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The small mammal fauna of Réserve Spéciale d'Analamazaotra, Madagascar: the effects of human disturbance on endemic species diversity

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This study represents the first long-term small mammal survey of the mid-altitude rain forest reserve of Analamazaotra, Madagascar. Twenty-three visits were made to the reserve between April 1988 and May 1990. Live-trapping with Sherman and pitfall traps at four sites subjected to varying levels of human disturbance revealed the presence of seven endemic tenrec species, three endemic rodent species and an introduced rat. Greater species richness was demonstrated at the most undisturbed site, though individual species abundance was reduced. Human disturbance associated with tourism was correlated with a decrease in endemic species richness and an increase in abundance of introduced rats. Forest subjected to infrequent logging by local people exhibited an intermediate level of species richness. It is recommended that core areas of the reserve be left undisturbed in order to preserve small mammal species diversity.

Keywords: conservation and tourism; habitat disturbance; mid-altitude rain forest; Nesomyinae; Tenrecidae

Introduction

The small mammal fauna of Madagascar comprises species from the Insectivora and Rodentia. Besides two species of shrew (Soricidae), which are probably recent human introductions (Eisenberg and Gould, 1984), all insectivores are in the endemic family Tenrecidae which includes at least 24 species (Nicoll and Rathbun, 1990; Stephenson, 1991). Besides the cosmopolitan *Mus musculus*, *Rattus rattus* and *R. norvegicus*, the rodent fauna comprises ten species in seven endemic genera which are artificially grouped in the subfamily Nesomyinae of the family Cricetidae (Petter, 1972, 1975).

Since the description of type specimens collected largely in the nineteenth century, few attempts have been made to survey the small mammal fauna of Madagascar. Very little is known of the general biology and ecology of most species. Known distribution patterns indicate that centres of small mammal species richness and endemism are located in eastern tropical rain forest (Carleton and Schmidt, 1990; Nicoll and Rathbun, 1990) yet this habitat is under severe threat from deforestation (e.g. Chauvet, 1972; Jolly and Jolly, 1984; Green and Sussman, 1990). Surveys of faunal taxa are, therefore, imperative to identify key conservation species and to determine species distributions and factors affecting them (e.g. IUCN/UNEP/WWF, 1984; Mittermeier *et al.*, 1987; Nicoll and Langrand, 1989; Nicoll and Rathbun, 1990).

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Of the limited number of small mammal surveys conducted in Madagascar in recent years (Stephenson, 1987; Thompson *et al.*, 1987; Raxworthy and Rakotondraparany, 1988; Duckworth and Rakotondraparany, 1990), the greatest number of species (19) has been recorded in the mid-altitude rain forest of Réserve Spéciale (RS) d'Analamazaotra (Nicoll *et al.*, 1988). This reserve was originally created as a haven for the largest Malagasy primate, *Indri indri*. However, the close proximity of the reserve to the capital city, Antananarivo, easy access by train and the presence of habituated and easily seen lemurs, has resulted in this reserve becoming a popular visiting site for foreign tourists. An increase in tourism has potential economic benefits for local communities but can also have potentially negative environmental effects on protected areas (IUCN/UNEP, 1986). To date there has been no attempt to quantify the effects of tourism on any reserve in Madagascar.

This project represents the first long-term, year-round small mammal trapping survey to be carried out in Madagascar. The aims were:

(i) to determine small mammal species richness, distribution and abundance in RS Analamazaotra.

(ii) to determine the effects of human disturbance on species distributions.

Materials and methods

Study site

RS Analamazaotra (sometimes referred to as Périnet) is situated next to the village of Andasibe, 30 km east of Moramanga, in Toamasina (Tamatave) Province at 18°28′S, 48°28′E (Fig. 1). Andasibe is on the Antananarivo–Toamasina railway line which facilitates easy access from the capital city and the coast.

The reserve lies on the eastern escarpment between 930 and 1040 m altitude and covers an area of 810 ha. Annual rainfall averages 1700 mm, with peak precipitation in January and a reduction during the relatively dry period from June to October (Nicoll and Langrand, 1989). Average monthly temperatures range from 14°C in August to 24°C in January. The dominant habitat in Analamazaotra is mid-altitude tropical rain forest. The forest canopy is composed of *Weinmania*, *Tambourissa*, *Symphonia*, *Dalbergia*, *Ravensara* and *Vernonia* (Nicoll and Langrand, 1989). Woody vegetation is generally dense and epiphytic mosses, ferns and orchids are abundant.

