ECOTROPICA 2: 109–120, 1996

SPECIES RICHNESS OF FOREST-DWELLING BIRDS, RODENTS AND INSECTIVORES IN A PLANTED FOREST OF NATIVE TREES: A TEST CASE FROM THE ANKARATRA, MADAGASCAR

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Résumé. Des résultats sont présentés sur une étude menée sur les oiseaux, les rongeurs et les mammifères insectivores de la Forêt de Nosiarivo (2000 m) dans le Massif de l'Ankaratra sur le Haut Plateau Central de Madagascar. Cette forêt a été replantée avec une espèce d'arbre autochtone à la fin du XVIIIème siècle et est actuellement largement isolée de toute autre forêt naturelle en étant entourée par des zones herbeuses anthropiques et des plantations exotiques de pins. Des données sur la richesse en espèces de ces trois groupes de vertébrés sont présentées. L'avifaune et la faune micro-mammallienne de l'Ankaratra sont comparées avec celles de zones de forêts pluviales des montagnes de l'est de Madagascar à des altitudes similaires pour vérifier si les forêts replantées de l'Ankaratra présentent une richesse spécifique comparable. Nous constatons qu'en général il n'existe pas de changement net en terme de richesse spécifique tant pour la faune micro-mammallienne que pour la faune avienne.

Abstract. Results are presented of a bird, rodent, and insectivore survey conducted in the Nosiarivo Forest (2000 m) on the Ankaratra Massif, Central High Plateau, Madagascar. This forest was replanted with one species of native tree at the end of the 18th-century, and is now isolated from other natural forests and is surrounded by anthropogenic grassland and exotic pine plantations. Data are presented on the species richness of these three vertebrate groups. The avian and small mammal faunas of Ankaratra are also compared with extensive areas of montane eastern humid forest at similar elevation elsewhere on Madagascar, to assess if the replanted Ankaratra forest has a comparable level of species richness. The general conclusion is that there is no clear change in species richness for small mammals and birds. *Accepted 25 November 1996.*

INTRODUCTION

One important issue in modern conservation biology is the ability of animals to recolonize disturbed habitats. The majority of research to date on this topic has focused on the effects of fragmentation and logging of natural forests. Few studies, particularly in the tropics, have been able to address the question of what types of animals are able to survive in, recolonize or utilize native tree plantations (e.g., Wilson & Johns 1982, Carlson 1986, Ganzhorn 1987). These factors are pertinent in many areas of the world where there has been extensive alteration of native habitat and managers of prorected areas contemplate reintroduction of animals through plantations of native trees in an attempt to reconstruct portions of the former habitat.

In this paper we review data on the rodent, insectivore, and bird faunas in a high mountain forest on the Ankaratra Massif that was replanted with native Malagasy trees at the end of the 18th-century. This nearly monospecific forest is now largely isolated from natural forests and is surrounded by anthropogenic grassland and pine plantations. Until at least the early 1930s this plantation of native trees was connected by corridors of forest to a larger area of natural forest. We also compare the rodent, insectivore and bird faunas of Ankaratra with extensive areas of montane eastern humid forest elsewhere on Madagascar, to assess if the replanted Ankaratra forest has a reduced species richness.

SITE AND METHODS

The Central High Plateau is a vast region extending nearly the complete length of Madagascar and, depending on how it is defined, representing around

40% of the island. Only a few sites on the high plateau retain any vestige of their former forest cover (e.g., Ambohitantely, Anjozorobe, and Ankaratra), and little is known about the fauna that has disappeared from this region over the past few millennia, let alone during the past century. For example, excavations of Holocene sites on the Central High Plateau show that the species richness of prosimians was probably close to double that of the extant lemur fauna of the region (MacPhee *et al.* 1985, Godfrey *et al.* 1997).

The Ankaratra Massif is volcanic in origin and dates from the Quaternary, and the summit of Tsiafajavona at 2643 m is the third highest peak on the island. The Manjakatompo Forestry Station, established in 1922, is located on the eastern slopes of

