estimated to be 1300 m (Andreone, pers. comm.) and in a zone of montane forest distinctly drier than the 1950 m site. The flora in this section of the reserve is moist montane forest in primary condition. These additional records suggest that the species ranges across the montane/sclerophyllous forest zone of the Anjanaharibe-Sud Massif, from approximately 1300 m to 1950 m near the summit. Beyond these two localities and five specimens, the distribution of the newly discovered genus is unknown.

ECOLOGY AND REPRODUCTION—Of the specimens collected in 1994, two individuals were obtained on the ground, by the opening of a hole into the base of a large tree and under tree roots in a natural tunnel that appeared to be a distinctly trampled runway, and the third was obtained on a horizontal, deeply moss-covered limb (28 cm diameter with, and 21 cm diameter without, the moss) of a large tree. The second and third trap locations were within 5 m of one another. The habitat where *Voalavo gymnocaudus* were captured in 1994 is dwarf upper montane/sclerophyllous forest, a vegetational belt found just below the summit and typified by lush epiphytic growth and profuse moss cover on plant and ground surfaces (see Chapter 11). Although little rain fell during the brief visit in late November, the upper slopes around the 1950 m camp were often shrouded in clouds, and mossy surfaces were generally drenched with moisture.

Two of three individuals taken in 1994 are males, one adult with scrotal testes (7 × 5 mm) and distended, convoluted epididymides and one younger individual with undescended testes. The female had one placental scar on each uterine horn but no embryos and retained slightly enlarged mammae (1-0-2). The two individuals collected on the western slopes in February 1996 were an adult female, with distended mammae and apparently having nursed, and a young male, with testes abdominal in position.

SPECIMENS EXAMINED—12.2 km WSW of Befingitra, 1950 m (FMNH 154040, 154041, 154267); RS d'Anjanaharibe-Sud, western slope, 14°46′S, 49°26′E, ca. 1300 m (FMNH 156162, 156163).

Discussion

As a preamble to our discussion, we emphasize the preliminary nature of any attempt to formulate definitive statements about nesomyine diversity patterns, distributions, ecology, and reproductive biology. Little critically gathered information is available on this group, and much of that has emerged in just the past decade. Because the field study of the RS d'Anjanaharibe-Sud was conducted over a period of less than 2 months, the window of time is too brief to support conclusions about reproductive seasonality and other populational phenomena or to rigorously contrast the findings with those from distant sites, such as the RNI d'Andringitra. Additional longer-term, site-intensive survey work is necessary to document whether clear patterns exist, particularly along altitudinal transects, and to understand their genesis. Finally, we stress that although important advances in our knowledge of the distribution and kinds of nesomyine rodents have been made in the past decade, there remain substantial geographic and taxonomic deficiencies that impede thorough comparisons of rodents from various places on the island (Carleton & Schmidt, 1990; see also Voss & Emmons, 1996, for a continental perspective on tropical diversity foundations). The additions of new genera and species to the Nesomyinae, through field discoveries and museum-based revisions (Carleton, 1994; Carleton & Goodman, 1996; Chapter 11), are revealing the unsuspected variety of an insular rodent group once described "as an exceptionally poor fauna with little speciation" (Paulian, 1984: p. 153).

Trapping Effort and Sampling Confidence

The 1994 small-mammal survey of the eastern slopes of the RS d'Anjanaharibe-Sud, from 875 in lowland moist forest, to 1260 and 1550 m in montane forest, and through 1950 m in sclerophyllous forest, produced nine species of native rodents as well as the ubiquitous *Rattus rattus*. Only two nesomyines were previously documented from the area (*Eliurus minor* and *Nesomys rufus*), and the inventory thus added records of an additional seven kinds, including a new species of *Eliurus* and a new genus and species of Nesomyinae (Chapter 11). During 7 weeks of field work, 2,600 trap-nights of sampling effort were apportioned among the four elevation sites (Table 12-1, Fig. 12-2) and yielded 117 mammals (Table 12-4), including 101 rodents, 15 insectivores (*Setifer setosus, Microgale cowani, M. dobsoni, M. gymnorhyncha, M. monticola, M. principula,* and *M. talazaci*; see Chapter 10), and one lemur (*Cheirogaleus major*; see Chapter 14).

