ECOTROPICA 3: 109–118, 1997

ANNUAL VARIATION IN SPECIES DIVERSITY AND RELATIVE DENSITY OF RODENTS AND INSECTIVORES IN THE PARC NATIONAL DE LA MONTAGNE D'AMBRE, MADAGASCAR

Steven M. Goodman[1,2], Jörg U. Ganzhorn[3]*, Link E. Olson[1,4], Mark Pidgeon[2] & Voahangy Soarimalala[5]

[1]Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, USA
[2]WWF, BP 738, Antananarivo (101), Madagascar
[3]Deutsches Primatenzentrum, Kellnerweg 4, D-37077 Göttingen, Germany
[4]Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois 60637, USA
[5]Département de Biologie Animale, BP 906, Université d'Antananarivo, Antananarivo (101), Madagascar

Résumé. La variation saisonnière d'une communauté de petits mammifères d'une forêt humide dans le Parc National de la Montagne d'Ambre au nord de Madagascar a été étudiée sur trois ans. Nous abordons les variations annuelles dans la densité relative et la diversité spécifique des rongeurs endémiques (Sous-famille des Nesomyinae), des insectivores endémiques (Famille des Tenrecidae) et de *Rattus rattus* introduit, cette dernière espèce étant abondante dans les forêts dégradés et dans les forêts intactes. Les insectivores montrent une variation importante dans les taux de capture sur les trois années, en particulier pour les espèces les plus communément capturées (ex.: *Microgale drouhardi*). *Rattus rattus* était le rongeur le plus communément capturé, représentant plus des trois quarts des animaux dans les lignes de capture, alors que les rongeurs ou les insectivores endémiques n'ont, sur aucune période, totalisé plus de 10% des captures d'animaux. En se référant aux résultats obtenus dans d'autres sites de l'île aux mêmes altitudes avec une végétation similaire, le succès de capture des rongeurs endémiques est réduit, ce qui est probablement dû à une forme d'exclusion par compétition avec *Rattus*.

Abstract. Seasonal variation in the small mammal community of a humid forest site, Parc National de la Montagne d'Ambre, in northern Madagascar, was studied over the course of three years. We assess yearly variation in relative density and species diversity of endemic rodents (Subfamily Nesomyinae) and insectivores (Family Tenrecidae) and introduced *Rattus rattus*, the latter species is abundant in disturbed and undisturbed forests within the park. Insectivores showed considerable variation in capture rates between the three years, particularly amongst the most commonly captured species (e.g., *Microgale drouhardi*). *Rattus rattus* was the most commonly captured rodent, accounting for more than three-quarters of the animals in the trap lines, and endemic rodents and insectivores never made up more than 10% of the animals captured during the coarse of any season. On the basis of comparisons to other sites on the island at the same elevation and with similar vegetation, the capture success rate of endemic rodents was suppressed and this is presumably related to some form of competitive exclusion with *Rattus*. *Accepted 9 October 1997.*

Key words: Madagascar, rodents, insectivores, population cycles.

INTRODUCTION

The native rodent and insectivore faunas of Madagascar are all endemic to the island and show a high level of diversity. Recent systematic studies and field work have yielded undescribed genera of rodents and new species of both rodents and insectivores. Even with this increase of information on the systematics and geographical distribution of terrestrial small mammals of the island, major gaps remain in basic knowledge of the ecology and natural history of these species. In recent years conservation projects on the island associated with the management of existing reserves have been evaluating different taxonomic groups for their possible utility in ecological monitoring. Except for the studies of Rakotondravony (1992) and Stephenson (1994) little is known about seasonal fluctuations in small mammal populations in the humid forests of the island, and long-term studies are important in understanding population variation in these animals and their potential use for ecological monitoring. Further, over the past few decades *Rattus rattus* has been invading relatively intact native forest (Goodman 1995) and there is

* Current address: University of Hamburg, Department of Ecology and Conservation, Martin Luther King Platz 3, 20146 Hamburg, Germany.

some evidence that their diet overlaps with several native mammals (Goodman & Sterling 1996).

We report on a 3-year study of the insectivore and rodent faunas in a humid forest in northern Madagascar. We assessed yearly variation in relative density and species diversity. Within this forest there are large numbers of *Rattus rattus*. Information on population trends at the site and a comparison to other forest blocks at similar elevations elsewhere on the island, without large populations of *Rattus*, provide insight into the effects this introduced species might be having on the native small mammal fauna.