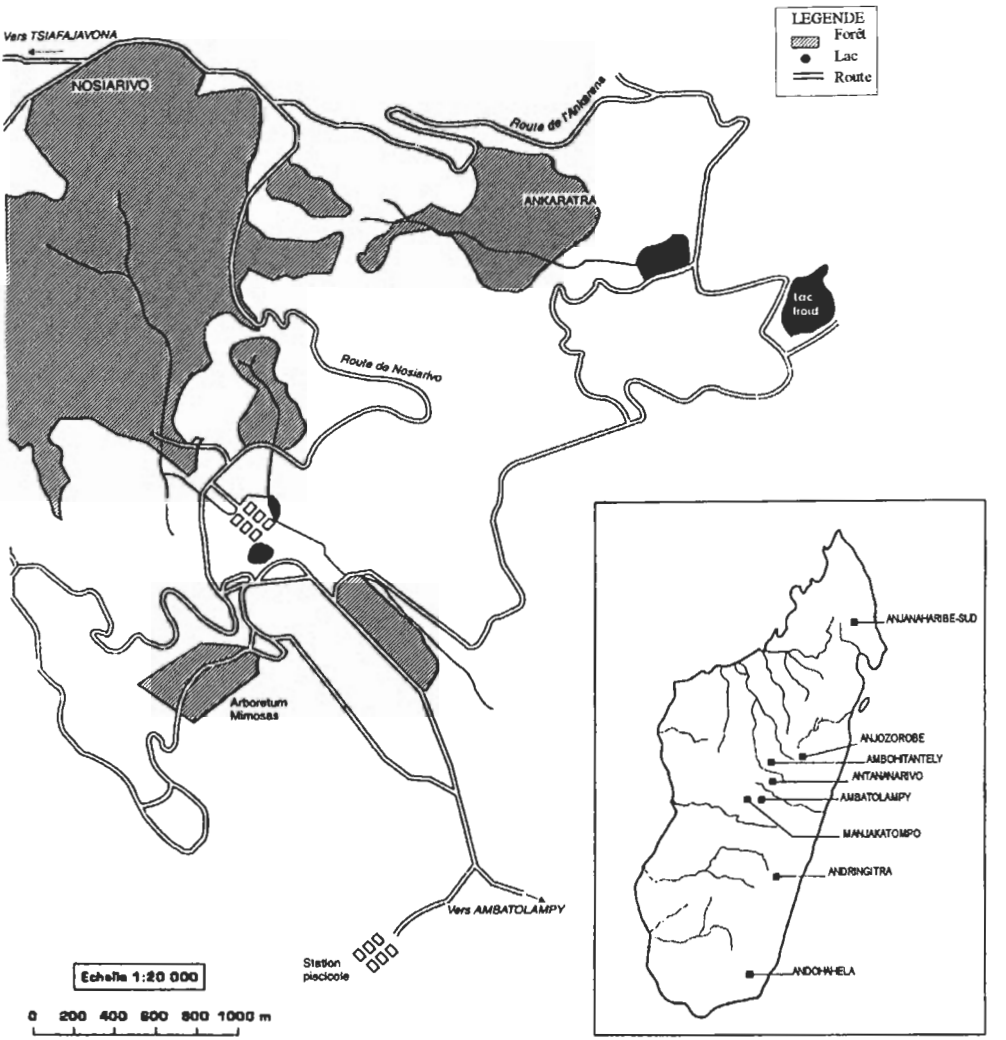

FIG. 1. Map showing the general plan of the Manjakatompo Forestry Station, including the Nosiarivo Forest (adapted from Anonymous 1995). Other localities noted in the paper are indicated on the inset map of Madagascar.

the massif (Fig. 1). The station covers an area of about 8300 ha, 2300 ha of which have been replanted with exotic trees and 650 ha are covered with natural forest (Nicoll & Langrand 1989), although a large portion of the latter is secondary and mixed with invasive exotic trees.

Between 10 and 17 February 1996 we conducted an inventory of the birds and small mammals inhabiting the Nosiarivo Forest, 2 km (by air) NNW of the Manjakatompo Forestry Station, 19°20.7'S, 47°18.2'E, at approximately 2000 m. The botanical inventory was done the following week. The annual precipitation in the vicinity of the station is about 2000 mm per year (Nicoll & Langrand 1989) and at slightly higher elevation in the Nosiarivo Forest approximately 2300 mm (Mussard 1991).

Small mammals were studied using two different trapping methods: live traps and pitfall buckets. Two trap lines, each composed of 75 traps (15 Nationals and 60 Shermans), were placed in the forest for a total of five trap-nights each. Bait consisted of peanut butter mixed with ground corn flour. Traps were checked once at dawn and again in the late afternoon, during the latter visit fresh bait was placed in each trap. A trap in use for a 24-hour period is considered one "trap-night".

