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PATTERNS OF ELEVATIONAL DISTRIBUTION OF BIRDS AND SMALL MAMMALS IN THE HUMID FORESTS OF MONTAGNE D'AMBRE, MADAGASCAR

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Résumé. Les résultats obtenus le long d'un transect altitudinal réalisé sur les versants de la Montagne d'Ambre, dont le sommet culmine à 1475 m, localisée dans l'extrême nord de Madagascar sont ici présentés. La forêt est de type humide sempervirent au-dessus de 600 m d'altitude et est de type transitionnel ou de type sec caducifolié au dessous de 600 m. Les insectivores, les rongeurs et les oiseaux ont fait l'objet d'une étude au niveau de trois paliers altitudinaux localisés à 340m, 1000 m et 1340 m sur le versant nord est du massif. Les mammifères et les oiseaux présentent une diversité spécifique relativement faible comparée à celle constatée 2e au niveau d'autres sites forestiers humides de Madagascar. Plusieurs éventuelles raisons sont évoquées pour expliquer ces différences. La forêt humide sempervirente de la Montagne d'Ambre, qui se développe sur un substrat géologique récent, est actuellement isolée d'autres blocs forestiers du même type localisés au sud de ce dernier. Au cours du Pléistocène Ancien et de l'Holocène, le massif de la Montagne d'Ambre était connecté à d'autres blocs de forêt localisés au sud de ce dernier par l'intermédiaire de corridors forestiers. A la suite de changements climatiques, les zones forestières de basse altitude de cette région ont considérablement évoluées. Aujourd'hui, les forêts de basse altitude du versant sous le vent sont des forêts de transition entre la forêt pluviale sempervirente et la forêt sèche caducifoliée. De plus des éruptions volcaniques intervenues au Quaternaire ont probablement considérablement affectées l'habitat naturel de la zone sommitale du massif de la Montagne d'Ambre. Enfin, *Rattus rattus* a colonisé en masse la forêt humide sempervirente, et à travers la compétition qu'elle a établie, ou de par un processus direct de prédation, cette espèce pourrait être responsable de la disparition de certains éléments de la faune locale.

Abstract. Results are presented of an elevational transect of the slopes of Montagne d'Ambre (summit at 1475 m), extreme northern Madagascar. The forest is classified as humid on the higher slopes above about 600 m and as transitional or dry deciduous below 600 m. Insectivores, rodents, and birds were surveyed at three sites (340, 1000, and 1350 m) along the northeastern slope. Mammals and birds had relatively low species richness when compared to other humid forest sites on Madagascar. Several possible reasons are presented for these differences. The humid forests on Montagne d'Ambre, a geologically recent formation, are currently isolated from similar habitats to the south. During the Late Pleistocene and Holocene Montagne d'Ambre was connected to areas further south by corridors of humid forest. As a result of climatic shifts there has been a drastic change in the lowland habitats of this region.The remaining lowland forests on the moist side of the mountain are transitional between dry deciduous and humid forest. Further,Quaternary volcanic eruptions may have greatly altered the habitat on the upper portion of the mountain. Finally, *Rattus rattus* has colonized the humid forest en masse and through competitive exclusion or direct predation may be displacing some of the native fauna. *Accepted 16 September 1996.*

Key words: Madagascar, birds, rodents, insectivores, humid forest, elevational variation.

INTRODUCTION

Studies of the distribution of animals along an altitudinal transect in mountainous regions provide useful information on the ecology, habitat preferences, and species replacement of organisms along an elevational gradient. Such information is often the key to understanding biogeographic distributions of various biotic elements. For example, the Late Pleistocene or Holocene history of connections between forests, particularly for animals restricted to what are presently isolated and botanically unique high mountain zones (Brown 1971, Diamond & Hamilton 1980, Fjeldså 1992), has been an interesting use of such data.

Madagascar is an ideal place to examine some of these interactions and test hypotheses associated with changes in vegetational structure in recent geological time and connections and disjunctions between montane biotas (e.g., Raxworthy & Nussbaum 1996, 1997). Montane communities on the island show considerable levels of endemism and Late Pleistocene and Holocene climatic shifts are well documented. Parallel to the eastern coast of Madagascar are a series of mountains, many of which reach 2000 m in elevation, that have distinct vegetional zones ranging from lowland forest, montane forest, sclerophyllous forest, to areas of open ericoid and rupicolous vegetation. Over the past few years there has been considerable effort in conducting elevational transects on Madagascar (e.g., Raxworthy & Nussbaum 1994), including multidisciplinary studies (Goodman 1996). Herein we present information on the elevational distribution of birds, rodents and insectivores along an elevational transect conducted in the forest of Montagne d'Ambre, Madagascar. We then examine several ecological and historical biogeographic hypotheses to explain the patterns observed along the transect.