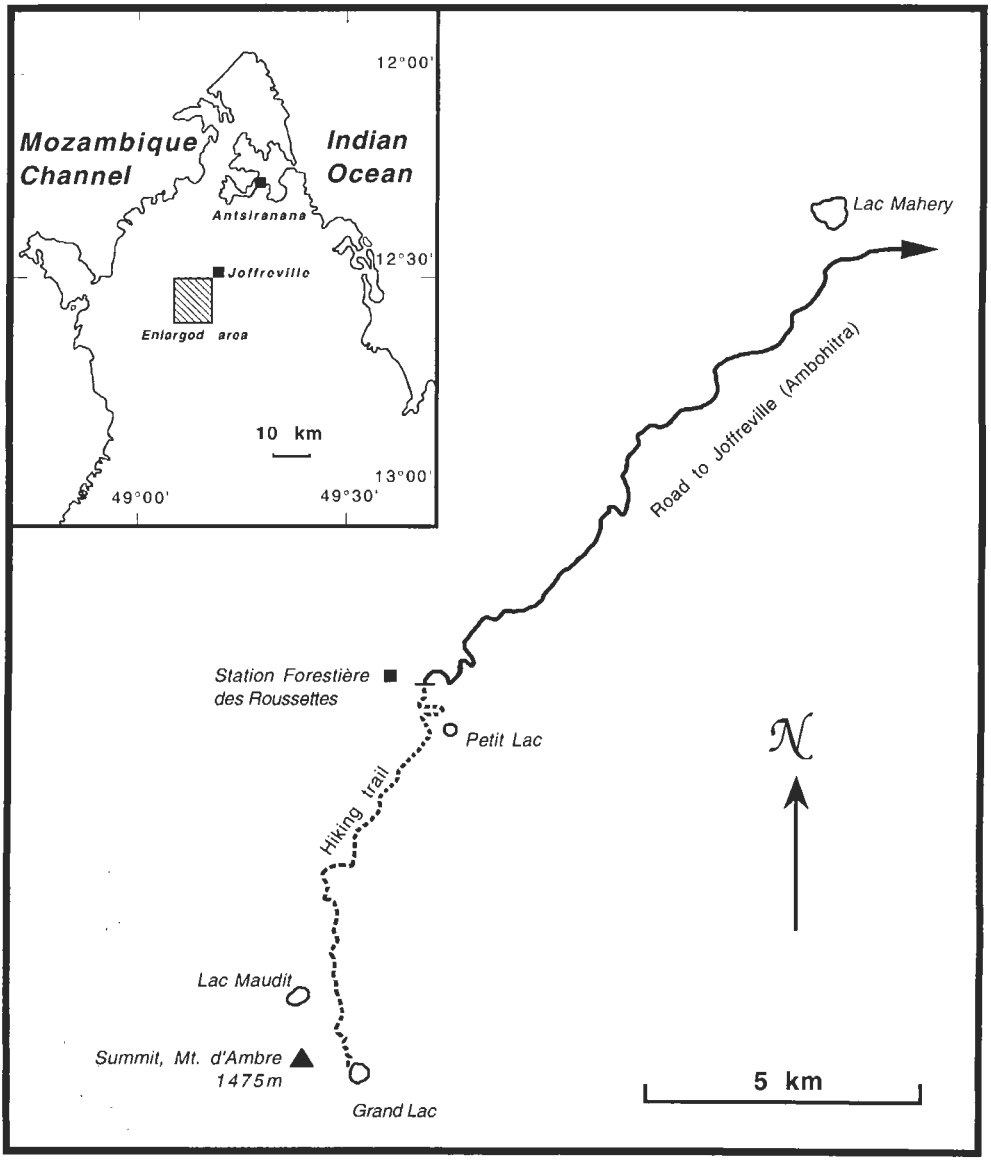

FIG. 1. Map of study area in the Parc National de la Montagne d'Ambre, Madagascar. The inset in the upper left hand corner is of the northern portion of Madgascar.

STUDY AREA AND METHODS

Montagne d'Ambre (Amber Mountain or Ambohitra in Malagasy) is located at the northern end of the island (Fig. 1). The study site, within the Parc National (PN) de la Montagne d'Ambre, is humid forest. We worked in the immediate vicinity of the Station Forestière des Roussettes located 5.5 km SW Joffreville (Ambohitra), between 900 and 1200 m, 12°31'S, 49°10'E. The site was visited between 26 March and 6 April 1994, 29 March and 5 April 1995, and 18 and 24 April 1996. For further information on the park see Nicoll & Langrand (1989), Raxworthy & Nussbaum (1994), and Goodman *et al.* (1996).