Pitfall trap lines were 100 m long and consisted of 11 buckets (275 mm deep, 290 mm top internal diameter, 220 mm bottom internal diameter), each 10 m apart and sunk into the ground to rim level. A continuous horizontal dark brown plastic drift fence traversed the complete line and bisected the rim of each bucket. Approximately 5 cm of the lower edge of the plastic was buried in the ground to prevent small animals from passing under the plastic. A pitfall bucket in place for a 24-hour period is referred to as a "bucket-day".

Point counts, general bird observations, and bird netting were conducted along trails within the Nosiarivo Forest. The original intent with the point counts was to obtain measures of relative bird density. However, since this technique relies extensively on vocalizing birds and the survey was conducted after the breeding season, the data obtained were insufficient to draw any conclusions about relative density or compare this measurement to other sites on the island censused during the breeding season. All of the various bird survey techniques were used to compile the Nosiarivo Forest species list.

DESCRIPTION OF THE LOCAL BOTANICAL COMMUNITY

The vestiges of forest on the steep, east-facing slopes of the Ankaratra Massif between about 1700 and 2000 m are dominated by relatively few species of plants, most of which are distributed in the vestige forests at similar elevations across the Central High Plateau. (The inclusion of the botanical communities occurring on the high mountains of this region (e.g., Ankaratra and Andringitra) with the Central High Plateau flora is in part an over-simplification, since each of these mountains has distinctive floristic characteristics.) Trees form a dense wind-swept canopy of on average 8–12 m in height (occasionally up to 16 m), under which understory development is limited to a sparse shrub layer 1–2 m tall, arching bamboo, and ground cover suffrutescent herbs. Dense epiphytic growth of mosses, lichens and orchids envelop trunks and branches.

A portion of the Nosiarivo Forest is composed of what appears to be even-aged, nearly monospecific stands of *Weinmannia bojeriana* (Cunoniaceae), particularly in an area around the ancient royal Tankaratra tombs; the trees were purportedly planted by local people several hundred years ago (see below). This tree has wind-dispersed seeds, intolerant of germination or recruitment in shaded areas. Seedlings of *Weinmannia* are common in open areas, and along the forest edge. If planted in a high density, as appears to be the case, the resulting dense shade may have deterred recruitment of many species, and apparently continues to do so. Two other striking features of this forest in comparison to other Malagasy humid forests at similar altitude are the nearly complete lack of understory plants, and the rarity of vines and lianas; the former is presumably a result of the dense canopy layer and, more importantly, the forest is seasonally used as a cattle pasture.

Rand (1936: 161, 163) described the vegetation of Ankaratra on the basis of his 1929 visit to the area, "The slopes of the greater part of the mountain were grass-covered and supported a growth of heath and bracken. Little grassy swamps were common at the base of the mountain. On the slopes, just above Monjakatompo [= Manjakatompo], was an area of humid forest, an isolated remnant of the forest that once covered the greater part of the central portion of Madagascar. This wooded area was of the humid forest type, with large trees hung with lianas and mosses. Tree-ferns were common and in some places there

was considerable undergrowth. It was cool here, with mist lying over the lower ground in the morning, the hills rising through it like islands through a snow-covered, frozen sea..." The extensive areas of grassland on the mountain are not natural vegetation formations, but are the result of human-set fires (Perrier de la Bâthie 1927, Nicoll & Langrand 1989, Raxworthy & Nussbaum 1996).

HISTORICAL INFORMATION ON THE REGION AND SITE

On the basis of oral history, which was subsequently written down by Mussard (1991), towards the end of the 18th-century the Tankaratra King and his family organized the massive planting of native trees to reforest areas of the mountain, including Nosiarivo (Mussard, pers. comm.). The Nosiarivo Forest has great value to the modern descendants of the Ankaratra living in the region and is the subject of numerous taboos. To a large extent this forest is protected under local tribal regulations and the principal human pressure is the seasonal presence of cattle, which severely damage the understory.

Between April 1929 and May 1931 the Mission Zoologique Franco-Anglo-Américaine (MZFAA) conducted a survey of Madagascar, focusing principally on birds, although mammal specimens were also collected, and members of the expedition visited numerous areas of the island (Rand 1932, 1935, 1936). A field party, based at the Manjakatompo Forestry Station, worked the Ankaratra Massif between 11 May to 2 June 1929. Specimens obtained during the mission were divided between the Muséum National d'Histoire Naturelle (MNHN), Paris; the British Museum (Natural History) (BM(NH)), London [now called The Natural History Museum]; and the American Museum of Natural History (AMNH), New York.

