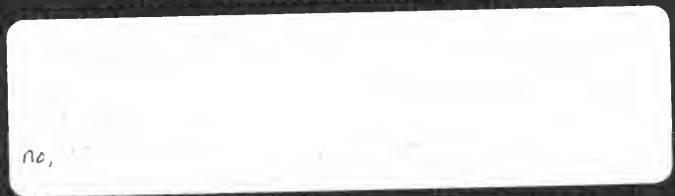


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no.

A Floral and Faunal Inventory of the Parc National de Marojejy, Madagascar: With Reference to Elevational Variation

Steven M. Goodman, Editor

August 31, 2000
Publication 1510

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LANGDON, E. J. M. 1979. Yagé among the Sionia: Cultural patterns in visions, pp. 63-80. In Browman, D. L., and R. A. Schwarz, eds., *Spirits, Shamans, and Stars*. Mouton Publishers, The Hague, Netherlands.

MURRA, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2, *The Andean Civilizations*. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

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**A Floral and Faunal Inventory
of the Parc National de
Marojejy, Madagascar**

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NEW SERIES, NO. 97

A Floral and Faunal Inventory of the Parc National de Marojejy, Madagascar: With Reference to Elevational Variation

Steven M. Goodman, Editor

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*World Wide Fund for Nature
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Preface

In this volume we present the results of a brief floral and faunal survey conducted in the Parc National (PN) de Marojejy, northeastern Madagascar, between 4 October and 20 November 1996. Since I began biotic inventories in Madagascar several years ago, numerous reports and publications on the plants and animals of the Marojejy Massif have fascinated me, in particular the volume produced by Henri Humbert in 1955 with the tantalizing title *Une merveille de la Nature à Madagascar: Première exploration botanique du massif du Marojejy et de ses satellites*. Thus, we were delighted to have the opportunity to visit this mountain and continue the work started by numerous other field scientists.

Our survey of the Marojejy Massif, organized by the World Wide Fund for Nature (WWF), Madagascar, was the fourth of five multidisciplinary large-scale biological and elevational inventories conducted on mountains in Madagascar over the past 5 years. This volume is the fourth inventory to be published in the *Fieldiana: Zoology* series. The previous volumes were inventories of the Réserve Naturelle Intégrale (RNI) d'Andringitra (now reclassified as a PN; *Fieldiana: Zoology*, n.s., no. 85, 1996), the Réserve Spéciale (RS) d'Anjanaharibe-Sud (*Fieldiana: Zoology*, n.s., no. 90, 1998), and the RNI d'Andohahela (now reclassified as a PN; *Fieldiana: Zoology*, n.s., no 94, 1999). Another volume on the RS du Pic d'Ivohibe and the corridor between this reserve and the PN d'Andringitra was recently published in French in the series *Recherches pour le Développement, Série Sciences Biologiques*, no. 15 (1999).

Many people and institutions provided assistance that made our inventory of the Marojejy Massif possible. Our colleagues in the Malagasy government, particularly the Direction des Eaux et Forêts, Association Nationale pour la Gestion des Aires Protégées (ANGAP), and members of the Commission Tripartite, provided the necessary permits to carry out this work; we owe much to their continued aid and collaboration. We are deeply indebted to WWF staff members based in Antananarivo and Andapa: Anjara Andriamanali-

na, Jean-Marc Garreau, Olivier Langrand (now of WWF Gabon), Patricia Lehmann, Anjara Mantantsara, Jean-Paul Paddock, Lantasoa Ramarojana, Gisèle Ramarosan, and Malalarisoa Razafimpahanana. The assistance of the inhabitants of Manantenina and Mandena is gratefully acknowledged, in particular M. Zézé Bruno, Roland Christophe, and Bevaio Jean Chrysostome. M. Razokiny and M. Simona Arsène of Eaux et Forêts, Andapa, helped with numerous aspects of this mission. We are also indebted in many ways to M. Ledada Rachel Razafindravao, our highly talented cook, who persevered under rather difficult conditions. Movements up and down a mountain by a research group and up to 40 porters can pose numerous problems; however, the logistical aid and competence of Mamy Ravokatra greatly facilitated this aspect of the mission.

The chapters in this volume have benefited from the comments of numerous reviewers. Those who waived anonymity are cited in the acknowledgments to the chapters they reviewed. John Weinstein, Field Museum of Natural History, helped with the preparation of many of the photographs that appear in this volume. William Burger, Scientific Editor of *Fieldiana*, and Marjorie Pannell, Managing Editor of the Field Museum Press, continued to provide valuable assistance in producing these volumes. Over the past 5 years, they have seen nearly 3,000 manuscript pages associated with these Madagascar monographs pass over their desks. For assistance with the translation of the abstracts into French, we thank Voninavoko Raminoarisoa, Bernardin Rasolonandrasana, and Lucienne Wilmé.

The 1996 biological inventory of the PN de Marojejy was made possible by grants from Kreditanstalt für Wiederaufbau (KfW) to WWF as part of the Projet de Conservation et de Développement Intégrés Marojejy/Anjanaharibe-Sud and from the Center for Biodiversity and Conservation of the American Museum of Natural History. KfW and the Schlinger Foundation provided partial subsidy for the publication of this volume.

S. M. Goodman
3 June 1999
Chicago

Chapter 1

Description of the Parc National de Marojejy, Madagascar, and the 1996 Biological Inventory of the Reserve

Steven M. Goodman¹

The past 10 years have witnessed an impressive expansion of scientific knowledge regarding Madagascar resulting from a variety of sources—symposia focused on the island's history and biological diversity (Ganzhorn et al., 1997; Goodman & Patterson, 1997; Lourenço, 1996), long-term field studies on a variety of plants and animals at several biological research stations (e.g., Ganzhorn & Sorg, 1996; Wright, in press); a wealth of behavioral, ecological, and taxonomic studies on particular organisms; rapid biological inventories of poorly known forested areas on the island (Goodman, 1996, 1998, 1999; Goodman & Langrand, 1994; Langrand & Goodman, 1997; Rakotondravony & Goodman, 1998; Ratsirarson & Goodman, 1998); and numerous popular guides to its biotic splendors (Dransfield & Beentje, 1995; Glaw & Vences, 1994; Langrand, 1990, 1995; Mittermeier et al., 1994; Morris & Hawkins, 1998). This nearly exponential increase in knowledge about Malagasy plants and animals has enabled scientists to synthesize new ideas associated with the biological patterns of the island to begin to understand, for example, the effects of ecological change during recent geological time. One of the critical uses of the newly available information is to strengthen conservation activities to safeguard what remains of this truly remarkable biota.

Even with these advances in comprehending the extant fauna and flora, major gaps remain in basic knowledge of the natural history and distribution of the great majority of Malagasy organisms. Further, a remarkable number of taxa new to science, including vertebrates, are being described each year from Madagascar. Because of

the continued high levels of habitat destruction (Whitmore, 1997) and the fact that very little of the original forest cover is left, the coming decade may be the last possible time to document the remaining patterns of biotic diversity for numerous sites on the island. Rapid biological inventories of previously unstudied or poorly known forested sites are critical to this effort.

This volume presents the results of a biological inventory conducted in the Parc National (PN) de Marojejy in northeastern Madagascar. The park lies within the Province d'Antsiranana and between the towns of Andapa and Sambava (Fig. 1-1). Fourteen scientists participated in the field inventory, which took place in the latter half of 1996.

In 1994 the eastern slopes of the Anjanaharibe-Sud Massif was the site of an intensive biological inventory (Goodman, 1998), part of a series of inventories of mountains ranging along the complete 13° latitudinal breadth that Madagascar encompasses. Data obtained on the massif, which lies more to the interior of the island and on the opposite side of the Andapa basin from the PN de Marojejy (but at nearly the same latitude), provide an excellent comparative base for examining patterns of congruence in the distribution of many different organisms along various latitudinal clines. The authors of several chapters in this volume have compared the survey information from the PN de Marojejy with the earlier data from the RS d'Anjanaharibe-Sud.

This chapter briefly reviews the history of the park, the organization of our 1996 field season in the park, geology, and climate. For further information about the mountain readers are referred to Humbert (1955), Guillaumet et al. (1975), Nicoll and Langrand (1989), and Safford and Duckworth (1990).

¹ Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605-2496, U.S.A.

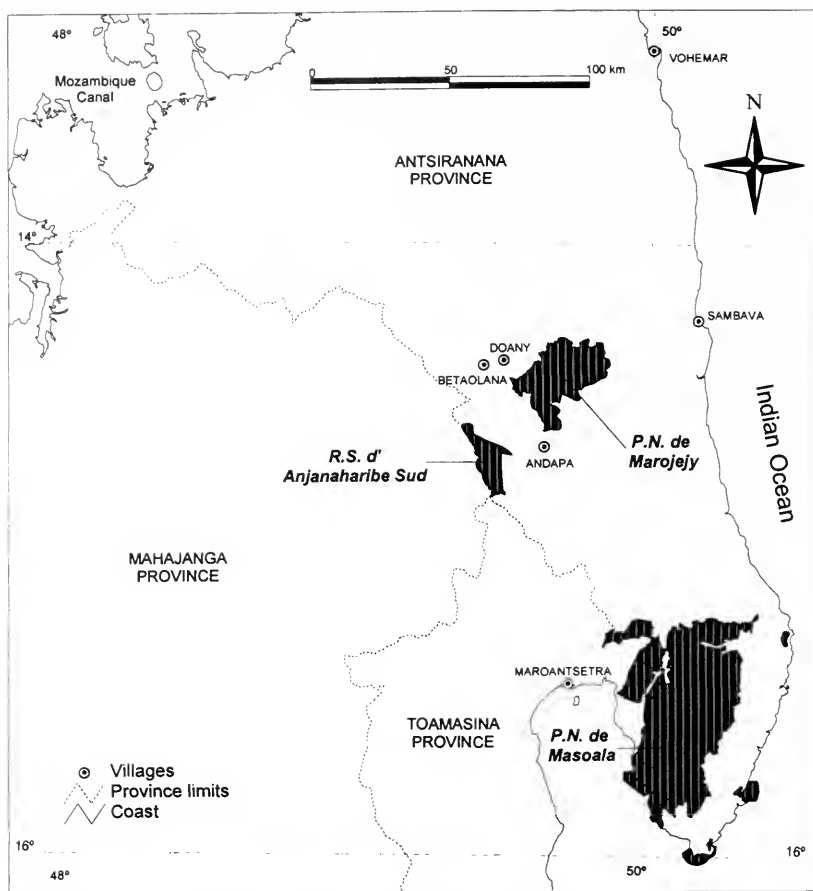


FIG. 1-1. Map of northeastern Madagascar showing the position of the Réserve Spéciale d'Anjanaharibe-Sud and the Parc National de Marojejy with respect to other sites, provincial limits, and towns in this part of the island.

Abbreviations Used in the Text

ANGAP	Association Nationale pour la Gestion des Aires Protégées
BM(NH)	The Natural History Museum, London (formerly British Museum [Natural History])
CNRE	Centre National de Recherche sur l'Environnement, Antananarivo
CNRS	Centre National de la Recherche Scientifique, Antananarivo
dbh	diameter at breast height
DEF	Direction des Eaux et Forêts
DRFP	Direction des Ressources Forestières et Piscicoles
FMNH	Field Museum of Natural History, Chicago
FTM	Foiben-Taosarintanin'i Madagasikara,

	Antananarivo (Institut National de Géodésie et Cartographie)
ha	hectare
IRSM	Institut de Recherche Scientifique de Madagascar
KfW	Kreditanstalt für Wiederaufbau
MBG	Missouri Botanical Garden, St. Louis
MNHN	Muséum National d'Histoire Naturelle, Paris
MRAD	Ministère de la Recherche Appliquée au Développement, Antananarivo
PBZT	Parc Botanique et Zoologique de Tsimbazaza, Antananarivo
PN	Parc National
RB	Réserve de Biosphère
RCP	La Recherche Coopérative sur Programme No. 225, under the Centre National de la Recherche Scientifique

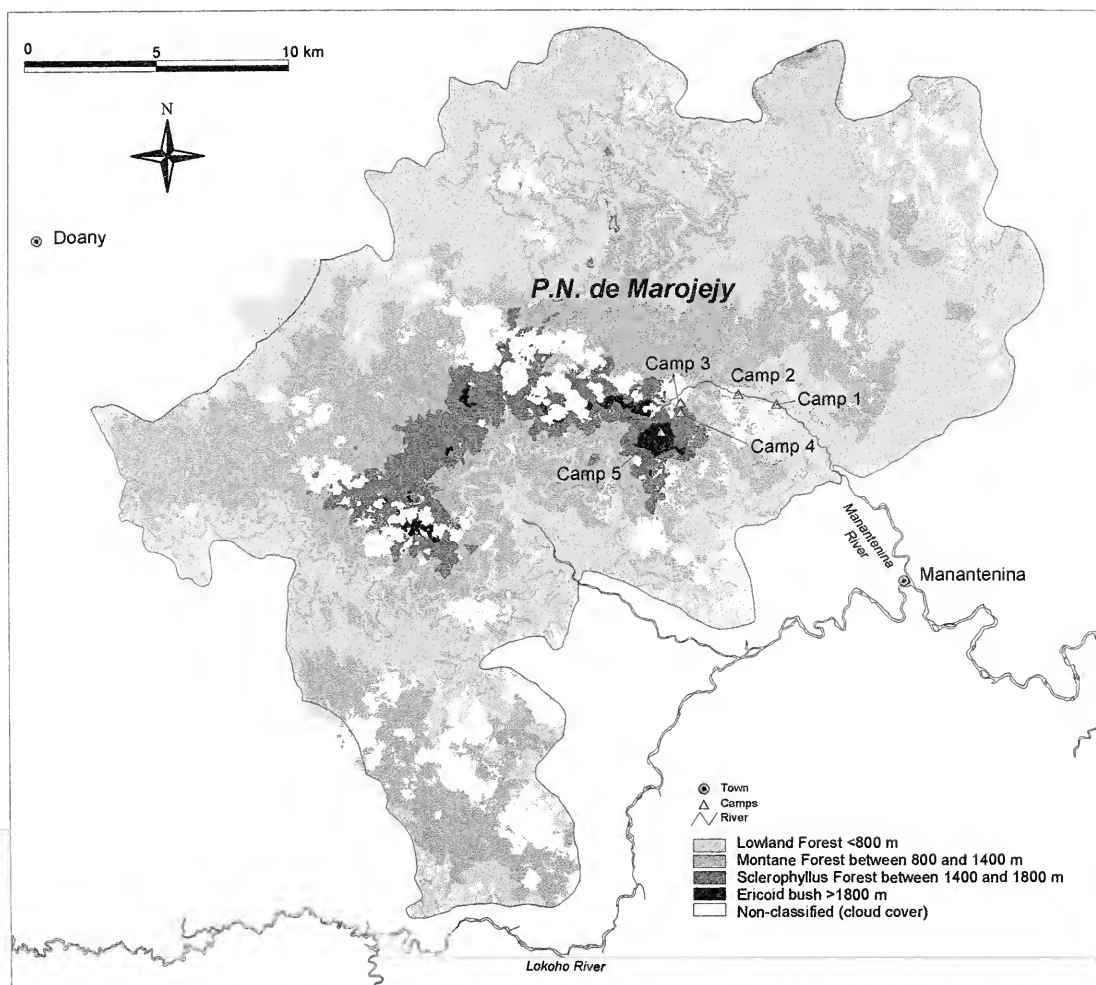


FIG. 1-2. Map of the approximate vegetational formations in the Parc National de Marojejy (modified after Razafy Fara, 1998). The locations of the camps occupied during the 1996 biological inventory of the reserve are indicated.

RNI	Réserve Naturelle Intégrale
RS	Réserve Spéciale
UADBA	Université d'Antananarivo Département de Biologie Animale
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Washington, D.C. (formerly United States National Museum)
WWF	World Wide Fund for Nature

The Marojejy Reserve

In early January 1952, after the exploration and remarkable discoveries of Henri Humbert con-

cerning the flora on the Marojejy Massif, a portion of this area was designated a réserve naturelle (Nicoll & Langrand, 1989). This decree was further modified on 1 June 1966 by another decree (no. 66-242) naming 60,150 ha of the region as the 12th Réserve Naturelle Intégrale (RNI) de Marojejy. Subsequently the status of this RNI was changed to that of a park, Parc National (PN) no. 13, by decree 98-375, signed on 19 May 1998 and published on 19 October 1998 (Gazetim-panjakan'ny, 1998), and the size of the park was reduced to 60,050 ha. The principal reason for this change in status was to provide opportunities for local people to benefit from ecotourism and regulated access to certain areas. Tourists have the right to enter a national park after purchasing tickets, but

TABLE 1-1. Surface coverage in the PN de Marojejy, based on LANDSAT TM images.*

Vegetational type and surface coverage	Surface area (ha)	Percent coverage
Dense humid forest with closed canopy and multiple strata	41,910	70.9
Dense humid forest with open canopy and a single stratum	10,128	17.1
Secondary forest with patches of cleared areas	5,365	9.1
Herbaceous formations (including ferns)	980	1.5
Covered in clouds	843	1.4

* Modified after Razafy Fara (1998).

protected areas with RNI status are only open to scientists carrying special permits.

The PN de Marojejy comprises a wide range of humid forest vegetational types, starting with lowland forest at about 75 m and culminating in large expanses above tree line of open ericoid bush and exposed rock in the summital zone. The principal peak is at 2132 m. The flora of the massif has been studied by many botanists (Dorr, 1997; Humbert, 1955), and a detailed checklist is currently in preparation (J. Miller, pers. comm.). More detailed analyses of the vegetational zones and the elevational stratification of the plant communities are presented in Chapters 2 and 3. Also, a number of works have been published on the terrestrial fauna of the reserve (Duckworth et al., 1995; Evans et al., 1992; Griveaud, 1960; Safford & Duckworth, 1990).

A recurrent theme in this book is the exceptional biological diversity of the PN de Marojejy in comparison with most of the reserves in the protected areas system of Madagascar. This richness is a result of the park encompassing a broad swath of elevational zones, starting from lowland formations and ranging continuously to high mountains.* The eastern foot of the Marojejy Massif begins within a few tens of kilometers from the Indian Ocean. In numerous other reserves on the island that include mountainous zones, the lowest represented forest starts at a distinctly higher elevation (e.g. Anjanaharibe-Sud and Andringitra). For many groups of land vertebrates, such as birds and the herpetofauna, there is a strong relationship between increasing elevation and decreasing species richness. Simply put, the lowland forests are the richest.

On the basis of patterns of vegetational coverage of the PN de Marojejy derived from LANDSAT TM images and ground-truthing (Razafy

Fara, 1998), nearly 90% of the reserve consists of dense, humid forest (Table 1-1). What is remarkable about this figure is that a large percentage of this habitat is forest below 800 m elevation (Fig. 1-2). We strongly suspect that the lowland forest is important in explaining the reserve's exceptionally high species richness. Few reserves in Madagascar cover broad elevational ranges with this high a percentage of lowland forest. An important exception is the Tsaratanana Massif, which includes a variety of habitats, from 227 m to the summit at 2876 m (Nicoll & Langrand, 1989). The RNI de Tsaratanana has not been the site of a multidisciplinary elevational inventory, and data are not available to compare its richness with Marojejy's. However, once the site has been extensively surveyed, it may show similarly high levels of species richness.

Transect Sites

During the 1996 inventory of the Marojejy Massif, coordinates for each site were determined with the use of a geographical positioning system, and the names for various localities were garnered from maps (Foiben Taosarintanin'i Madagasikara [FTM], 1974, 1977) and discussions with local people. A gazetteer is presented at the end of this volume (p. 275) for the localities mentioned in the text.