Trapping sites

Traps were set at three sites within the reserve and one site outwith the reserve (Fig. 2). Each site was subject to different levels of human disturbance, thereby allowing a comparison of species composition and abundance within these habitats. Estimates of human activity were made by calculating the percentage of study days (i.e. days during which trapping was implemented) on which habitat disturbance or people were observed at each study site.

Site A was at the southern end of the reserve on the northern side of the river (Fig. 2). Trap lines were laid up the slope from river level to the top of the ridge and along the ridge top. Although a path ran along the river edge, people were never seen within the forest at this site and there was no evidence of recent human activity. Estimated level of human activity = 0%.

Figure 1. Map of Madagascar to show location of Réserve Spéciale (RS) d'Analamazaotra.

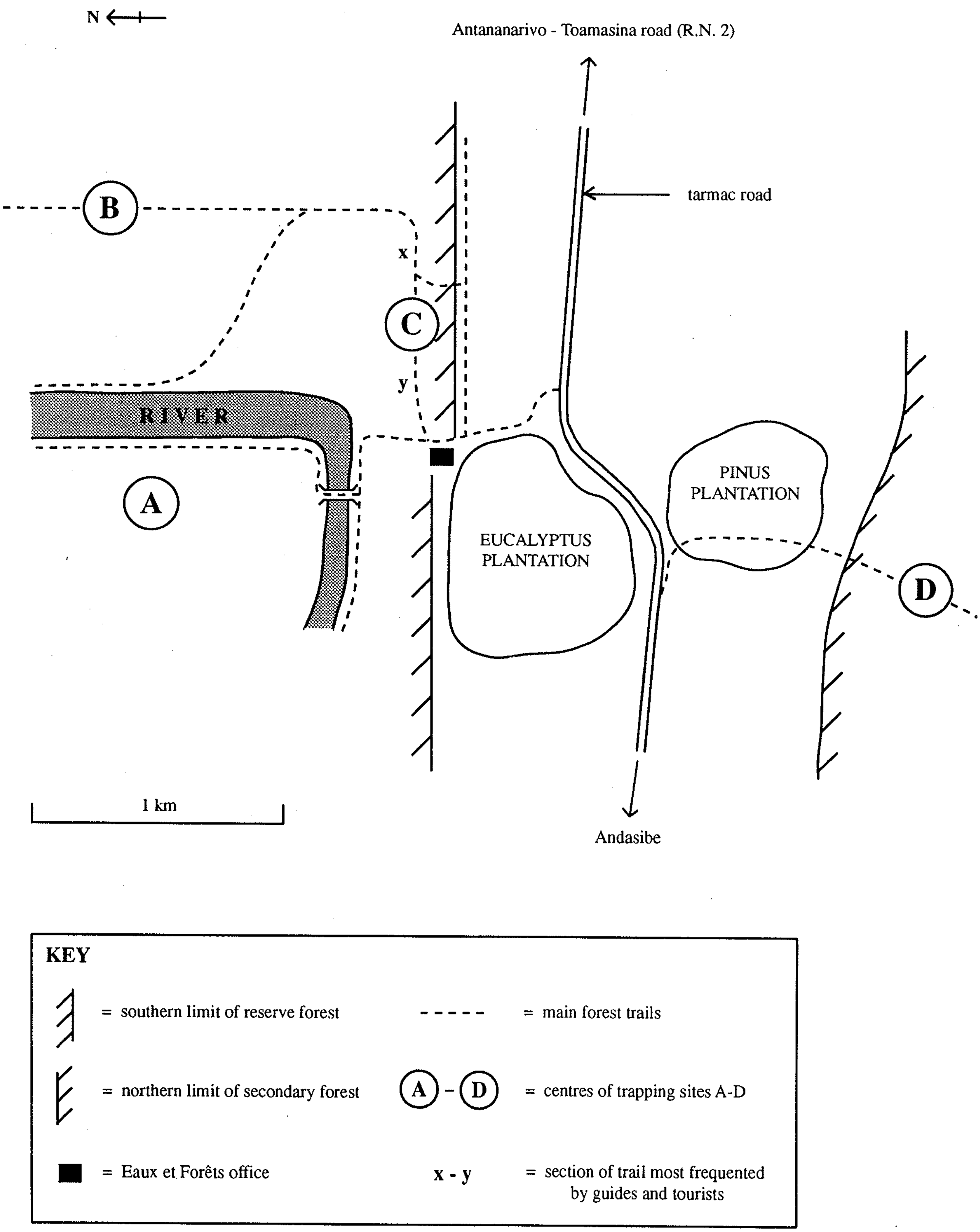

Figure 2. Diagrammatic map to illustrate positions of trapping sites in and around RS Analamazaotra.