Rand (1936, p. 161) noted that the MZFAA Ankaratra collections were from an altitude of 1800 m, which is higher than the Manjakatompo Forestry Station (1720 m). Elevational records mentioned on various specimen tags or in Richard Archbold's journal (archived in the AMNH Mammalogy Department) indicate that the team worked the slopes of Ankaratra at least from 1650 m to 1950 m. Thus, the zone of the MZFAA survey would have included the corridor between the Manjakatompo Forestry Station and the Nosiarivo Forest, and presumably the lower portion of the latter forest. A more recent collection of small mammals of the massif was made by M. Petter in February 1972, and the material is housed in the MNHN.

THE PREVIOUSLY KNOWN RODENT, INSECTIVORE AND BIRD FAUNAS OF THE ANKARATRA MASSIF

Species of the endemic rodent Subfamily Nesomyinae previously reported from Ankaratra include *Brachyuromys betsileoensis* (Carleton & Schmidt 1990) and the recently described genus and species *Monticolomys koopmani* (Carleton & Goodman 1996). The former species is widespread in the eastern portion of Madagascar and tends to occur in grassy meadows and marshland and the latter is only known from the upper slopes of the Ankaratra and Andringitra Massifs. No species of *Eliurus*, a widespread Nesomyinae genus, was previously reported from the massif. On the basis of Archbold's field notes, introduced *Rattus rattus* was well-established in the area by 1929.

On Madagascar there is a large radiation of insectivores belonging to the Family Tenrecidae. Several species have been previously reported or collected

TABLE 1. Small mammal trap success with live traps in the Nosiarivo Forest, Ankaratra.

Species	Total captured	Total % trap success (n = 750)
Rattus rattus	35	4.7%
Eliurus minor	1	0.1%
Monticolomys koopmani	1	0.1%
Microgale gracilis	1	0.1%
Total animals	38	5.1%

from the Ankaratra Massif: *Limnogale mergulus*, *Microgale dobsoni*, *M. talazaci*, *M. cowani*, *Setifer setosus*, and the introduced Soricidae *Suncus murinus* (Malzy 1965, MacPhee 1987, Nicoll & Langrand 1989, specimens in AMNH, BM(NH), MNHN).

The avifauna of Madagascar is composed of relatively few breeding species, of which about 50 % are endemic (Langrand 1995). The MZFAA reported 18 species in the general vicinity of the Manjakatompo Forestry Station (Delacour 1930, 1932, Rand 1936). Further, bird lists for the site are presented in Nicoll & Langrand (1989) and Anonymous (1995).

RESULTS

Thirty-eight individual small mammals, of four species, were captured in the live traps during an accrued total of 750 trap-nights (5.1 % trap success; Table 1). *Rattus* made up 35 of the 38 mammals, and single individuals of *Eliurus minor*, *Monticolomys koopmani*, and *Microgale gracilis* were also captured. In the pitfall traps, a total of 20 individuals of four insectivore species were captured in 176 bucket-days (Table 2). *Microgale cowani* was the most common animal in the pitfalls, making up 50% of those captured, and five *M. longicaudata*, three *M. thomasi*, and two *Setifer setosus* were also obtained.

Thirty-seven resident species of birds were observed in and around the Nosiarivo Forest, including 23 forest-dwelling species (Table 3). No species of bird was captured in the mist nets that was not seen or heard during general observations. Forest-dwelling species previously recorded from Ankaratra Mountain and not noted during our visit include *Aviceda madagascariensis*, *Accipiter madagascariensis*, *Canirallus kioloides*, *Cuculus rochii*, *Coracina cinerea*, *Dromaeocercus seebohmi*, *Newtonia amphichroa*, and *Foudia omissa* (Delacour 1930, Rand 1936, Nicoll & Langrand 1989, O. Langrand, pers. comm.). *D. seebohmi* was apparently common in open grassland at Ankaratra in 1929, and it also occurs in marshes in other humid forest areas (Wilmé & Langrand 1990). Species not previously recorded from the site include *Dryolimnas cuvieri* and *Falco eleonorae*, the latter being a Palaeartic breeding species that visits Madagascar during the northern winter.