Our inventory of the southeastern slopes of the Marojejy Massif was conducted in an ascending series of altitudinal transect zones, following the classic route established by earlier explorers and scientists who visited the site, such as L.-J. Aragon. H. Humbert, P. Griveaud, the field team under the direction of R. Paulian (Guillaumet et al., 1975), botanists from the Missouri Botanical Garden (MBG), a group from the University of London (Safford & Duckworth, 1990), and a number of other researchers. We worked in five altitudinal

* The terminology used for forest types on Madagascar is complicated. In Table 3-6 the various descriptive names of these classifications are compared.

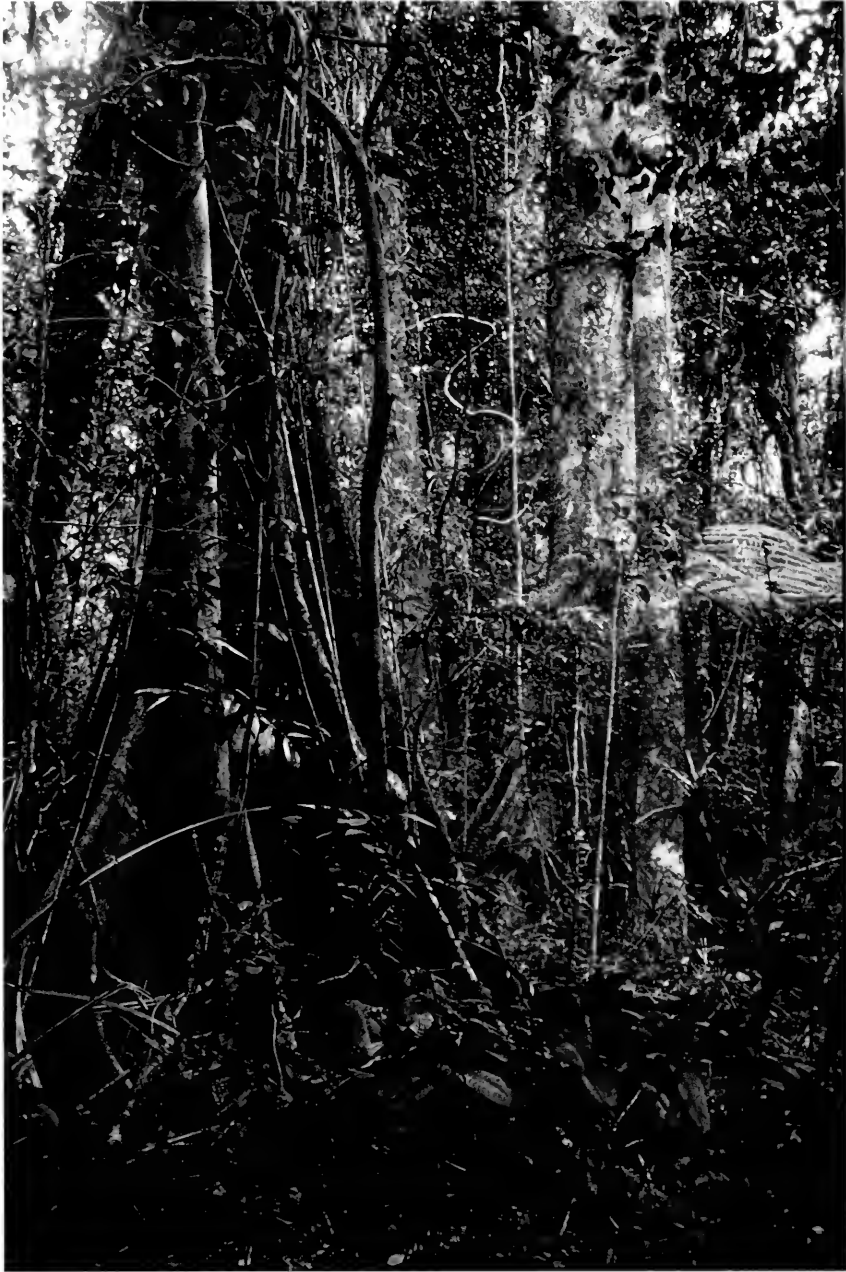


FIG. 1-3. Lower portion of a largely undisturbed area of forest (at ca. 500 m) with a thick understory, relatively dense lianas, and some remaining large trees. The vegetational types in the lowest elevational zone of the Marojejy Massif were a mixture of secondary forest, dense areas of bamboo, and relatively intact lowland forest. (Photograph by N. Messmer.)

zones (often referred to in this volume as transects or transect zones) on the mountain that were generally delimited by a ± 75 m elevational band centered on each of the five camps. Elevations were determined with the use of altimeters. The posi-

tion of each camp occupied during the survey is indicated in Figure 1-2 (p. 3).

450 m (camp 1) 4–14 October 1996
Madagascar: Province d'Antsiranana, Parc Na-



FIG. 1-4. View of Ambatotsondrona rising to 1261 m, just across the Manantenina River valley from our camp 2 at 775 m and along the Ambavaomby River. The forest at the foot of the mountain has a discontinuous canopy cover, presumably as a result of natural landslides, and secondary forest zones associated with human activities. (Photograph by F. Rakotondrainibe.)

tional de Marojejy, along tributary of Manantenina River, 8 km NW Manantenina, 14°26.2'S, 49°46.5'E.

775 m (camp 2) 14–24 October 1996

Madagascar: Province d'Antsiranana, Parc National de Marojejy, along a tributary of the Manantenina River, 10 km NW of Manantenina, 14°26.0'S, 49°45.7'E.

1325 m (camp 3) 24 October–4 November 1996

Madagascar: Province d'Antsiranana, Parc National de Marojejy, 11 km NW of Manantenina, Antranohofa, 14°26.2'S, 49°44.5'E.

1625 m (camp 4) 4–13 November 1996

Madagascar: Province d'Antsiranana, Parc National de Marojejy, 10.5 km NW of Manantenina, along a tributary near the source of the Andranomifototra River, 14°26.4'S, 49°44.5'E.

1875 m (camp 5) 13–20 November 1996

Madagascar: Province d'Antsiranana, Parc National de Marojejy, 11 km NW of Manantenina,

at the source of the Andranomifototra River, 14°26.8'S, 49°44.1'E.

Itinerary of the 1996 Expedition

From 3 to 6 September 1996, together with Désiré Ravelonarivo, Gisèle Ramarason, and a local guide, I conducted a quick reconnaissance of the area along the Manantenina–summit trail up to Antranohofa at 1250 m. Sites were chosen for our first three camps. After we descended to the village of Manantenina we met with the village elders and local officials to explain our presence in the area and discuss the plans for the inventory; we also engaged local people to work with the field group and established porter prices for the various stages of the mission. I then returned to Antananarivo by plane (via Sambava) to organize other aspects of the mission.

On 30 September 1996 a vehicle driven by M.



FIG. 1-5. View north, looking toward Ambatotsondrona (left center) and across the large areas of lowland forest that remain in the PN de Marojejy. The photograph was taken from the trail above the upper limit of the elevational transect centered at 775 m. The Manantenina River valley is just out of view at the bottom, (Photograph by S. M. Goodman.)

Ravokatra, in the company of M. Ledada, left Antananarivo for Andapa loaded with field gear and a good portion of the dried food provisions (excluding rice) for the mission. This journey, in a four-wheel-drive vehicle, took 3 days. On 2 October 1996 the group of researchers based in Antananarivo and those who had recently arrived from other countries to join the survey team flew from Antananarivo to Sambava, where they were met by WWF vehicles and driven to Andapa. The day of 3 October was spent in Andapa arranging baggage and provisions, including 600 kg of rice purchased locally, and paying courtesy visits to various government offices. Research materials and dried food provisions were separated according to camp (transect zone), packed in labeled and numbered rice sacks, and stored in a rat-proof, dry building in Andapa.

Early on the morning of 4 October 1996 the research group, baggage, and provisions for the first camp were driven to the village of Manantenina, where about 40 porters from this and neighboring villages awaited our arrival. We then

walked 3–4 hours to a site at 450 m and established our first camp.

Over the next 7 weeks the group, with the assistance of porters from villages at the foot of the mountain, changed study sites an additional four times and then descended to Manantenina on 20 November 1996. Most of the group returned to Andapa the same day, and on 22 November the vehicle headed back to Antananarivo with the specimens and research material; a number of the researchers returned to Antananarivo by plane (via Sambava).

The system for reprovisioning each camp was as follows. One or two days before each scheduled displacement to the next camp, a WWF employee in Andapa purchased fresh produce in the local market, and these goods, along with the dried provisions and research materials stocked in Andapa for the next camp, were transported to Manantenina. Prearranged rendezvous were organized with local porters to carry the material to the site we were preparing to leave. Once the porters had reached the research group, the baggage,



FIG. 1-6. View toward the northeast from an open area at about 1250 m and below camp 3 at Antranohofa. The peak in the center is Ambatotsondrona, a prominent feature opposite camp 2 at 775 m. Note the growth of bamboo in the valley bottom in the foreground and changes in vegetational cover along exposed ridges. (Photograph by S. M. Goodman.)

which included the new goods, goods from the existing camp, and the porters' food provisions, was reorganized and redistributed. This process took from a few minutes to several hours, and after it was completed the porters and field-workers climbed to the next site. Specimens from each site were temporarily stored in the abandoned camp. After each displacement, the porters on their way back down the mountain carried the specimens to Manantenina, where a WWF vehicle was waiting to transfer the specimens to the storage building in Andapa.

After the third camp the distances between the lowlands and our transect zones were too long to complete the round-trip during 1 day. After our displacement to camp 4 the porters spent the night in camp 2, and after we moved to camp 5 the porters passed the night at camp 3. On both occasions these camps had to be stocked with tarps for shelter, cooking pots, and provisions for the porters. Between 32 and 42 porters were needed for each displacement, with the exception of the final descent, which did not involve any provi-

sions and took about 25 people, not including the research group.

Compared with our study group's other elevational transects of mountainous regions in Madagascar, the survey of the Marojejy Massif was relatively simple from the point of view of logistics. The Manantenina-summit trail was established decades ago and has remained open owing to frequent use. People in the local villages are accustomed to working as porters and guides for scientific groups, distances between sites can be covered in a few hours, and the climb to the summital zone is not particularly steep.

During the field trip to the PN de Marojejy (4 October–20 November 1996) members of the scientific crew included S. M. Goodman (birds and small mammals), A. F. A. Hawkins (birds—camps 1 and 2 only), J. Legrand (insects—camps 1 and 2 only), N. Messmer (plants), T. Nguyen (insects—camps 1 and 2 only), E. Quinter (insects), P. J. Rakotomalaza (plants), F. Rakotondrainibe (ferns), B. Randriamampionina (ferns), D. Randriamasimanana (insects—camps 1 and 2 only),

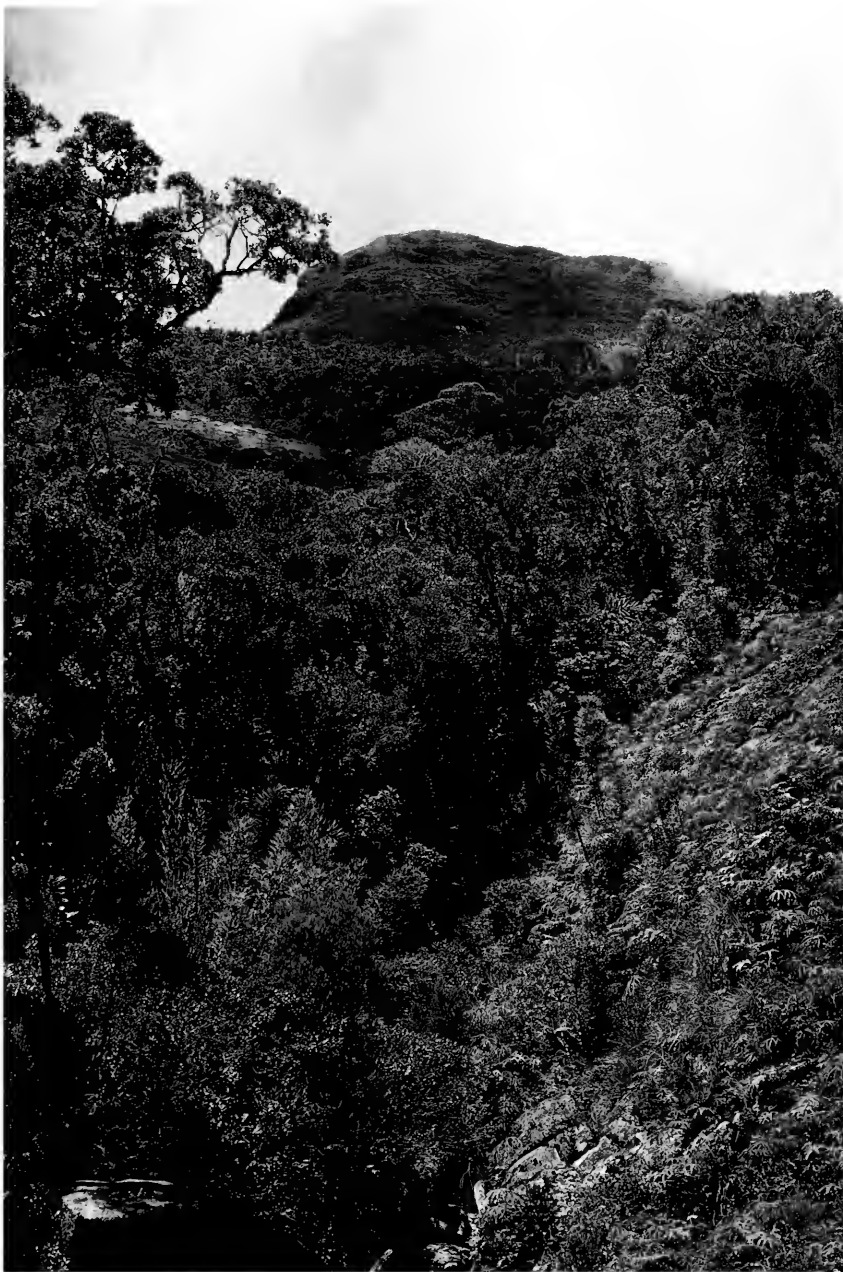


FIG. 1-7. Starting at about 1250 m, there are numerous areas of exposed rock or very shallow soils supporting bamboos, ferns, or small geophytic plants. This photograph was taken at about 1275 m and below camp 3 on the main trail leading down to camp 2. The view is toward the south. (Photograph by S. M. Goodman.)

A. Raselimanana (reptiles and amphibians), D. Ravelonarivo (plants), M. Ravokatra (birds and logistics), and J.-C. Razafimahaimodison (birds).

The group also included two to three local people from the villages of Mandena and Manantina, a cook, and visitors from the WWF project

in Andapa. The maximum number of people we had simultaneously in any one camp was about 22, not including porters. The names and addresses of all field and laboratory researchers who took part in this project are given at the end of this chapter (Appendix 1-1).



FIG. 1-8. View of exposed ridge at about 1600 m showing largely sclerophyllous vegetation. These slopes are regularly exposed to strong winds, heavy fog, and mist. (Photograph by N. Messmer.)

Logistics, Trail Systems, and Descriptions of the Various Study Zones

Our trajectory up the mountain followed the Manantenina–summit trail, and the first three camps were at sites already established along this path by researchers who had previously visited this slope of the massif. The vast majority of recent scientists who visited the massif used the Antranofofa site at 1325 m (our camp 3) as their base camp for work in the summital zone and climbed up and down each day. At a stiff pace it is possible to ascend from Antranofofa to the summital zone in about 4 hours. However, for our purposes this was not adequate, and we decided to establish two other camps between Antranofofa and the summital zone.

Chapters 2 and 3 of this volume present detailed descriptions of the pteridophyte and angiosperm plant communities occurring within each elevational zone. Here I restrict my comments to aspects of access, trails, and the general condition of each transect zone.

450 m

Our study area was close to the main valley of the Manantenina River and in an area of disturbed forest, at a site known locally as Ampanasankolana (Ampanasama Ankolony) or Bedinta. The camp was near the junction of two tributaries of the Manantenina River and about 4 hours' walk from Manantenina. The names of these tributaries were not consistent between local informants but are probably the Ambinantelo and Ampanasatogotra Rivers.

The habitats within the transect varied from heavily disturbed sites with low secondary growth (*savoka*) to zones of dense bamboo mixed with *Aframomum* (Zingiberaceae) to slightly disturbed lowland humid forest habitat (Fig. 1-3). Portions of this area had been cleared in the not too distant past for agricultural use, particularly coffee plantations (Humbert, 1955) and slash-and-burn practices (*tavy*). Most of the zones of secondary growth were regenerating *tavy* plots, as were probably also some of the nearly monospecific areas of bamboo. An extensive trail system existed



FIG. 1-9. Camp 5 at 1875 m, above the forest line. The vegetation immediately around the camp was a mixture of ericoid bush, dwarf palms, and herbaceous plants. The ground in low-lying areas was moist. The source of the Andranomifototra River is in this region. (Photograph by F. Rakotondrainibe.)

in this portion of the park and is regularly used by local people for collecting forest plants (medicinal and construction uses), hunting and fishing, and access to illegal *tavys* well hidden in various portions of the reserve. Photographs published in Humbert's monograph (1955, pl. 24, figs. 47 and 48) show the hills above Mandena and toward Mt. Behondroko as already a patchwork of forest and agricultural plots. In 1996 the level of habitat degradation was much more severe, and little forest remained on these hills.

775 m

This site was next to the Andampimbazaha Cascade, a waterfall along the Ambavaomby River about 100–150 m elevation above where it plunges into the Manantenina River. Across the main river valley is the distinct rock outcrop known as Ambatotsondrona (Fig. 1-4). The walk to the 775 m camp from the 450 m site takes about 1 hour and is along the trail leading to the summit.

In general, the forest below the 775 m camp site showed signs of human disturbance, mostly plant wood extraction for building materials, while above the camp the forest seemed largely intact. It was in this zone that the magnificent *Marojejya* palms, a genus discovered during Humbert's explorations on the Marojejy Massif, were clearly in evidence. Small trails existed throughout the upper portion of this transect zone, and these paths often ended in a small and well-hidden *tavy*, most of which had been recently abandoned, or at a site where a tree had been removed. Thus, it was clear that until very recently, local people harvesting forest products from the park had tried to conduct their activities off the beaten track. The Manantenina Valley and the low hills to the north still hold considerable areas of the original lowland and montane forest (Fig. 1-5).

1250 m

This site, known as Antranohofa, was within 3 hours' walking distance of camp 2 and along the



FIG. 1-10. The habitats occurring in the zone above camp 5 at 1875 and the summit varied from low ericoid bush, often with stands of bamboo and palms in the valley bottoms, to areas of low-growing herbaceous and woody vegetation, and finally bare exposed rock. The large dome at the top of the photograph is the summit of Marojejy, at 2132 m. (Photograph by F. Rakotondrainibe.)

trail leading to the summit. We designated the camp at 1325 m as the upper limit of the transect zone, with the midpoint 75 m below, at 1250 m. This locality is probably the Andilana of Humbert (1955) and the Andasy II of Griveaud (1960). Just

next to the campsite is a small tributary that has potable water most of the year, except at the end of the dry season. In early September, during the reconnaissance mission, this source was nearly dry. However, when we arrived to occupy the site

Mission O.R.S.T.O.M. XII-1958 Réserve N° 12.

P. GRIVEAUD.

Entomologiste de l'I.R.S.M. Tananarive
Recherches entomologiques dans le massif du Marojejy du
30-XI-58 au 18-XII-58.

