



Habitat use by endemic and introduced rodents along a gradient of forest disturbance in Madagascar

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Abstract. We used logistic and Poisson regression models to determine factors of forest and landscape structure that influence the presence and abundance of rodent species in the rain forest of Ranomafana National Park in southeastern Madagascar. Rodents were collected using live-traps along a gradient of human disturbance. All five endemic rodent species (*Nesomys rufus*, *N. audeberti*, *Eliurus tanala*, *E. minor* and *E. webbi*) and the introduced rat *Rattus rattus* were captured in both secondary and primary forests, but the introduced *Mus musculus* was only trapped in secondary forest. The abundance of *R. rattus* increased with the level of habitat disturbance, and it was most common in the heavily logged secondary forest. Furthermore, the probability of the presence of *R. rattus* increased with decreasing distance from forest edge and decreasing canopy cover, while the probability of presence increased with increasing herbaceous cover, altitude and overstory tree height. The species was never observed farther than 500 m away from human habitation or camp-site. *N. rufus* preferred selectively-logged forest at altitudes above 900 m a.s.l. Its probability of presence increased with increasing canopy cover, herbaceous cover and distance from forest edge, and with decreasing density of fallen logs, overstory tree height and distance from human habitation. *N. audeberti* preferred heavily-logged areas, while *E. tanala* was the only species occurring along the entire range of forest disturbance. We suggest that in the Ranomafana National Park the spread of *R. rattus* is associated with deforestation.

Key words: endemic species, habitat use, human disturbance, introduced species, Madagascar, rain forest, Ranomafana National Park, rodents

Introduction

Numerous studies in temperate forests have demonstrated that clearcutting and other forms of intensive forestry lead to increased population densities of certain species of rodents (e.g. Verme and Ozoga 1981; Monthey and Soutiere 1985). The few studies that have addressed this issue in a tropical rain forest have shown comparable results to those from temperate forest (Malcolm 1997; Struhsaker 1997).

In Madagascar, however, changes in rodent densities following forestry operations appear to differ from those found elsewhere. Although selective logging had minor effect on insectivores and rodents in the Kirindy dry forest (Ganzhorn et al.

1996), endemic rodents were generally more abundant in primary than in secondary forest in lowland rainforest of north-east Madagascar (Stephenson 1995). However, Stephenson (1995) studied lowland rainforests where rodent diversity is very low. Thus, logging might decrease population densities of native rodents in the rainforests of Madagascar. Satellite images and aerial photographs show a rapid decline in rainforest cover in eastern Madagascar (Green and Sussman 1990).

In addition to deforestation, the introduction of rodents may threaten native rodent species of Madagascar, all in the endemic subfamily Nesomyinae (Goodman 1995). The history of the introduction and colonisation of Madagascar by non-native rodents (*Rattus norvegicus*, *R. rattus* and *Mus musculus*) is not well known, but the earliest presence of commensal rats dates back to 11–14th century middens excavated at an archaeological site in northwestern Madagascar (Rakotozafy 1996; Radimilahy 1997). Later, especially *Rattus rattus* has invaded most the humid forests of eastern Madagascar (Goodman 1995). It has not only been found close to human habitation but also deep within undisturbed forests, e.g. in Andringitra National Park (Goodman and Carleton 1996).

Compared to the well-studied lemurs and other more charismatic groups of Malagasy animals, little is known about the rodents of the island. Illustrative of the poor knowledge of Nesomyinae is that five new rodent species have been described from Madagascar during the 1990s (Carleton 1994; Carleton and Goodman 1996, 1998). However, interest in Nesomyinae has been awakened in the past decades (see Goodman and Carleton 1998). Recent investigations of Malagasy rodents have provided new information about their elevational range (Goodman and Carleton 1996, 1998; Goodman et al. 1996), but other factors influencing their habitat use have been analysed in more detail only by Stephenson (1995) and Ganzhorn et al. (1996).

Our aim is to add to the scanty knowledge of the ecology Malagasy rodents by analysing the composition of the rodent fauna in the secondary and primary rain forest in Ranomafana National Park in the southeastern region of Madagascar. We determine factors influencing the presence and abundance of rodent species. In particular, we address the following questions for both endemic and introduced rodents: (1) which rodent species co-exist? (2) what are their species-specific habitat utilisation patterns? and (3) how does anthropogenic habitat disturbance affect the rodent community?

Materials and methods

Study area

Research was conducted in the Ranomafana National Park (RNP: 21°16', 47°20') east of the high plateau in southeastern Madagascar. Most of the park is mountainous (500–1500 m a.s.l) and consists of relatively undisturbed lowland rain forest and

cloud forest (Wright 1997). The annual rainfall is 2300–4000 mm, and monthly temperature means are 15–24 °C.

The protected core area of RNP, established in 1991, covers 43 500 ha, and the park is surrounded by a 3-km-wide peripheral zone which contains 93 villages with 25 000 residents (Grenfell and Robinson 1995). There are no villages within the park boundaries. Permits for small timber concessions had been issued for about two decades prior to the establishment of RNP. Eight timber exploiters had been granted selective logging concessions within the area now protected by the park, averaging 700 ha each, for the period between 1987 and 1991 (Wright 1992).