STUDY AREA

Montagne d'Ambre is located in the far northern portion of the island (Fig. 1) and the remaining natural forest is composed of two distinct types: the northeastern portion of the mountain is largely humid forest and the western side dry deciduous forest. The upper volcanic portion of the mountain was formed during the Upper Pliocene and Quaternary (Brenon 1972, Karche 1972 cited in Rossi 1974), and there is evidence of significant volcanic activity less than 8000 years ago (Battistini 1965). This is a very recent formation compared to other mountain chains slightly over 150 kilometers further south and southwest (Tsaratanana, Anjanaharibe-Sud, and Marojejy).

A significant portion of the remaining forested areas, particularly humid zones, are contained in the Parc National de la Montagne d'Ambre, a reserve of 18,200 ha (Nicoll & Langrand 1989). The upper portions of the massif trap storm systems moving in from the nearby sea and there is considerable variation in the rainfall along the mountain's slopes. Annual precipitation on the eastern side at 1000 m (Station Forestière des Roussettes) is approximately 3.9 m, as compared to 2.2 m per year at Joffreville (700 m and 5.5 km air distance from the station and close to the ecotone between humid and dry forest), and 1.3 m per year at Sakaramy (380 m and 15 km air distance from the station) (Donque 1975). This variation in precipitation gives rise to remarkable differences in vegetational and floristic structure. The remaining lowland forests below 700 m on the northeastern side of the mountain are largely transitional between humid and dry deciduous forest.

Our elevational transect was conducted at three sites along the northeastern slope of the mountain. Each elevational zone surveyed comprised an altitudinal band of approximately 75 m.

(1) 340 m – Province d'Antsiranana, Forêt de Sahantanana, 6.5 km NE Joffreville (Ambohitra), 12°26.5'S, 49°13.9'E, 5 to 9 April 1996, heavily disturbed transitional lowland forest.

(2) 1000 m – Province d'Antsiranana, Parc National de la Montagne d'Ambre, 5.5 km SW Joffreville (Ambohitra), forest in the vicinity of the Station Forestière des Roussettes, 12°31'S, 49°10'E, 17 to 26 March 1996, disturbed to slightly disturbed montane forest.

(3) 1350 m – Province d'Antsiranana, Parc National de la Montagne d'Ambre, Grand Lac (Matsabory Malio), 12 km SW Joffreville (Ambohitra), 12°36'S, 49°10'E, 27 March to 3 April 1996, undisturbed montane forest.

METHODS

Birds. Point count surveys were used to estimate relative bird abundance and to quantify differences in species' density as a function of altitude (Reynolds *et al.* 1980). On the basis of previous experience with censusing Malagasy forest birds, a distance of 125 m between consecutive point counts was adopted. This