- 1^{er} Camp. altitude 500m Ambinanitelo.
- 2^e - - 1.300m Andasy II
- 3^e - - 1.600m Ambodifiakarana
- 4^e - - 2.030m Matsobory

Arrivée au sommet le 11-XII-1958 à 10^h15

Ernest RAHARIZONINA Paul GRIVEAUD
assistant entomologiste Entomologiste

Pierre SOGA
Garde auxiliaire des Forêts

ent

Griveaud

Soga

Les documents contenus dans ce local ont été recopiés par M. P. Griveaud, Entomologiste de l'I.R.S.M. en mission de réserve pour l'I.R.S.M. au sommet le 13-XII-58

La plupart des papiers se trouvaient dans des bouteilles et tubes plus ou moins bien fermés, et sont détériorés par l'humidité, plusieurs devenus illisibles. Tous ont néanmoins été séchés et conservés.

La 1^{ère} ascension et reconnaissance du sommet du Marojejy. Est a été effectuée par le Capitaine ARAGON en 1937. En 1958, nous avons pu déchiffrer sur les documents trouvés ci. inclus. les passages suivants:

- Capitaine ENCKUD. (?) du S.G.M. en X-1947 (?)
- Professeur HUMBERT du Muséum d'Histoire Naturelle en XII-1948
- SABDUREAU Conservateur des Réserves Naturelles et Des ABBAYES de la Faculté de Sciences de Rennes en X-1956.
- Capitaine DRECHOU du S.G.M. en IX-1957

En outre, apparaissait le nom AMIEUX (?) de Sambava et il a été signalé l'ascension du sommet par deux Pères Catholiques ayant à côté une statuette de la Vierge qui se trouve en contrebas et au sud du pylon.

L'altitude au som. - on a vérifié par nous, avec altimètre Suisse "Ekomen" : ascension : soit de 2090^m
barométrique de 595^m

P. GRIVEAUD. XII-1958

FIG. 1-11. Messages left in a container cached in a small cairn at the principal summit of the Marojejy Massif at 2132 m. Top. A note left by P. Griveaud concerning his December 1958 trip to the mountain describes the members of the group and the sites they visited. Much of the information collected by Griveaud during this trip focused on insects, but he also published some information on the birds and mammals occurring on the massif (Griveaud, 1960). When he visited the summit in 1958 he found numerous slips of paper left behind by earlier visitors to the site. Most slips had badly deteriorated. Griveaud recopied certain messages of historical interest and added the fresher slip of paper to the cairn bottle (bottom). Among the notes in his distinctive handwriting is information on the 1937 visit of Aragon, the first person to reach the summit, and records of passage of such notable individuals as Professor H. Humbert. The Griveaud recapitulation is also in poor shape, and we reproduce it here to continue the archival tradition.

in late October there was a considerable amount of water. In addition, there was a permanent stream within 100 m by foot below the camp. There were few signs of human activity in the Antranohofa transect, with the exception of an occasional cut tree of *Evodia* sp. (*bilahy*), the bark of which is used to make an alcoholic beverage known as *betsa-betsa*.

About 400 m walking distance below the Antranohofa camp, on the trail leading back to camp 2, there is a precipitous drop in the topography, from which one can look down into the Manantenina River valley. From this lookout point it is also possible to see Ambatotsondrona, the massif just across the Manantenina Valley from our camp 2 (Fig. 1-6). In this area of the trail there were

TABLE 1-2. Summary of minimum and maximum temperatures and precipitation during the 1996 expedition to PN de Marojejy.

Periods of measurement within each transect	Temperature (°C)*		Rainfall (mm)†
	Minimum	Maximum	
450 m	10, 13.0–17.0	10, 17.0–23.0	8, 2.0–40.0
4–14 October	14.7 ± 1.10	20.1 ± 1.87	10.6 ± 12.68
750 m	10, 13.0–18.0	10, 19.0–27.0	7, 1.0–27.5
15–23 October	15.9 ± 1.58	23.2 ± 2.14	12.2 ± 10.76
1325 m	9, 10.0–13.0	9, 19.0–23.0	5, 1.0–23.0
24 October–3 November	11.4 ± 0.83	21.3 ± 1.56	8.0 ± 7.8
1550 m	9, 9.0–13.0	9, 15.0–18.0	6, 0.5–45.0
4–13 November	11.0 ± 1.40	16.5 ± 1.17	11.0 ± 15.84
1875 m	7, 8.0–13.0	7, 18.0–23.0	5, 0.5–1.0
14–20 November	9.9 ± 1.64	21.0 ± 1.69	0.6 ± 0.2

* Data are presented as number of records, range, mean, and ± standard deviation.

† Data are presented as number of days with rain, range, mean, and ± standard deviation.

numerous sites with exposed rock or very shallow soils supporting bamboo, ferns, or small geophytic plants (Fig. 1-7).

1550 m

Our camp 4 was about 1¼ hours' walk from camp 3. The site was at 1550 m, which marked the lower end of the transect (1550–1700 m, centered at 1625 m). The camp was along the Andranomifototra River and accessible by a newly cut path, about 1 km from the main summit trail. The camp was within an extensive area of montane and mossy forest. The only signs of human activity that we found in this area were a few trees of *bilahy* that had been cut and their bark removed.

This zone encompassed the ecotones between montane and sclerophyllous forest, particularly on ridges that were exposed to wind (Fig. 1-8). In the protected valleys the vegetational structure had more of a montane forest aspect.

1875 m

The site of our camp 5 was above the tree line on the flat portion of a ridge overlooking the source of the Andranomifototra River (Fig. 1-9). The camp was about 300 m from the main summit trail and a 1.5–2 hours' climb from camp 4. The site afforded easy access to the summital zone, the open ericoid bush, and the upper limit of the sclerophyllous forest. On clear days we had spectacular views of the Lokoho and Manantenina riv-

er systems, the Indian Ocean, and at night the lights of Sambava. The walk from the camp to the summit took about an hour. The habitats in this region varied from low ericoid bush, often with stands of bamboo and palms in the valley bottoms, to areas with low-growing herbaceous and woody vegetation, and finally bare exposed rock (Fig. 1-10).

As mentioned earlier, numerous missions to Marojejy had reached the summit of the massif. It is customary among mountain enthusiasts on Madagascar to place notes recording their passage in a cairn at the summits of the major peaks. At the summit of Marojejy we found an old jar with messages left by groups that had successfully reached this point. Several of the older messages or those written on poor-quality paper were in poor condition, and some were already illegible. Messages that we considered important from a historical perspective were carried back to Andapa by Jean-Marc Garreau, photocopied, returned to the site, and placed in a new, hermetically sealed plastic container. Two of these messages had been written by P. Griveaud in his distinctive penmanship, one recounting his ascent to the summit in 1958 and the other recapitulating portions of messages in poor condition found at the time of his passage (Fig. 1-11).

Geology

The Marojejy Massif covers an area approximately 32 km from east to west and 22 km from north to south. The massif is lithologically com-

TABLE 1-3. Historical meteorological data from weather stations at Sambava and Andapa.*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Precipitation												
Sambava (1933-1960)												
Rainfall (mm)	283	269	243	243	150	161	147	144	102	95	129	253
Number of days with rain	17	16	16	16	14	16	18	18	16	16	14	17
Andapa (1935-1960)												
Rainfall (mm)	347	345	282	165	74	75	86	103	68	61	89	269
Number of days with rain	23	21	21	19	17	18	21	21	16	14	13	19
Temperatures												
Sambava (1941-1960)												
Average maximum (°C)	31.5	31.6	31.5	30.6	29.4	27.8	26.9	26.9	27.6	28.7	29.9	30.8
Average minimum (°C)	22.2	22.1	22.2	21.5	19.9	18.3	17.6	17.8	18.0	19.0	20.5	21.6
Andapa (1950-1963)												
Average maximum (°C)	30.4	29.9	30.0	28.5	27.2	24.9	24.0	24.2	25.4	27.3	29.2	30.2
Average minimum (°C)	19.2	19.2	19.4	18.3	16.0	14.4	13.6	13.5	13.6	14.7	16.8	18.5

* Data from Petit (1971).

plex, with portions being granitic, granite-dioritic, malagachitic, and a section toward the summit area composed of gneiss. On the basis of information presented by Humbert (1955), Karche and Petit (1969), and Petit (1971), I will briefly describe the geology of the massif along the Manantenina summit slope. Above the main Manantenina River valley the first major cascade occurs above 700 m (in the vicinity of our camp 2) and the rock is generally a form of gneiss interstratified with charnockitic, syenitic, and migmatitic rock. Between about 700 m and 1200 m the formation is largely charnockite and syenite. From about 1200 m the rock, which rises to form the summit of the mountain, is principally granite, with intrusions of white and rose quartz.

Meteorology

One of the difficulties in interpreting weather patterns in the PN de Marojejy is the lack of data from the immediate environs of the massif: the nearest weather stations are along the coast, at Sambava (about 50 km direct distance), and further inland, at Andapa (about 50 km direct distance) (Fig. 1-1). The mean annual precipitation is 2,296 mm at Sambava and 1,883 mm at Andapa (Donque, 1975). Rainfall is probably higher on the Marojejy Massif, and there is certainly elevational variation on the mountain with respect to precipitation and temperature. To establish a weather profile for Marojejy, we measured minimum and maximum daily temperatures (°C) and amount of precipitation every 24-hour period (Table 1-2).

As expected, daily minimum temperatures were generally lower with increasing elevation. An exception was the mean minimum temperature at 750 m (15.9°C), which was warmer than at 450 m (14.7°C). One explanation for this observation is that the 750 m campsite was in an exposed area with considerable amounts of open dark-colored rock that absorbed and retained a greater amount of solar energy. Another possibility is that the valley in which our 450 m camp was located acts as a cold air funnel.

In contrast to minimum temperatures, daily maximum temperatures across the altitudinal gradient deviated substantially from a simple model of decreasing values with increasing elevation. The 750 m camp had the highest mean daily temperature, perhaps because of the exposed nature

of the site. The 1330 m site had a slightly higher mean daily maximum than the site at 450 m. The camp at 1875 m was in an open area above the tree-line and exposed to direct solar radiation, which accounts for the high daily temperatures relative to the 1625 m site.

Levels of rainfall showed no clear pattern in relation to the elevational sequence of our study sites. To a large extent the amount of rainfall was equal across the four lower zones within the forest. The main differences between the five sites occurred at the 450 m and 1675 m camps, where several heavy showers (40–45 mm) swelled the average daily rainfall figure. Although the rainy season in this part of Madagascar normally begins in earnest by December, there was no clear pattern of an increase in number of days with rain per transect zone during our inventory of Marojejy. At Sambava, the driest month over the course of the year on average is October (Petit, 1971; Table 1-3, this chapter). Eighty percent of the days we were present at 450 m had rain, 70% at 750 m, 55% at 1330 m, 66% at 1675 m, and 71% at 1875 m. The most unusual rainfall pattern was seen at the 1875 m camp. During the 7 days we were present at the site, the maximum rainfall on any given day was 1.0 mm, and in general most precipitation occurred as dew and heavy morning mist.

Literature Cited

- DONQUE, G. 1975. Contribution géographique à l'étude du climat de Madagascar. Nouvelle Imprimerie des Arts Graphiques, Antananarivo, vii + 478 pp.
- DORR, L. J. 1997. Plant collectors in Madagascar and the Comoro Islands. Royal Botanic Gardens, Kew, xlv + 524.
- DRANSFIELD, J., AND H. BEENTJE. 1995. The palms of Madagascar. Royal Botanic Gardens, Kew, xii + 475 pp.
- DUCKWORTH, J. W., M. I. EVANS, A. F. A. HAWKINS, R. J. SAFFORD, AND R. J. WILKINSON. 1995. The lemurs of Marojejy Strict Nature Reserve, Madagascar: A status overview with notes on ecology and threats. *International Journal of Primatology*, **16**: 545–559.
- EVANS, M. I., J. W. DUCKWORTH, A. F. A. HAWKINS, R. J. SAFFORD, B. C. SHELDON, AND R. J. WILKINSON. 1992. Key bird species of Marojejy Strict Nature Reserve, Madagascar. *Bird Conservation International*, **2**: 201–220.
- FOIBEN TAOSARINTANIN'I MADAGASIKARA. 1974. Maroambihy, 1:100,000, feuille XY-36. Foiben Taosarintanin'i Madagasikara, Antananarivo.
- . 1977. Andapa, 1:100,000, feuille W-36. Foiben Taosarintanin'i Madagasikara, Antananarivo.
- GANZHORN, J. U., B. RAKOTOSAMIMANANA, L. HANNAH, J. HOUGH, L. IYER, S. OLIVIERI, S. RAJAOBELINA, C. RODSTROM, AND G. TILKIN. 1997. Priorities for biodiversity conservation in Madagascar. *Primate Report*, **48-1**: 1–81.
- GANZHORN, J. U., AND J.-P. SORG, EDs. 1996. Ecology and economy of a tropical dry forest in Madagascar. *Primate Report, Special Issue*, **46-1**: 1–382.
- GAZETIM-PANJAKAN'NY. 1998. Decret no. 98-375 portant changement de statut de la Réserve naturelle intégrale no. 12 de Marojejy en Parc national no. 13. *Gazetim-panjakan'ny Repoblikan'i Madagasikara*, 19 Oktobra 1998, pp 3137–3144.
- GLAW, F., AND M. VENCES. 1994. A fieldguide to the amphibians and reptiles of Madagascar. *Zoologisches Forschungsinstitut und Museum Koenig, Bonn*, 480 pp.
- GOODMAN, S. M., ED. 1996. A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. *Fieldiana: Zoology, n.s.*, **85**: 1–319.
- , ED. 1998. A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation. *Fieldiana: Zoology, n. s.*, **90**: 1–246.
- , ED. 1999. A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahelo, Madagascar: with reference to elevational variation. *Fieldiana: Zoology, n. s.*, **94**: 1–297.
- GOODMAN, S. M., AND O. LANGRAND, EDs. 1994. Inventaire biologique: Forêt de Zombitse. *Recherches Pour le Développement, Série Sciences Biologiques, Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, No. Spécial*, 106 pp.
- GOODMAN, S. M., AND B. D. PATTERSON. 1997. Natural change and human impact in Madagascar. *Smithsonian Institution Press, Washington, D.C.*, xiii + 432 pp.
- GRIVEAUD, P. 1960. Une mission entomologique au Marojejy. *Naturaliste Malgache*, **12**: 43–55.
- GUILLAUMET, J.-L., J.-M. BETSCH, C. BLANC, P. MORAT, AND A. PEYRIERAS (under the direction of R. Paulian). 1975. Etude des écosystèmes montagnards dans la région malgache. III. Le Marojejy. IV. L'ltremo et l'Ibity. Géomorphologie, climatologie, faune et flore (Campagne RCP 225, 1972–1973). *Bulletin du Muséum National d'Histoire Naturelle, 3e série, Ecologie générale*, no. 309, **25**: 29–67.
- HUMBERT, H. 1955. Une merveille de la Nature à Madagascar. Première exploration botanique du massif du Marojejy et de ses satellites. *Mémoires de l'Institut Scientifique de Madagascar, série b*, **6**: 1–210.
- KARCHE, J. P., AND M. PETIT. 1969. Grand traits géomorphologiques du Marojejy central. *Semaine Géologique (Antananarivo)*, pp. 105–109.
- LANGRAND, O. 1990. Guide to the birds of Madagascar. *Yale University Press, New Haven*, xi + 364 pp.
- . 1995. Guide des oiseaux de Madagascar. *Delachaux et Niestlé, Lausanne*, 415 pp.
- LANGRAND, O., AND S. M. GOODMAN, EDs. 1997. Inventaire biologique: Forêt de Vohibasia et d'Isoky-Vohimena. *Recherches Pour le Développement, Série Sci-*

- ences Biologiques, Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, no. 12, 197 pp.
- LOURENÇO, W. R., ED. 1996. *Biogéographie de Madagascar*. ORSTOM Editions, Paris, X + 588 pp.
- MITTERMEIER, R. A., I. TATTERSALL, W. R. KONSTANT, D. M. MEYERS, AND R. B. MAST. 1994. *Lemurs of Madagascar*. Conservation International, Washington, D.C., 356 pp.
- MORRIS, P. A. J., AND A. F. A. HAWKINS. 1998. *The birds of Madagascar: A photographic guide*. Pica Press, East Sussex, xi + 316 pp.
- NICOLL, M. E., AND O. LANGRAND. 1989. *Madagascar: Revue de la conservation et des aires protégées*. World Wide Fund for Nature, Gland, xvii + 374 pp.
- PETIT, M. 1971. *Contribution à l'étude morphologique des reliefs granitiques à Madagascar*. L'Imprimerie Centrale, Antananarivo, 307 pp.
- RAKOTONDRAVONY, D., AND S. M. GOODMAN, EDs. 1998. *Inventaire biologique: Forêt d'Andranomay, Anjozorobe. Recherches Pour le Développement, Série Sciences Biologiques, Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, no. 13, 110 pp.*
- RATSIRARSON, J., AND S. M. GOODMAN, EDs. 1998. *Inventaire biologique de la Forêt Littorale de Tampolo (Fenoarivo Atsinanana). Recherches Pour le Développement, Série Sciences Biologiques, Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, no. 14, 261 pp.*
- RAZAFY FARA, F. L. 1998. *Rapport sur la typologie de la végétation et des occupations de sol dans le Parc National de Marojejy et du corridor forestier. Département des Eaux et Forêts, Antananarivo, 18 pp.*
- SAFFORD, R. J., AND J. W. DUCKWORTH, EDs. 1990. *A wildlife survey of Marojejy Reserve, Madagascar. ICBP Study Report 40. International Council for Bird Preservation, Cambridge, England.*
- WHITMORE, T. C. 1997. *Tropical forest disturbance, disappearance, and species loss, pp. 3-12. In Laurence, W. F., and R. O. Bierregaard, Jr., eds., Tropical forest remnants: Ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, xv + 616 pp.*
- WRIGHT, P. C., ED. In press. *Biodiversity science and village economics: Madagascar's Ranomafana National Park*. Covelo, Island Press.
- Carleton, M. D., Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.
- Gautier, L., Conservatoire et Jardin Botaniques de la Ville de Genève, Case Postale 60, CH-1292, Chambésy/Genève, Switzerland.
- Goodman, S. M., Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605-2416, U.S.A., and World Wide Fund for Nature, Aires Protégées, B.P. 738, Antananarivo (101), Madagascar.
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Appendix 1-1

Participants in the Project (Field and Laboratory)

A total of 24 scientists and field-workers from five different countries were involved in this multidisciplinary study. This number included field participants listed in the previous section as well as researchers responsible for some of the laboratory studies. The addresses of all scientific participants are given below.