Six study sites were selected and visited between 15 September and 29 November 1996 and 1998. Three of these sites are located in primary forests (i.e., unlogged or slightly selectively logged forest): Vatoharanana (VT), Valohoaka (VL) and Miaranony II (M2). Selective logging in VT included removal of over 1000 trees in 1986 (Balko 1998). The logging history of M2 has not been documented but there are signs of a previous slight selective logging. VL has never been exploited (Wright 1997). Another three study sites are in secondary forests (i.e., heavily logged forest): Talatakely (TK), Ambotalahy (AL) and Miaranony I (M1) (Figure 1). Sites AL and M1 located in the peripheral zone are still exploited by local people. The site at TK is in an area that was a village from 1935 to 1947, and was heavily exploited for timber in 1986–1990 (Wright 1997). Since 1990, TK is a site for a research station containing two research cabins, campsites and extensive trail system. The mean altitude of trapping squares was 642 m in M1, 667 m in M2, 895 m in AL, 977 m in TK, 1019 m in VT and 1066 m in VL. For further information about the study sites see Wright (1997) and Balko (1998).

Field methods and trapping protocol

Each of the six study sites included 10 (M1 and M2) or 12 (other sites) trapping plots. In addition to these plots, 44 similar trapping plots were monitored between 12 October and 3 December, 1998 to determine the distribution of *Rattus rattus*. These trapping plots were placed along three lines between the primary forest areas and areas where *R. rattus* was known to occur. Specifically, there were 12 plots between TK and VT, 12 between VH and Ambatovory village (Figure 1) and four between M1 and M2. The remaining 16 trapping plots were situated in highly disturbed areas, close to Ambodiamontana and Ambotalahy villages. In total we operated 112 trapping plots.

Each trapping plot was a square measuring 20 × 20 m. We placed one large, locally made live-trap (10 × 10 × 29 cm: Ramiarinjanahary 1999) and one small live-trap (2.5 × 7.8 × 6.5 cm: Ugglan special, Grahnab, Marieholm, Sweden), and one pitfall trap (9 cm in diameter, 15 cm in depth) in each corner of the trapping plots for three nights. In 1998, 2/3 of the plots had three small live-traps instead of four (see Results). Most of the live-traps were placed on the ground, while 4% were set above the ground on fallen logs, lianas or live branches. The distance between neighbouring

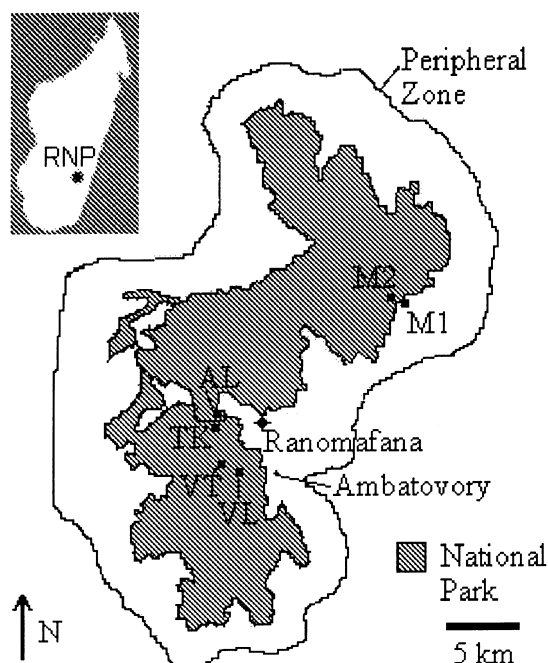


Figure 1. Map of RNP with an inset of Madagascar. Squares mark the study of annual monitoring.

trapping plots was at least 100 m. In each study site half of the 10 or 12 plots were situated in valleys and other half on ridges. Live-traps were baited daily, generally between 15:00 and 17:00 hrs, with banana slices and peanut butter.

Traps were checked twice per day, in the morning beginning at 07:00 hrs and in the afternoon. Captured animals were sexed, examined for reproductive condition, weighed and measured for head and body, tail, ear length and hindfoot without claw. Species identification was based on morphological criteria provided by Carleton (1994), Carleton and Goodman (1996) and Goodman and Carleton (1996). All captured individuals of *Rattus rattus* and *Mus musculus* were sacrificed, but most individuals of endemic species were released after measuring and earmarking. To study endoparasites, 14 individuals of *Nesomys rufus*, 2 individuals of *N. audeberti* and 3 individuals of *Eliurus tanala* were collected in 1998. These results will be presented elsewhere. In addition, one individual per species from the 1996 study was preserved as a voucher specimen in the collection of Université d'Antananarivo.