Sampling techniques used for small mammals included pit-falls and two types of live traps (Goodman *et al.* 1996). Each pit-fall line was composed of 11 plastic buckets. Three lines were used in each of the elevational zones. A "bucket night" is defined as one bucket in place for a 24-hour period (dawn to dawn). Each trap line consisted of Sherman Live traps and National Live traps in a ratio of 4:1 (Goodman *et al.* 1996). A "trap night" is defined as one trap in use for a 24-hour period (dawn to dawn).

During the three seasons, all small mammals trapped were removed from the site of capture. *Rattus* were destroyed or prepared as specimens and native mammals were either collected or released in areas away from trap and pit-fall lines. The ears of released small mammals were notched to facilitate recognition of recaptured individuals. Voucher specimens are deposited in the Field Museum of Natural History, Chicago, and the Département de Biologie Animale, Université d'Antananarivo. For rodents we follow the arrangement of Musser & Carleton (1993) and for insectivores MacPhee (1987) and Jenkins *et al.* (1997).

RESULTS

Species accumulation curves. To assess the completeness of the seasonal inventories with respect to species richness, we plotted the number of species of insectivores captured in the pit-falls (Fig. 2a). These resulting species accumulation curves indicate that, in general, 2 to 3 days of pit-fall trapping with three lines (11 buckets each) in different microhabitats was generally sufficient to reach an asymptote in the addition of species not previously captured. The

TABLE 1. Pit-fall trap success for three separate lines in 1994, 1995, and 1996 based on seven nights of trapping (77 bucket nights/line) in the Parc National de la Montagne d'Ambre.

Site	line 1 Jardin Botanique			line 2 near Petit Cascade			line 3 above Petit Cascade		
Habitat	slightly degraded with exotic trees			slightly degraded			slightly degraded		
Year	1994	1995	1996	1994	1995	1996	1994	1995	1996
Species									
Tenrec ecaudatus	0	1	13	0	0	0	5	0	0
Microgale drouhardi	3	7	23	0	20	32	12	21	25
Microgale fotsifotsy	0	3	2	2	4	3	0	1	0
Microgale longicaudata	2	1	3	1	0	2	5	2	0
Microgale talazaci	2	2	1	0	3	5	0	1	0
*Suncus murinus**	0	0	0	0	2	0	0	1	0
total individuals	7	14	42	3	29	42	22	26	25
total individuals combined across years		63			74			73	
total number of species	3	5	5	2	4	4	3	5	1
total number of species combined across years		5			5			6	