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Chapter 2

Pteridophyte Diversity Patterns Along an Elevational Gradient in the Parc National de Marojejy, Madagascar

France Rakotondrainibe¹

Abstract

A study of the pteridophytes of the Parc National de Marojejy was conducted as part of an ongoing biological inventory program of protected areas in Madagascar, operating since 1993. A total of 239 species or infraspecific taxa in 70 genera were recorded. Of that total, 105 (43.9%) are endemic to Madagascar, and 6 are known only from the park. Its high level of floristic richness may be explained in large part by several observations: the Marojejy reserve lies in the wettest part of the island; its complex geomorphology generates a great number of biotopes; moist evergreen forest covers a wide altitudinal range, from 400 to 2000 m; and its former status as a strict nature reserve has been retained until mid-1998. Compared to the pteridophyte floras of other massifs studied in Madagascar (Anjanaharibe-Sud and Andohahela), that of Marojejy has a relatively large number of species in the genera *Lindsaea* and *Grammitis*, and lower richness in *Asplenium*, although the latter is still the dominant genus as elsewhere in the island. Floristic data gathered on 194 species and varieties observed in 18 plots covering a total area of 14,100 m² were analyzed using two complementary numerical methods: correspondence analysis and hierarchical ascending classification. Four floristic groups were distinguished between 400 and 2000 m elevation on the eastern slope of Marojejy, each of which was characterized regarding several features, including generic and specific composition, average density of the species present, “exclusively characteristic” and “preferentially characteristic” species, and the range and percentages of growth forms present. The altitudinal zones occupied by these floristic groups were compared to those of the vegetation types previously described on the massif. Floristic similarity coefficients were calculated for the pteridophytes occurring in each altitudinal zone on Marojejy for comparison with those in the corresponding zones on Anjanaharibe-Sud ca. 35–40 km farther inland; the results show that the pteridophyte flora of Marojejy is most distinctive at middle altitudes, between 1250 and 1350 m.

Résumé

L'étude des Ptéridophytes du Parc National de Marojejy a été réalisée dans le cadre des campagnes d'inventaire biologique menées depuis 1993 dans les aires protégées de Madagascar. Un total de 239 espèces ou variétés réparties en 70 genres a été recensé. Parmi elles, 105 soit 43,9% sont endémiques de Madagascar et 6 endémiques du parc. La position géographique du massif du Marojejy dans la région la plus arrosée de l'île, la géomorphologie complexe du massif qui abrite de nombreux biotopes, sa couverture forestière continue entre 400 et 2000 m

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d'altitude et le statut de réserve intégrale qui lui a été attribué entre 1952 et 1998, expliquent en grande partie cette richesse floristique élevée. Les traits caractéristiques de cette flore par rapport à celle d'autres massifs malgaches (Anjanaharibe-Sud et Andohahela) sont la richesse relative en taxons appartenant aux genres *Lindsaea* et *Grammitis* et une moindre diversité en *Asplenium* qui reste cependant le genre dominant comme sur l'ensemble de l'Ile. Les données floristiques relevées sur 18 parcelles totalisant 14.100 m² et concernant 194 espèces ou variétés sont traitées par deux types d'analyses multivariées complémentaires: une classification ascendante hiérarchique et une analyse factorielle des correspondances. Quatre groupements floristiques sont ainsi mis en évidence. Pour chacun d'eux, nous précisons: la composition générique et spécifique, la densité moyenne des espèces, les espèces caractéristiques exclusives et préférentielles, le spectre des types biologiques. La position de ces groupements par rapport à l'étagement connu des formations végétales du parc est discutée. La comparaison des coefficients de similitude floristique, étage par étage, des quatre groupements de Ptéridophytes du Marojejy avec ceux du massif de l'Anjanaharibe-Sud distant seulement de 35–40 km montre que la spécificité de la flore du Marojejy est la plus grande au niveau des altitudes moyennes, entre 1250 et 1350 m.

Introduction

Of all the large mountain massifs in Madagascar, Marojejy was the last to be discovered but has the best known flora (Des Abbayes, 1961; Guillaumet et al., 1975; Humbert, 1955; Koechlin et al., 1974). Humbert (1955) was the first botanist to collect in the region. Between 1948 and 1951 he traveled throughout the principal massif of Marojejy as well as the massifs of Beondroka and Mainborondro, located slightly to the east, Ambatosoratra, to the south, Anjenabe and Betso-manga, to the north, and several surrounding valleys, including the Lokoho, Antsahabe, Manantenina, and Androranga. The pteridophyte specimens that Humbert took back to the Muséum National d'Histoire Naturelle (MNHN) in Paris were studied by Tardieu-Blot, who published (in Humbert, 1955) a preliminary list of 107 species and varieties of pteridophytes, including descriptions of 11 new species, 8 of which were considered to be locally endemic: *Asplenium andapense* Tardieu, *A. marojejyense*,* *Blechnum humberitii*, *B. longepetiolatum*, *Blotiella coriacea*, *Deparia marojejyensis* (Tardieu) Kato, *Elaphoglossum cerussatum* Tardieu, and *E. marojejyense*.

More recent studies of plant specimens collected in the Parc National (PN) de Marojejy prior to the present expedition (cf. Humbert and collaborators in 1959–1960; Guillaumet in 1972; Miller and collaborators in 1988–1989) and deposited at the herbarium of the Laboratoire de Phanérogamie, MNHN, have added 61 taxa to Tardieu-

Blot's initial list (Rakotondrainibe, unpubl. data), bringing the total number of pteridophytes to 168. In contrast, 211 species and varieties of pteridophytes have been identified from the Réserve Spéciale (RS) d'Anjanaharibe-Sud (Rakotondrainibe & Raharimalala, 1998), which is about three times smaller in area than the PN de Marojejy (18,255 vs. 60,050 ha) and is separated from it by a corridor of intact forest only about 35–40 km in length (Fig. 2-1). This suggests that assessments of pteridophyte species diversity at Marojejy were substantially underestimated.

The present inventory of pteridophyte species occurring along the eastern slope and the summit area of the Marojejy Massif was conducted between 4 October and 20 November 1996. The principal objective was to supplement the list of pteridophytes known from the reserve and to evaluate the density of the various taxa present and their altitudinal distribution. An integrated conservation and development program is currently being conducted in the Marojejy/Anjanaharibe-Sud reserves, and an assessment of the most highly threatened species (whether because of small population size or restricted geographic distribution) is of potential value in this context.

Methodology

The present study was conducted using a standardized methodology described earlier for inventory work performed in 1994 at RS d'Anjanaharibe-Sud (Rakotondrainibe & Rahari-

* Names of authors of the taxa mentioned in Table 2-3 are not given in the text.

malala, 1998) and PN d'Andohahela (Rakotondrainibe, 1999). Two phases were involved: (1) an inventory of the pteridophytes present along an altitudinal transect on the eastern slope running between the lowest point in the reserve and its summit, the entire length of which is exposed to the trade winds, and (2) ecological surveys in a series of 800 m² plots representative of the various biotopes present, from which an evaluation can be made of the diversity of the pteridophyte communities present along the transect.

Floristic Survey

Five base camps were established along the trail situated on the east slope and leading to the summit area of the Marojejy Massif, between 400 m and 2132 m altitude: camp 1 at 450 m, camp 2 at 775 m, camp 3 at 1225 m, camp 4 at 1625 m, and camp 5 at 1875 m (see Chapter 1). The inventory work was conducted within a radius of 2 km around each camp and along the main trail from the point where it enters the park along the banks of the Manantenina River, 3 km northwest of the village of Mandena, to the summit (see Chapter 1).

All voucher specimens are deposited at the herbarium of the Département des Recherches Forestières et Piscicoles, Centre National de la Recherche Appliquée au Développement DRFP/FOFIFA in Antananarivo (TEF), and the Laboratoire de Phanérogamie, MNHN. Duplicates of most of the specimens collected will also be sent to the Missouri Botanical Garden (MO) and the Royal Botanic Gardens, Kew (K).

In most cases, generic delimitations follow those proposed by Kramer and Green (1990), although for certain genera whose circumscription is controversial and which are in need of revision, particularly for the Malagasy flora, more classical concepts have been used: Thelypteridaceae follow the system of Holttum (1974), and Grammitidaceae are classified according to Pichi-Sermolli (1977), but the genus *Cochlidium* has been separated from *Xiphopteris* according to Bishop (1978). The identification of species and varieties was done using monographs for the genus *Lastreopsis* (Tindale, 1965), and the families Lindsaeaceae (Kramer, 1972) and Thelypteridaceae (Holttum, 1974). Circumscription of the other species follows treatments in the *Flore de Madagascar et des Comores* (Stefanovic et al., 1997; Tardieu-Blot, 1951–1971), except for *Pyrrosia rhodesiana*, *Ctenopteris flabelliformis*, *Elaphoglossum*

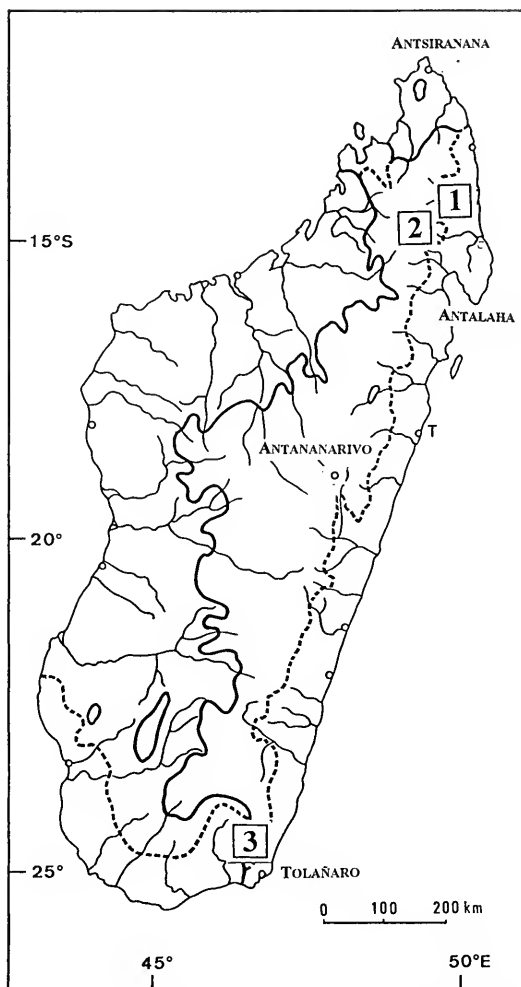


FIG. 2-1. Location of the PN de Marojejy (1), RS d'Anjanaharibe-Sud (2), and PN d'Andohahela (3) in Madagascar.

petiolatum ssp. *salicifolium*, and *Lycopodiella caroliniana*, which follow the most recent African floras (Schelpe, 1970; Schelpe & Diniz, 1979).

Ecological Sampling

Previous studies in Madagascar, at sites similar to those found on the eastern slope of Marojejy with intact or only slightly disturbed forest and relatively uniform soil (Table 2-1), have shown that altitude and topography influence the floristic composition of pteridophyte communities (Rakotondrainibe, 1999; Rakotondrainibe & Guillermin, 1990; Rakotondrainibe & Raharimalala, 1988).

TABLE 2-1. Characteristics of the study plots on the eastern slopes of the PN de Marojejy.

Parameter evaluated	Plot					
	P1	P2	P3	P4	P5	P6
Area (m ²)	800	800	800	700	800	800
Altitude (m)	520	510	530	470	780	740
Topographic position	middle slope	lower slope	plateau	middle slope	ridge	alluvial terrace
Exposure	S-SW	S-SE	N-NW	SW	N-E	
Slope (°)	10–15	5–10	5–10	45–50	15	0–2
Canopy height (m)	25	18–20	18–20	15–18	15–18	18–25
Woody plant cover (%)	65	45–50	60	40–45	45–50	35–45
Herbaceous plant cover (%)	15–20	20–50	10–15	7–10	10–15	20
Litter thickness (cm)	1–2	1–2	0.2–0.5	0.5–5	4–6	3
Humus thickness (cm)	0–0.5	0	0	0	7–9	15–50
Soil characteristics	yellow-ochre clay	yellow-ochre clay-sand	yellow-ochre clay-sand	yellow-ochre clay-sand	yellow-ochre clay-sand	yellow-ochre clay with stones

Stratified sampling procedures were therefore used in the present study: 18 plots covering a total area of 14,100 m² were delimited along the altitudinal transect, situated on slopes (plots P1–P15) and along streams (R1–R3). The altitudinal and topographic distributions of the plots, as well as other physical and biological features, are presented in Tables 2-1 and 2-2. The locations of the plots were not selected at random; instead, each plot was established in an area in which both the vegetation and the physical characteristics of the milieu were considered to be homogeneous. Each plot had a rectangular or near rectangular form. The surface area of each plot was 800 m², except for P4 (700 m²) and P13, P14, and P15 (600 m² each), which were situated in narrow or fragmented biotopes. The abundance of each species was, however, always calculated (by extrapolation if necessary) for a standard area of 800 m². In each plot, two kinds of information were recorded. First, species abundance was coded on a non-linear scale according to the following categories: 1, a single individual or colony; 2, 2–4 individuals or colonies; 3, 5–9 individuals or colonies; 4, 10–19 individuals or colonies; 5, 20–49 individuals or colonies, and 6, more than 50 individuals or colonies. Second, the growth form of each species was noted, as follows: T/r, always terrestrial, or terrestrial and more rarely epilithic; E/r, always

epiphytic, or epiphytic and more rarely epilithic; R, strictly epilithic; L, lianescent; and T/E/r, terrestrial, epiphytic, or more rarely epilithic. The criteria used to assess homogeneity within a plot, the method used to count individuals and colonies, and the definitions of the growth forms used here are given in Rakotondrainibe and Raharimalala (1998). Epiphytic species in the upper layers of the forest were identified using binoculars, and as a consequence, at least for the smallest species in the families Hymenophyllaceae and Grammitidaceae, their density was almost certainly underestimated above 12–15 m.

Data Analysis

The floristic data collected from the plots were treated using two complementary types of multivariate analyses (SPAD, version 3): correspondence analysis (CA) and hierarchical ascending classification (HAC) (Benzécri & Benzécri, 1984; Lebart et al., 1997). Using a data matrix in which species were plotted against sample plots, application of these methods results in a double classification of columns (plots) and rows (species) in which plots with similar species composition (and therefore presumably similar environments) are grouped together. The relations among the various

TABLE 2-1. *Extended.*

Plot								
P7	P8	P9	P10	P11	P12	P13	P14	P15
800	800	600	800	800	800	600	600	600
820	1300	1290	1290	1540	1550	1530	1920	1900
middle slope	middle/lower slope	ridge	higher slope	lower slope	ridge	middle slope	ridge	lower slope
N	N-NE		N	E-SE	NE	S	E	N
20	15-20	0-5	20-30	15	5-15	10-15	15	5-10
18-20	18	8-12	18	12-15	2-8	10-12	1-3	6-8
50-60	30-35	40-50	40-45	20-35	30-35	40	25-40	35-40
25	25-30	30-40	10 + moss	35	30-50 (+ moss)	7	100 (moss)	40-50 (moss)
4-7	4-5	9-10	0	1-2	10-20	?	10-20	1-2
6-7	1	10-15	40-60	50-120	10-20	?	80	40
yellow-ochre clay-sand	yellow-ochre clay with stones	yellow-ochre clay-sand	yellow-ochre clay-sand	?	White clay-sand	yellow-ochre clay-sand		

elements of the matrix are measured using the χ^2 distance (Lebart et al., 1997).

HAC generates a tree or dendrogram comprising a hierarchical and progressive grouping of plot units and/or species units in sets of increasing size. The criterion used for grouping units into a class is the average of the weighted distances. CA generates scatter diagrams of plot and/or species points represented in the plane of pair-wise sets of axes resulting from the analysis. Each axis explains a percentage of the variance among the points. The dispersion of the clusters of points along a given axis is here an expression of an ecological gradient.

The data matrix used for the two analyses listed, in rows, all 194 species recorded in the plot studies, against columns representing each of the 18 plots sampled (P1-P15 and R1-R3). Each cell of the matrix contained the corresponding abun-

dance code (1-6) as defined above. The two analyses assess clusters of plots and/or species, which can then be interpreted with regard to their ecology. The relative contribution of a species to the variance expressed by a given axis will be higher when a species is both abundant and present in a limited number of plots. Species present in a cluster of plots are referred to as "characteristic" when their contribution to the fraction of the variance expressed by the axis by which the group was identified is $\geq 1.8\%$. "Exclusively characteristic" species are those that belong to a single cluster of plots, and "preferentially characteristic" species belong to at least two clusters. The threshold value of 1.8% was chosen a posteriori because it allows for the elimination of species that are too widely distributed, those that are infrequent, and those whose distribution is erratic. It should be noted that the concept of "character-

TABLE 2-2. Characteristics of PN de Marojejy study plots in forest located along streams.

Plot	Area (m ²)	Altitude (m)	Width of stream-bed (m)	Nature of streambed	Flow
R1	800 (200×4)	490-510	1-3	large granitic rocks + sand	gentle
R2	800 (200×4)	750-810	2-6	large granitic rocks + sand	variable with sudden flows
R3	800 (200×4)	1290-1310	2-4	large granitic rocks + sand	gentle

TABLE 2-3. Pteridophytes of PN de Marojejy: Floristic composition, habit type, and altitudinal distribution.

No.	Taxa	400– 550 m	740– 840 m	1250– 1350 m	1500– 2132 m	Habit type
1	* <i>Amauropelta bergiana</i> (Schltdl.) Holttum	–	–	+	+	T
2	* <i>Amauropelta</i> sp. 1 (FR 3349)	+	+	–	–	T
3	* <i>Angiopteris madagascariensis</i> de Vriese	+	–	–	–	T
4	<i>Antrophyum boryanum</i> (Willd.) Kaulf.	+	+	+	–	E
5	* <i>Antrophyum malgassicum</i> C. Chr.	+	+	–	–	E
6	* <i>Arthropteris monocarpa</i> (H. L. Cordem.) C. Chr.	–	+	+	–	T/E/r
7	* <i>Arthropteris orientalis</i> (J. F. Gmel.) Posth. var. <i>subbiaurita</i> (Hook.) C. Chr.	+	+	–	–	E
8	* <i>Arthropteris palisotii</i> (Desv.) Alston	+	–	–	–	E
9	* <i>Asplenium affine</i> Sw. var. indet. (FR 3430)	–	+	–	–	T
10	<i>Asplenium afzellii</i> Rosend.	+	+	+	+	T/E
11	* <i>Asplenium bipartitum</i> Bory ex Willd.	+	+	–	–	E
12	* <i>Asplenium cancellatum</i> Alston	+	+	–	–	E
13	<i>Asplenium cuneatum</i> Lam.	+	+	–	–	E/r
14	* <i>Asplenium dregeanum</i> Kunze	+	+	–	–	E/r
15	* <i>Asplenium friesiorum</i> C. Chr.	–	–	+	–	E
16	<i>Asplenium herpetopteris</i> Baker var. <i>herpetopteris</i>	+	+	+	+	E/r
17	* <i>Asplenium herpetopteris</i> Baker var. <i>acutipinnatum</i> (Bonap.) Tardieu	+	+	–	–	E
18	* <i>Asplenium herpetopteris</i> Baker var. <i>villosum</i> (Bonap.) Tardieu	+	+	–	–	E
19	* <i>Asplenium inaequilaterale</i> Willd.	+	+	–	–	T/r
20	<i>Asplenium marojejense</i> Tardieu	–	+	–	–	T/r
21	* <i>Asplenium nidus</i> L.	+	+	–	–	E
22	<i>Asplenium normale</i> D. Don	–	–	+	+	T
23	<i>Asplenium obscurum</i> Blume	–	+	–	–	T/r
24	<i>Asplenium pellucidum</i> Lam.	+	+	+	–	E/r
25	* <i>Asplenium petiolulatum</i> Mett.	–	+	–	–	E
26	<i>Asplenium sandersonii</i> Hook.	–	+	+	–	E
27	* <i>Asplenium thunbergii</i> Kunze	–	+	–	–	T/E
28	<i>Asplenium unilaterale</i> Lam. et A. aff. <i>unilaterale</i> (FR 3394)	+	+	+	–	T/r
29	<i>Asplenium variabile</i> Hook. var. <i>paucijugum</i> (F. Ballard) Alston	+	–	–	–	T/E
30	* <i>Asplenium</i> sp. nov. 1 ined. (FR 3357)	+	–	–	–	E/r
31	<i>Athyrium scandicinum</i> (Willd.) C. Presl var. <i>scandicinum</i>	–	–	+	+	T
32	* <i>Athyrium scandicinum</i> (Willd.) C. Presl var. <i>bipinnata</i> Rakotondr.	–	–	+	+	T
33	* <i>Belvisia spicata</i> (L.f.) Mirb.	+	+	+	+	E
34	* <i>Blechnum attenuatum</i> (Sw.) Mett.	–	+	+	–	T/E/r
35	* <i>Blechnum bakeri</i> (Baker) C. Chr.	–	–	+	–	R
36	<i>Blechnum humbertii</i> Tardieu	–	–	+	+	T
37	* <i>Blechnum ivohibense</i> C. Chr.	–	–	+	+	T
38	<i>Blechnum longepetiolatum</i> Tardieu.	–	–	–	+	T
39	<i>Blechnum madagascariense</i> Tardieu.	–	–	–	+	T
40	* <i>Blechnum simillimum</i> (Baker) Diels	+	+	+	+	T/E/r
41	* <i>Blechnum simillimum</i> (Baker) Diels fa. <i>binerve</i> (Hook.) Tardieu	–	–	–	+	T/r
42	* <i>Blechnum simillimum</i> (Baker) Diels var. <i>xiphophyllum</i> (Baker) Tardieu	–	–	+	–	T
43	<i>Blotiella coriacea</i> (Tardieu) Rakotondr. comb. nov.	–	–	+	+	T
44	* <i>Blotiella madagascariensis</i> (Hook.) Tryon	–	+	+	+	E
45	<i>Bolbitis auriculata</i> (Lam.) Alston	+	+	–	–	T/r
46	* <i>Bolbitis humblotii</i> (Baker) Ching	–	+	–	–	T
47	* <i>Cheilanthes</i> sp. nov. 1 ined. (FR 3621, 3692)	–	–	–	+	T
48	<i>Christella dentata</i> (Forssk.) Brownsey & Jermy	+	–	–	–	T
49	<i>Christella distans</i> (Hook.) Holttum	+	–	–	–	T
50	* <i>Cochlidium serrulatum</i> (Sw.) L. E. Bishop	–	+	+	+	E
51	<i>Coniogramme madagascariensis</i> C. Chr.	–	–	+	–	T