Habitat variables

Twelve variables of forest and landscape structure were measured by the same person at each of the 112 trapping plots in 1998: canopy cover (percentage of canopy cover directly above trapping plot, estimated by eye to within 5%), fallen log density (0 = no

fallen logs, 1 = 1–2 fallen logs, 2 = 3–10 fallen logs, 3 = 10–20 fallen logs, 4 = > 20 fallen logs), herbaceous cover (percentage of herbaceous cover: 0 = no cover, 1 = 1–25%, 2 = 25–50%, 3 = 50–75%, 4 = 75–100%), liana stem density (0 = no lianas, 1 = 1–9 lianas, 2 = 10–20 lianas, 3 = > 20 lianas), overstory tree height (estimation to within 5 m), altitude (measured using a Peet Bros altimeter and altitude for the cabin as 931 m as the calibration value (Tan-Alkis 1997), meters), distance from a building (distance from the plot to nearest building or permanent satellite campsite, meters), distance from a field (distance from the plot to nearest recently cultivated field, meters), distance from human habitation (distance from the plot to nearest house, permanent satellite campsite or to recently cultivated field, meters), distance from forest edge (if plot was situated in open area, e.g. in secondary bush, value was negative, meters), distance from stream (distance from plot to nearest stream, water depth >20 cm, meters) and slope (estimation within 5°). All values represent the mean of the plot area (20 × 20 m). Distances above 200 m were measured using a Garmin 12 XL GPS-navigator, while distances below 200 m were estimated by eye.

All trapping plots were also divided into four categories of human disturbance: (1) secondary bush, (2) heavily logged forest, (3) selectively logged forest and (4) pristine forest. If the exact logging history of the trapping plot was not known, it was estimated by the occurrence of the following plant indicator species of forest disturbance: *Clidemia hirta*, *Dombeya* sp., *Harunga madagascariensis*, *Psidium cattleianum*, *Ravenala madagascariensis* (Lowry et al. 1997). Some natural phenomena like cyclons may also produce the same form of regeneration. Anyway, the effects of cyclons and heavy winds on forest are quite similar than forest cutting. Thus, we think it is better to use indicator species than only the successional stage.

Data analyses

We used logistic and Poisson regression models to examine the effect of various environmental factors on the presence and abundance of the rodent species in 1998. The 12 forest or landscape variables (see above) were used as explanatory variables.

Logistic regression was used to examine the determinants of the presence of the four commonest rodent species. Odds ratios (OR) were used to characterise quantitatively the effects of the explanatory variables on presence of the species (Collett 1991; Nieminen et al. 1999).

Poisson regression was used to model the effects of explanatory variables on the abundance of *R. rattus*, *N. rufus* and the pooled abundance of all Nesomyinae. Species abundance data are often problematic: one can never know whether an observation with no individuals of a species is only due to insufficient effort or a manifestation of real non-presence of the species. In a sense, one can not tell how ‘deep’ a zero is. Our solution is to include in the abundance analysis only those zero observations that according to the logistic model had at least 30% probability of species presence (Lindenmayer et al. 1991). Without the elimination of some of the empty plots we

would have included extreme variable values which only indicate presence but not abundance of the studied species. We tracked the best-fit model (i.e., the one with the smallest deviance) by the forward stepwise procedure, including statistically significant (at the 5% level) variables into the model (Nicholls 1989). All analyses were conducted using STATISTIX for Windows (Analytical Software 1996).

Results

Captures of mammals

Seven species of rodents (209 individuals) were caught in the RNP in 1996 and 1998 (Table 2). In addition, the large live-traps captured two species of primates (*Cheirogaleus major*, *Microcebus rufus*), one carnivore (*Galidia elegans*), and one insectivore (*Setifer setosus*). Pitfalls and small live-traps caught insectivores (*Microgale* spp. and *Suncus murinus*). Small live-traps were not successful as only 11 (5%) of the 209 captured rodents were caught by them. Thus, the absence of the fourth small live-trap in some squares in 1998 did not affect the results much. Pitfall traps did not capture any rodents.

Effects of human disturbance on rodent occurrence

All five endemic rodent species and *Rattus rattus* were found in both secondary and primary forests, but *Mus musculus* was trapped only in secondary forests (Table 1). *R. rattus* was by far the most abundant species (61 individuals), but it was scarce in primary forest: only one individual was captured in Vatoharanana, 200 m from a campsite, which had been continuously used between May and November 1998. If the campsite and Talatakely research station are classified as inhabited by humans, then *R. rattus* was never observed farther than 500 m away from human habitation or cultivated fields. During both study years, the total number of endemic rodents was higher in the primary forests (21 individuals in 1996, 34 in 1998) than in the secondary forests (9 individuals in 1996, 21 in 1998) (Table 1).

The 112 trapping plots were divided into four categories of human disturbance in 1998 (secondary bush, heavily-logged forest, selectively-logged forest and pristine forest). When the abundances of rodents are compared between different disturbance categories it is worth noting that most of the forest structure and landscape variable measurements differed between the four categories (Table 2). The highly disturbed trapping plots were situated much closer to buildings, fields and forest edges than were those of unlogged ones. Canopy cover decreased and herbaceous cover increased as a function of disturbance.