*Species introduced to Madagascar

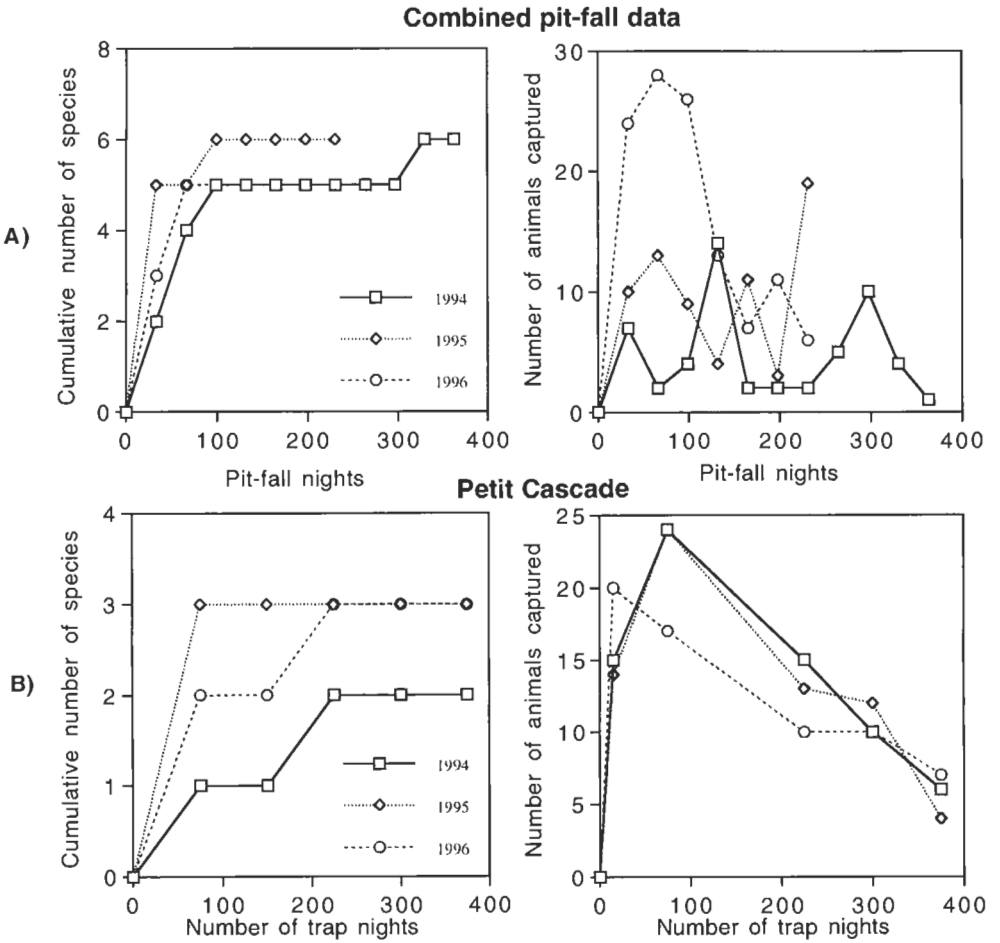

FIG. 2. Legend see page 113.

exception was in 1994 when, between the third and and ninth day of trapping, no new species was added, and on the tenth and final day the introduced *Suncus murinus* was captured for the first time.

Because the number of trap nights between trap lines was not equal, we have plotted the species accumulation curves for rodents by trap line. Further, although insectivores were captured in live traps, no species was captured that was not also obtained in the pit-fall buckets, and thus we have limited these curves to rodent species. The maximum number of rodent species obtained in any trap line was three: two endemic (in the genus *Eliurus*) and one introduced (*Rattus*). For the Petit Cascade (Fig. 2b) and Camp Line (Fig. 2c) trap lines the species accumulation curves reached a plateau after the first to third night of trapping. In 1995 the Jardin Botanique (Fig. 2d) trap line was in place a total of seven nights and no new species was added after the first night. In 1996 this line was in place for eight nights and species not previously captured that year were added the first, fourth, and sixth night of trapping. The number of traps used along this trail in 1994 was fewer (30/night) than in 1995 and 1996 (50/night) and the results are not plotted. However, *Rattus* was captured the first night and *E. majori* and *E. webbi*