Site B was situated in the south-east of the reserve. Trap lines were positioned either side of the main ridge-top trail that runs south-north. Trails led off at intervals from the main path and these were used occasionally by local people and visitors looking for *Indri*. Estimated level of human activity = 50%.

Site C was also in the south-east of the reserve. Trap lines were positioned either side of the main ridge-top trail that runs east-west (x–y in Fig. 2). This site was in the centre of the range of the most habituated troop of *Indri* and, therefore, attracted a large number of reserve visitors. Local guides searched the site for lemurs every day. This disturbed forest was traversed by numerous pathways and had the highest abundance of herbaceous vegetation of any site. Estimated level of human activity = 100%.

The situations of the sites meant that the relative level and frequency of human disturbance increased from Site A to Site C.

Site D was outwith the reserve. It was situated about 1 km south of the Andasibe road in secondary forest. The forest had a high density of woody and herbaceous stems and a large number of fallen logs. Local people occasionally felled trees for timber and firewood. This site was therefore a mixture of disturbed and undisturbed secondary forest. Estimated level of human activity = 5%. However, the purpose of the visits (logging rather than tourism) meant they had a greater impact on the habitat.

Trapping protocol

Small mammals were live-trapped an average of ten times at each trapping site during 23 visits to the reserve between April 1988 and May 1990. All sites were trapped during summer and winter, every second or third month, to preclude any significant seasonality effects on trap success.

Sherman traps and pitfall traps were employed. Large (9 × 7.5 × 23 cm) aluminium Sherman traps (H.B. Sherman Traps, Inc., Tallahassee, Florida, USA) were baited with dried fish or fresh shrimps. This bait was selected due to its proven effectiveness with tenrecs (Stephenson, 1987; Nicoll *et al.*, 1988). Each Sherman was placed in a transparent plastic cover to afford protection against the rain. Pitfall traps were plastic plant propagators (Stuart Plastics Ltd., Croydon, London, UK), 20 cm in depth and 12 cm in diameter. Each trap was set by digging a hole in the soil causing minimum disturbance to the habitat. The plastic propagator was then sunk into the hole below the leaf-litter/root mat layer. Holes in the base facilitated water drainage. When traps were not in use they were filled with twigs and dead leaves.

Traps were set in lines in positions known or suspected to maximize small mammal captures such as alongside fallen logs or tree roots, under low palms, in herbaceous cover and in deep leaf litter. Some Sherman traps were positioned along potential aerial walkways such as angled branches or fallen trees. Some traps were also positioned randomly in open ground to ensure most possible foraging habits were accounted for.

Traps were checked each morning between 0600–0900 h. Captured animals were weighed, sexed and examined for reproductive condition. Species identification was based on the keys by Genest and Petter (1974) and Petter (1975). Captured individuals were marked with unique ear clips (Twigg, 1975) before being released.

Results

Small mammal captures

Seven tenrec species and four rodent species were captured during 4521 Sherman trap nights and 811 pitfall trap nights (Table 1). Two additional species (the tenrec, *Hemicentetes semispinosus* and the endemic rodent, *Nesomys rufus*) were frequently observed foraging in the study area but were never trapped. Similarly, the large endemic rodent, *Brachytarsomys albicauda*, was also recorded in the reserve but was never trapped. This species was found nesting in tree holes.

Ten of the eleven species captured were caught in Sherman traps. Sherman traps placed off the ground on potential aerial walkways caught *Microgale talazaci* and *Eliurus minor*, though both species were also captured on the ground. Only two species (*Microgale cowani* and *Oryzorictes hova*) were caught by pitfall trapping. On average, Sherman traps caught 41.6 small mammals for every 1000 trap nights whereas, in the same number of trap nights, pitfall traps caught only 2.5 animals. Therefore, Sherman traps were 17 times more efficient than pitfalls. Shermans were 9 times more efficient at capturing tenrecs but it is noteworthy that only pitfall trapping yielded the fossorial tenrec, *O. hova*.