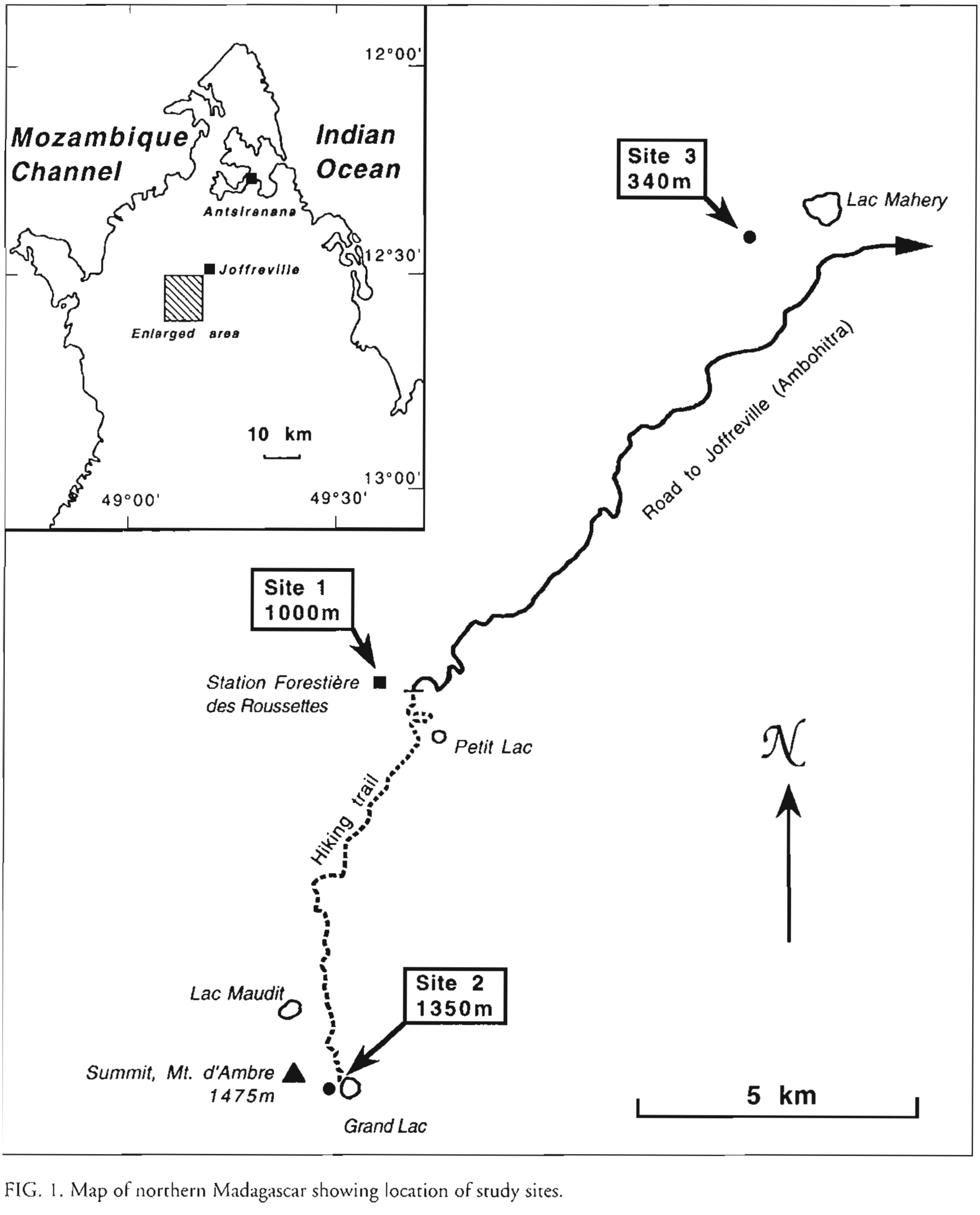

FIG. 1. Map of northern Madagascar showing location of study sites.

distance is presumed to be large enough to avoid counting the same individuals of most common species in two consecutive point counts, but not too far apart as to lose scarce species. Twenty-five sites were used in each zone, and each site was counted three times during a 10 minute period within three hours after sunrise (about 05h30 to 08h30) when most species are vocally active. Within each elevational zone, the point count sites were visited during different periods within the 3 hours of morning survey to avoid any possible time effects. Point counts were conducted along the same trail systems and in the same habitats as the small mammal surveys.

Small mammals. Sampling techniques used for small mammals included pit-falls and two types of live traps. The pit-fall traps were composed of 11 plastic buckets (275 mm deep, 290 mm top internal diameter, 220 mm bottom internal diameter), sunk in the ground at 10 m intervals with the upper rims flush with ground level. Small holes were drilled in the bottom of the buckets to allow water drainage. A black plastic drift fence 100 m long and 0.5 m high was stapled in a vertical position to thin wooden stakes. The fence bottom was buried about 5 cm deep into the ground using leaf litter or soil and positioned to run across the middle of each pit-fall trap. The traps were checked each morning and late afternoon. After heavy rain the buckets were sponged dry. Three lines were used in each of the elevational zones. A "bucket-day" is defined as one bucket in place for a 24 hour period (dawn to dawn).

Each line of traps consisted of Sherman live traps (9 x 3.5 x 3 inch) and National live traps (16 x 5 x 5 inch) in a ratio of 5:1. Traps were installed in a linear pattern along pre-existing trails with approximately 20% in elevated positions. They were placed at sites to maximize capture rates (i.e., next to burrow entrances, along runways, and along "natural" trunk or liana bridges). Distances between traps was variable, although on average 5-7 m separated individual traps. Traps were baited daily, generally between 15h00 and 17h00, with a fresh mixture of finely ground peanut butter and corn grain. Animals not retained for specimens were released and, when necessary, the ears of released small mammals were notched to facilitate recognition of recaptured individuals. Traps were visited at least twice per day, once at dawn and again in the late afternoon. A "trap-day" is defined as one trap in use for a 24-hour period (dawn to dawn).

Voucher specimens of small mammals are deposited in the Field Museum of Natural History, Chicago, and the Département de Biologie Animale, Université d'Antananarivo.