Overall trap success, based on all small mammals captured (rodents, insectivores, and lemur) and total trap-nights (2,600), was highest at 1260 m (10.5%, 63 animals in 600 trap-nights) and ranged from 1.8 to 4.8% at the other three locales (875 m: 1.8%, 18 animals in 1,000 trap-nights; 1550 m: 4.8%, 24 animals in 500 trap-nights; and 1950 m: 2.4%, 12 animals in 500 trap-nights). When results are restricted to rodents obtained in the first 500 trap-nights within an elevational zone (the standardized trapping regimen), the percentage of trap return is nearly the same (Table 12-4), varying from 2.4% (at 875 and 1950 m) to 10.6% (1260 m). Except for the slightly higher success rate at 1260 m (>10%), these percentages are more or less typical of trap-line efficiencies from other rodent surveys at different elevational zones on Madagascar (Stephenson, 1993; Goodman & Ganzhorn, 1994; Stephenson et al., 1994; Goodman & Carleton, 1996; Goodman et al., 1996) and on other large Old World tropical islands (Heaney et al., 1989; Rickart et al., 1991, 1993).

Most rodent species captured in the RS d'Anjanaharibe-Sud may be generally characterized as either terrestrial or scansorial. Two species are strictly ground-dwelling (*Gymnuromys roberti* and *Nesomys rufus*), and one is probably strictly arboreal (*Brachytarsomys albicauda*), habits that are predicted by the bodily proportions and hind-foot morphology of the species. The activity sphere and locomotory mode of the remainder may be termed scansorial, although three were more often trapped on the ground (*Rattus rattus, Eliurus grandidieri,* and *E. tanala*) and three others in predominantly arboreal situations (*E. majori, E. minor,* and *E. webbi*). Too few *Voalavo gymnocaudus* were obtained to say much about its climbing behavior, but the animal's broad hind-feet and relatively long tail intimate scansorial proclivities. At other sites, such as RNI d'Andringitra, *E. webbi* is known to inhabit subterranean burrows, and although some individuals were trapped on the ground, the majority were obtained from arboreal sets (Goodman, 1994; Goodman & Carleton, 1996). No pronounced intraspecific trend was found in proportions of individuals taken on and off the ground; in contrast, there appeared to be shifts in microhabitat utilization by certain *Eliurus* species in zones of sympatry in the RNI d'Andringitra (Goodman & Carleton, 1996). Because no trap was placed more than 3 m off the ground (Table 12-1), canopy specialists, for which no evidence presently exists for such animals in Malagasy humid forest, would likely have been overlooked.

Two different types of evidence, derived from species accumulation curves and analogous results from other small-mammal inventories, support the premise that the trapping effort was suitable to establish basic rodent diversity within the