Comparison Between Trap Sites

The greatest number of small mammal species was found at Site A (Table 2) where all species recorded in this study were represented. Site A was the only trap locality for *Tenrec ecaudatus*, *Microgale taiva*, *O. hova* and *E. minor* and the only site where the two small *Microgale* species, *M. cowani* and *M. melanorrhachis*, were caught sympatrically.

Table 1. Small mammal captures at Réserve Spéciale d'Analamazaotra, April 1988 – May 1990. Trapping methods: S = Sherman trap, P = pitfall trap.

Species	Trapping method	No. captures	No. individuals
Tenrecidae:			
Tenrec ecaudatus	S	1	1
Setifer setosus	S	28	21
Microgale talazaci	S	62	59
Microgale cowani	S,P	6,1	7
Microgale melanorrhachis	S	2	2
Microgale taiva	S	1	1
Oryzorictes hova	P	1	1
Rodentia:			
Eliurus myoxinus	S	6	6
Eliurus minor	S	3	3
Gymnuromys roberti	S	3	3
Rattus rattus	S	77	62
Total		191	166

Table 2. Distribution and abundance of small mammal species at four trapping sites in and around Réserve Spéciale d'Analamazaotra. Data presented as numbers of individuals captured per 1000 Sherman trap nights to compensate for different numbers of trap nights at each site. Captures per 1000 pitfall trap nights presented in parentheses. Total number of individuals captured in each taxon are calculated from Sherman trap results only. See text for description of trap sites.

Species	Site			
	A	B	C	D
T. ecaudatus	0.5	–	–	–
S. setosus	5.1	4.0	5.3	4.2
M. talazaci	3.1	23.3	15.9	20.1
M. cowani	1.5 (1.6)	2.0	2.6	–
M. melanorrhachis	0.5	–	–	0.8
M. taiva	0.5	–	–	–
O. hova	(1.6)	–	–	–
E. myoxinus	2.5	1.0	–	–
E. minor	1.5	–	–	–
G. roberti	0.5	–	–	1.7
R. rattus	10.7	16.2	26.5	13.4
Total no. tenrecs	11.2	29.4	23.8	25.1
Total no. endemic rodents	4.6	1.0	0	1.7
Total no. small mammals	26.5	46.6	50.3	40.2

During the survey, two *H. semispinosus* were observed foraging on the river-side path at the bottom of Site A, so this species also probably occurs within the forest. Field observations on body size, morphology, diet and trap site of the eight sympatric tenrecs (Table 3) suggest ecological differences between all but the two smallest species. Of these, *M. cowani* was caught towards the top of the ridge in traps positioned under young palm trees and *M. melanorrhachis* was caught in herbaceous growth near the foot of the ridge, less than 15 m from the forest edge and some 50 m from the nearest *M. cowani* capture site. Therefore, these species may utilize different microhabitats.

Although species richness at Site A was high, the relative abundance of small mammals (as measured by the number of individuals trapped per 1000 trap nights) was lower than for any other site.

The lowest number of species was recorded from Site C (Table 2). The three most common tenrecs and *Rattus rattus* were the only small mammals trapped here. All of these species, except *M. talazaci*, were found in greater abundance than at any other site. *R. rattus* was more abundant than the other species combined.

Site B yielded the same species as Site C with the addition of *Eliurus myoxinus*. This rodent was probably the sub-species *E.m. tanala* (Carleton and Schmidt, 1990).

At Site D, one of the rarest tenrec species, *M. melanorrhachis*, and one of the least trapped endemic rodents, *Gymnuromys roberti*, were both recorded. Trap sites for these

Table 3. Ecological data on sympatric tenrec species at Site A, RS Analamazaotra.

Species	Abundance (% of total)	Body mass (g)	Niche	Diet
T. ecaudatus	4	>750	Terrestrial	Omnivore
S. setosus	42	200	Terrestrial	Omnivore
H. semispinosus	not trapped	110	Semifossorial	Earthworms
O. hova	4	40	Fossorial	Earthworms
M. talazaci	25	37	Scansorial	Invertebrates & vertebrates
M. taiva	4	26	Terrestrial	Invertebrates & vertebrates?
M. melanorrhachis	4	11.5	Terrestrial	Invertebrates
M. cowani	17	10.5	Terrestrial	Invertebrates

two species were in some of the least disturbed secondary forest and greater than 40 m from the main forest trail.

Across all trapping sites, *M. talazaci* was the dominant native species. *Setifer setosus* and *R. rattus* were also caught at each locality. *R. rattus* was notably most abundant at the most disturbed site (C) where endemic species richness was lowest. It was least abundant at the least disturbed site (A) where endemic species richness was highest. The results suggest that the number of endemic small mammal species, and in particular the number of tenrec species, is greatest in undisturbed forest, although the densities of most species are reduced in such habitat.