RESULTS

Small mammals. The species accumulation curves based on the combined results of pit-fall and live trap techniques indicate that no new species of mammals were trapped within the 340 m zone after two nights, in the 1000 m zone after five nights, and in the 1350 m zone a near plateau was reached after three nights, although an additional species was added in the sixth and final night (Fig. 2). Generally an asymptote in the species accumulation curve was reached for native insectivores before native rodents. On the basis of these tabulations we conclude that the small mammal fauna along our transect was well-documented.

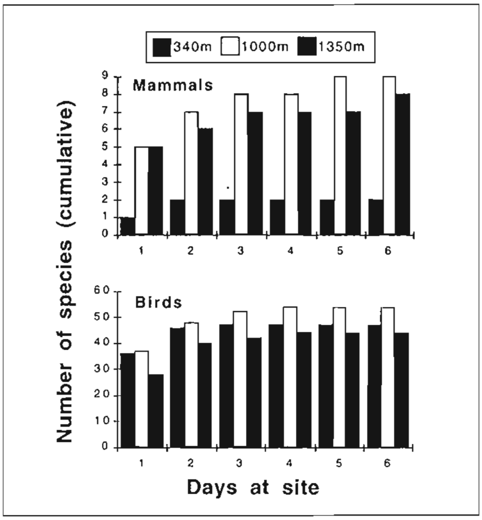

FIG. 2. Species accumulation curves by elevational zone for small terrestrial mammals (rodents and insectivores) and birds. For each group of animals data presented is the combined results of all techniques employed.

The results with Sherman and National traps are as follows (Table 1): 750 trap nights in the 340 m zone yielded one animal (introduced *Rattus rattus*) (0.1% capture rate); 975 trap nights in the 1000 m zone resulted in the capture of 185 animals (19.0% capture rate), including 116 *R. rattus* (62.7% of captures), 8 individuals (4.3%) of two native rodents (*Eliurus webbi* and *E. majori*), 60 (32.4%) insectivores (*Tenrec ecaudatus*, *Microgale talazaci*, *M. melanorrhachis*, and introduced *Suncus murinus*), and one (0.1%) carnivore (*Galidia elegans*); and 750 trap-nights in the 1350 m zone resulted in 121 animals (16.1% capture rate), including 103 (85.1% of captures) *R. rattus*, 1 (0.8%) native rodent (*Eliurus majori*), 14 (11.6%) insectivores (*Tenrec ecaudatus*, *Microgale talazaci*, and *M. melanorrhachis*), and 3 (2.5%) carnivores (*Galidia elegans*).

TABLE 1. Summary of small mammal captured with Sherman and National traps during the 1996 field season in the Parc National de la Montagne d'Ambre in three elevational zones of the mountain. Figures in parentheses are accrued number of trap nights for each trap line.

		340 m		1000 m			1350 m	
	total captured	1 (n = 300)	2 (n = 450)	3 (n = 375)	4 (n = 400)	5 (n = 200)	6 (n = 450)	7 (n = 300)
habitat[1]		dl	dl	sdm	dme	un	un	un
species								
Rattus rattus	220	1	0	44	46	26	67	36
Eliurus majori	5	0	0	1	2	1	1	0
Eliurus webbi	4	0	0	2	2	0	0	0
Microgale melanorrhachis	8	0	0	3	2	0	3	0
Microgale talazaci	35	0	0	7	14	8	5	1
Tenrec ecaudatus	30	0	0	8	12	5	2	3
Suncus murinus	1	0	0	0	1	0	0	0
Galidia elegans	4	0	0	0	1	0	3	0
total animals	306	1	0	65	80	40	81	40
total capture (%)	12.4	0.3	0.0	17.3	20.0	20.0	18.0	13.3
total capture endemics (%)	3.4	0.0	0.0	5.6	8.3	7.0	3.1	1.3
total capture endemic rodents %	0.4	0.0	0.0	0.8	1.0	0.5	0.2	0.0

1 Habitat definitions: dl = disturbed lowland forest, dmc = disturbed montane forest with exotic trees, sdm = slightly disturbed montane forest, un = undisturbed montane forest.

Pit-fall trapping techniques (Table 2) resulted in 153 accrued pit-fall nights in the 340 m zone with 1 (0.7%) insectivore (*Microgale brevicaudata*) captured; 231 pit-fall nights in the 1000 m zone with 115 (50%) insectivores captured, including 6 (5.2% of captures) *Microgale talazaci*, 86 (75%) *M. melanorrhachis*, 5 (4.3%) *M. longicaudata*, 5 (4.3%) *M.* nov. sp., and 13 (11.3%) *Tenrec ecaudatus*; 209 pit-fall nights in the 1350 m zone with 150 (72%) insectivores captured, including 10 (6.7% of captures) *Microgale talazaci*, 120 (80%) *M. melanorrhachis*, 15 (10%) *M. longicaudata*, 2 (1.3%) *M. parvula*, 1 (0.6%) *Tenrec ecaudatus*, and 2 (1.3%) introduced *Suncus murinus*.