There was a significant difference in the abundance of *Rattus rattus* among the different habitat types (Kruskal–Wallis, $P < 0.001$). The same was true for *Neso-*

Table 1. Number of individuals trapped for each rodent species in different forested areas in 1996 and 1998 (total number of trapping squares is shown in parentheses).

Species	Secondary forest						Primary forest						Total					
	TK (12)		AL (12)		MI (10)		VT (12)		VL (12)		M2 (10)		Sec. for (34)		Prim. for (34)		Additional squares (44)	
	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998
<i>Mus musculus</i>	-	-	-	-	2	3	-	-	-	-	-	-	2	3	-	-	-	-
<i>Rattus rattus</i>	1	1	22	24	7	5	-	1	-	-	-	-	30	30	-	1	27	-
<i>Eliurus minor</i>	1	1	-	-	-	-	1	-	1	-	-	-	1	1	2	-	-	-
<i>Eliurus tanala</i>	-	1	1	4	-	1	5	5	3	2	-	-	1	6	8	7	4	-
<i>Eliurus webbi</i>	-	1	-	-	-	-	1	1	-	-	-	-	-	1	1	1	2	-
<i>Nesomys audeberti</i>	-	8	-	-	-	2	-	-	-	-	2	2	-	10	2	2	11	-
<i>Nesomys rufus</i>	1	3	6	-	-	-	5	15	3	9	-	-	7	3	8	24	14	-
Total rodents	3	15	29	28	9	11	12	22	7	11	2	2	41	54	21	35	58	-
Total nesomyines	2	14	7	4	-	3	12	21	7	11	2	2	9	21	21	34	31	-

Table 2. Mean (\bar{X}), median (Md) and standard deviation (SD) for forest and landscape structure variable measurements for four disturbance categories.

Variable	Secondary bush ($n = 20$)			Heavily logged forest ($n = 42$)			Selectively logged forest ($n = 32$)			Pristine forest ($n = 18$)		
	\bar{X}	Md	SD	\bar{X}	Md	SD	\bar{X}	Md	SD	\bar{X}	Md	SD
Canopy cover	13.2	5	16.7	67.0	72.5	19.9	81.6	80	4.5	84.2	85	5.8
Fallen log density	1.0	1	0.8	1.6	2	0.8	2.2	2	0.6	2.1	2	0.5
Herbaceous cover	2.8	3	0.6	2.1	2	0.7	2.0	2	0.6	1.9	2	0.7
Liana stem density	0.1	0	0.2	1.2	1	0.8	2.1	2	0.8	1.7	2	0.7
Overstory tree height	10.0	10	5.2	24.3	25	5.3	30.5	30	4.1	28.6	27.5	6.6
Altitude	795.5	845	128.9	893.2	911.5	120.4	908.4	991	150.7	930.3	1046	198.3
Distance from house	234.0	150	251.3	446.7	440	291.8	670.3	650	460.2	2227.8	2650	622.0
Distance from field	38.5	5	69.1	336.9	245	300.8	1301.9	1245	688.9	1344.4	1800	671.2
Distance from human habitation	38.5	5	69.1	262.6	195	238.5	520.3	450	335.1	1344.4	1800	671.2
Distance from forest edge	1.5	0	70.3	221.0	75	280.3	1214.1	1105	759.3	1344.4	1800	671.2
Distance from stream	83.0	55	71.3	134.5	110	97.7	108.0	80	100.8	103.1	75	91.1
Slope	23.2	20	19.8	28.0	35	19.1	18.0	12.5	18.5	23.1	22.5	18.7

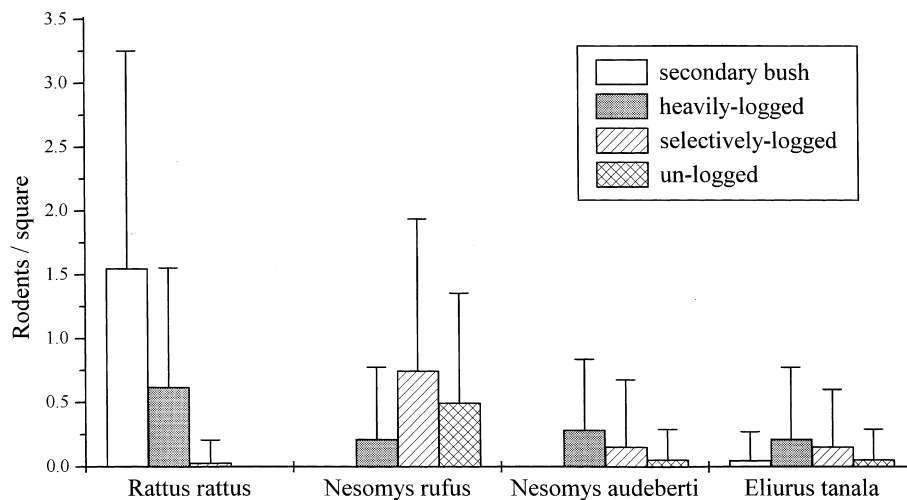


Figure 2. The mean abundance of different rodent species per trapping square in different categories of natural state in RNP in 1998.