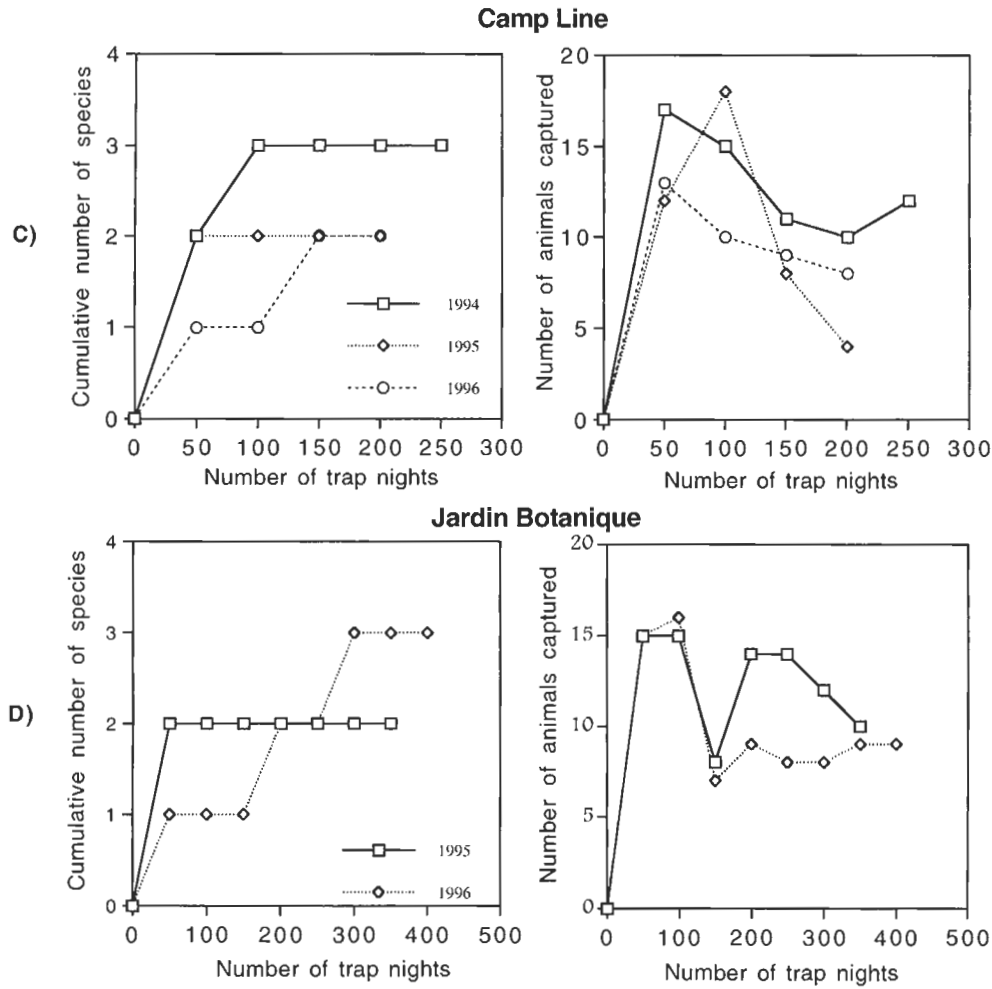

FIG. 2. Species accumulation curves (left column) and number of trap captures plotted as a function of trapping effort (right column) for three seasons (1994–1996) in the forest near the Station Forestière des Roussettes, Parc National de la Montagne d'Ambre: insectivores captured in the pit-falls (all lines combined) (A), and insectivores and rodents in three different live trap lines Petit Cascade (B), Camp Line (C), and Jardin Botanique (D).

were taken the fifth night. In all years of this study the only rodent species captured along the Cascade Touristique trail was *Rattus* and in each year this species was obtained the first night of trapping.

General trapping results. There was considerable variation in the number of insectivores captured in each pit-fall line between years, although the combined results per line of the number of individuals and species across the three seasons are similar (Table 1).

For *Microgale drouhardi* there were considerable fluctuations in the number of individuals captured in each line across the three years (Table 1) and per year (1994, 15; 1995, 48; 1996, 80).

Rattus rattus was the most commonly taken animal in the trap lines, accounting for 513 of the 659 (77.8 %) captures (Table 2). Two species of nesomynice rodents, *Eliurus majori* and *E. webbi*, were obtained in the trap lines. Native rodents and

TABLE 2. Small mammal trap success over the course of three seasons along four different trap lines in the Parc National de la Montagne d'Ambre.

Forest type	Jardin Botanique degraded with mixed exotic trees			Camp Line primary			Petit Cascade slightly degraded			Cascade Touristique heavily degraded with exotic trees		
Year	1994	1995	1996	1994	1995	1996	1994	1995	1996	1994	1995	1996
Trap nights	150[a]	350	350	200	200	200	375	375	375	175	175	120
Species												
Rattus rattus	37 (25)[b]	77 (22)	47 (13)	55 (28)	28 (14)	26 (13)	64 (17)	43 (11.5)	43 (11.5)	28 (16)	49 (28)	16 (13)
Eliurus majori	1 (0.6)	0	2 (0.6)	3 (1.5)	6 (3)	1	0	3 (0.8)	1 (0.3)	0	0	0
Eliurus webbi	1 (0.6)	5 (1.4)	2 (0.6)	1 (0.5)	0	0	1 (0.3)	10 (2.6)	2 (0.5)	0	0	0
Suncus murinus	0	0	1 (0.3)	0	1 (0.5)	0	0	1 (0.3)	0	0	0	0
Tenrec ecaudatus	0	3 (0.9)	12 (3.5)	5 (2.5)	1 (0.5)	0	0	2 (0.5)	8 (2.1)	1 (0.6)	2 (1.1)	4 (3.3)
Microgale drouhardi	0	1 (0.3)	2 (0.6)	1 (0.5)	1 (0.5)	5	1 (0.3)	2 (0.5)	3 (0.8)	0	1 (0.6)	0
Microgale talazaci	0	2 (0.6)	14 (4)	0	5 (2.5)	8	4 (1.1)	6 (1.6)	7 (1.9)	0	0	0
Galidia elegans	0	0	1 (0.3)	0	0	0	0	0	0	0	0	2 (1.6)
total number of animals	39	88	81	65	42	40	70	67	64	29	52	22
total number of animals excluding *Rattus*	2	11	34	10	14	14	6	24	21	1	3	6

[a] Number is total accrued trap nights for each trap line per year.

[b] Number in parentheses is the percent trap success.

insectivores never made up more than 10% of the animals captured during the course of any season. Introduced *Suncus murinus* was rarely captured in pit-fall or trap lines and is apparently rare in the PN de la Montagne d'Ambre. A total of 4050 trap nights in the vicinity of the station accrued during the three years of trapping, 3045 of which were the standardized trap lines (Table 2). The only species of rodent captured in the balance of the 1005 trap nights not reported in this paper was a single individual of *E. minor*. This animal was taken in 1994 in an area of mostly exotic trees.