Two species of small mammals occur in the 340 m zone, 9 at 1000 m zone, and 8 at 1350 m. The number of native small mammals recorded in each elevational zone was: 1 at 340 m, 7 at 1000 m, and 6 at 1350 m (Table 3). Within each zone introduced small mammals were trapped: at 340 m *Rattus rattus* and at 1000 and 1350 m *R. rattus* and *Suncus murinus*. The number of *Rattus* in the 1000 and 1350 m zones was exceptionally high and there is evidence that through direct and indirect competitive exclusion, this animal may be displacing native mammals.

Birds. The species accumulation curves within each elevational zone (Fig. 2) indicate that few species were added to the local list after three days of survey, which supports the extrapolation that the bird fauna in each zone is relatively well-known. On the basis of combined general observations and point counts 47 species were recorded in the 340 m zone, 54 in the 1000 m zone, and 44 in the 1350 m zone. When restricted to forest-dwelling species the tabulations for each zone are 23, 37, and 22 (respectively; Table 4). Of the 34 forest-dwelling species recorded on the mountain, 25 (78%) are endemic to Madagascar and an additional 9 species also occur on nearby western Indian Ocean Islands. Thus, the complete forest avifauna is endemic to the Malagasy Region.

In general, bird species found across the three elevational zones had more-or-less constant relative densities between altitudes (Table 5) which can be divided into common species (*Nectarinia souimanga*),

TABLE 2. General information and capture rate for pit-fall traps used during the 1996 elevational transect of Montagne d'Ambre. Individuals marked and recaptured are not included in tally.

	Pit-fall line number								
	7	8	9	1	2	3	4	5	6
altitude	300 m	315 m	335 m	980 m	1010 m	1060 m	1300 m	1320 m	1380 m
position	valley	slope	crest	valley	slope	slope	plain	valley	slope
vegetation	disturbed lowland forest	disturbed lowland forest	disturbed lowland forest	disturbed montane forest	slightly disturbed montane forest	intact montane forest	marsh edge montane forest	intact montane forest	intact montane forest
total bucket-days	54	55	44	77	77	77	77	66	66
total small mammals captured	1	0	0	43	45	27	60	50	40
total capture %	1.8	0	0	55.8	58.4	35.1	77.9	75.8	60.6
Microgale talazaci	0	0	0	1	5	0	2	2	6
M. melanorrhachis	0	0	0	24	35	27	47	41	32
M. longicaudata	0	0	0	3	2	0	10	3	2
M. nov. sp.	0	0	0	2	3	0	0	0	0
M. parvula	0	0	0	0	0	0	0	2	0
M. brevicaudata	1	0	0	0	0	0	0	0	0
Tenrec ecaudatus	0	0	0	13	0	0	1	0	0
Suncus murinus	0	0	0	0	0	0	0	2	0

TABLE 3. Altidudinal ranges of small mammals in the humid forest of Montagne d'Ambre, Madagascar. Data from 650 m and 1150 m are derived from Raxworthy & Nussbaum (1994), who used a parallel system of pit-falls but no live traps. Thus, their results for rodents is potentially incomplete.

Taxon	340 m	650 m	1000 m	1150 m	1350 m
Microgale talazaci		X	X	X	X
M. melanorrhachis			X	X	X
M. longicaudata		X	X	X	X
M. nov. sp.		X	X	X	
M. parvula				X	X
M. brevicaudata	X	X			
Tenrec ecaudatus			X	X	X
Setifer setosus		X			
Suncus murinus [1]			X	X	X
Rattus rattus [1]	X		X	X	X
Eliurus majori			X	X	X
E. webbi		X	X		
total species	2	6	9	9	8
total native insectivores	1	5	5	6	5
total native rodents	0	1	2	1	1

1 Species introduced to Madagascar.

TABLE 4. Bird species recorded during elevational transect of Montagne d'Ambre.
Key to table: *status* – * = endemic to Madagascar, (*) = endemic to region (Madagascar, Comoros, Mascarenes & Seychelles), M = migrant, N = nesting on Madagascar but not endemic to region, I = introduced; *habitat* – A = aquatic (including sea shore), F = forest dwelling, O = open country, M = mixed forest and open country, S = aerial foraging.