TABLE 2-3. *Continued.*

No.	Taxa	400– 550 m	740– 840 m	1250– 1350 m	1500– 2132 m	Habit type
52	* <i>Ctenitis ochrorachis</i> (Baker) Tardieu var. <i>violacea</i> Rakotondr.	–	+	+	–	T
53	* <i>Ctenitis poolii</i> (C. Chr.) Tardieu	+	–	–	–	T
54	* <i>Ctenitis warburii</i> (C. Chr.) Tardieu	+	–	–	–	T
55	* <i>Ctenitis</i> sp. nov. 1 ined. (FR 3558)	–	–	+	–	T
56	<i>Ctenopteris alboglandulosa</i> (Bonap.) Tardieu	–	–	+	+	E
57	* <i>Ctenopteris devoluta</i> (Baker) Tardieu	–	+	+	+	E
58	* <i>Ctenopteris elastica</i> (Bory) Copel.	+	+	+	–	E
59	* <i>Ctenopteris flabelliformis</i> (Poir.) J. Sm.	–	–	–	+	E
60	<i>Ctenopteris humbertii</i> (C. Chr.) Tardieu	–	–	–	+	E
61	* <i>Ctenopteris</i> sp. 1 cf. <i>C. humbertii</i> (FR 3484, 3615 bis)	–	–	+	+	E
62	* <i>Ctenopteris villosissima</i> (Hook.) Harley	–	–	+	+	E
63	* <i>Ctenopteris zenkeri</i> (Hieron.) Tardieu	–	+	+	–	E
64	* <i>Cyathea</i> aff. <i>albida</i> Tardieu	–	–	+	–	T
65	<i>Cyathea alticola</i> (Tardieu) Tindale	–	–	–	+	T
66	* <i>Cyathea approximata</i> Bonap.	–	–	+	+	T
67	* <i>Cyathea bellisquamata</i> Bonap. var. <i>basilobata</i> C. Chr.	–	–	+	+	T
68	* <i>Cyathea boivinii</i> Mett.	+	+	–	–	T
69	* <i>Cyathea borbonica</i> Desv. var. ? (FR 3282)	+	–	–	–	T
70	* <i>Cyathea bullata</i> (Baker) Rakotondr.	–	+	+	+	T
71	* <i>Cyathea bullata</i> (Baker) Rakotondr. var. <i>mada- gascariensis</i> (Bonap.) Rakotondr.	–	+	–	–	T
72	* <i>Cyathea costularis</i> Bonap.	+	+	–	+	T
73	* <i>Cyathea coursii</i> (Tardieu) Rakotondr.	–	–	+	–	T
74	* <i>Cyathea decrescens</i> Mett.	+	+	+	+	T
75	* <i>Cyathea dregei</i> Kunze	–	+	+	+	T
76	* <i>Cyathea dregei</i> Kunze var. <i>polyphlebia</i> C. Chr.	–	–	–	+	T
77	* <i>Cyathea ligulata</i> Tardieu	+	+	–	–	T
78	* <i>Cyathea longipinnata</i> Bonap.	+	–	–	–	T
79	* <i>Cyathea melleri</i> (Baker) Domin var. <i>melleri</i>	+	+	+	–	T
80	* <i>Cyathea perrieriana</i> C. Chr.	–	–	+	–	T
81	* <i>Cyathea serratifolia</i> Baker et <i>C. aff. serratifolia</i> (FR 3379)	–	+	–	–	T
82	* <i>Cyclosorus interruptus</i> (Willd.) H. Itô	–	+	–	–	T
83	* <i>Davallia chaerophylloides</i> (Poir.) Steud.	+	+	–	–	E
84	<i>Davallia repens</i> (L.f.) Kuhn (= <i>Humata repens</i> (L.f.) Diels)	+	+	–	–	E
85	* <i>Deparia parvisora</i> (C. Chr.) M. Kato et <i>D. aff.</i> <i>parvisora</i> (FR 3346)	+	+	+	–	T
86	* <i>Deparia</i> sp. 1 (FR 3445, 3447) et var. (FR 3446)	–	+	–	–	T
87	* <i>Dicranopteris linearis</i> (Burm.f.) Underw.	–	+	+	+	T
88	<i>Didymochlaena microphylla</i> (Bonap.) C. Chr.	–	+	–	–	T
89	* <i>Diplazium andapense</i> (Tardieu) Rakotondr.	–	–	+	–	T
90	* <i>Diplazium dilatatum</i> Blume	–	+	–	–	T
91	<i>Diplazium nemorale</i> (Baker) Schelpe	+	+	–	–	T
92	* <i>Diplazium proliferum</i> (Lam.) Thouars	+	+	–	–	T
93	* <i>Drynaria willdenowii</i> (Bory) T. Moore	+	–	–	–	E
94	* <i>Dryopteris mangindranensis</i> Tardieu	–	+	+	–	T
95	* <i>Elaphoglossum achroalepis</i> (Baker) C. Chr.	–	–	–	+	E
96	<i>Elaphoglossum acrostichoides</i> (Hook. & Grev.) Schelpe	–	–	+	+	T/E
97	* <i>Elaphoglossum angulatum</i> (Blume) T. Moore	–	–	–	+	T
98	* <i>Elaphoglossum aubertii</i> (Desv.) T. Moore	–	–	+	+	T/E
99	* <i>Elaphoglossum decaryanum</i> Tardieu	–	+	–	–	E
100	* <i>Elaphoglossum deckenii</i> (Kuhn) C. Chr. var. <i>rufi- dulum</i> (Willd. ex Kuhn) Tardieu	–	–	+	+	E
101	<i>Elaphoglossum forsythii-majoris</i> H. Christ	–	–	–	+	E

TABLE 2-3. *Continued.*

No.	Taxa	400– 550 m	740– 840 m	1250– 1350 m	1500– 2132 m	Habit type
102	* <i>Elaphoglossum humbertii</i> C. Chr.	–	–	+	+	E
103	<i>Elaphoglossum leperancluii</i> (Fée) Moore	–	+	–	+	T/E
104	* <i>Elaphoglossum leucolepis</i> (Baker) Krajina ex Tardieu	–	+	+	+	E
105	<i>Elaphoglossum marojejense</i> Tardieu	–	+	–	–	E
106	* <i>Elaphoglossum petiolatum</i> (Sw.) Urb. ssp. <i>salici-</i> <i>folium</i> (Willd. ex Kaulf.) Schelpe	–	+	–	–	E/r
107	* <i>Elaphoglossum scolopendriforme</i> Tardieu et E. aff. <i>scolopendriforme</i>	–	+	+	+	E
108	<i>Elaphoglossum</i> aff. <i>sieberi</i> (Hook. & Grev.) T. Moore	+	+	+	+	E
109	<i>Elaphoglossum spathulatum</i> (Bory) T. Moore	+	–	–	–	R
110	* <i>Elaphoglossum subsessile</i> (Baker) C. Chr.	–	+	+	+	T/E
111	* <i>Elaphoglossum</i> sp. 5 (FR 3458, 3472, 3475, 3611, 3701)	–	+	+	+	E
112	* <i>Elaphoglossum</i> sp. 6 (FR 3496, 3514, 3520, 3550, 3616)	–	–	+	+	T/E
113	* <i>Elaphoglossum</i> sp. 7 (FR 3574, 3582, 3607)	–	–	+	+	E
114	* <i>Elaphoglossum</i> sp. 10 (FR 3485, 3488, 3489, 3646, 3408)	–	+	+	+	E
115	* <i>Elaphoglossum</i> sp. 11 (FR 3468, 3593)	–	–	+	+	T/E
116	* <i>Gleichenia madagascariensis</i> C. Chr.	–	–	–	+	T
117	* <i>Gleichenia polypodioides</i> (L.) J. E. Smith.	–	–	–	+	T
118	<i>Grammitis barbatula</i> (Baker) Copel.	–	–	+	–	E
119	* <i>Grammitis copelandii</i> Tardieu	–	–	+	+	E
120	<i>Grammitis cryptophlebia</i> (Baker) Copel.	–	–	–	+	E
121	* <i>Grammitis ebenina</i> (Maxon) Tardieu	–	–	+	+	E
122	<i>Grammitis gilpiniae</i> (Baker) Tardieu	–	+	+	+	E
123	<i>Grammitis holophlebia</i> (Baker) Copel.	–	–	+	+	E
124	* <i>Grammitis kyimbilensis</i> (Brause) Copel.	–	+	+	–	E
125	* <i>Grammitis microglossa</i> (C. Chr.) Ching	–	–	–	+	E
126	* <i>Grammitis obtusa</i> Willd. ex Kaulf.	–	–	–	+	E
127	<i>Grammitis synsora</i> (Baker) Copel.	–	+	–	–	E
128	* <i>Grammitis</i> sp. 1 (FR 3589, 3629, 3668, 3668 bis)	–	–	+	+	E
129	* <i>Grammitis</i> sp. 3 (FR 3663)	–	–	–	+	E
130	* <i>Histiopteris incisa</i> (Thunb.) J. Sm.	–	–	–	+	T
131	* <i>Huperzia cavifolia</i> (C. Chr.) Tardieu	+	+	+	–	E
132	* <i>Huperzia megastachya</i> (Baker) Tardieu	+	+	+	+	T/E
133	* <i>Huperzia obtusifolia</i> (P. Beauv.) Rothm.	–	–	–	+	T
134	* <i>Huperzia ophioglossoides</i> (Lam.) Rothm.	+	+	–	+	E
135	* <i>Huperzia pecten</i> (Baker) Tardieu	–	+	+	–	E
136	* <i>Huperzia suberecta</i> (Lowe) Tardieu	–	–	–	+	R
137	* <i>Huperzia squarrosa</i> (G. Forst.) Trevis.	–	–	+	+	E
138	* <i>Huperzia trigona</i> (C. Chr.) Tardieu	–	–	+	+	E
139	* <i>Huperzia verticillata</i> (L.f.) Trevis.	–	–	+	+	E
140	* <i>Hymenophyllum capillare</i> Desv. var. ? (FR 3487)	–	–	+	+	E
141	* <i>Hymenophyllum deltoideum</i> C. Chr.	–	–	+	+	E
142	* <i>Hymenophyllum fumaroides</i> Willd. et <i>H.</i> aff. <i>fu-</i> <i>marioides</i> (FR 3365, 3652, 3700)	–	–	–	+	T/E
143	* <i>Hymenophyllum heimii</i> Tardieu	–	–	+	+	E
144	<i>Hymenophyllum hirsutum</i> (L.) Sw.	–	+	+	+	T/E/r
145	* <i>Hymenophyllum humbertii</i> C. Chr.	–	–	+	+	T/E
146	* <i>Hymenophyllum inaequale</i> (Poir.) Desv.	–	–	+	+	E
147	* <i>Hymenophyllum parvum</i> C. Chr. (= <i>H. capense</i> Schräd.)	–	+	+	+	E
148	* <i>Hymenophyllum polyanthos</i> (Sw.) Sw.	–	+	+	+	E
149	* <i>Hymenophyllum poolii</i> Baker	–	–	+	+	T/E
150	* <i>Hymenophyllum sibthorpioides</i> Mett.	–	+	+	+	T/E
151	* <i>Hymenophyllum tunbrigense</i> (L.) Smith	–	–	+	+	E

TABLE 2-3. *Continued.*

No.	Taxa	400– 550 m	740– 840 m	1250– 1350 m	1500– 2132 m	Habit type
152	<i>*Hymenophyllum veronicoides</i> C. Chr.	–	–	+	–	E
153	<i>*Hymenophyllum viguieri</i> Tardieu	+	–	–	+	E
154	<i>*Lastreopsis subsimilis</i> (Hook.) Tindale	–	–	+	–	T
155	<i>Lepisorus excavatus</i> (Bory ex Willd.) Moore	–	+	+	+	E
156	<i>*Lindsaea blotiana</i> K. U. Kramer	–	+	+	+	T
157	<i>*Lindsaea coursii</i> (Tardieu) K. U. Kramer	–	–	+	+	E
158	<i>*Lindsaea ensifolia</i> Sw.	–	+	–	–	T
159	<i>Lindsaea flabellifolia</i> (Baker) Kuhn	–	+	+	–	T
160	<i>Lindsaea goudotiana</i> (Kunze) Kuhn	–	–	+	–	E
161	<i>*Lindsaea madagascariensis</i> Baker	–	–	–	+	E
162	<i>*Lindsaea millefolium</i> K. U. Kramer	–	+	–	–	T/E
163	<i>*Lindsaea odontolabia</i> (Baker) K. U. Kramer	–	+	–	–	E
164	<i>Lindsaea odorata</i> Roxb.	–	–	–	+	R
165	<i>*Lindsaea sp. nov. 1</i> (FR 3605)	–	–	–	+	T/E
166	<i>*Lomariopsis crassifolia</i> Holttum	–	+	–	–	T/E
167	<i>Loxogramme humblotii</i> C. Chr.	+	+	–	–	E/r
168	<i>Loxogramme lanceolata</i> (Sw.) C. Presl. et <i>L. aff. lanceolata</i> (FR 3645)	+	+	+	+	E
169	<i>*Lycopodiella caroliniana</i> (L.) Pic. Serm.	–	–	–	+	T
170	<i>*Lycopodiella cernua</i> (L.) Pic. Serm.	–	+	+	+	T
171	<i>*Lycopodium zanclophyllum</i> Wilce	–	–	–	+	T
172	<i>*Lygodium lanceolatum</i> Desv.	+	–	–	–	L
173	<i>*Macrothelypteris torresiana</i> (Gaudich.) Ching	+	+	–	–	T
174	<i>*Marattia fraxinea</i> Sm. ex J. F. Gmel.	+	+	+	–	T
175	<i>Microlepia madagascariensis</i> C. Presl	+	+	+	–	T
176	<i>Microsorium punctatum</i> (L) Copel.	+	+	+	–	E
177	<i>*Monogramma graminea</i> (Poir.) Schkuhr	+	+	–	–	E
178	<i>Nephrolepis biserrata</i> (Sw.) Schott	+	+	–	–	T/E/r
179	<i>*Nephrolepis tuberosa</i> (Bory) C. Presl	–	+	+	–	E
180	<i>Odontosoria melleri</i> (Hook.) C. Chr.	–	+	–	+	T
181	<i>Oleandra distenta</i> Kunze	+	+	+	–	E
182	<i>Ophioglossum palmatum</i> L.	–	–	–	–	E
183	<i>Ophioglossum pendulum</i> L.	+	–	–	–	E
184	<i>*Pellaea angulosa</i> (Bory) Baker	–	+	–	–	T
185	<i>Phymatosorus scolopendria</i> (Burm. f.) Pic. Serm.	+	+	+	–	E
186	<i>*Pityrogramma calomelanos</i> (L.) Link	+	–	–	–	T
187	<i>*Pityrogramma humbertii</i> C. Chr.	–	–	–	+	T
188	<i>Pityrogramma humbertii</i> C. Chr. var. ? (FR 3687)	–	–	–	+	T
189	<i>*Platycerium madagascariense</i> Baker	–	+	+	–	E
190	<i>*Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.	+	–	–	+	E
191	<i>Pneumatopteris remotipinna</i> (Bonap.) Holttum	+	+	+	+	T
192	<i>Pneumatopteris subpennigera</i> (C. Chr.) Holttum	–	+	+	–	T
193	<i>Pseudocyclosorus pulcher</i> (Bory ex Willd.) Holttum	–	+	–	–	T
194	<i>*Pseudophegopteris cruciata</i> (Willd.) Holttum	–	+	–	–	T
195	<i>*Pteris catoptera</i> Kunze et <i>P. aff. catoptera</i> (FR 3584)	+	+	+	–	T
196	<i>*Pteris cretica</i> L.	–	+	–	–	T
197	<i>*Pteris elongatiloba</i> Bonap. var. <i>remotivenia</i> Bonap.	+	–	–	–	T
198	<i>*Pteris pseudolonchitis</i> Bory ex Willd.	–	+	–	–	T
199	<i>*Pteris woodwardioides</i> Bory ex Willd.	+	–	–	–	T
200	<i>*Pyrrosia rhodesiana</i> (C. Chr.) Schelpe	–	+	–	–	E
201	<i>Rumohra adiantiformis</i> (G. Forst.) Ching	+	+	+	+	E
202	<i>Rumohra lokohoensis</i> Tardieu	–	–	+	+	T/E
203	<i>Saccoloma henriettae</i> (Baker) C. Chr.	–	–	+	+	T
204	<i>*Schizaea dichotoma</i> L.	+	+	–	–	T
205	<i>*Schizaea pectinata</i> (L.) Sw.	–	–	–	+	T
206	<i>*Selaginella fissidentoides</i> (Hook. & Grev.) Spring fa <i>fissidentoides</i>	+	+	–	–	T

TABLE 2-3. *Continued.*

No.	Taxa	400– 550 m	740– 840 m	1250– 1350 m	1500– 2132 m	Habit type
207	* <i>Selaginella goudotana</i> Spring var. <i>goudotana</i>	–	+	–	–	T
208	* <i>Selaginella hildebrandtii</i> A. Braun ex Hieron.	–	+	–	–	T/r
209	* <i>Selaginella pervillei</i> Spring	+	–	–	–	T
210	* <i>Selaginella polymorpha</i> Badre (= <i>S. pectinata</i> Spring)	+	+	+	–	T
211	* <i>Selaginella unilateralis</i> Spring	–	–	+	+	T
212	<i>Sphaerostephanos arbuscula</i> (Willd.) Holttum	–	+	–	–	T
213	* <i>Sphenomeris chinensis</i> (L.) Maxon	–	+	–	–	T
214	* <i>Stenochlaena tenuifolia</i> (Desv.) Moore	+	+	–	–	T/E
215	* <i>Sticherus flagellaris</i> (Bory) St John	–	+	+	+	T
216	<i>Tectaria gemmifera</i> (Fée) Alston et <i>T. aff. gemmifera</i> (FR 3281)	+	–	–	–	T
217	<i>Tectaria humbertiana</i> Tardieu	–	+	–	–	T
218	* <i>Tectaria magnifica</i> (Bonap.) Tardieu	–	+	–	–	T
219	* <i>Trichomanes bipunctatum</i> Poir.	+	+	+	–	E
220	* <i>Trichomanes bonapartei</i> C. Chr.	+	+	+	+	E
221	* <i>Trichomanes borbonicum</i> Bosch	–	+	+	+	E/r
222	<i>Trichomanes cupressoides</i> Desv.	+	+	+	+	T/r
223	* <i>Trichomanes digitatum</i> Sw.	–	+	+	+	E
224	* <i>Trichomanes erosum</i> Willd.	+	+	+	+	E
225	* <i>Trichomanes lenormandii</i> Bosch	+	+	+	–	E
226	* <i>Trichomanes longilabiatum</i> Bonap.	+	–	–	–	R
227	* <i>Trichomanes meifolium</i> Bory ex Willd.	–	+	+	+	T/E
228	* <i>Trichomanes montanum</i> Hook.	–	+	+	–	E
229	* <i>Trichomanes montanum</i> Hook. var. ? (FR 3339)	+	–	+	–	E/r
230	* <i>Trichomanes rigidum</i> Sw.	–	+	+	+	T
231	<i>Trichomanes speciosum</i> Willd.	+	–	+	–	L
232	<i>Vittaria ensiformis</i> Sw.	+	+	–	–	E
233	* <i>Vittaria humblotii</i> Hieron.	–	+	+	–	E
234	<i>Vittaria scolopendrina</i> (Bory) Thwaites	+	–	–	–	E
235	<i>Xiphopteris mysuroides</i> (Sw.) Kaulf.	–	–	–	+	E
236	* <i>Xiphopteris oosora</i> (Baker) Alston var. <i>micropecten</i> C. Chr.	–	–	–	+	E
237	* <i>Xiphopteris sikkimensis</i> (Hieron.) Copel.	–	–	–	+	E
238	* <i>Xiphopteris</i> sp. 3 (FR 3613, 3680)	–	–	–	+	E
239	* <i>Xiphopteris</i> sp. 4 (FR 3519)	–	–	+	–	E

Species endemic to Madagascar are indicated in **boldface type**. Species endemic to PN de Marojejy are indicated in **boldface type and underlined**.