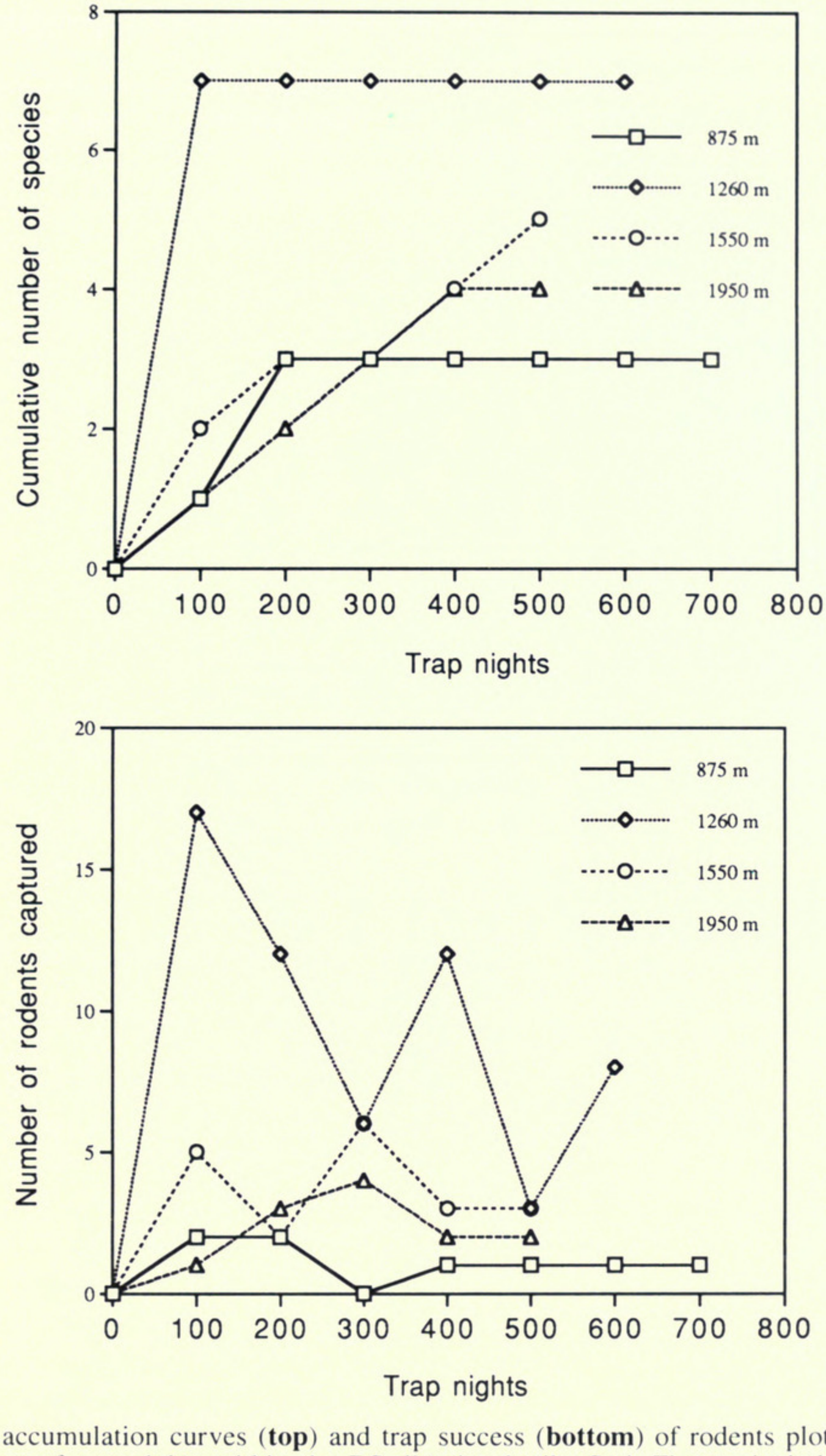

FIG. 12-2. Species accumulation curves (**top**) and trap success (**bottom**) of rodents plotted for each elevational zone against the number of trap-nights within the RS d'Anjanaharibe-Sud. Figures include both Nesomyinae and introduced *Rattus rattus*.

reserve. Plots of the cumulative number of species documented at each elevational zone over the duration of trapping disclose distinct plateaus before the end of each respective trapping session (Fig. 12-2). No additional rodent species were encountered after 100–400 trap-nights, depending on the elevational zone and the ultimate number of species eventually recorded at each. The asymptote in species accumulated per zone did not result from diminishing trap success, because there was no parallel decrease in overall trap success during the course of the survey period (Fig. 12-2).

The number and composition of rodent species documented thus far for other places in the eastern humid forest provide circumstantial evidence about those that might be expected to occur in the RS d'Anjanaharibe-Sud. Three general localities, RNI d'Andringitra, Parc National de Ranomafana, and RS d'Analamazaotra (Périnet), qualify for such faunal comparisons: they are floristically

TABLE 12-4. Number of individuals of small mammals captured in the RS d'Anjanaharibe-Sud during 500 trap-nights within the four elevational zones surveyed.

Species	875 m	1260 m	1550 m	1950 m
Microgale cowani			1	
Microgale dobsoni		2		
Microgale gymnorhyncha		1		
Microgale monticola			1	
Microgale principula			1	
Microgale talazaci		1	2	
Setifer setosus	4			
Rattus rattus	1	2	13	1
Eliurus grandidieri		21	1	
Eliurus majori		6	2	4
Eliurus minor	1	6		
Eliurus tanala		5		
Eliurus webbi	5			
Gymnuromys roberti		1		
Nesomys rufus		8	3	4
Voalavo gymnocaudus				3
Cheirogaleus major	1			
Total individuals	12	53	24	12
% Trap success	2.4	10.6	4.8	2.4
Total rodents	7	49	19	12
% Rodent trap success	1.4	9.8	3.8	2.4
Total nesomyine	6	47	6	11
% Nesomyine trap success	1.2	9.4	1.2	2.2