mys rufus ($P = 0.002$) and *N. audeberti* ($P = 0.03$), but no significant difference was detected in the abundance of *Eliurus tanala* ($P = 0.6$) (Figure 2). Catches of *R. rattus* increased with increasing disturbance and the species was most common in secondary bush, where *N. rufus* did not occur at all. *N. rufus* occurred in all the other habitat types being most abundant in selectively-logged forest. Also *N. audeberti* was absent from the secondary bush and it preferred the heavily-logged sites. *E. tanala* occurred in all the four habitat types, also in the secondary bush. Two individuals of *E. webbi* were caught in heavily-logged areas and two in selectively-logged areas. The single *E. minor* specimen discovered in 1998 was in heavily-logged forest, but in 1996 *E. minor* was caught also in selectively logged and unlogged sites. Thus, it appears that none of the endemic species preferred unlogged forest.

Elevational range of rodent occurrence

Eliurus tanala, *Nesomys audeberti* and *Rattus rattus* were captured virtually across the whole range of surveyed altitudes (600–1120 m a.s.l.), but *N. rufus* was captured only in higher altitudes (above 925 m a.s.l.) (Figure 3). The abundance of *R. rattus* peaked between 870 and 950 m a.s.l. Both *E. minor* and *E. webbi* were caught between 900 and 1050 m a.s.l., while *Mus musculus* was discovered between 600 and 850 m a.s.l.

Logistic regression models for the presence of rodent species

The best-fit logistic regression model for the presence of *Rattus rattus* in 1998 included six environmental variables (Table 3). The probability of presence in a trapping plot increased with increasing herbaceous cover, altitude and overstorey tree height.

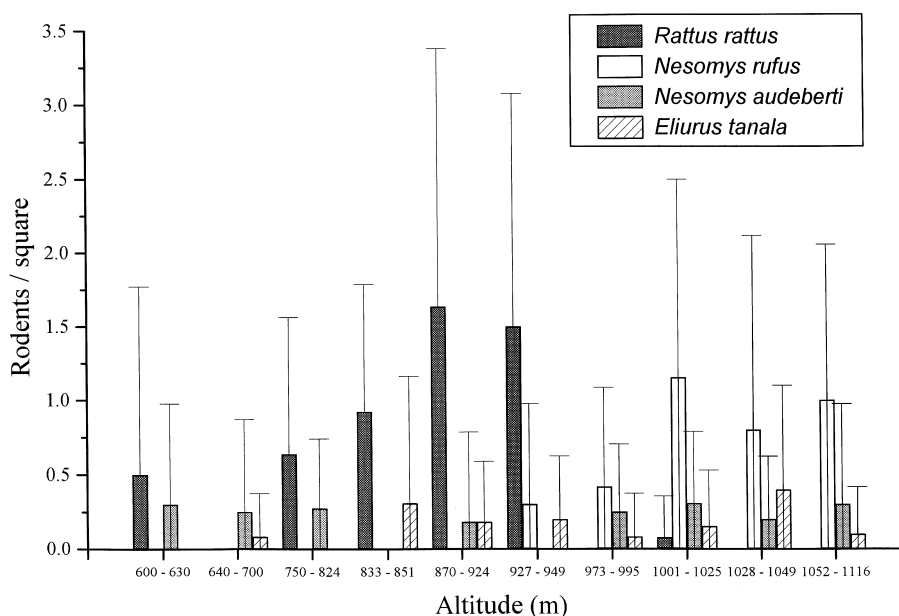


Figure 3. Number of rodents captured per trapping square in different elevational zones in RNP in 1998. Each value is the mean of 10–13 trapping plot.

The probability of presence decreased with increasing distance from forest edge, from human habitation, and with increasing canopy cover. These results indicate that the species avoids closed forest away from human habitation.

The adequacy of the model was estimated by means of calculations specified in Table 4. Error rate of the model was 9.8%, sensitivity 92.1% and specificity 90.1% at level $P \geq 0.3$. Thus, *R. rattus* was absent only from 8% of sites where it was predicted to occur and was present at less than 10% of sites from which it was predicted to be absent. Five squares where *R. rattus* was predicted to occur but was absent in 1998 had been studied also in 1996 and three of them were occupied by *R. rattus* in 1996. Thus, the species prefers relatively pristine conditions but can also occur in the vicinity of buildings.

Probability of presence of *Nesomys rufus* increased with increasing distance from forest edge, increasing canopy cover and increasing herbaceous cover. Probability of presence decreased with increasing density of fallen logs, increasing overstory tree height and increasing distance from buildings (Table 3). Error rate of the model was 9.8%, sensitivity 91.3% and specificity 89.9%. In one of seven squares where *N. rufus* was predicted to occur, it was absent in 1998, but was present in 1996.

According to the best-fit model, distance from buildings and from fields had a negative effect, and the overstory tree height and distance from human habitation had a positive effect on the presence of *N. audeberti* (Table 3). Error rate of the model was 19.6%, sensitivity 33.3% and specificity 89.4%. Hence, the model was able to predict

Table 3. Parameter estimates of the logistic regression model for the probability of presence of various rodent species. Only variables with $P < 0.05$ are included. For further interpretation of OR, see Collett (1991).