* New records for PN de Marojejy.

T = terrestrial; E = epiphytic; R = strictly epilithic; r = occasionally epilithic; L = lianescent; + = present; – = absent; FR = initials of the collector's name, France Rakotondrainibe.

istic" species in the present context is based on the ecological amplitude of one species and its abundance, rather than on its constancy in a vegetation unit, as often utilized by phytosociologists.

Results

General Floristic Inventory

SPECIES RICHNESS—Table 2-3 lists all the taxa observed on the eastern slope and in the summit

area of the PN de Marojejy, inside and outside the 18 plots, between 400 and 2132 m altitude, and indicates the growth form (terrestrial, epiphytic, or epilithic) and altitudinal distribution of each taxon. The delimitation of the altitudinal zones is explained below.

A total of 239 species and varieties of pteridophytes, representing 70 genera, were identified. The most speciose genera are *Asplenium* (20 spp. and 2 varieties), *Elaphoglossum* (21 spp.), *Cyathea* (16 spp. and 2 varieties), *Hymenophyllum* (14 spp.), *Trichomanes* (13 spp. and 1 variety), *Grammitis* (12 spp.), *Lindsaea* (10 spp.), *Blechn-*

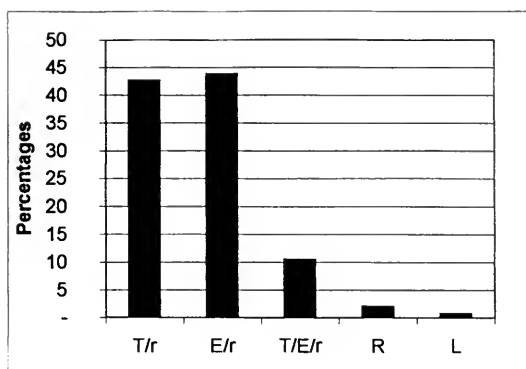


FIG. 2-2. Percentages of the whole pteridophyte flora (239 species and varieties listed in Table 2-3) by habit type in the PN de Marojejy. T/r = always terrestrial or terrestrial and more rarely epilithic; E/r = always epiphytic or epiphytic and more rarely epilithic; R = strictly epilithic; L = lianescent; T/E/r = terrestrial, epiphytic or more rarely epilithic.

num (7 spp. and 2 varieties), *Huperzia* (9 spp.), and *Ctenopteris* (8 spp.). The 171 taxa marked with an asterisk in Table 2-3 are new records for the PN de Marojejy.

ENDEMISM—The 105 reserve species endemic to Madagascar are indicated in Table 2-3 by bold characters; they represent 43.9% of the pteridophyte flora of the park. An additional 18 species are endemic to the Malagasy region, which includes Madagascar, the Mascarenes (Réunion, Mauritius, and Rodrigues), the Seychelles, and the Comoro Islands, bringing the total number of regional endemics to 123 taxa (51.5% of the total).

Among the species endemic to the Marojejy Massif, only six have been observed during the present expedition on the eastern slope: *Blechnum longepetiolatum*, *Cheilanthes* sp. nov. 1, *Cyathea alticola*, *Elaphoglossum* sp. nov. 11, *Lindsaea* sp. nov. 1, and *Tectaria humberiana*. Several other endemic species were collected by Humbert on the western slope of the massif and nearby areas, including *Asplenium andapense* Tardieu, *Deparia marojejensis* (Tardieu) Kato, *Diplazium marojejense* (Tardieu) Rakotondr., and *Elaphoglossum cerussatum* Tardieu. Among the other species considered by Tardieu as endemic to Marojejy, *Blotiella coriacea* was recorded by Perrier de la Bâthie (Bâthie, no. 15297P!) in the Tsaratanana Massif, and *Asplenium marojejense*, *Blechnum humberii*, and *Elaphoglossum marojejense* have since been recorded by the present author in other reserves within the country (Rakotondrainibe & Quansah, 1994; Rakotondrainibe & Raharimalala,

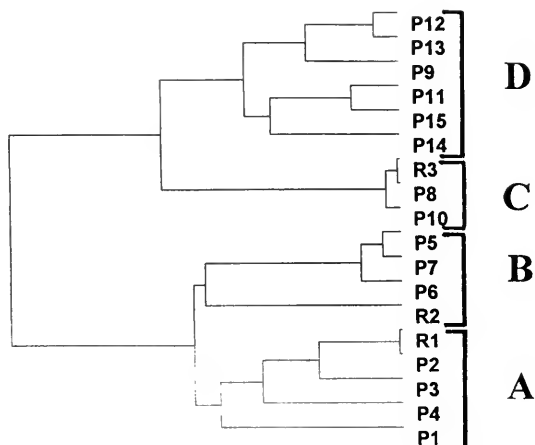


FIG. 2-3. Hierarchical ascending classification (HAC) tree using a matrix of 18 plots (P1–P15, R1–R3) and 194 species of pteridophytes recorded in the PN de Marojejy. The criterion used for grouping units into a class is the average of the weighed distances.

1996, 1998). One widespread species, *Arthropteris palisotii*, is currently known in Madagascar only from the Marojejy Massif, but additional populations occur in West Africa, the Comoros, Sri Lanka, Java, and several areas in Oceania (Tardieu-Blot, 1964).

GROWTH FORMS—The percentage of each habit type represented in Figure 2-2 was calculated using the data in Table 2-3. Approximately equal percentages of pteridophyte species and varieties are either (1) terrestrial or more rarely epilithic (T/r) (42.7%) or (2) epiphytic or epiphytic and more rarely epilithic (E/r) (43.9%); 10.5% of the taxa are variously terrestrial, epiphytic, or epilithic (T/E/r), whereas strictly epilithic (R) (2.1%) or lianescent species (L) (0.8%) are rare.

Distribution of Taxa

ECOLOGICAL GRADIENTS AND CHARACTERISTIC TAXA—The tree obtained by HAC from the data matrix (not given here) of the study plots (P1–P15 and R1–R3) against the 194 species recorded collectively in all the plots is presented in Figure 2-3. By sectioning the tree between nodes 32 and 33, four groups of plots are defined on the basis of their floristic composition: group A (P1, P2, P3, P4, R1), group B (P5, P6, P7, R2), group C (P8, P10, R3), and group D (P9, P11, P12, P13, P14, P15).

Using the positions of groups A through D,

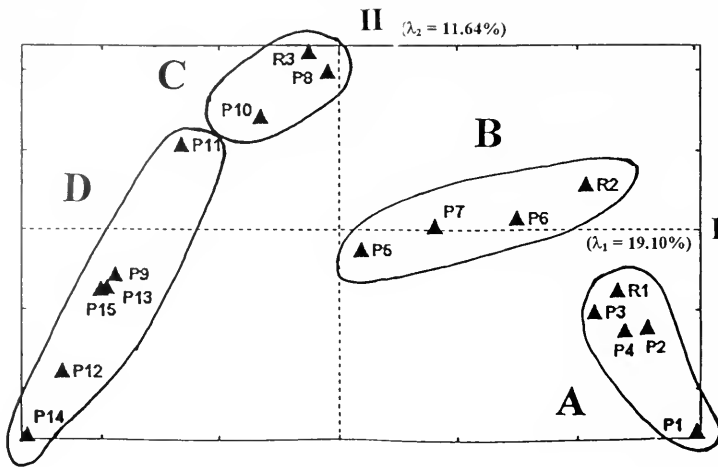


FIG. 2-4. Correspondence analysis (CA) of the matrix of 18 plots and 194 pteridophyte species recorded in the PN de Marojejy: projection on axes I and II of all the plots (P1–P15, R1–R3). Group A = plots at low altitude (470–530 m); group B = plots at middle altitude (740–820 m); group C = plots at middle altitude (1290–1310 m); group D = plots at high altitude (1530–1920 m).

axes I–II (Fig. 2-4), I–III (Fig. 2-5), and I–IV (Fig. 2-6), and the ecological information given in Table 2-1 and 2-2, it is possible to evaluate the ecological gradients responsible for the floristic heterogeneity among pteridophytes on the eastern slope of the Marojejy Massif. Axes I, II, and IV show the same altitudinal gradient, whereas axis III reflects a topographic gradient that is striking but localized. Along axis I, group A, comprising plots at low altitude (470–530 m), is separated

from group D, made up of plots at high altitude (1530–1920 m), whereas groups B (740–820 m) and C (1290–1310 m), at middle altitudes, occupy an intermediate position on this axis. Axis II separates groups A and B and groups C and D, respectively. The projection of plot points on axes I–IV shows fine-scale heterogeneity among the plots constituting group D, which can be further divided into two subgroups, D1 (P9, P12, P13) and D2 (P11, P14, P15), as indicated in Figure

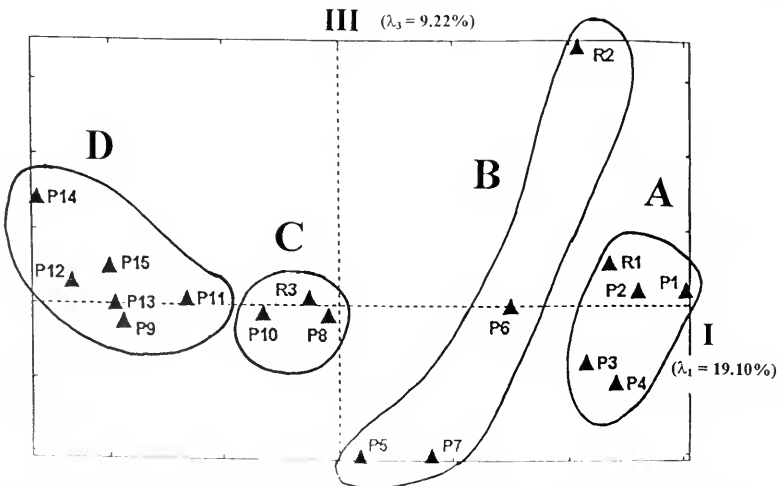


FIG. 2-5. Correspondence analysis (CA) of the matrix of 18 plots and 194 pteridophytes species recorded in the PN de Marojejy: projection on axes I and III of all the plots (P1–P15, R1–R3). Group A = plots at low altitude (470–530 m); group B = plots at middle altitude (740–820 m); group C = plots at middle altitude (1290–1310 m); group D = plots at high altitude (1530–1920 m).

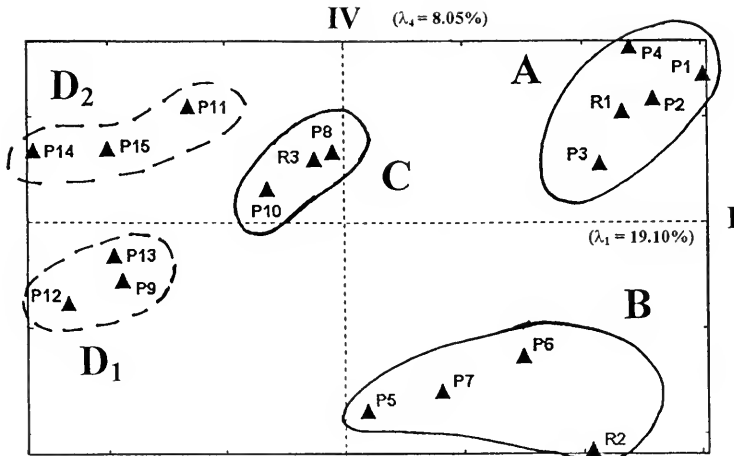


FIG. 2-6. Correspondence analysis (CA) of the matrix of 18 plots and 194 pteridophytes species recorded in the PN de Marojejy: projection on axes I and IV of all the plots (P1–P15, R1–R3). Group A = plots at low altitude (470–530 m); group B = plots at middle altitude (740–820 m); group C = plots at middle altitude (1290–1310 m); group D = plots at high altitude (1530–1920 m).

2-6 and in the dendrogram of Figure 2-3. In Figure 2-5 the parcels belonging to group B are scattered along axis III in relation to their topographic position: plots P7 and P5, situated respectively on a ridge and mid-slope, have negative values; plot R2, located along the banks of a creek, has a positive value; plot P6, however, on a raised alluvial terrace, has an intermediate value. It should be noted that the position of plot P9 on both the tree and the two-dimensional projections is not consistent with the overall pattern of altitudinal distribution described above. Instead, although this plot is located at 1290 m, it clearly belongs to group D on the basis of its floristic composition. The distinctive topographic position of plot P9, on a ridge that is exposed to the elements, is probably sufficient to explain this anomaly. This plot was established on a very narrow, straight, nearly flat ridge with abrupt slopes on both sides that further accentuate the ridge effect. Moreover, the physiognomy of the vegetation in P9 is exceptional for this altitude; it is a low forest about 8–12 m tall (Table 2-1) and comprised of trees whose twisted branches are covered with epiphytes.

On the basis of floristic composition of the pteridophytes in the plots, four altitudinal zones can thus be recognized on the eastern slope of the PN de Marojejy (as indicated in the column headings of Table 2-3):

Zone A, at low altitude, studied at plots between 400 and 550 m (P1, P2, P3, P4, R1)

Zone B, at lower mid-altitude, studied between 740 and 840 m (P5, P6, P7, R2)

Zone C, at upper mid-altitude, studied between 1250 and 1350 m (P8, P10, R3)

Zone D, at high altitude, studied between 1500 and 1900 m (P9, P11, P12, P13, P14, P15)

The sampling method used did not, however, permit a precise determination of the upper and lower altitudinal limits of these zones. On the other hand, it was possible to detect the influence of topography on the species composition of the pteridophytes, which appeared to be restricted to zone B, between 740 and 840 m.

Plot P9, at 1290 m on a ridge, has been included in zone B on the basis of its floristic composition, even though it occurs considerably higher on Marojejy. This reassignment only emphasizes how difficult it is to establish fixed altitudinal limits between floristic zones whose distribution is influenced not only by altitude but also by local topographic conditions.

The 49 characteristic species (including both exclusively and preferentially characteristic species) for each of the altitudinal and/or topographic zones (ridges, mid-slopes, bottomlands, and creek banks) are listed in Table 2-7. As indicated above, each of these species contributes at least 1.8% to the variance of one or more of the four axes defined in the factorial analysis, in particular to axes

TABLE 2-4. Percentages of the pteridophyte flora (239 species and varieties listed in Table 2-3) by habit types for each altitudinal zone in PN de Marojejy.

Habit type	Zone A 400– 550 m	Zone B 740– 840 m	Zone C 1250– 1350 m	Zone D 1500– 2132 m
T/r	40.2	43.1	32.8	34.5
E/r	47.5	45.4	52.5	48.7
T/E/r	7.3	11.5	13.1	15.0
R	2.5	0.0	0.8	1.0
L	2.5	0.0	0.8	0.0

T/r = always terrestrial or terrestrial and more rarely epilithic; E/r = always epiphytic or epiphytic and more rarely epilithic; R = strictly epilithic; L = lianescent; T/E/r = terrestrial, epiphytic, or more rarely epilithic.

I, II, and IV for the altitudinal indicator species and to axis III for the topographic indicators.

FLORISTIC CHARACTERISTICS OF THE ALTITUDINAL ZONES—Percentages of the pteridophyte flora (239 species and varieties listed in Table 2-3) by habit type for each altitudinal zone are indicated in Table 2-4. Table 2-5 shows the total number of species and genera of the whole pteridophyte flora (i.e., the generic and overall species richness) for each altitudinal zone, along with the number and percentage of species endemic to Madagascar and the mean number of species per 800 m² plots (species density). Table 2-6 lists the largest genera and the number of species and varieties belonging to them that occur within each altitudinal zone. The highest generic and species richness occurred in zone B (56 genera and 130 species), whereas the greatest species density was observed at a somewhat higher altitude, in zone C (60 species/800 m²). The level of species endemism increases progressively with altitude, from 36.6% in zone A to a maximum of 49.5% in zone D. The percentage of epiphytic species is always higher than for terrestrial taxa, regardless of altitude, and reaches a maximum value between 1250 and 1350 m in zone C. However, the percentage of species that

TABLE 2-6. Species richness for each altitudinal zone of the 10 largest pteridophyte genera in PN de Marojejy.

Genus	Zone A 400– 550 m	Zone B 740– 840 m	Zone C 1250– 1350 m	Zone D 1500– 2132 m	Total 400– 2132 m
<i>Asplenium</i>	14	18	7	3	22
<i>Elaphoglossum</i>	2	10	13	17	21
<i>Cyathea</i>	7	9	9	8	18
<i>Hymenophyllum</i>	1	4	12	13	14
<i>Grammitis</i>	0	3	8	10	12
<i>Trichomanes</i>	8	10	12	7	13
<i>Lindsaea</i>	0	5	4	5	10
<i>Huperzia</i>	3	4	6	7	9
<i>Blechnum</i>	1	2	6	6	9
<i>Ctenopteris</i>	1	3	6	6	8

can be either epiphytic or terrestrial increases with altitude, as the moss layer on the ground becomes more widespread and thicker. Above 1500 m, and especially near 1800 m, the moss coat present on tree trunks and branches is continuous with the thick layer on the ground, sometimes making it difficult to distinguish between epiphytic and terrestrial species. Above 2000 m the forest gives way to a high-altitude xerophytic grassland in which all the fern species are terrestrial.