similar to the RS d'Anjanaharibe-Sud, encompass similar elevational spans, and have been extensively surveyed for rodents. Ten, eight, and nine species of Nesomyinae have been reported from Andringitra, Ranomafana, and Analamazaotra, respectively, whereas the native rodent fauna of the Anjanaharibe-Sud Massif totals nine (Table 12-5). The composition of rodents is broadly parallel among the four areas, largely due to several species (e.g., *Eliurus minor, E. tanala, E. webbi, Gymnuromys roberti,* and *Nesomys rufus*) that have extensive geographic ranges and broad elevational occurrence in eastern humid forests of the island. Five of the nine currently known species of *Eliurus* have been documented in the RS d'Anjanaharibe-Sud (Carleton, 1994; Chapter 11). On the basis of present distributional records, other nesomyine species reach their northern limits either in the region of the Sihanaka Forest (*Brachyuromys betsileoensis*) or the Central High Plateau (*B. ramirohitra, E. penicillatus, E. petteri,* and *Monticolomys koopmani*); none of these would be reasonably expected in the RS d'Anjanaharibe-Sud.

One other species may inhabit portions of the reserve, namely *Nesomys audeberti,* a form with an extensive north/south range in eastern lowland moist forest (Carleton & Schmidt, 1990; Goodman & Carleton, 1996). Because it has been collected in the vicinity of Antongil Bay and because the reserve contains some areas with lower-lying forest than the 875 m altitudinal zone, this large, white-bellied *Nesomys* may also occur locally. Excepting this species, we believe that the species accumulation curves and comparisons of species richness in eastern forest offer persuasive support that the rodent fauna of the RS d'Anjanaharibe-Sud has been largely, although perhaps not exhaustively, documented.

Elevation and Rodent Associations

No species of Nesomyinae was captured across the complete range of the altitudinal survey (875–1950 m), although two, *Eliurus majori* and *Nesomys rufus,* were found in the three higher zones (Table 12-6). As in the RNI d'Andringitra (Goodman & Carleton, 1996), the only clear example of elevational replacement of congeners involves *E. webbi* and *E. majori,* the former discovered only in the lowest zone (875 m) and the latter documented from 1260 to 1950 m. Two species in the Andringitra study, *E. minor* and *Gymnuromys*

TABLE 12-5. Comparison of nesomyine rodents documented to date for adequately censused regions in eastern humid forests.

Species	**Anjanaharibe-Sud* 875–1950 m**	**Andringitra† 720–2450 m**	**Ranomafana‡ 575–1225 m**	**Analamazaotra§ 500–1300 m**
Mus musculus		X		
Rattus rattus	X	X	X	X
Brachytarsomys albicauda	X		X	X
Brachyuromys betsileoensis		X	X	X
Brachyuromys ramirohitra		X		
Eliurus grandidieri	X			
Eliurus majori	X	X		
Eliurus minor	X	X	X	X
Eliurus petteri				X
Eliurus tanala	X	X	X	X
Eliurus webbi	X	X	X	X
Gymnuromys roberti	X	X	X	X
Monticolomys koopmani		X		
Nesomys audeberti		X	X	X
Nesomys rufus	X	X	X	X
Voalavo gymnocaudus	X			
Number of species of Nesomyinae	9	10	8	9

* This study.
† Goodman and Carleton (1996); Langrand and Goodman (1997); Goodman (unpubl. data).
‡ Carleton and Schmidt (1990); Ryan et al. (1993, in prep.); specimens in USNM.
§ Compiled from Carleton and Schmidt (1990); Carleton (1994); specimen in USNM; Stephenson (1993).

roberti, demonstrated seemingly broad ecological tolerance, occurring throughout the vegetational zones of the survey (720–1625 m) in relatively low densities (Goodman & Carleton, 1996). In contrast, their presence is apparently restricted in the RS d'Anjanaharibe-Sud (*E. minor* at the 875 and 1260 m levels and *G. roberti* only at 1260 m). We strongly suspect that their elevational range on this mountain is similarly extensive and that such differences are artifactual, arising through a combination of low density and chance and given the brevity of the trapping periods.