ANALYSIS AND DISCUSSION

A critical issue associated with the extant native birds and small mammals of the Nosiarivo Forest is if the species richness of these groups is comparable to other sites of natural forest at similar elevations? The best comparison that could be made to examine this question is with areas of unfragmented forest on the Central High Plateau, a region that had extensive areas of forest a few hundred years ago. However, few remaining forested sites exist in this vast area of Madagascar and the best candidate for the comparison would be the forest of Anjozorobe, a forest block still attached to the eastern humid forest. However, the highest point in the Anjozorobe Forest is around 1600 m and the bird and small mammal faunas are not well-known. Many groups of birds and species of small mammals typical of eastern humid forest, the largest area of remaining wet forest on the island, are absent from the Central High Plateau (Stephenson *et al.* 1994, Langrand & Wilmé 1997), including Ankaratra, and it is unknown if this represents their natural distribution or the effects of habitat fragmentation and subsequent local extinction. Thus, herein we compare the bird and mammal faunas of the Nosiarivo Forest to two sites, Andohahela and Anjanaharibe-Sud, that are part of the main eastern humid forest block.

TABLE 2. Small mammal trap success with pit-fall buckets in the Nosiarivo Forest, Ankaratra.

Species	Total captured	Total % trap success (n = 176)
Microgale thomasi	3	1.7%
Microgale cowani	10	5.7%
Microgale longicaudata	5	2.8%
Setifer setosus	2	1.1%
Total animals	20	11.4%

TABLE 3. Comparison of the resident birds in three high mountain areas of Madagascar. See Table 4 for more information on each forest block. Forest-dwelling species are preceded by an asterisk (*)

Species	Ankaratra [1] 2000 m	Andohahela [2] 1875 m	Anjanaharibe-Sud [3] 1950 m
**Aviceda madagascariensis*	(+)		
**Polyboroides radiatus*	+		
**Accipiter madagascariensis*	+		
**Accipiter francesii*	+		
**Accipiter henstii*			+
**Buteo brachypterus*	+	+	+
Falco newtoni	+		
Falco peregrinus	+		
Dryolimnas cuvieri	+		
**Canirallus kioloides*	(+)	+	
**Sarothrura insularis*	+		
**Streptopelia picturata*	+	+	+
**Alectroenas madagascariensis*	+	+	
**Coracopsis vasa*		+	
**Coracopsis nigra*		+	+
**Cuculus rochii*	+	+	+
**Coua reynaudii*		+	+
**Coua caerulea*		+	+
Tyto alba	+		
**Otus rutilus*	+		
Asio capensis	+		
Caprimulgus madagascariensis	+		
Zoonavena grandidieri		+	+
Apus melba		+	+
Apus barbatus	+	+	+
**Atelornis crossleyi*		+	+
**Leptosomus discolor*	+	+	
**Philepitta castanea*		+	
**Neodrepanis hypoxantha*		+	+
Phedina borbonica	+	+	+
Motacilla flaviventris	+	+	
**Coracina cinerea*	+	+	
**Phyllastrephus cinereiceps*		+	
**Hypsipetes madagascariensis*	+	+	+
**Copsychus albospecularis*	+		
Saxicola torquata	+	+	+
**Pseudocossyphus sharpei*	+	+	+
**Nesillas typica*	+	+	+
**Dromaeocercus brunneus*		+	+
Dromaeocercus seebohmi	(+)		
**Cryptosylvicola randrianasoloi*		+	+
**Newtonia amphichroa*		+	+
**Newtonia brunneicauda*	+	+	+
**Terpsiphone mutata*	+		

Species	Ankaratra [1] 2000 m	Andohahela [2] 1875 m	Anjanaharibe-Sud [3] 1950 m
**Neomixis viridis*		+	
**Oxylabes madagascariensis*		+	
**Crossleyia xanthophrys*		+	
**Nectarinia souimanga*	+	+	+
**Nectarinia notata*	+		
**Zosterops maderaspatana*	+	+	+
**Xenopirostris polleni*		+	
**Tylas eduardi*		+	
**Dicrurus forficatus*		+	
Corvus albus	+		
**Ploceus nelicourvi*		+	
**Foudia omissa*	+	+	+
Foudia madagascariensis	+	+	
Lonchura nana	+		
Total number of species	37	39	24
Total number of forest-dwelling species	23	32	19

[1] Records presented in brackets are based on the 1929 visit to the area by the MZFAA and were not recorded during the 1996 inventory of the Nosiarivo Forest or reported by Nicoll & Langrand (1989).
[2] Based on Goodman et al. (in press).
[3] Based on Hawkins et al. (in press).