Discussion

Species richness and abundance

Trapping with Sherman and pitfall traps revealed the presence of eleven small mammal species. Pitfall traps were less effective but, as in previous studies in Madagascar (Stephenson, 1987; Nicoll *et al.*, 1988), they were the only traps to catch the fossorial tenrec, *O. hova*. In lowland forest in the north-east, Stephenson (1987) discovered a new species of *Microgale* through pitfall trapping (see Jenkins, 1988), emphasizing the importance of this technique to any small mammal survey in Madagascar.

In the present study, the tenrec *H. semispinosus* and the endemic rodents *N. rufus* and *B. albicauda* were sighted in the study area yet failed to be caught by either type of trap. Although the large body size and specialized diets of these species may account for their absence in the trap record, they illustrate the limitations of any small mammal survey in measuring true community structure. Nonetheless, in the undisturbed forest of Site A, eight tenrec species were recorded sympatrically. This represents an extremely diverse insectivore fauna when compared with other tropical habitats (see Fleming, 1975). The co-existence of so many species may be possible due to the wide differentiation of body size and food habits, and microhabitat segregation between the smaller species of *Microgale* (Stephenson, 1987, 1991).

A previous study of Analamazaotra (Nicoll *et al.*, 1988) also employed pitfall and Sherman traps. As with the present study, *M. talazaci* and *R. rattus* were the most frequently trapped small mammals (Nicoll *et al.*, 1988). This is typical of most tropical small mammal communities which contain one or two common species and many uncommon species (Fleming, 1975). Additional species recorded by Nicoll *et al.* (1988) are the tenrec *Microgale* (=*Leptogale*) *gracilis*, the introduced shrew, *Suncus murinus* and the house mouse, *Mus musculus*. *M. gracilis* was recorded on a trapping grid that incorporated part of Site D (M.E. Nicoll, personal communication). The absence of this species from the present study is either due to chance or a decline in population density.

Eisenberg and Gould (1970) visited Analamazaotra in 1967 and caught 18 *M. talazaci* in 539 trap nights. This represents 33.4 animals per 1000 trap nights, a higher capture frequency than obtained at any site in the present study. Eisenberg and Gould (1970) found *M. talazaci* most abundant where *R. rattus* was absent and Heim de Balsac (1972) questioned whether the apparent rarity of many *Microgale* species is a direct result of introduced rats and shrews. In the present study, endemic small mammal species richness was highest in undisturbed forest where *R. rattus* was least abundant. Other studies trapped endemic rodents less frequently in disturbed areas where *R. rattus* was abundant (Stephenson, 1987; Nicoll *et al.*, 1988). Whether the correlation between an increase in *R. rattus* abundance and a reduction in endemic species richness at disturbed sites is related to changes in habitat structure or the occurrence of interspecific competition is, as yet, unclear.

Species vulnerability to disturbance

The findings reported in the present study suggest that endemic species richness in and around Analamazaotra is reduced in areas exploited for tourism and logging. These conclusions are based on the assumption that animals not present in the trap record at disturbed sites were not present in the small mammal community. They also assume that absent species could have occurred at a site, or used to occur there, but disappeared due to disturbance. A variety of factors can affect trap success (see Fleming, 1975) and failure to trap an animal may be due to chance. Alternatively, a species may be absent from a site for reasons other than disturbance. For example, the site may be outwith the species' range. Only further trapping across a range of sites can confirm the absence of certain species from disturbed forest, and only the concurrent monitoring of changes in mammal communities with changes in disturbance levels will establish cause and effect. However, there is no reason to suppose that the locations of the disturbed sites in the present study were outwith any species' range so the assumptions were probably not violated. Furthermore, circumstantial evidence from previous studies (Eisenberg and Gould, 1970; Heim de Balsac, 1972; Stephenson, 1987, 1991) suggests that endemic species are often less numerous in disturbed areas inhabited by introduced rats. Also it may be more than coincidence that the endemic tenrec *M. gracilis*, previously recorded at Site D (Nicoll *et al.*, 1988), was absent from the trapping record after the site had been subjected to logging. Whatever the potential pitfalls in drawing conclusions from trapping data, 'failure to consider the absence of species in a sample undoubtedly results in the loss of information' (Green, 1971).