SPECIES RICHNESS—Nesomyine diversity was greatest at 1260 m, a survey zone with six species, but declined at both lower and higher elevations to four species (875 m) or three species (1550 and 1950 m) (Table 12-6). This midelevational peak in rodent species richness approximately coincides with the lower extent of montane forest, according to these trapping results. Furthermore, this elevational zone appears to be the region of the mountain where lowland and montane rodent faunas overlap, thus perhaps giving rise to a higher species richness at intermediate elevations. On

TABLE 12-6. Elevational zonation of rodents within the RS d'Anjanaharibe-Sud based on the trapping results of the 1994 inventory.

Species	**875 m**	**1260 m**	**1550 m**	**1950 m**
Rattus rattus	+	+	+	+
Brachytarsomys albicauda	+			
Eliurus grandidieri		+	+	
Eliurus majori		+	+	+
Eliurus minor	+	+		
Eliurus tanala	+	+		
Eliurus webbi	+			
Gymnuromys roberti		+		
Nesomys rufus		+	+	+
Voalavo gymnocaudus				+
Total species	5	7	4	4

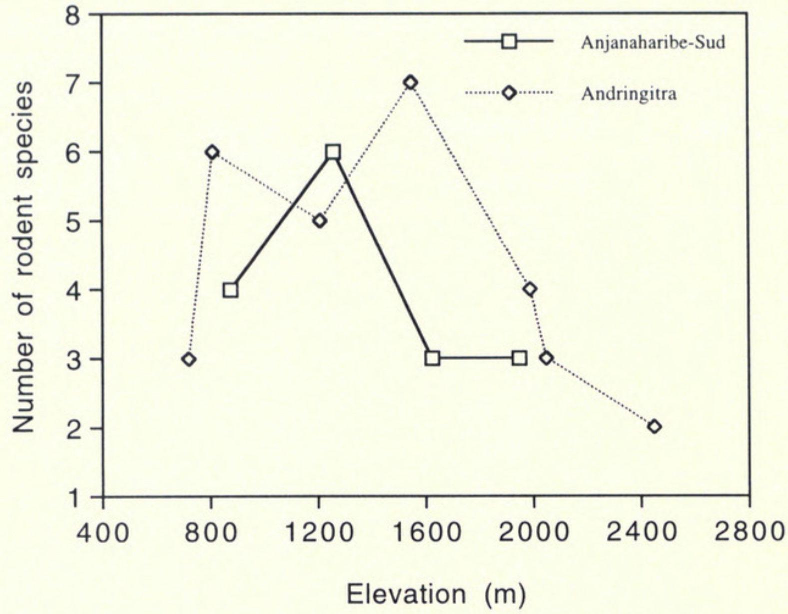

FIG. 12-3. Number of Nesomyinae rodents documented at various elevational zones in the humid forests of the RS d'Anjanaharibe-Sud (squares) and the RNI d'Andringitra (diamonds) using standardized trapping regimens. The Andringitra data are based on Goodman and Carleton (1996), Langrand and Goodman (1997), and Goodman (unpubl. data).

the Andringitra Massif, a site with typical vegetational zonation of eastern humid forest (Lewis et al., 1996), the highest species richness of native rodents, with seven species, was found at 1625 m (Fig. 12-3); at lower elevations species richness varied from three species at 720 m to six at 810 and 1210 m; at higher elevations it varied from five at 1990 m (just below tree line) to one at 2050 and 2450 m (Goodman & Carleton, 1996; Langrand & Goodman, 1997; Goodman, unpubl. data). The pattern at Andringitra and Anjanaharibe-Sud of rodent species richness along an elevational gradient appears to be more or less typical of other mountains in the Old World tropics and subtropics, including continental land masses and large islands, where the greatest rodent diversity is generally within the upper portion of montane forest (e.g., Rupp, 1980; Yalden, 1988; Heaney & Rickart, 1990; Yu, 1994). One of the better examples from Old World tropical forests of a midelevational bulge in rodent species richness is along the slopes of Mount Kinabalu, Borneo, where rodent diversity peaks at 1400 m across a transect from about 700 to 3200 m (Md. Nor, pers. comm.). This pattern of midelevational humps in species richness has been noted for many other groups of tropical invertebrates and vertebrates (Rosenzweig & Abramsky, 1993; Rahbek, 1995, 1997), but see Patterson et al. (in press) for a different pattern in the New World tropics.