The generic and species composition of the pteridophyte flora on the eastern slope of Marojejy changes with altitude, as follows (cf. Tables 2-6 and 2-7):

Between 400 and 550 m, the genera *Asplenium* (14 spp.), *Trichomanes* (8 spp.), and *Cyathea* (7 spp.) are the most speciose. Three exclusively characteristic species occur, as well as three preferentially characteristic species.

Between 740 and 840 m, the same three genera are represented by a large number of species, *Asplenium* (18 spp.), *Trichomanes* (10 spp.), and *Cyathea* (9 spp.), along with *Elaphoglos-*

TABLE 2-5. Generic richness, species richness, and endemism rate of the pteridophyte flora (239 species listed in Table 2-3) and mean number of species per 800 m² plots, for each altitudinal zone in PN de Marojejy.

Character	Zone A 400–550 m	Zone B 740–840 m	Zone C 1250–1350 m	Zone D 1500–2132 m
Number of genera	41	56	43	33
Total number of species	82	130	122	113
Number of Malagasy-endemic species	30	49	55	55
Percentage of Malagasy-endemic species	36.6	37.7	45.1	49.5
Mean number of species/800 m ²	30.2	48.0	60.0	38.3

sum (10 spp.). There are many more exclusively characteristic species (9) and preferentially characteristic species (8).

Between 1250 and 1350 m, *Elaphoglossum* is even more speciose (13 spp.), as are *Hymenophyllum* (12 spp.) and *Trichomanes* (12 spp.); the genera *Cyathea* (9 spp.) and *Grammitis* (8 spp.) are also well represented. Only one exclusively characteristic species is present, but 6 preferentially characteristic species were recorded.

Between 1500 and 2132 m altitude, *Elaphoglossum* (17 spp.) is particularly diversified, along with *Hymenophyllum* (13 spp.) and *Grammitis* (10 spp.). Five exclusively characteristic species and 2 preferentially characteristic species are found here.

Zone C, between 1250 and 1350 m, exhibits features typical of a transition zone, with a greater number of preferentially characteristic species than exclusively characteristic species. Zone C also shows a sharp decrease in the number of taxa belonging to *Asplenium*, which is a dominant genus at lower altitudes, coupled with a marked increase in species diversity in *Elaphoglossum* and *Hymenophyllum*, both of which are especially well represented at higher altitudes in zone D.

Discussion

Sampling Quality—Rare Taxa

A total of 239 species and varieties of pteridophytes were recorded on Marojejy. Of that total, 194 taxa (81.2%) were present in one or more of the 18 sample plots examined. Among the 45 remaining pteridophytes, observed only outside the plots, some are rare within the reserve or even in Madagascar as a whole, including *Asplenium affine*, *A. obscurum*, *Bolbitis humblotii*, *Cyathea borbonica* var. ?, *C. bullata* var. *madagascariensis*, *C. aff. albida*, *C. longipinnata*, *C. serratifolia*, *Drynaria wildenowii*, *Elaphoglossum forsythii-majoris*, *E. spatulatum*, *Grammitis barbatula*, *Huperzia obtusifolia*, and *Selaginella goudotiana* each of which was seen only once or twice. Several other rare pteridophytes are known from only one to four localities in the entire country, including *Blechnum simillimum* var. *xiphophyllum*, *Cheilanthes* sp. nov. 1, *Ctenitis warburii*, *C.* sp. nov. 1, *Ctenopteris* sp. aff. *humbertii*, *Diplazium*

dilatatum, *Grammitis microglossa*, *Huperzia saururus*, *Lastreopsis subsimilis*, *Lindsaea ensifolia*, *L. odontolabia*, *Tectaria humbertiana*, *Trichomanes longilabiatum*, and *Xiphopteris* sp. nov. 4. Other species are restricted to narrow and fragmented biotopes in which it would be difficult or impossible to delimit 800 m² plots that contain a homogeneous vegetation. These include *Blechnum bakeri* and *B. ivohibense*, which occur preferentially at the bases of large rocks; *Cyclosorus interruptus*, which grows in swampy areas; *Macrothelypteris torresiana* and *Odontosoria melleri*, which are found in open areas; and *Elaphoglossum petiolatum* ssp. *salicifolium*, *Lindsaea odorata*, *Pityrogramma calomelanos*, *Sphaerostephanos arbuscula*, and *Sphenomeris chinensis*, which colonize rocky banks of rivers and streams. In addition, three species and one variety (*Lycopodiella caroliniana*, *Pityrogramma humbertii*, *P. humbertii* var. ?, and *Schizaea pectinata*) appear to be restricted on Marojejy to xerophytic grasslands found above the upper limit of forests, between 2000 and 2132 m, a biotope that has a total of only eight pteridophyte species and that was not sampled quantitatively as part of the present study. In all, only one species and two varieties of pteridophytes known to occur rather frequently in forest habitats on Marojejy were absent from the study plots: *Asplenium herpetopteris* var. *acutipinnata*, *Athyrium scandicinum* var. *bipinnata*, and *Nephrolepis tuberosa*.

The shapes of the species–area curves (Figs. 2-7A–D) indicate that the sample plots are both floristically homogeneous and representative of the biotopes in which they were located. The curves for the 18 plots are regular and give no indication of intermediate plateaus, suggesting that the boundaries of each plot fell entirely within a single biotope. Each of the curves shows a clear asymptote, except for P13 (Fig. 2-7D), which covered only 600 m², and P8, P10, and R3 (Fig. 2-7C), which had particularly rich pteridophyte floras, with about 60 species each. For pteridophytes, the minimal plot size needed in the PN de Marojejy to establish a nearly complete sample of the floristic composition thus appears to be between 600 and 1,000 m², the precise size being a function of the level of species richness of the biotope sampled. In practice it is often difficult to establish plots as large as 1,000 m² in which the vegetation is homogeneous, especially at higher altitudes above 1500 m and on ridges. The average value of 800 m² adopted for the present study thus

TABLE 2-7. List of exclusive (Ex.) and preferential (Pr.) characteristic species* and ecological preferences of each species in PN de Marojejy.

No.	Taxa	Zone							Preferential biotope
		A	B	C	D	A + B	B + C	C + D	
1	<i>Amauropelta bergiana</i>			Pr.					stream banks
2	<i>Amauropelta</i> sp. 1	Ex.	Pr.						
3	<i>Angiopteris madagascariensis</i>			Pr.				Ex.	
6	<i>Arthropteris monocarpa</i>								
11	<i>Asplenium bipartitum</i>		Pr.					Ex.	
12	<i>Asplenium cancellatum</i>							Ex.	
13	<i>Asplenium cuneatum</i>	Pr.						Ex.	
14	<i>Asplenium dregeanum</i>		Pr.					Ex.	
20	<i>Asplenium marojejyense</i>		Ex.					Ex.	middle slopes and stream banks
21	<i>Asplenium nidus</i>							Pr.	
28	<i>Asplenium unilaterale</i>								
29	<i>Asplenium variabile</i> var. <i>paucijugum</i>	Ex.							
34	<i>Blechnum attenuatum</i>			Pr.			Ex.		
38	<i>Blechnum longepetiolatum</i>								
45	<i>Bolbitis auriculata</i>	Pr.						Ex.	
67	<i>Cyathea bellisquamata</i> var. <i>basilobata</i>			Pr.					Ex.
72	<i>Cyathea costularis</i>		Pr.						middle slopes and ridges
74	<i>Cyathea decrescens</i>							Pr.	middle slopes
77	<i>Cyathea figulata</i>		Pr.						stream banks
83	<i>Davallia chaerophylloides</i>		Pr.						middle slopes
84	<i>Davallia repens</i>		Pr.						middle slopes
86	<i>Deparia</i> sp. 1		Ex.						stream banks
88	<i>Didymochlaena microphylla</i>		Ex.						streams banks
89	<i>Diplazium andapense</i>			Ex.					
91	<i>Diplazium nemorale</i>							Ex.	stream banks
94	<i>Dryopteris mangintraensis</i>		Pr.						middle slopes and ridges
105	<i>Elaphoglossum marojejyense</i>		Ex.						
113	<i>Elaphoglossum</i> sp. 7							Ex.	
116	<i>Gleichenia madagascariensis</i>				Ex.				
119	<i>Grammitis copelandii</i>							Ex.	
120	<i>Grammitis cryptophlebia</i>								
129	<i>Grammitis</i> sp. 3								
142	<i>Hymenophyllum fumarioides</i>			Pr.					
150	<i>Hymenophyllum sibirhioides</i>		Ex.						middle slopes and ridges
162	<i>Lindsaea millefolium</i>			Ex.					middle slopes
166	<i>Lomariopsis crassifolia</i>							Pr.	
178	<i>Nephrolepis biserrata</i>		Ex.					Ex.	
185	<i>Phymatosorus scolopendria</i>	Ex.							

TABLE 2-7. Continued.

No.	Taxa	Zone							Preferential biotope
		A	B	C	D	A + B	B + C	C + D	
192	<i>Pneumatopteris subpennigera</i>								stream banks
193	<i>Pseudocyclosorus pulcher</i>		Ex.						stream banks
200	<i>Pteris woodwardioides</i>								
202	<i>Rumohra lokoensis</i>			Pr.				Ex.	
203	<i>Saccolloma henriettae</i>			Pr.					
208	<i>Selaginella hildebrandtii</i>		Ex.						stream banks
218	<i>Tectaria magnifica</i>		Ex.						stream banks
219	<i>Trichomanes bipunctatum</i>					Pr.			
224	<i>Trichomanes erosum</i> †							Ex.?	
229	<i>Trichomanes montanum</i> var. ?		Pr.?						
230	<i>Trichomanes rigidum</i>							Ex.	middle slopes and ridges

* Characteristic species are those that contribute to at least 1.8% of the variance of one or the other of the factorial axes. Characteristic species restricted to a single altitudinal stage are referred to as "exclusively characteristic." Characteristic species that have a higher coefficient of abundance in the constituent plots of one stage compared to elsewhere are referred to as "preferentially characteristic."

† Zone A = 470–530 m; zone B = 740–820 m; zone C = 1290–1310 m; zone D = 1540–1900 m (cf. data matrix: 194 species × 18 plots, not given here).

‡ Potential error in the field in the determination of *Trichomanes erosum* and *T. montanum* var. ?.

appears to be an acceptable compromise (see also Rakotondrainibe, 1989).

The stratified sampling method used here does not make it possible to determine precise upper and lower altitudinal limits for the floristic groups of pteridophytes defined in the study. Continuous sampling along an altitudinal transect would be necessary, but this method was not compatible with the logistical constraints of the fieldwork performed or with the objectives of the multidisciplinary approach adopted, which were to evaluate the overall biodiversity of a protected area in a limited amount of time (45–60 days).

Vegetation Stages and Floristic Groups of Pteridophytes on the Eastern Slope of the Marojejy Massif

Humbert (1955) and Guillaumet et al. (1975) recognized four principal vegetation types on the Marojejy Massif: (1) moist evergreen forests of low and middle altitude, from sea level to ca. 800 m; (2) montane forests, or moss forests with an herbaceous lower layer (the latter term used by Perrier de la Bâthie, 1921), between ca. 800 and 1450 m; (3) dense sclerophyllous high-altitude forests, or lichen forests, between about 1400–1450 and 1850 m; and (4) montane thickets or ericoid bushland, above about 1900 m. The physiognomy and the flora of these four vegetation types on Marojejy were described in detail by Humbert (1955) and remain essentially unaltered to this day, except in some areas around 400–550 m altitude, where the primary forest has given way to a more open formation, often dominated by a native bamboo species (*Ochlandra capitata* E. G. Camus) or a Zingiberaceae (*Aframomum angustifolium* K. Schum.).

The pattern of distribution of pteridophytes generally coincides with that of the vegetation types, although some exceptions can be noted at both lower and upper ends of the altitudinal gradient, where water or humidity can become a limiting factor, as follows:

Between 400 and 850 m the physiognomy of the vegetation changes progressively along the eastern slope and shifts imperceptibly from low- to middle-altitude forest. However, the pteridophyte groups A and B, whose limit occurs in this same area, have very different floristic compositions, as indicated by their respective positions on the first two axes of the CA and their separation at a high level in the HAC. Pteridophytes are par-

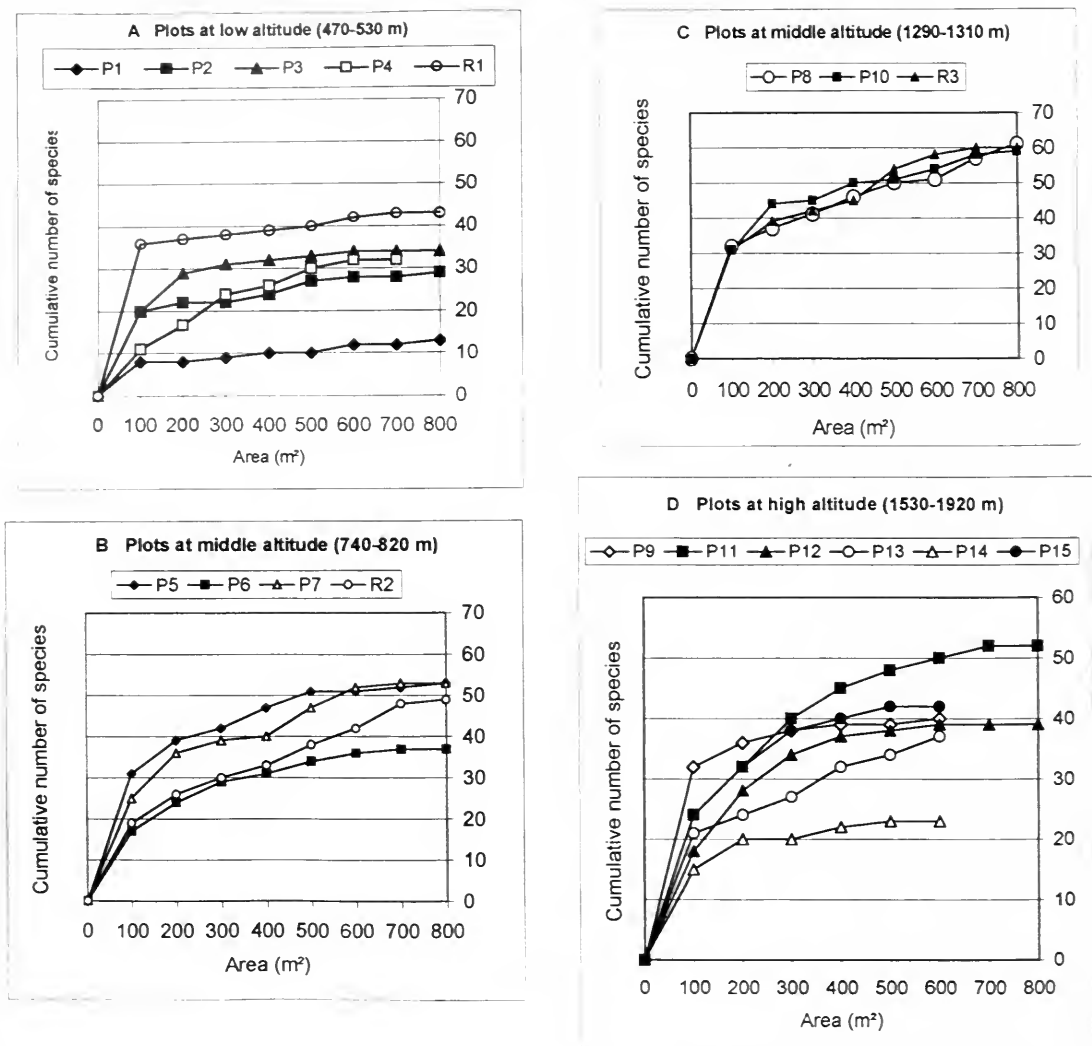


FIG. 2-7. Accumulation curves of pteridophyte diversity in each plot within the PN de Marojejy. **A**, plots at low altitude (470–530 m); **B**, plots at middle altitude (740–820 m); **C**, plots at middle altitude (1290–1310 m); **D**, plots at high altitude (1530–1920 m).

ticularly sensitive to soil and atmospheric humidity (Dzwonko & Kornas, 1994; Kornas, 1993; Rakotondrainibe & Guillerm, 1990; van der Werff, 1990; Young & Leon, 1991). At low altitudes of 400–500 m, i.e., below the zone in which substantial condensation of fog takes place, the presence of even a short dry season prevents the most drought-intolerant species from growing, such as *Asplenium sandersonii*, *Blechnum attenuatum*, *Blotiella madagascariensis*, *Cochlidium serrulatum*, *Ctenopteris devoluta*, *C. zenkeri*, *Cyathea bullata*, and numerous species of *Elaphoglossum*, *Grammitis*, *Hymenophyllum*, and *Lind-*

saea. These same taxa occur, however, toward 750–850 m, at least on the lower slopes and in the valleys, where conditions favor their presence.

By contrast, at the other end of the altitudinal spectrum, between 1500 and 2000 m, an abrupt shift occurs at about 1800 m, from sclerophyllous forest to montane thicket vegetation, whereas little change occurs in the floristic composition of the pteridophytes. The plots comprising group D are separated into two subgroups, D1 and D2 (P12, P13, P9 and P11, P14, P15, respectively) only along axis IV of the CA, and even then at a rather low level in the HAC. This relative homogeneity

of the pteridophyte flora in such drastically different ecological conditions is surprising. The species typical of sclerophyllous forests, in which the canopy reaches 8–15 m in height, grow in a shaded, continually moist forest environment, whereas those in the montane thickets occur in a low vegetation type that is subjected to marked daily variations in temperature and insolation. The latter species are, however, small in size, grow among mosses that are saturated with water, and form layers around branches and a dense carpet on the ground. Thus, it is possible that water reserves in the substrate may allow species that are sensitive to microclimatic variations to survive and occur abundantly in the more buffered parts of the sclerophyllous forest. Lack of data on the amount of sunshine received on the summit of Marojejy prevents the formulation of any formal hypotheses. However, Guillaumet et al. (1975) indicated that measurements made at 2050 m altitude during the month of November (one of the driest in the region) showed that the soil was permanently saturated with water at a depth of only 3 cm below the surface. If this observation accurately reflects the situation on Marojejy throughout the year, it would explain the relative homogeneity of the pteridophyte groups above 1500 m altitude. Observations made in the equivalent vegetation types in the Anjanaharibe-Sud Massif, located at approximately the same latitude but 35–40 km farther inland, support this idea. There, contrary to what has been found on Marojejy, the floristic composition of the pteridophytes in montane thicket vegetation is statistically different from that found in adjacent sclerophyllous forest (Rakotondrainibe & Raharimalala, 1998). Observations in the field showed, however, that during November 1996, the moss layer in the montane thicket, which occurs on a narrow ridge at 1950 m altitude, just below the summit, dries out rapidly in the midday sunshine. These observed differences confirm the idea that pteridophytes are valuable indicators of microclimate.