Species	Predictor variables	Estimate	P-value	OR ^a	95% confidence interval of OR
<i>Rattus rattus</i>	Constant	-13.224	0.006		
	Distance from forest edge ^b	-0.232	0.008	0.79	0.67-0.94
	Herbaceous cover	2.196	0.009	8.98	1.74-46.34
	Distance from human habitation ^b	-1.214	0.012	0.30	0.12-0.77
	Altitude ^b	0.970	0.014	2.64	1.21-5.72
	Overstory tree height	0.221	0.040	1.25	1.01-1.54
	Canopy cover	-0.060	0.042	0.94	0.89-1.00
<i>Nesomys rufus</i>	Constant	-10.287	0.033		
	Distance from forest edge ^b	0.486	0.000	1.63	1.24-2.13
	Canopy cover	0.237	0.003	1.27	1.08-1.48
	Fallen log density	-2.669	0.006	0.07	0.01-0.46
	Overstory tree height	-0.484	0.012	0.62	0.42-0.90
	Distance from house ^b	-0.168	0.020	0.85	0.73-0.97
	Herbaceous cover	2.230	0.024	9.29	1.34-64.28
<i>Nesomys audeberti</i>	Constant	-4.228	0.001		
	Distance from house ^b	-0.319	0.002	0.73	0.59-0.89
	Distance from human habitation ^b	0.557	0.002	1.74	1.23-2.48
	Overstory tree height	0.141	0.006	1.15	1.04-1.27
	Distance from field ^b	-0.200	0.031	0.82	0.68-0.98
<i>Eliurus tanala</i>	Constant	-7.814	0.002		
	Liana stem density	-1.309	0.010	0.27	0.10-0.73
	Fallen log density	1.114	0.014	3.05	1.25-7.41
	Altitude ^b	0.583	0.030	1.79	1.06-3.03
Total Nesomyinae	Constant	-2.119	0.003		
	Distance from human habitation ^b	0.385	0.001	1.47	1.17-1.85
	Distance from house ^b	-0.272	0.001	0.76	0.65-0.89
	Canopy cover	0.047	0.001	1.05	1.02-1.08
	Liana stem density	-0.772	0.021	0.46	0.24-0.89

^a Values above one indicate increase in presence probability with increasing explanatory variable value.

^b 100 m.

much more accurately the absence of *N. audeberti* than its presence. However, it is worth noting that all these measures depend on the limit value ($P \geq 0.3$). This species appears to prefer slightly more disturbed sites than does *N. rufus*.

The probability of the presence of *Eliurus tanala* increased with increasing density of fallen logs and altitude (Table 3). Liana stem density had negative effects on the probability of occupancy. Error rate of the model was 17.0%, sensitivity 28.6% and specificity 90.8%.

We also analysed the occurrence of the pooled catch of all endemic Nesomyinae. The probability of occurrence of these species was positively affected by distance from human habitation and canopy cover, and negatively by distance from buildings and liana stem density (Table 3). Error rate of the model was 42.9%, sensitivity

Table 4. Calculation of model adequacy measures for the logistic regression model developed for the estimated probability of presence of species studied. All measures were calculated at the level $P \geq 0.3$ (see Lindenmayer et al. 1991).

a	= The number of squares where species studied was correctly predicted to be present
b	= The number of squares where species studied was predicted to be absent but was present
c	= The number of squares where species studied was predicted to be present but was absent
d	= The number of squares where species studied was correctly predicted to be absent
N	= The total number of squares
Error rate	= An estimate of the number of incorrect predictions $((c + b)/N)$
Sensitivity	= A measure of the ability of the model to predict the presence of studied species at a square $(a/(a + b))$
Specificity	= The ability of the model to correctly predict that studied species will not occur on a given square $(d/(c + d))$

95.7% and specificity 29.2%. The pooled model was able to predict more accurately the presence of these species than their absence, a finding contrary to the species specific models of *N. audeberti* and *E. tanala*. This result is possibly caused by the smaller numbers of trapping plots occupied by *N. audeberti* (19) and *E. tanala* (17) as compared to all endemic Nesomyinae (49).

Poisson regression models of the abundance of rodents

Only trapping squares where *R. rattus* was present or was predicted to be present at the level $P \geq 0.3$ using logistic regression analyses were included in the Poisson modeling of the abundance ($n = 35$). Based on this analysis the abundance of *R. rattus* increased with increasing distance from forest edge, density of fallen logs and altitude. Abundance decreased with decreasing distance from fields, liana stem density and distance from a stream (Table 5). Most of these explanatory factors were different than in the model of the presence of *R. rattus* and the effect of the distance from forest edge was in the opposite direction.

For *N. rufus* no model included statistically significant variables at the 5% level ($n = 30$). More than one *N. audeberti* or *E. tanala* were captured only in a few trapping plot. Hence, the Poisson regression was not used to model the abundance of these species.

The total abundance of endemic rodents was positively affected by altitude and distance from human habitation, and negatively by distance from buildings ($n = 95$) (Table 5).