RELATIVE POPULATION DENSITY AND BIOMASS—As with species richness, relative density of rodent populations, as estimated by the number of individuals per 100 m of trap line, reached its highest level at 1260 m, with 9.3 individuals/100 m (Table 12-7). The highest density measured at any other elevation was about half this number (4.7 individuals/100 m at the 1550 m locality) and was smallest at the lowest elevation sampled, 875 m (1.0 individuals/100 m). Furthermore, the peak in estimated population density for each species of Nesomyinae was likewise recorded in the 1260 m zone; however, the variation in relative numbers of *Eliurus majori* and *Nesomys rufus,* found in three of four zones (1260–1950 m), is trivial across this 700 m swath of montane forest. Only the introduced *Rattus rattus* deviated from this pattern and, as measured by total number of captures or relative density, was most common in the 1550 m zone.

In the RNI d'Andringitra, sparse population densities were also reported for the lowest elevation sampled, 720 m in lowland moist forest, but density increased regularly with ascension into montane zones (Goodman & Carleton, 1996). Unlike Anjanaharibe-Sud, the greatest density was instead measured at the highest point of the transect, 1625 m within the lower reaches of sclerophyllous forest. For example, nearly a fourfold increase in the relative density of *Nesomys rufus* was recorded between 810 and 1625 m.

Because the nine species trapped in the RS d'Anjanaharibe-Sud vary 10-fold in average adult

TABLE 12-7. Relative numbers of rodents (number of individuals trapped per 100 m of trap line) in the four elevational zones of the RS d'Anjanaharibe-Sud.*

Species	875 m (730)	1260 m (520)	1550 m (396)	1950 m (423)	Grand† mean
Rattus rattus	0.13	0.38	3.25	0.24	0.82
Eliurus grandidieri		3.99	0.25		2.40
Eliurus majori		1.14	0.50	0.96	0.90
Eliurus minor	0.13	1.14			0.56
Eliurus tanala		0.95			0.95
Eliurus webbi	0.69				0.69
Gymnuromys roberti		0.19			0.19
Nesomys rufus		1.52	0.75	0.96	1.05
Voalavo gymnocaudus				0.72	0.72
All rodents	0.96	9.31	4.75	2.88	4.20
% Captures of native rodents	86.5	95.9	31.6	91.7	80.5

* Number in parentheses is total length (in m) of trap lines for each zone.
† Averaged only for elevational zones in which a species was captured.

body weight (Table 12-2), ranging from around 22 g (*Voalovo gymnocaudus*) to more than 200 g (*Brachytarsomys albicauda*), rodent abundance on the slopes of the reserve may differ when measured by relative biomass compared with estimates of population density. However, the pattern of rodent biomass does parallel that derived for density estimates (Table 12-7), attaining the largest values at 1260 m whether viewed as total biomass or as average biomass per species (Table 12-8). The 1260 m bulge in relative biomass does not appear to be simply related to species diversity, because the zone also supports a higher average total biomass per species than do others on the massif. All measures of rodent abundance, species diversity, population density, and standing biomass, suggest that the habitat at 1260 m, near the lower boundary of montane forest, is the most productive within the RS d'Anjanaharibe-Sud.

Again, these results depart slightly from the picture derived for the rodent fauna of RNI d'Andringitra (Goodman & Carleton, 1996). There, estimated total biomass of rodents increased in relation to elevation, being highest at the top of the transect (1625 m), but the largest average biomass per species was recorded for a lower site (1210 m). Nevertheless, species diversity and most indices of abundance within the reserves appear to be closely coupled, with higher population densities and total biomass obtained in the zone having the most species (1625 m in the RNI d'Andringitra versus 1250 m in the RS d'Anjanaharibe-Sud). In view of the unknown level of sampling error inherent in these statistics and sample comparisons, further long-term investigations are required to verify whether the altitudinal profiles of species richness and population abundances are meaningfully different between

TABLE 12-8. Estimated biomass (g) of rodents trapped along an elevational transect in the RS d'Anjanaharibe-Sud.*

Species	875 m	1260 m	1550 m	1950 m
Rattus rattus	106	211	1,374	106
Eliurus grandidieri		1,109	53	
Eliurus majori		565	188	377
Eliurus minor	37	221		
Eliurus tanala		530		
Eliurus webbi	360			
Gymnuromys roberti		156		
Nesomys rufus		1,287	482	643
Voalavo gymnocaudus				66
Number of species	3	7	4	4
Total biomass	503	4,079	2,097	1,192
Average total biomass/species	168	583	524	298

* Summations from average weight of adults captured over the first 500 trap-nights within each zone.