Species	Status	Habitat	340 m	1000 m	1350 m
Phalacrocorax africanus	N	A			X
Ardeola ralloides	N	A			X
Lophotibis cristata	*	F	X	X	X
Aviceda madagascariensis	*	F		X	
Accipiter madagascariensis	*	F		X	
Accipiter francesii	(*)	M	X	X	X
Accipiter henstii	*	F		X	X
Polyboroides radiatus	*	F	X	X	
Falco zoniventris	*	F		X	
Falco newtoni	(*)	O	X	X	
Falco eleonorae	M	O	X		X
Margaroperdrix madagascariensis	*	O	X		X
Coturnix coturnix	N	O	X		
Turnix nigricollis	*	O	X	X	
Dryolimnas cuvieri	(*)	A		X	X
Sarothrura insularis	*	M	X	X	X
Gallinula chloropus	N	A			X
Streptopelia picturata	(*)	F	X	X	X
Oena capensis	N	O	X		
Treron australis	(*)	M	X		
Alectroenas madagascariensis	*	F	X	X	X
Coracopsis vasa	(*)	F	X	X	X
Coracopsis nigra	(*)	F	X	X	X
Cuculus rochii	*	M	X		X
Coua cristata	*	F	X	X	
Centropus toulou	(*)	M	X	X	X
Otus rutilus	(*)	F	X	X	X
Asio madagascariensis	*	F	X	X	X
Asio capensis	N	O			X
Ninox superciliaris	*	F	X	X	
Tyto soumagnei	*	F		X	
Caprimulgus enarratus	*	F		X	
Caprimulgus madagascariensis	(*)	M	X	X	X
Zoonavena grandidieri	(*)	S	X	X	X
Apus melba	N	S	X		X
Apus barbatus	N	S	X	X	X
Alcedo vintsioides	(*)	A	X	X	X
Ispidina madagascariensis	*	F		X	
Merops superciliosus	N	O	X		
Eurystomus glaucurus	N	M	X		X
Atelornis pittoides	*	F		X	
Leptosomus discolor	(*)	F	X	X	X
Phedina borbonica	(*)	S	X		X

Species	Status	Habitat	340 m	1000 m	1350 m
Motacilla flaviventris	*	O		X	
Coracina cinerea	(*)	F	X	X	X
Phyllastrephus madagascariensis	*	F	X	X	
Phyllastrephus zosterops	*	F		X	
Hypsipetes madagascariensis	N	M	X	X	X
Copsychus albospecularis	*	F	X	X	X
Pseudocossyphus sharpei	*	F		X	X
Nesillas typica	(*)	M		X	X
Newtonia amphichroa	*	F		X	X
Newtonia brunneicauda	*	F	X	X	X
Neomixis tenella	*	F	X	X	
Terpsiphone mutata	(*)	F	X	X	X
Oxylabes madagascariensis	*	F		X	X
Nectarinia souimanga	(*)	M	X	X	X
Nectarinia notata	(*)	M	X	X	X
Zosterops maderaspatana	(*)	M	X	X	X
Calicalicus madagascariensis	*	F	X	X	X
Vanga curvirostris	*	F	X	X	X
Leptopterus chabert	*	M	X		
Cyanolanius madagascarinus	(*)	F	X	X	X
Dicrurus forficatus	(*)	M	X	X	
Hartlaubius auratus	*	M	X	X	
Ploceus nelicourvi	*	F		X	X
Foudia madagascariensis	*	O	X	X	
Foudia omissa	(*)	F		X	
Lonchura nana	*	O		X	X
Total species			47	54	44
Total forest species			23	37	22

moderately common (*Hypsipetes madagascariensis*, *Zosterops maderaspatana*), and rare (*Coracopsis nigra*, *Cyanolanius madagascarinus*, *Vanga curvirostris*). Exceptions to this include *Newtonia brunneicauda* which was rarer at 340 m than at the upper two elevations and *Terpsiphone mutata* which was less common in the upper zone than in the lower two.

DISCUSSION

Small mammals. The small mammal fauna of Montagne d'Ambre is relatively depauperate compared to other mountainous humid forest areas on Madagascar (Goodman & Carleton 1996, Goodman *et al.* 1996, Goodman, unpublished). Furthermore, it is the only mountain with humid forest that we have surveyed to date that does not hold any recognized endemic small mammals or any of the highly specialized semi-fossorial shrew-tenrecs (e.g., *Microgale gymnorhyncha* and *M. gracilis* found in montane humid forest across much of eastern Madagascar). All of the small mammals recorded on the mountain have broad distributions across the eastern humid forest. On the basis of these points, we conclude that this fauna does not show any indications of being isolated from other humid regions of Madagascar, lacks specialists, and thus may be recently derived from areas of humid forest to the south.