The Réserve Spéciale d'Anjanaharibe-Sud in northeastern Madagascar is an area of approximately 32,100 ha of humid forest within the elevational range 500–2064 m, and the Réserve Naturelle Intégrale d'Andohahela (parcel 1) in southeastern Madagascar comprises about 63,100 ha of humid forest within the elevational range 350–1972 m (Nicoll & Langrand 1989). Both of these sites have been surveyed over the past few years using identical techniques to our inventory of the Nosiarivo Forest (Tables 3 and 4). The collections of small mammals from the RNI d'Andohahela are still under study, and the number of species recorded at the 1875 m site is preliminary.

Mammals. Eleven species of small mammals (all insectivores) were captured in the pit-fall buckets at 1875 m at Andohahela and the capture rate was rather high (57.8%). This is compared to both Nosiarivo and Anjanaharibe-Sud where four species of small mammals (all insectivores) were captured in a comparable number of bucket-days and the capture rate was 11.4% and 10.6% (respectively). The 1950 m zone of Anjanaharibe-Sud is part of a large tract of primary forest and several kilometers from areas with signs of human disturbance.

For live traps, eight species of small mammals (four insectivores and four rodents) were captured in Andohahela and the trap success rate was 3.7%. The number of small mammal species captured at Nosiarivo was four (three rodents and one insectivore) and at Anjanaharibe-Sud also four (all rodents), and trap success was 5.1% and 2.4% (respectively). At all three forests introduced *Rattus* were captured and when this species is removed from the live captures the trapping success for rodents at each site was: Andohahela – 2.5% (three native species), Nosiarivo – 0.4% (two native species), and Anjanaharibe-Sud – 2.2 % (three native species). *Rattus* was extremely common in the Nosiarivo Forest and they were found in a variety of microhabitats. At other humid forest sites on the island, there is evidence of broad overlap in the diets of *Rattus* and endemic rodents (Goodman & Sterling 1996). Thus, the low relative density of small mammals in the Nosiarivo Forest, as measured by trap success, may be the result of *Rattus* displacing native rodents through some form of competition or perhaps direct predation.

The insectivore community of Nosiarivo is comparable in species richness and density to the intact forest of Anjanaharibe-Sud and both are

TABLE 4. Comparison of density and species richness of small mammal communities in three high mountain zones of Madagascar.

	Ankaratra	Andohahela	Anjanaharibe-Sud
altitude	2000 m	1875 m	1950 m
forest type	upper montane/ sclerophyllous	upper montane/ sclerophyllous	upper montane/ sclerophyllous
estimated natural forest cover[1]	650 ha	63,100 ha	32,100 ha
total days rain/total days	6/7	6/7	3/6
total rain during survey	27 mm	30 mm	25 mm
minimum temperature[2] °C	5.6-12.8 10.2 ± 3.0	6.1-12.2 9.2 ± 2.3	8.5-13 11.8 ± 1.4
maximum temperature °C	15.6-21.1 18.8 ± 2.4	11.1-25.6 18.8 ± 6.0	17.0-21.0 18.5 ± 1.4
PITFALLS[3]			
number pitfall-days	176	187	198
number species small mammals captured	4	~11	4
number small mammals captured	20	108	21
TRAPS			
number trap-nights	750	815	500
number species small mammals captured	4	~8	4
trap success	5.1%	3.7%	2.4%
number of small mammals captured at each site	38	25	12
percent *Rattus*	92 %	20 %	8 %
OVERALL			
number of species captured at each site	8	~15	8
number of native species captured at each site	7	~14	7

[1] Figure based on Nicoll & Langrand (1989)
[2] Temperature data presented as minimum-maximum, mean ± standard deviation.
[3] Records from Andohahela based on Goodman & Jenkins (in prep.) and Anjanaharibe-Sud on Goodman & Jenkins (in press).
[4] Records from Andohahela based on Goodman & Carleton (in prep.) and Anjanaharibe-Sud on Goodman & Carleton (in press).

depauperate in comparison to Andohahela. Why Andohahela and Anjanaharibe-Sud should have such vast differences is not the subject of this paper. What we would like to emphasize is that there is no clear difference in species richness or density between Anjanaharibe-Sud and Nosiarivo. Thus, there is no demonstrable negative effect of fragmentation and isolation in the Nosiarivo Forest for the insectivore community. Insectivores are apparently resilient to habitat fragmentation and degradation, and have been able to colonize the Nosiarivo Forest or sustain expected levels of species richness.