TABLE 12-9. Multiple captures of rodents in a single trap within each elevational zone in the RS d'Anjanaharibe-Sud.*

Elevation	Total species	Number of traps with captures	Traps with multiple captures: Same species	Traps with multiple captures: Different species
875 m	3	11	1	0
1260 m	6	35	12	8
1550 m	4	11	4	2
1950 m	4	9	2	0

* Not standardized for trap-nights.

the RS d'Anjanaharibe-Sud and RNI d'Andringitra.

Abundance and biomass have been used as measures of variation in species richness along elevational transects in the tropics (Terborgh, 1977; Graham, 1990). The relationship between specific diversity and these two factors seems to be consistent with the distribution of rodents on mountains in Madagascar. Further studies that collate aspects of forest productivity and its association with rodent species richness may help to sort out what forces mold these patterns. The possibility that the elevational distribution of rodents and their density vary between mountains on Madagascar could provide a natural system to explore hypotheses associated with productivity models (Rosenzweig & Abramsky, 1993).

MULTIPLE CAPTURES IN SINGLE TRAP SETS—In this section, instances of multiple captures by the same trap set are consolidated, both those involving individuals of the same species and those belonging to different species. We compile such examples, not necessarily as any indication of competition, but simply to document microhabitat overlap and local syntopy. Long-term, single-site field studies are required to conclude partitioning of resources or interference competition for them and to demonstrate social organization and mating systems.

At least one trap station within each elevational zone secured two or more conspecifics, but the number of such multiple successes varied considerably. The only discernable pattern is the predictable correlation that the level with the most rodent species and largest populations, 1260 m, contained the most instances of multiple captures (Table 12-9). In a few cases, three or more individuals of *Rattus rattus*, *Eliurus grandidieri*, and *E. tanala* were taken in the same trap in various combinations over the term the line was in place, suggesting some sort of "trap competition" (Patterson et al., 1989; Yu, 1994). The number of multiple captures in traps placed within this elevation zone deviated from a Poisson distribution ($p < 0.01$). No clear sex ratio pattern emerged for conspecifics taken in the same set, disallowing any inference about a species' social organization. Eight of 13 *R. rattus* captured at 1550 m were taken in three traps, all within 70 m of one another and on a man-made trail that had been in existence for several years. The age or sex of the trapped individuals supplies no evidence that these rodents were clearly living in family groups or monogamous couples. Rather, it appears that they have a clumped distribution along the trail in this elevational zone.

Like conspecific associations, the incidence of interspecific captures was highest at 1260 m (Table 12-9). All of these were taken in ground placements, although 43 of the 100 live traps in this zone were situated in arboreal settings. Examples of microhabitat overlap between species include the following: *Eliurus grandidieri* and *E. tanala,* in traps set under roots or boulders and within 5 m of a stream margin; *E. grandidieri* and *Rattus,* at an opening under roots and a small boulder; *E. grandidieri* and *Nesomys rufus,* in traps positioned at an opening in root entanglement and at the hollowed-out base of a massive tree; *E. grandidieri* and *E. majori,* in leaf litter close to a small stream; and *E. majori* and *Rattus,* at the opening of a large cavity under tree roots. In one case, on consecutive days, an *E. minor* and *Microgale gymnorhyncha* (FMNH 154028) entered a trap placed near an opening under roots and at the edge of dense herbaceous vegetation. The single above-ground trap station (at 1550 m) that yielded an interspecific catch involved *E. majori* and *Rattus,* collected in a trap placed 1.5 m high on a nearly horizontal tree trunk.

INTRA- AND INTERSPECIFIC DIFFERENCES IN REPRODUCTION—Knowledge of reproductive physiology and seasonality of breeding is meager for most species of Nesomyinae. Other than anecdotal observations, the only information published on variation along an elevational transect comes from the RNI d'Andringitra (Goodman & Carleton, 1996). Here we augment this previous study and summarize information on breeding condition of the Anjanaharibe-Sud rodents.