Raxworthy & Nussbaum (1994) presented information on the elevational distribution of small mammals on the same slope we surveyed, but with censused zones centered at 650 and 1150 m. They used an identical pit-fall sampling technique. Thus, a comparison of the insectivores they captured with our results allows us to examine the question of how comprehensive rapid faunal inventories are in the documentation of species richness of a given site. There is nearly complete overlap in the species of

TABLE 5. Bird species densitiy per hectare derived from Distance Sampling.[1]

Species	340 m	1000 m	1350 m
Coracopsis nigra	1.4 (0.5–3.8) (CV = 28.4 %)	1.8 (0.4–2.9) (CV = 18.90 %)	1.6 (0.5–4.3) (CV = 23.45 %)
Phyllastrephus madagascariensis	2.3 (1.8–3.0) (CV = 11.15 %)	1.7 (0.7–4.2) (CV = 22.45 %)	
Phyllastrephus zosterops		17.5 (7.30–20.9) (CV = 22.9 %)	
Hypsipetes madagascariensis	2.7 (1.3–5.7) (CV = 19.04 %)	2.6 (1.4–5.0) (CV = 16.43 %)	2.1 (1.0–4.4) (CV = 18.60 %)
Pseudocossyphus sharpei		2.2 (0.3–5.2) (CV = 28.40 %)	1.5 (0.5–4.8) (CV = 21.56 %)
Nesillas typica		15.2 (6.9–23.5) (CV = 20.07 %)	21.5 (15.7–27.4) (CV = 17.54 %)
Newtonia amphichroa		12.8 (3.8–21.4) (CV = 30.10 %)	2.4 (1.2–6.9) (CV = 18.52 %)
Newtonia brunneicauda	3.0 (1.0–9.0) (CV = 26.22 %)	7.5 (3.5–16.1) (CV = 19.07 %)	8.8 (7.8–11.5) (CV = 22.25 %)
Terpsiphone mutata	1.9 (0.7–3.6) (CV = 25.33 %)	2.1 (1.2–6.4) (CV = 23.57 %)	+
Oxylabes mdagascariensis		15.4 (6.6–25.5) (CV = 21.23 %)	2.3 (0.4–6.2) (CV = 18.90 %)
Nectarinia souimanga	12.5 (5.7–27.3) (CV = 19.22 %)	8.3 (4.5–15.3) (CV = 15.34 %)	11.9 (5.2–27.7) (CV = 21.15 %)
Zosterops maderaspatana	4.8 (2.0–7.6) (CV = 34.0 %)	2.7 (1.2–6.4) (CV = 21.14 %)	5.4 (2.6–10.8) (CV = 18.98 %)
Calicalicus madagascariensis	+	2.5 (1.3–4.6) (CV = 16.23 %)	+
Vanga curvirostris	0.4 (0.1–1.3) (CV = 21.09 %)	0.7 (0.2–2.2) (CV = 24.67 %)	0.2 (0.1–0.5) (CV = 11.34 %)
Cyanolanius madagascarinus	1.5 (0.4–6.0) (CV = 28.34 %)	1.0 (0.2–2.9) (CV = 19.76 %)	0.5 (0.3–1.9) (CV = 21.34 %)
Ploceus nelicourvi		15.1 (5.3–21.8) (CV = 27.5 %)	+

[1] Data was pooled from each 3 day survey using distance intervals of 0, 10, 20, 30, 40, 50 and 100 m (Buckland *et al.* 1993). Results presented as density/ha, minimum and maximum density based on 95 % confidence interval, and coefficient of variation (CV). A plus-sign (+) signifies that a species was present within an elevational zone, but available data are not sufficient to calculate density.

insectivores they documented on the mountain and our 1996 survey. The only exception is *Setifer setosus*, of which they captured four at their 650 m zone in 1,089 (0.4% capture rate) bucket-days. This apparently uncommon species was not recorded during the 1996 survey. The elevational ranges presented by Raxworthy & Nussbaum (1994) for insectivores on the mountain, particularly the genus *Microgale*, are in direct concordance with our results. The use of the same pit-fall technique at other sites on the island has resulted in the capture of numerous species of small insectivores not obtained through other trapping techniques (Sherman and National traps), while these other techniques rarely yield species not captured with pit-falls (Goodman *et al.* 1996). Thus, we conclude that pit-fall traps are efficient in capturing and documenting insectivores, and in general 5-6 nights with three lines, each composed of 11 buckets, is sufficient to reach an asymptote in the species accumulation curve.