Almost any alteration to tropical forest ecosystems affects the abundance and composition of the mammal fauna (Delany and Happold, 1979). However, the effects of habitat change will vary between species (e.g. Beatley, 1976; Emmons, 1984; Pahl *et al.*, 1988). The first species to disappear might be those that are least abundant within the community or those that are specialists on particular vegetation types (Terborough and Winter, 1978; Emmons, 1984). Species that favour dense vegetation cover may even increase in abundance following disturbance (e.g. Jeffrey, 1977; Kasenene, 1984; Happold and Happold, 1987). Vulnerability to disturbance can also depend on factors such as body size (Burbidge and McKenzie, 1989; Bennett, 1990) and the position of a species on the r-K continuum of life history strategies (Laurance, 1991).

In the present study, there is evidence of interspecific variation in the effects of disturbance on small mammals in Malagasy rain forest. Although *G. roberti* was trapped most frequently in forest subjected to occasional logging, *Eliurus* species were not found in logged forest and were trapped more frequently in undisturbed primary forest. *S. setosus* was abundant in disturbed forest. Other tenrecs in the subfamily Tenrecinae, such as *H. semispinosus* and *T. ecaudatus*, have also been recorded in disturbed habitats (Gould and Eisenberg, 1966; Eisenberg and Gould, 1970; Ganzhorn *et al.*, 1990), so large tenrec species may be able to adapt to altered habitats. In the present study, some tenrecs of the subfamily Oryzorictinae (*M. talazaci* and *M. cowani*) were abundant in disturbed forests but other species, such as *M. taiva* and *O. hova*, were trapped only in undisturbed habitats. *M. melanorrhachis* was recorded in both primary and secondary forest but may be restricted to certain microhabitats.

In Madagascar, the loss of small mammal species from disturbed habitats may be associated with a decline in floral species richness (Stephenson, 1987; Ganzhorn *et al.*, 1990), which also affects lemur diversity (Hawkins *et al.*, 1990). In addition, most reptile species in Madagascar are dependent on primary rain forest habitats (Raxworthy, 1988). Therefore, the decline of small mammal species richness in disturbed forests may be an indicator of a more widespread loss of biodiversity within the ecosystem. If disturbance results in local species extinction, high species diversity may never be re-established (Jordan, 1986).

Recommendations

There is reason to suspect that tourism will continue to expand around RS Analamazaotra. The reserve is ideal for visitors because: (i) Andasibe is easily accessible by train from Antananarivo, and is a convenient stop–over on the route to Toamasina (a popular seaside tourist attraction); (ii) hotel accommodation at Andasibe railway station attracts overnight stops; (iii) Andasibe is within walking distance of the reserve; (iv) there are numerous local guides to show visitors *Indri* and other reserve wildlife.

The present study found endemic mammalian species richness lowest in areas most heavily visited by tourists. Therefore, a conflict of interests may be arising. With the development of ecological tourism proposed for other Malagasy nature reserves (Hawkins *et al.*, 1990; Rakotoarison *et al.*, 1993), it is vital that further research is conducted into potential environmental impacts. Specific recommendations can be made in light of the present study:

(i) A programme of survey and monitoring needs to be implemented at Analamazaotra to assess quantitatively the impact of visitors on faunal and floral communities. The present study suggests that small mammals may be ideal indicators of faunal and floral diversity. Small mammal trapping studies could be augmented by using standardized methodologies to measure the effects of human trampling on vegetation (Cole and Bayfield, 1993). Future work needs to monitor species populations and human activity concurrently to determine population changes over time and to establish cause and effect. The survey work needs to be replicated at a number of sites within the reserve.

(ii) There is urgent need for faunal and floral surveys outwith the reserve to determine the effects of different levels of logging on rain forest habitats.

(iii) Until more data are obtained, trends already detected within small mammal distributions suggest that the cutting of new paths or clearings should be avoided since this may facilitate access to exotic small mammal species. Inner core areas of the reserve should be left undisturbed wherever possible to safeguard microhabitats favoured by rarer endemic species.

The Réserve Spéciale d'Analamazaotra attracts large numbers of visitors and is, therefore, an integral part of the tourist industry in Madagascar. The growth of this tourist industry should have beneficial consequences for local and national economic development. However, there is urgent need for a better understanding of the potential environmental impacts of human disturbance on protected areas. If tourism in Analamazaotra continues to expand unchecked, protected habitats may be altered, jeopardising the conservation of endemic species diversity.

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