DISCUSSION

Population cycles. Two long-term field studies have been conducted in Madagascar humid forest that provide insight into the seasonal cycles of small mammal numbers. Between November 1980 and October 1982 rodents were systematically trapped, marked and released, generally on a monthly basis, in the Andranomay Forest (1300 m) near Anjozorobe (Rakotondravony 1992). *Rattus rattus* and *Eliurus* spp. showed considerable variation in effective population size during this 24-month study with asynchronous population cycles between the two genera. *R. rattus* reached an effective population high in March–April 1980 and thereafter population levels never reached 25% of this peak. Within *Eliurus* spp. approximately the same relative differences between the low and high points of effective population size were measured, but the peak in the cycle was during the latter portion of 1981.

At two sites, Réserve Spéciale (RS) d'Analamazaotra (930–1040 m) and RS d'Ambohitantely (1448–1662 m), small mammals were systematically trapped, marked, and released on average once per month between April 1988 and May 1990 (Stephenson 1994). At both sites there was considerable variation in the number of individuals and species of small mammals (rodents and insectivores combined) captured per month, with highest trap success from May to June and the periods of lowest trapping success varied between the sites. The number of species captured per month varied from two to six at Analamazaotra and three to four at Ambohitantely.

During our three-year study in the PN de la Montagne d'Ambre there was considerable annual variation in the total number of insectivores captured (Table 1). For virtually all of the insectivore species trapped in the standardized pit-fall lines, there was marked annual variation in the number of individuals and species richness with each line. When these measures are averaged across the three years, the total number of individuals and species captured in each line were: line 1–63 individuals and 5 species, line 2–74 individuals and 5 species, and line 3–73 individuals and 6 species. Thus, on a broad scale there were few differences between the lines, although they were placed in different microhabitats with varying degrees of human disturbance.

For the trap lines there were varying patterns of annual trap success (Table 2). On the basis of standardized trap success for each trap line, no generalization can be made about variation in annual population cycles (Fig. 3). When the trap lines are combined by year, there was a decline in the number of *R. rattus* captured per 100 trap nights from 20 in 1993, 18 in 1994 to 12.6 in 1996. Endemic rodents varied from 0.8 individuals/100 trap nights in 1993 and 1995 to 2.2 individuals/100 trap nights in 1994, and endemic insectivores steadily increased from 1.3 individuals/100 trap nights in 1993 to 6.0 individuals/100 trap nights in 1996. Further, given that all captured rodents were removed from the local population (collected or displaced to another area) and that there was not necessarily a subsequent decline in the number captured, this implies relatively high local densities for recruitment.

Even though our surveys of the small mammals of the PN de la Montagne d'Ambre were conducted during approximately the same season, there was considerable annual variation in relative numbers of individuals captured. This result, combined with rhe non-synchronized patterns of seasonal cycles between *Rattus*, endemic rodents and insectivores demonstrated by Rakotondravony (1992) and Stephenson (1994), provides no basis for generalization on annual periods of highest relative density of native and introduced small mammals in humid forests of Madagascar. The factors that influence these population cycles (e.g., rainfall, temperature, phenology of fruit and seed production) are not well known.

The effects of Rattus. Demonstration that *Rattus rattus* is negatively effecting the native rodent species is not simply a matter of documenting high population levels of *Rattus* within forest blocks. It is possible that native rodent populations have remained at normal levels despite elevated *Rattus* numbers. No data are available on the species richness or relative density of nesomyine rodents in the PN de la Montagne

d'Ambre before invasion of this forest by *Rattus*. Thus, we must turn to parallel studies of rodents in the Réserve Naturelle Intégrale (RNI) d'Andringitra (Goodman & Carleton 1996) and the RS d'Anjanaharibe-Sud (Goodman & Carleton in press), in primary forest with similar vegetation, and at approximately the same elevation as our study site in the PN de la Montagne d'Ambre. The low number of endemic rodent and insectivore species within the PN de la Montagne d'Ambre is consistent with the much lower than expected numbers of tree and lemur species as compared to similar forest types on the island (Ganzhorn *et al.* 1997). These differences may be due to a combination of factors including geologically recent volcanic activity on the mountain and its isolated humid forest habitat (Raxworthy & Nussbaum 1994, Goodman *et al.* 1996).

The RS d'Anjanaharibe-Sud, in northeastern Madagascar, is approximately 32,100 ha of humid forest within the elevational range 500–2064 m, and the RNI d'Andringitra in southeastern Madagascar is about 31,000 ha within the elevational range 650–2658 m (Nicoll & Langrand 1989), of which less than half is humid forest. Both sites have been recently surveyed with identical techniques to the study conducted in the PN de la Montagne d'Ambre. We compare only the two trap lines (Camp Line and Petit Cascade) within relatively intact forest.