Discussion

Rodent fauna of RNP

Rattus rattus and eight species of Nesomyinae, including all five species captured by us are known to occur in RNP (Carleton and Schmidt 1990; Ryan et al. 1993). *Mus*

Table 5. Parameter estimates of the Poisson regression model for the probability of abundance of *Rattus rattus* and total nesomyinae. Only variables with $P < 0.05$ are included.

Species	Predictor variables	Estimate ^a	<i>P</i> -value
<i>Rattus rattus</i>	Constant	-3.014	0.064
	Distance from field ^b	-0.873	0.002
	Distance from forest edge ^b	0.758	0.006
	Fallen log density	0.696	0.010
	Altitude ^b	0.442	0.019
	Liana stem density	-0.546	0.022
	Distance from stream ^b	-0.424	0.050
Total nesomyine	Constant	-2.762	0.011
	Distance from house ^b	-0.290	0.002
	Distance from human habitation ^b	0.184	0.006
	Altitude ^b	0.290	0.013

^a Effect on mean abundance (/individuals) by one unit increase in the variable.

^b Variable/100.

musculus, which we discovered both on the edge of field in Miaranony and inside houses in Ambatolahy village, has not previously been documented from the national park (Goodman and Carleton 1998). In other areas in Madagascar, *M. musculus* is found in houses, rice fields, savannas and marsh, but never in closed forests (Langrand and Goodman 1997; Rakotondravony and Randrianjafy 1998).

We did not capture three species of Nesomyinae previously recorded from RNP, namely *Brachytarsomys albicauda*, *Brachyuromys betsileoensis* and *Gymnuromys roberti*. The possible reason for the absence of *B. albicauda* from our traps is that the species is arboreal and known to be difficult to trap using standard techniques (Goodman and Carleton 1996), and we placed only a few traps above the ground. The ecological monitoring team of RNP uses more traps above the ground than we did, and they captured *B. albicauda* in the park both in 1996 and in 1998 (W. Rakotonirina, per. comm.).

Brachyuromys betsileoensis was absent from our data probably because all our traps were located below 1120 m a.s.l. Previously, *B. betsileoensis* has been captured in RNP at 1225 m a.s.l. (Carleton and Schmidt 1990) and at Andringitra the species has been recorded only at 1700–1900 m a.s.l. (Goodman and Carleton 1996).

The third species not collected by us, *Gymnuromys roberti*, is terrestrial and has been reported at elevations 500–1800 m a.s.l. (Goodman and Carleton 1996). *G. roberti* has been observed in RNP close to Talatakely at 950 m a.s.l. (Carleton and Schmidt 1990) and close to Miaranony at 700 m a.s.l. in 1999 (J.T. Lehtonen, unpublished).

Elevational range of the species

Regarding elevational range of the endemic species our results corroborate earlier studies (Goodman and Carleton 1996, 1998; Goodman et al. 1996). In our study,

Nesomys rufus was discovered only in high altitudes (above 925 m a.s.l), while *N. audeberti* was captured virtually across the whole range of surveyed altitudes (600–1120 m a.s.l). These two species co-occurred only in Talatakely research station (977 m a.s.l.) and its surroundings indicating a fairly clear separation in elevational occurrence. Whether this is caused by different habitat requirements or interspecific interactions is not known.

Previous studies in Madagascar and in the Old World tropical forests have shown a mid-elevational peak in native rodent species richness (Goodman and Carleton 1998). Our results corroborate this pattern. Only two endemic species were present at altitudes below 900 m a.s.l., whereas five species occurred at elevations above 900 m a.s.l.

Population densities of *Rattus rattus* have been documented to peak at ca. 1600 m a.s.l. in two study sites in Madagascar (Réserve Spéciale d'Anjanaharibe-Sud and Parc National d'Andringitra) (Goodman and Carleton 1996, 1998). In our study, however, *R. rattus* densities peaked at a much lower elevation, about 900 m a.s.l. Furthermore, peak density in RNP was much higher (13 rats/100 trap-nights of large live-traps) than the density peaks in the RS d'Anjanaharibe-Sud (3 rats/100 trap-nights) or in Andringitra (1 rat/100 trap-nights). The density contrast between Ranomafana and the two other areas is at least partly caused by different trapping methods. Firstly, Goodman and Carleton (1996, 1998) did not trap in highly disturbed areas, where *R. rattus* density was highest in our study. Secondly, Goodman and Carleton (1996, 1998) trapped for five nights, whereas our periods were three nights. The number of rodents captured tends to decrease after 100–300 trap-nights in the same site in Madagascar (Goodman and Carleton 1998). Our trapping effort was 120–144 trap-nights/site (3 days), which probably did not deplete the local rat population as much as 200–240 trap-nights (5 days) would have done.