Levels of rodent reproduction were moderately high on the slopes of the RS d'Anjanaharibe-Sud, signs of active breeding evident in 55% (1950 m)

TABLE 12-10. Reproductive condition of all rodents captured (standard live traps and pitfall traps) in the RS d'Anjanaharibe-Sud.*

	875 m		1260 m		1550 m		1950 m		875–1950 m	
Species	**A/S**	**M/F**	**A/S**	**M/F**	**A/S**	**M/F**	**A/S**	**M/F**	**A/S**	**M/F**
Rattus rattus	0/1	0/1	4/0	4/0	7/1	4/4	0/1	1/0	11/3	9/5
Brachytarsomys albicauda	1/0	0/1							1/0	0/1
Eliurus grandidieri			13/13	10/16	1/0	0/1			14/13	10/17
Eliurus majori			4/4	7/1	2/0	2/0	2/2	0/4	8/6	9/5
Eliurus minor	1/1	1/1	5/2	5/2					6/3	6/3
Eliurus tanala	0/1	1/0	3/3	3/3					3/4	4/3
Eliurus webbi	6/2	3/5							6/2	3/5
Gymnuromys roberti			2/1	1/2					2/1	1/2
Nesomys rufus			5/3	6/2	2/2	1/3	2/1	1/2	9/6	8/7
Voalavo gymnocaudus							2/1	2/1	2/1	2/1
Total	8/5	5/8	36/26	36/26	12/3	7/8	6/5	4/7		
% Individuals captured in reproductive state	62		58		80		55			

* A = adults; F = females with large mammae, carry embryos, or lactating; M = males with scrotal testes; and S = subadults.

to 80% (1550 m) of the specimens collected within an elevation (Table 12-10). Moreover, no clinal trend with elevation is suggested for this data. In the RNI d'Andringitra, there was a directional pattern of increasing reproductive activity at higher altitudes, ranging from only 25% of the rodents sampled at 720 m to more than 80% at 1625 m. Whether such a trend is manifested within any species in the RS d'Anjanaharibe-Sud is unclear, because few taxa were found across a broad range of altitudes or the number of individuals captured is insufficient to draw conclusions.

The timing of the Anjanaharibe survey (mid-October through November) was chronologically in advance of the one conducted in Andringitra (mid-November through mid-December). In the survey of the RNI d'Andringitra (22°13′S), very few juvenile or subadult rodents were captured. Furthermore, the ratio of adults to subadults and the number of adults in or approaching a sexually mature state indicate that the Andringitra inventory was conducted at the beginning of a reproductive season. In the RS d'Anjanaharibe-Sud (14°45′S), the proportions are different, particularly for the genus *Eliurus*, in which a smaller percentage of the individuals trapped were in reproductive condition and a significant portion were subadults. Such differences in the reproductive condition and age structure of rodents captured at these two sites may implicate seasonal or latitudinal factors to account for the considerable variation in these variables.

Acknowledgments

We are grateful to the Direction des Eaux et Forêts and l'Association Nationale pour la Gestion des Aires Protégées for authorization to conduct this study, in particular to M. Henri Finoana, Mme. Miadana Harisoa Faramalala, and Mme. Célestine Ravaoarinoromanga. We thank the various museum curators who allowed us to examine specimens under their care: Guy Musser, American Museum of Natural History, New York; Paula Jenkins and Jean Ingles, The Natural History Museum, London; Lawrence Heaney and Bruce Patterson, Field Museum of Natural History, Chicago; Malcolm J. Largen, Merseyside County Museums, Liverpool; Maria Rutzmoser, Museum of Comparative Zoology, Cambridge, Massachusetts; Francis Petter and Michel Tranier, Muséum National d'Histoire Naturelle, Paris; Chris Smeenk, Rijksmuseum van Natuurlijke Histoire, Leiden; and Hans Baggøe and Mogens Andersen, Universitets Zoologisk Museum, Copenhagen. Shukor Md. Nor kindly provided information on his studies of Bornean rodents. Bruce Patterson and Jim Ryan provided critical comments on an earlier version of this manuscript.

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