Although there was variation in the trapping results in the PN de la Montagne d'Ambre over the three seasons ($Chi^2 = 19.23$; df = 2; $P < 0.001$), the average number of nesomyine rodents captured was very low compared to the RNI d'Andringitra and the RS d'Anjanaharibe-Sud ($Chi^2 = 29.61$; df = 2; $P < 0.001$; Table 3), where there were low levels of *Rattus* in the forest. Thus it appears, on the basis of these comparisons, that the high levels of *Rattus* in the relatively intact forests of the PN de la Montagne d'Ambre might be having a negative effect on the native rodents. This effect is not restricted to

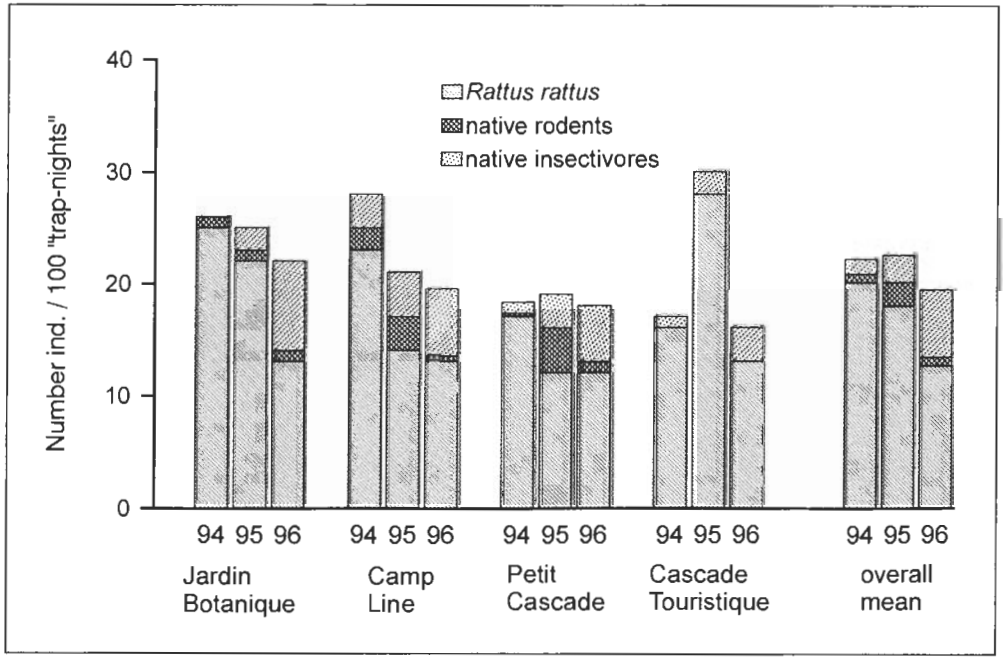

FIG. 3. Proportions of introduced rodents (*Rattus rattus*) and native insectivores and rodents captured in four different live trap lines over three seasons (1994–1996) and overall mean for the four lines. All trap lines in the vicinity of the Station Forestière des Roussettes, Parc National de la Montagne d'Ambre. The number of individuals captured is standardized per 100 trap nights.

TABLE 3. Comparison of introduced and native rodent trap success in the relatively intact forests of Parc National de la Montagne d'Ambre and two other intact humid forest sites using the same techniques.

	Montagne d'Ambre[a]			Anjanaharibe-Sud[b]	Andringitra[c]
	1993 (575)[d]	1994 (575)	1995 (575)	1994 (500)	1993 (625)
Number of *R. rattus* captured (% trap success)	119 (20.7)	71 (12.3)	69 (12.0)	2 (0.4)	4 (0.6)
Number of native rodents captured (% trap success)	5 (0.9)	19 (3.3)	4 (0.7)	47 (9.4)	40 (6.4)
Number of native rodenr species captured	2	2	2	6	5

[a] Combines the trapping results of the Petit Cascade and Camp Line trap lines.
[b] Based on Goodman & Carleton (in press), transect zone centered at 1260 m.
[c] Based on Goodman & Carleton (1996), transect zone centered at 1210 m.
[d] Figure in parenrheses below year is the total number of accrued trap nights.

forests within a few kilometers of the reserve limit or in close proximity to human disturbance. In 1996 near the summit of Montagne d'Ambre, in more-or-less undisturbed forest, in 750 trap nights 103 *R. rattus* and one nesomyine rodent were captured (Goodman *et al.* 1996). Further, at these other two localities with similar vegetation characteristics and elevation as our site in the PN de la Montagne d'Ambre the ratio of *R. rattus* to native nesomyine rodents decreases with increasing species richness of native rodent species (Spearman rank correlation: $rs = -1$, $P = 0.05$). Though sample size is small, this relationship furthur supports the premise that *R. rattus* is competing with or actually outcompeting the native rodents.