Birds. The survey was conducted at the end of the breeding season when densities are probably at an annual peak and when the morning chorus is reduced in intensity and duration. Thus, for several species the relative densities estimated with point count techniques may not be directly comparable with data gathered at other sites during the peak breeding season. Nonetheless, we feel that the combined observational and point count data are sufficiently complete to draw some conclusions about differences between the bird fauna of Montagne d'Ambre and other sites on Madagascar.

Compared to other surveyed mountainous sites with humid forest, Montagne d'Ambre has a distinctly depauperate bird fauna. For example, in the humid forests of the RNI d'Andringitra 66 species were recorded at 810 m, 56 at 1210 m, and 46 at 1625 m (Goodman & Putnam 1996); in the RNI d'Andohahela 59 at 400 m, 64 at 800 m, 62 at 1200 m, 47 at 1600 m, and 38 at 1900 m (Goodman *et al.* in press); and in the Réserve Spéciale d'Anjanaharibe-Sud 74 at 860 m, 69 at 1260 m, 49 at 1550 m, and 25 at 1950 m (Hawkins *et al.* in press). Furthermore, the general pattern at these three sites is a decrease in species richness as a function of elevation - at Montagne d'Ambre there is a distinct mid-elevational bulge at 1000 m.

Due to their dispersal ability, species richness in birds is expected to be little affected by the mountain's isolation – however, this is not the case. Numerous forest-dwelling species, including generalist species, are apparently inhibited to dispersal across non-forested areas or perhaps across different types of forested habitats.

GENERAL CONCLUSIONS

A comparison of the species richness of small mammals and birds along an elevational gradient on Montagne d'Ambre to other well-documented humid forest sites on the island indicates that the small mammal and bird faunas are depauperate. We propose that this pattern can be explained by four possible factors. First, the humid forest on Montagne d'Ambre, resting on a geologically recent formation, is currently isolated from parallel habitats. During the recent geological past Montagne d'Ambre's only connections were to lowland forest further south, a habitat generally depauperate in rodents and insectivores. If montane species were able to colonize the mountain, they may not have locally survived the Late Pleistocene and early Holocene climatic vicissitudes. During warmer dry periods in the Late Pleistocene there is evidence of the retreat of montane forest habitats towards summital zones (Gasse *et al.* 1994, Burney 1988, 1997). The peak of Montagne d'Ambre is at 1475 m, which may have been too low to harbor montane habitat for humid forest animals. An analysis of the biogeographic relationships of reptiles in the humid forests of Madagascar (Raxworthy & Nussbaum 1997) has shown that the fauna of Montagne d'Ambre shares much closer affinity to Ankarana and the Sambirano region further west (Manongarivo, Nosy Be, and Tsaratanana). This is best explained by a broad corridor of lowland humid forest previously connecting these regions. Subsequent climatic shifts, particularly due to changes in rainfall patterns, have resulted in the isolation of these humid forest areas. Parallel data are not available for the bird and small mammal faunas of Ankarana and the mountains of the Sambirano to determine if this pattern is consistent across other land vertebrate groups.

Second, Quaternary volcanic activity on Montagne d'Ambre may have given rise to extensive and immediate changes in the forest community. The areas surrounding our 1000 m and 1350 m camps experienced volcanic activity less than 8000 years ago (Battistini 1965).

Third, the remaining lowland forests on the moist side of Montagne d'Ambre contain transitional forest, and the small mammal and bird species composition is depauperate and not representative of lowland humid forests elsewhere on the island. The position of Montagne d'Ambre relative to the sea results in a halo effect where the upper half of the mountain receives considerable rainfall and contains humid forest, while the lower half is distinctly drier and includes transitional forest. Thus, the unusual elevational distributions of the fauna can in part be explained by the orographic position of the mountain.

Fourth, *Rattus rattus* has invaded the humid forests of Montagne d'Ambre and is extremely common. Rats were captured on the ground, in elevated holes in trees, and on suspended lianas. On the basis of feeding experiments and excavation of rat burrows it is known that there is broad overlap in the diets of *R. rattus* and the endemic rodents (Goodman & Sterling 1996). There is evidence that rats are currently displacing the native rodents through competitive exclusion and perhaps direct predation. Furthermore, the large numbers of *Rattus* in the humid forests of Montagne d'Ambre might have devastating effects for birds, particularly ground-dwelling species, whose nests would be subject to predation by *Rattus*. Thus, it is possible that elements of the bird and small mammal faunas of the mountain have already been locally extirpated and our tabulation of the species diversity within an elevational zone is lower than during the pre-*Rattus* period. On the basis of a 1930 zoological expedition to the mountain, however, there is no evidence that any species of bird (Rand 1936), rodent (Carleton & Schmidt 1990), or insectivore (MacPhee 1987) has been lost during the intervening period.

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