The total species richness of native rodents at the three high mountain sites varied from three at Andohahela and Anjanaharibe-Sud to two at Nosiarivo. The most important difference between these sites was in the relative density of native rodents, as measured by trap success, which was distinctly lower at Nosiarivo than the other two sites. We assume that this is related to the fragmented nature of the Nosiarivo Forest, its close proximity to human settlements that *Rattus* have presumably colonized the forest from, and competitive exclusion by *Rattus* of the native rodent fauna. However, forest-dwelling *Rattus*

on Madagascar are known to have substantial season fluctuations in population size (Rakotondravony 1992). *Eliurus majori* is a typical rodent of montane forest and is missing from Nosiarivo. It is known from Andohahela, Anjanaharibe-Sud and the Central High Plateau site of Anjozorobe (specimens in the Département de Biologie Animale, Université d'Antananarivo).

Birds. Thirty-seven bird species have been recorded in the general region of the Nosiarivo Forest, of which 23 are forest-dwelling species; 39 at 1875 m at Andohahela, of which 32 are forest-dwelling; and 24 at 1950 m at Anjanaharibe-Sud, of which 19 are forest-dwelling (Table 3). Thus, in comparison to two other high mountain sites on Madagascar there is no clear indication of a reduction in general species richness in the Nosiarivo Forest.

Two endemic families (Mesitornithidae and Brachypteraciidae) and two endemic subfamilies (Couinae and Philepittinae) known from other humid forest sites have not been recorded at Ankaratra. *Atelornis crossleyi* (Brachypteraciidae), *Coua reynaudii*, *C. caerulea* (Couinae), and *Neodrepanis hypoxantha* (Philepittinae) occur in the high elevation zones of both Andohahela and Anjanaharibe-Sud, and *Philepitta castanea* (Philepittinae) is only known from this zone in Andohahela – these species are not necessarily restricted to montane forest at these sites. These five species have not been recorded in the isolated forests of Ambohitantely (Langrand 1995) or Montagne d'Ambre (Nicoll & Langrand 1989). Of the 23 forest-dwelling bird species recorded at Ankaratra, two belong to endemic genera (*Newtonia* and *Pseudocossyphus*) and ten others are endemic species to the island.

In terms of ecological guilds (Wilmé 1996), the high mountain Ankaratra avifauna holds fewer insectivorous species (35%) when compared to the montane avifaunas in Andohahela (53%), Anjanaharibe-Sud (42%), Ambohitantely (37%), and Montagne d'Ambre (43%). Predatory bird species are more common at Ankaratra and represent 27% of the avifauna, as compared to 9% at Andohahela, 16% at Anjanaharibe-Sud, 27% at Ambohitantely, and 18% at Montagne d'Ambre. The basis for these differences is unknown, but they might be related to a combination of factors associated with isolation and vegetational structure.

Of the forest-dwelling species listed in Table 3, seven of the eight species that are restricted to montane zones of eastern humid forest are absent from Ankaratra (*Atelornis crossleyi*, *Neodrepanis hypoxantha*, *Phyllastrephus cinereiceps*, *Dromaeocercus brunneus*, *Cryptosylvicola randrianasoloi*, *Newtonia amphichroa*, and *Crossleyia xanthophrys*). The montane species occurring at all three of these sites is *Pseudocossyphus sharpei*. Thus, it would appear that Ankaratra is depauperate in bird species generally restricted to montane forests and the species occurring at this site have broad elevational distributions. The response to the question if this pattern reflects the natural distribution of these montane taxa or is the result of the isolation and fragmentation of Ankaratra will have to await ornithological exploration of the Anjozorobe Forest.

Flora. In one sense, the large monospecific stand of native *Weinmannia* in the Nosiarivo Forest becomes a biological desert for granivorous and frugivorous vertebrates, in much the same way as a plantation of pine trees in a tropical zone. Few seeds of either understory or canopy bird-dispersed taxa reach the interior of the densely planted stand, the weedy edge bird-dispersed plant species are *Solanum mauritianum* (Solanaceae, native to South America) and *Maesa lanceolata* (Myrsinaceae, common in montane Africa and questionably native to Madagascar). Both of these plants are incapable of recruitment in dense shade, dominating feeding areas just outside of the *Weinmannia* stand. *Schismatoclada* sp. (Rubiaceae), a slender shrub to treelet, was found along the forest edge and in canopy openings. Other common native tree species included *Alberta* sp. (Rubiaceae) and *Dicoryphe viticoides* (Hamamelidaceae). Two dominant understory plants were *Croton* sp. (Euphorbiaceae) and *Plectranthus* sp., both of which are abiotically dispersed.