Food-trial experiments of *Rattus* and nesomyine rodents in captivity and the excavation of foods cached in rodent burrows, show evidence for some overlap in the diets of native and introduced rodents, and some lemur species (Goodman & Sterling 1996). *Rattus* also have considerably higher reproductive potential (Hayssen *et al.* 1993; Goodman & Carleton 1996, in press) than nesomyine rodents. An eradication program of *Rattus* within the park is insufficient to ameliorate this problem, since the large recruitment population that exists in inaccessible forests and in surrounding areas as human commensals would rapidly recolonize trapped areas.

It has been postulated that the introduced soricid *Suncus murinus* may compete with or prey upon tenrecid insectivores, primarily *Microgale* spp. (Heim de Balsac 1972). Our results from PN de la Montagne d'Ambre show *Suncus* has colonized areas within relatively intact forests (also see Goodman *et al.* 1996). However, their numbers remain low and there is no evidence that they are having a negative effect on the endemic insectivore fauna.

ACKNOWLEDGMENTS

Our research in Madagascar has been authorized by the Direction des Eaux et Forêts, Association Nationale pour la Gestion des Aires Protégées, and the Commission Tripartite. We are particularly thankful to Henri Finaona, Faramalala Miadana Harisoa, and Célestine Ravaoarinoromanga for issuing permits. The field work was supported by the ICDP-Montagne d'Ambre, WWF, Madagascar. For logistic help we wish to thank the WWF staff in Antsiranana and Joffreville. The résumé was kindly translated from the English by Lucienne Wilmé.

REFERENCES

Ganzhorn, J.U., Malcomer, S., Andrianantoanina, O., & S.M. Goodman. 1997. Habitat characteristics and lemur species richness in Madagascar. Biotropica 29: 331–343.

Goodman, S.M. 1995. *Rattus* on Madagascar and the dilemma of protecting the endemic rodent fauna. Conserv. Biol. 9: 450–453.

Goodman, S.M., Andrianarimisa, A., Olson, L.E., & V. Soarimalala. 1996. Patterns of elevational distribution of birds and small mammals in the humid forests of Montagne d'Ambre, Madagascar. Ecotropica 2: 87–98.

Goodman, S.M., & M.D. Carleton. 1996. The rodents of the Réserve Naturelle Inrégrale d'Andringitra, Madagascar. Fieldiana: Zoology, new series 85: 257–283.

Goodman, S.M., & M.D. Carleton. In press. The rodents of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. Fieldiana: Zoology.

Goodman, S.M., & E.J. Sterling. 1996. The utilization of *Canarium* (Burseraceae) seeds by vertebrates in rhe Réserve Naturelle Intégrale d'Andringitra, Madagascar. Fieldiana: Zoology, new series 85: 83–89.

Hayssen, V., van Tienhoven, A., & A. van Tienhoven. 1993. Asdell's patterns of mammalian reproduction. Ithaca.

Heim de Balsac, H. 1972. Insectivores. Pp. 629–660 *in* Battistini, R., & G. Richard-Vindard (eds.). Biogeography and ecology in Madagascar. The Hague.

Jenkins, P.D., Raxworthy, C.J., & R.A. Nussbaum. 1997. The descriprion of a new species of *Microgale* (Insectivora, Tenrecidae), with comments on the status of four related taxa. Bull. Brit. Mus. (Zoology) 63: 1–12.

MacPhee, R.D.E. 1987. The shrew tenrecs of Madagascar: Systematic revision and Holocene distribution (Tenrecidae, Insectivora). Amer. Mus. Novit. 2889: 1–45.

Musser, G.G., & M.D. Carleton. 1993. Family Muridae. Pp. 501–755 *in* Wilson, D.E., & D.M. Reeder (eds). Mammal species of the world: a taxonomic and geographic reference. 2nd edition. Washington, D. C.

Nicoll, M.E., & O. Langrand. 1989. Madagascar: Revue de la conservation et des aires protégées. Gland.

Rakotondravony, D.S. 1992. Etude comparée de rrois rongeurs des milieux malgaches: *Rattus norvegicus* Berkenhout (1769), *Rattus rattus* Linné (1757) et *Eliurus* sp. (Biologie et dynamique des populations). These de 3ème cycle, Etablissement d'Enseignement Superieur des Sciences, Université d'Antananarivo, Madagascar.

Raxworthy, C.J., & R.A. Nussbaum. 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. Biol. Conserv. 69: 65–73.

Stephenson, P.J. 1994. Seasonality effects on small mammal trap success in Madagascar. J. of Trop. Biol. 10: 439–444.