Factors influencing the occurrence of endemic species

None of the endemic rodent species occurred exclusively in primary forest, and none of the three most common endemic species (*Nesomys rufus*, *N. audeberti* and *Eliurus tanala*) was more abundant in unlogged areas than in selectively logged areas. Therefore, controlled selective logging may not pose a major threat to the endemic rodent species in Ranomafana, at least for the common species. However, strongly human-modified habitats are inhospitable for the endemic species as a single individual of *E. tanala* was the only endemic rodent captured in secondary bush representing the most disturbed site along our environmental gradient. In previous studies also *Brachyuromys ramirohitra* and *N. rufus* were captured on farmland but only close to a forest (Rakotondravony and Randrianjafy 1998). However, according to our results, *N. rufus* especially seemed to suffer from heavy logging. The increasing probability of presence of *N. rufus* as a function of increasing herbaceous cover and canopy cover, and decreasing density of fallen log is in agreement with its terrestrial way of

life (Ryan et al. 1993; Goodman and Carleton 1996, 1998). Hence, slight human disturbance in the form of selective logging does not seem to affect the endemic rodents much, but heavy logging is associated with loss of endemic rodents in Ranomafana.

Our finding that selective logging has only minor effects on native rodents corroborates most studies from tropical forests (Ganzhorn et al. 1996; Malcolm 1997; Struhsaker 1997). Stephenson's (1995) study in lowland rain forest of north-east Madagascar is the only one suggesting adverse effects. However, in that study *E. webbi* was the only endemic rodent species represented more than two trapped individuals.

As in most studies in Madagascar, the catches of most endemic rodent species was quite low in our study. The low numbers were reflected as somewhat contradictory results in our statistical analyses, and preclude us from making definite conclusion about their habitat use.

Factors influencing the occurrence of the introduced rat

Cutting or otherwise disturbing native forest has been proposed to create habitats favourable for *Rattus rattus* (Nicoll et al. 1988; Stephenson 1993, 1995), and for instance, in Andranomay, in the highlands, the abundance of *R. rattus* was higher in the fields than in the forest (Rakotondravony 1992). Our study supports this view as the abundance of *R. rattus* increased with increasing disturbance of the habitat. However, the relationship appears to be confounded by various factors. Previous studies in tropical rainforest (Struhsaker 1997) and also our own data show that logging reduces canopy cover and increases ground cover vegetation. Logistic regression analyses suggested three factors which could be effects of logging and deforestation: an increase in the herbaceous cover, a decrease in the canopy cover, and distance from forest edge. It was remarkable that also an increase in the overstorey tree height was predicted to increase the probability of the presence of *R. rattus*, which contradicts the logging effect pattern. Although *R. rattus* prefers highly disturbed and open areas, it seems to favour modified habitats with some big trees remaining. Hence, examination of the detailed effects of logging and deforestation provide a more comprehensive picture of the factors affecting the presence of *R. rattus* than merely logging.

Overall, our analyses indicated that *R. rattus* favours disturbed sites close to human habitation. However, even semi-permanent campsites attract the species. A single mature female was captured deep in the primary forest in Vatoharana, 200 m from the campsite in 1998, and one individual was collected at same site in 1997 by the ecological monitoring team of RNP (A. Dalecky, pers. comm.). Vatoharana campsite had been used continuously between May and November 1998, and there has been a rather large and exposed garbage pit there in the recent years. These observations have important consequences as regards the expansion of *R. rattus*. Although it appears that primary forest is not a habitat favoured by the species, the stray individuals in the forest rely on the semi-permanent campsites for food, and may be able to establish a permanent population there. Therefore, in order to prevent the further invasion of

the primary forest by *R. rattus* it is important not to log in the primary forest or leave exposed garbage.

It seems that the effects of human disturbance on the occurrence of *R. rattus* vary from region to region. Contrary to the situation in Ranomafana, in lowland rainforest of north-east Madagascar (Stephenson 1995) and in some other old world tropical countries (Musser 1987; Heaney et al. 1989), other studies in Madagascar suggest that *R. rattus* is not more common in disturbed forest close to human habitation than in primary forests (Goodman 1995; Goodman and Carleton 1996, 1998).

Previous studies have suggested that *R. rattus* competes with nesomyine rodents because of broad overlap in their food preferences (Goodman and Sterling 1996), and because the abundance of *R. rattus* at certain sites far exceeds that of the native rodents (Goodman et al. 1997). We did not include the abundance of *R. rattus* as an explanatory variable in the models for the endemic species because we do not know whether possible negative effect of *R. rattus* on the probability of the presence of some endemic species is caused by their different habitat selection or by interspecific competition. However, it is possible that especially the rarest endemic species, which are the most difficult to study, are the most threatened by rats. For instance, the fairly rare and small-sized *Eliurus minor* and *E. webbi* are partly arboreal like *R. rattus*, and may therefore interact with rats. Since even selective logging promotes the invasion by *R. rattus*, the nature of competitive interactions with native rodents should receive detailed study.

Conclusion

Our models were successful in predicting the presence of *Rattus rattus* and *Nesomys rufus* (i.e. low error rate in the models). However, studies from other areas are needed to test the interpretation based on the models. So far, we can suggest that clearcutting is detrimental to the endemic rodents but beneficial for *R. rattus*. Therefore, protecting primary forest from being logged also prevents the spread of *R. rattus*.

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