Among canopy trees, disseminules clearly adapted for dispersal by birds and lemurs (all locally extirpated) consist of fleshy berries, shiny seeds that mimic fleshy berries, and arillate seeds. Fleshy red to purple to black berries are exhibited by *Ilex mitis* (Aquifoliaceae), *Cassinopsis madagascariensis* (Icacinaceae), *Polyscias* spp. (Araliaceae), and *Tarenna* sp. (Rubiaceae). The bright yellow-orange dehiscent capsule of *Evodia madagascariensis* (Rutaceae) contrasts with the shiny blue-black seeds revealed inside. Dehiscent fruits of *Pittosporum humbertii* and *P. pachyphyllum* (Pittosporaceae), as well as *Tambourissa parvifolia* (Monimiaceae), expose orange-red "arillate" seeds. Understory shrubs with fleshy berries include

Oncostemum (Myrsinaceae), *Pauridiantha paucinervis* (Rubiaceae), and *Psychotria* sp. (Rubiaceae). Several tree species possess larger fleshy berries potentially taken by birds with larger gapes (e.g., *Alectroenas*), including *Garcinia* sp. (Clusiaceae), *Symphonia* sp. (Clusiaceae), and *Syzygium emirnense* (Myrtaceae).

In general, the dense, even-aged monoculture of an abiotically dispersed species would seem to preclude, or at least delay (until natural disturbances provide suitable sites for recruitment, which today may be colonized by weedy exotics), the establishment of both biotically and abiotically dispersed understory plant species, as well as biotically dispersed canopy tree species. However, whatever food plants for rodents, insectivores, and birds remain within the forest they are apparently sufficient to maintain a species richness of these three groups which is comparable to the intact humid forest site of Anjanaharibe-Sud.

GENERAL CONCLUSIONS

Many of the small mammal species of the Nosiarivo Forest were trapped in disturbed areas at the edge of the planted forest and it is clear that the rodents and insectivores currently living in the Nosiarivo Forest are not particularly sensitive to disturbance. Three species, of which single individuals were captured, are particularly noteworthy. *Monticolomys koopmani*, currently only known from higher elevations on Ankaratra and Andringitra, was captured in an open area of heavily disturbed *Weinmannia* forest. *Microgale gracilis*, a rarely captured shrew-tenrec that is presumed to be semi-fossorial, was taken at the ecotone between heavily disturbed *Weinmannia* forest and a recently burned pine plantation. *M. dobsoni* was trapped in a pine plantation just below the Nosiarivo Forest. Further, on the basis of our field work and information on the museum tickets of specimens collected by the MZFAA and Petter at Ankaratra, several species of shrew-tenrecs survive in heavily disturbed habitats (e.g., *Microgale talazaci*, *M. dobsoni*, and *M. cowani*). Although prosimians are known from other Central High Plateau forests (Nicoll & Langrand 1989), we did not find this group on the Ankaratra Massif. Lemurs were not recorded on the mountain in 1929 during the MZFAA (Delacour 1932). A few humid forest lemur species have been recorded at elevations above 1800 m at other sites on the island (Albignac 1970, Schmid & Smolker, in press) and in other isolated Central High Plateau forests (e.g., Ambohitantely; Stephenson *et al.* 1994).

In summary, several hundred years have passed since the planting of the *Weinmannia* forest of Nosiarivo, and in general expected levels of species richness for rodents, insectivores, and birds in this forest are more-or-less similar to those observed at two sites with similar habitat in the eastern humid forest. These groups seem resilient to the effects of habitat degradation and isolation. The colonization of this forest by *Rattus* has apparently had an impact on the native rodents of the forest. On the basis of a comparison with large tracts of forest at similar elevation, the species richness of rodents, insectivores and rodents in the Nosiarivo Forest does not appear to be depauperate.

ACKOWLEDGEMENTS

Our research in Madagascar has been authorized by the Direction des Eaux et Forêts and the Commission Tripartite. We are particularly thankful to Henri Finaona and Jasper Rahajaharison for issuing permits. Mussard Andriamanana of the GTZ project in Ambatolampy provided important information on the history of the Ankaratra Forest. The field work was conducted during a training course for students at the Université d'Antananarivo which was supported by the Ecology Training Programme of WWF, Madagascar. We are grateful to Rob Voss, Paula Jenkins, and Michel Cuisin for access to specimen material in their care. For comments on an earlier draft of this paper we are indebted to Jörg Ganzhorn, Frank Hawkins and Olivier Langrand.

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