Species Richness

The biodiversity of three protected areas in eastern Madagascar (PN de Marojejy, PN d'Andohahela, and RS d'Anjanaharibe-Sud) (Fig. 2-1) has now been studied using identical methods. Among these areas, Marojejy has by far the richest pteridophyte flora, with 239 species, as

compared to 207 and 211 species, respectively, for the other two areas (Rakotondrainibe, 1999; Rakotondrainibe & Raharimalala, 1998), an observation that can be explained by climatic, biological, and geomorphological factors. The PN de Marojejy is located only 45 km from the east coast of Madagascar in a region with the highest rainfall in the country (Donque, 1975). The east slope of the massif is directly exposed to the trade winds; annual rainfall at sea level in Antalaha averages 2150 mm, and it is almost certainly higher between 500 and 2132 m on Marojejy. Mean temperature in Antalaha is 29.8°C in the warmest month and is 18.1°C in the coolest month; thus it has a warm, humid climate particularly favorable for the growth of ferns. The Anjanaharibe-Sud Massif has a similar climate, although it is most likely somewhat less humid due to its more inland location. The PN d'Andohahela, situated in extreme southeastern Madagascar, just outside the tropics, is in an area with a somewhat cooler and drier climate (Donque, 1975; Rakotondrainibe, 1999). At both Marojejy and Andohahela, primary forest (including montane thickets) that has been minimally affected by humans covers a wide altitudinal belt, from 400 to 2000 m. By contrast, at Anjanaharibe-Sud the lower limit of the native forest does not extend below 800 m except for a few patches near 600 m altitude. Also, PN de Marojejy and PN d'Andohahela are approximately the same size (60,050 and 63,100 ha, respectively), much larger than RS d'Anjanaharibe-Sud (18,255 ha). Unlike the two other reserves, Marojejy is surrounded by several associated massifs, and air flow in the numerous valleys and along the slopes generates a multitude of microclimates that can support greater levels of biodiversity.

In the three massifs studied to date, species richness and species density peak in the mid-altitudinal level, between 750 and 1350 m, i.e., in the zone where condensation from fog and orographic precipitation occur, where topography has the most influence, and where the diversity of habitats is thus greatest. This appears to be a widespread phenomenon: in Panama, where the highest peaks terminate at 3374 m, pteridophyte richness is greatest between 500 and 1500 m (Lellingner, 1985); in South Africa the maximum richness occurs between 1000 and 1500 m on massifs that reach to 3000 m, and in the high massifs of East Africa pteridophyte richness is greatest between 1500 and 2000 m (Jacobsen & Jacobsen, 1989). On Mt. Kinabalu, in Borneo, which reach-

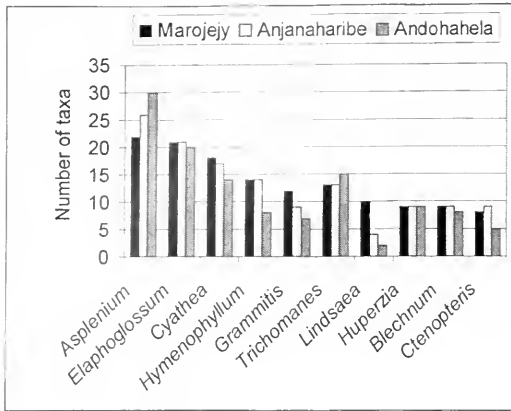


FIG. 2-8. Species richness of the 10 largest pteridophyte genera in the PN de Marojejy, RS d'Anjanaharibe-Sud, and RNI d'Andohahela.

es to 4175 m altitude, maximum diversity was observed at about 1500 m (Parris et al., 1992).

Figure 2-8 shows the number of taxa (species and varieties) of the 10 most speciose pteridophyte genera in the Marojejy, Anjanaharibe-Sud, and Andohahela reserves. The pteridophyte flora of Marojejy is distinctive in being relatively poor in members of the genus *Asplenium* (22 taxa vs. 26 and 30, respectively, for the other two areas) and having more representatives of the genera *Grammitis* (12 taxa vs. 9 and 7) and especially *Lindsaea* (10 taxa vs. 4 and 2). The other genera listed have approximately equivalent numbers of taxa in the Marojejy and Anjanaharibe-Sud reserves, and in most cases there are fewer representatives in PN d'Andohahela. It is not possible at present to suggest a possible explanation for these observed differences in floristic composition, but ecological and geographic factors surely play a role. Mapping now under way to depict the distributions of taxa with restricted ranges in Madagascar and to assess their affinities with taxa present in other floristic zones should, however, make it possible to formulate hypotheses.

Floristic Distinctiveness

The fern flora of the Marojejy Massif has a high level of endemism, but it also exhibits strong floristic similarities with its closest neighbor, the Anjanaharibe-Sud Massif. Table 2-8 shows the coefficients of floristic similarity (Ps) (Sørensen, 1948) between the two areas, calculated on the

TABLE 2-8. Degree of similarity of the pteridophyte flora of PN de Marojejy and RS d'Anjanaharibe-Sud by altitudinal zone (Ps = Sørensen coefficient of similarity calculated on the basis of the quantitative plot data).

Altitudinal zone (m)	Ps (%)*
740–2000	74.2
740–1000	66.0
1250–1350	59.1
1500–2000	61.3

* $Ps = 200 \times C/A+B$, where A = species number in the PN de Marojejy, B = species number in the RS d'Anjanaharibe-Sud, and C = species number shared between the PN de Marojejy and RS d'Anjanaharibe-Sud.

basis of the quantitative plot data. Analysis of the full set of plots located between 740 and 2000 m (i.e., the range of altitudes at which primary forest occurs at both sites) yields a very high coefficient of similarity ($Ps = 74.2\%$). Comparison of the different altitudinal zones, however, shows the strongest differences in the floristic composition occurring in the middle altitude zone, between 1250 and 1350 m ($Ps = 59.1\%$), which is characterized by the presence of a closed, high tree canopy. Homosporous pteridophytes, with their very light diaspores that can travel over great distances, are the most likely pteridophyte taxa to disperse between relatively isolated forest blocks such as Marojejy and Anjanaharibe-Sud. However, the exchange of diaspores between the two massifs may be impeded at middle altitudes, where a closed forest canopy presents a barrier to dispersal. This might explain in part the lower level of floristic similarity at these altitudes.

Figure 2-9 summarizes the chorology of the 239 species and varieties of pteridophytes ob-

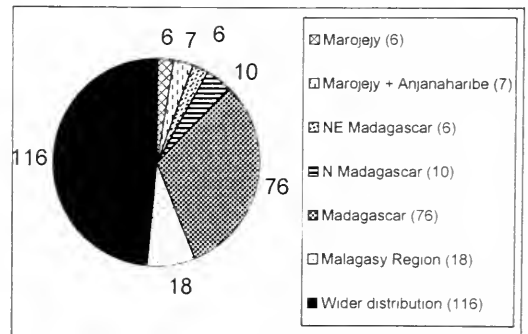


FIG. 2-9. Number of taxa (species and varieties) locally and regionally endemic among the 239 pteridophytes known from the eastern slopes of the Marojejy Massif.

served on the eastern slope of Marojejy. A total of 6 taxa are endemic to the massif; 7 are known only from Marojejy and Anjanaharibe-Sud; 6 are restricted to the northeastern region of Madagascar, including these two reserves as well as the Masoala Peninsula and the areas around Vohémar and Mananara-Nord; and 10 taxa have distributions covering the northern part of Madagascar, north of a line from Mananara-Nord to Antsohy.

The floristic distinctiveness of Marojejy increases with altitude (Table 2-5). The number and percentage of species endemic to Madagascar increase regularly between 400 and 2000 m, and four of the six species known only from the eastern slope of the massif are found in the highest altitudinal zone. It is difficult to explain the observed discrepancy between the strong floristic similarity and the presence of several taxa endemic to each of these two massifs, which are in close geographical proximity and have comparable altitudinal ranges and geological features. It would be interesting to observe the species diversity of the corridor forests between the two reserves.

Conclusions

An assessment of the pattern of distribution of pteridophyte taxa present on the eastern slope of the Marojejy Massif was conducted using complementary numerical methods. The results provide baseline data on the current species richness, floristic composition, and endemism of the area. Because the park is about to be opened to ecotourism, it is hoped that this study will be useful to those responsible for the Marojejy/Anjanaharibe-Sud Integrated Conservation and Development Project in their effort to manage and conserve the biodiversity of these protected areas, which are without doubt among the richest in Madagascar.

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Literature Cited

- BENZÉCRI, J. P., AND F. BENZÉCRI. 1984. *Pratique de l'analyse des donnés. I. Analyse des correspondances, exposé élémentaire*, 2^e ed. Bordas, Paris, 456 pp.
- BISHOP, L. E. 1978. Revision of the genus *Cochlidium* (Grammitidaceae). *American Fern Journal*, **68**(3): 76–94.
- DES ABBAYES, H. 1961. Lichens récoltés à Madagascar et à la Réunion (Mission H. Des Abbayes, 1956). I. Introduction. II. Parméliacées. *Mémoires Institut Scientifique de Madagascar, série B*, **10**(2): 81–122.
- DONQUE, G. 1975. Contribution géographique à l'étude du climat de Madagascar. Nouvelle Imprimerie des Arts Graphiques, Antananarivo, Madagascar, 477 pp.
- DZWONKO Z., AND J. KORNAS. 1994. Patterns of species richness and distribution of pteridophytes in Rwanda (Central Africa): A numerical approach. *Journal of Biogeography*, **21**: 491–501.
- GUILLAUMET, J.-L., J.-M. BETSCH, C. BLANC, P. MORAT, AND A. PEYRIERAS (sous la direction de R. PAULIAN). 1975. Etude des écosystèmes montagnards dans la région malgache. III. Le Marojejy. IV. L'Itremo et l'Ibity. Géomorphologie, climatologie, faune et flore (Campagne RCP 225, 1972–1973). *Bulletin du Muséum National d'Histoire Naturelle, série 3*, **309** (Ecologie générale 25): 29–67.
- HOLTUM, R. E. 1974. Thelypteridaceae of Africa and adjacent islands. *Journal of South African Botany*, **40**: (2) 123–128.
- HUMBERT, H. 1955. Une merveille de la nature à Madagascar: Première exploration du massif du Marojejy et de ses satellites. *Mémoires Institut Scientifique de Madagascar, série B*, **6**: 1–210.
- JACOBSEN, W. B. G., AND N. H. G. JACOBSEN. 1989. Comparison of the pteridophyte flora of southern and eastern Africa, with special reference to high-altitude species. *Bulletin du Jardin Botanique National de Belgique*, **59**: 261–317.
- KOECHLIN, J., J.-L. GUILLAUMET, AND P. MORAT. 1974. Flore et végétation de Madagascar. J. Cramer Verlag, Vaduz, 687 pp.
- KORNAS, J. 1993. The significance of historical factors and ecological preference in the distribution of African pteridophytes. *Journal of Biogeography*, **20**: 281–286.
- KRAMER, K. U. 1972. The Lindsaeoid ferns of the Old World, IX. Africa and its islands. *Bulletin du Jardin Botanique National de Belgique*, **42**: 305–345.
- KRAMER, K. U., AND P. S. GREEN. 1990. Pteridophytes and gymnosperms. In Kubitzki K., ed., *The Families and Genera of Vascular Plants*. Springer-Verlag, Berlin, 404 pp.
- LEBART, L., A. MORINEAU, AND M. PIRON. 1997. *Statistique Exploratoire Multidimensionnelle*, 2^e ed. Dunod, Paris, 439 pp.

- LELLINGER, D. B. 1985. The distribution of Panama's pteridophytes. *Monographs in Systematic Botany*, Missouri Botanical Garden, St. Louis **10**: 43–47.
- NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des aires protégées. *World Wide Fund for Nature*, Gland, xvii + 374 pp.
- PARRIS, B. S., R. S. BEAMAN, AND J. H. BEAMAN. 1992. The plants of Mount Kinabalu I. Ferns and fern allies. *Royal Botanic Gardens*, Kew, 165 pp.
- PERRIER DE LA BATHIE, H. 1921. La végétation malgache. *Annales de l'institut botanico-géologique colonial de Marseille*, sér. 3, **9**: 1–268.
- PICHI-SERMOLLI, R. E. G. 1977. Tentamen Pteridophytorum genera in taxonomicus ordinem redigendi. *Webbia*, **31**: 313–512.
- RAKOTONDRAINIBE, F. 1989. Etude floristique, biologique, phytogéographique et écologique des fougères et plantes alliées de la forêt d'Ambohitantely (forêt tropicale d'altitude). Thèse de Doctorat, Université de Lille, 304 pp.
- . 1999. Pteridophytes of the eastern slope of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: Distribution and floristic analysis, pp. 25–49. *In* Goodman, S. M., ed., A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **94**: 1–297.
- RAKOTONDRAINIBE, F. AND J. L. GUILLERM. 1990. Modèle de répartition horizontale des Ptéridophytes le long d'un gradient d'humidité lié à la topographie: le cas d'une forêt naturelle à Madagascar. *Candollea*, **45**: 591–598.
- RAKOTONDRAINIBE, F. AND F. RAHARIMALALA. 1996. The pteridophytes of the eastern slope of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 76–82. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **85**: 1–319.
- . 1998. The pteridophytes of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: Floristic analysis and altitudinal distribution, pp. 9–38. *In* Goodman, S. M., ed., A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **90**: 1–246.
- RAKOTONDRAINIBE, F. AND N. QUANSAH. 1994. The diversity and originality of the pteridophytes of the forest of Manongarivo Special Reserve (north-west Madagascar). *Fern Gazette*, **14**(7): 259–268.
- SAFFORD, R. AND W. DUCKWORTH. EDs. 1990. A wildlife survey of Marojejy Nature Reserve, Madagascar: Report of the Cambridge Madagascar Rainforest Expedition, 1988. Study Report no. 40. International Council for Bird Preservation, Cambridge, 172 pp.
- SHELPE, E. A. C. L. E. 1970. Pteridophyta. *In* Exell, A. W., and E. Launert, eds., *Flora Zambesiaca*. Crown Agents, London, 254 pp.
- SHELPE, E. A. C. L. E., AND M. A. DINIZ. 1979. Pteridophyta. *In* Mendes, E. J. ed., *Flora de Moçambique*. Junta de Investigações Científicas do Ultramar, Centro de Botânica, Lisboa, 257 pp.
- SØRENSEN, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Det Kongelige Danske Videnskabsbernes Selskab. Biologiske Skrifter*, **5**(4): 1–34.
- STEFANOVIC, S., F. RAKOTONDRAINIBE, AND F. BADRÉ. 1997. Sélaginellacées. *In* Morat, P., ed., *Flore de Madagascar et des Comores*, Paris, 68 pp.
- TARDIEU-BLOT, M. L. 1951–1971. Les Ptéridophytes. *In* Humbert, H., ed., *Flore de Madagascar et des Comores*. Muséum National d'Histoire Naturelle Paris.
- . 1955. Les Fougères du massif du Marojejy et Annexes, pp. 219–243. *In* Humbert, H. ed. Une merveille de la nature à Madagascar: Première exploration du massif du Marojejy et de ses satellites. *Mémoires Institut Scientifique de Madagascar*, série B, **6**: 1–210.
- . 1964. Les Ptéridophytes. *In* A. Aubréville, ed., *Flore du Gabon*. Muséum National d'Histoire Naturelle, Paris, 228 pp.
- TINDALE, M. D. 1965. A monography of the genus *Lastreopsis* Ching. *Contributions of the New South Wales National Herbarium*, **3**(5): 249–339.
- VAN DER WERFF, H. 1990. Ferns as indicators of vegetation types in the Galapagos archipelago. *Monographs in Systematic Botanical Gardening*, Missouri Botanical Garden, St. Louis **32**: 79–92.
- YOUNG, K. R., AND B. LEON. 1991. Diversity, ecology and distribution of high-elevation pteridophytes within Rio Abiseo National Park, north-central Peru. *Fern Gazette*, **14**(1): 26–39.

Chapter 3

Structure and Floristic Composition of the Vegetation of the Parc National de Marojejy, Madagascar

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Abstract

A rapid biological inventory was conducted along an altitudinal transect in the Parc National de Marojejy, Madagascar, between 4 October and 20 November 1996. Ten linear samples of 100 m were studied in five different elevational zones spanning 500 to 1950 m, and in a broad assortment of forest types. Five hundred eighty-four species of vascular plants representing 73 families were censused in the linear samples. In addition, nine 0.1 ha temporary plots were established in the lower four elevational zones. The data obtained provide quantitative and qualitative information on the structure, biometrics, and floristics of the vegetation on the Marojejy Massif.

Structural data revealed a progressive decrease in tree height and tree diameter as a function of altitude. The density of trees ≥ 10 cm dbh was highest in mid-elevation plots. Basal area was greatest at the lower altitudes. Dominant families changed gradually with altitude. Species diversity was maximum at 1200 m. Although there was little similarity between samples, some clusters were apparent and confirmed the trend observed in forest structure. The floristic and structural differences between ridges and slopes at the same elevation were in general as important as the differences between one ridge sample and the slope sample at an altitude 400 m higher.

Generally, the results of this study support Humbert's (1955, 1965) classification, but underline the importance of topography in delimitation of forest types and the gradual transitions from one type to another. Four hundred seventy-five fertile plants were collected, adding information to an already relatively well-known flora, based on the extensive collections of Humbert (1955) and several other more recent collectors.

Résumé

Une mission d'inventaire biologique rapide a été menée aux mois d'octobre et novembre 1996 le long d'un gradient altitudinal dans le Parc National de Marojejy, Madagascar. Dix relevés linéaires de 100 m et neuf parcelles de 0.1 ha ont été étudiées, fournissant ainsi des données quantitatives et qualitatives, permettant l'étude floristique, structurale et biométrique de la végétation du massif du Marojejy. Cinq cent quatre-vingts quatre espèces de plantes vasculaires réparties en 73 familles ont été recensées dans les dix relevés linéaires.

Sur la base des données structurelles, on observe une diminution progressive de la hauteur des arbres et de leur diamètre en fonction de l'altitude. La densité des arbres ≥ 10 cm dbh atteint sa valeur maximale dans les parcelles de moyenne altitude. L'aire basale est maximale

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dans les parcelles de basse altitude. Les familles dominantes changent progressivement avec l'altitude. La diversité spécifique atteint son maximum à 1200 m. Malgré une faible similarité entre les relevés, des regroupements sont possibles confirmant les tendances observées au niveau de la structure. Les différences floristiques et structurales entre crête et versant à une altitude donnée sont en général aussi importantes que celles observées entre un relevé de crête et le relevé de pente 400 m plus haut.

De manière générale, les résultats de cette étude confirment la classification de Humbert (1955, 1965), mais soulignent l'importance de la topographie dans la délimitation des types de végétation, ainsi que la nature graduelle du passage d'un type de végétation à un autre. Quarante six quinze échantillons de plantes fertiles ont été récoltés, s'ajoutant à ceux de Humbert (1955), ainsi qu'à ceux d'autres récolteurs, complétant ainsi petit à petit la connaissance de la biodiversité floristique du Parc National de Marojejy.

Introduction

The remarkable flora of the Marojejy Massif was first encountered by Henri Humbert during his exploration of the northern mountains of Madagascar, which also included the other mountains ringing the Andapa basin and the Tsaratanana Massif (Koechlin et al., 1974). Humbert visited Marojejy on several occasions and considered it one of the most beautiful and impressive massifs of Madagascar; in a 1955 monograph he described it as "Une merveille de la nature à Madagascar" [A wonder of nature in Madagascar]. Humbert collected almost 2,500 specimens in the Marojejy area (ca. 2,100 from the actual reserve), which contributed significantly to establishing the floristic diversity of this mountain. However, his account was published as a series of notes and in no way is a comprehensive floristic treatment of the massif. Humbert (1955) also proposed a classification of the Marojejy forests, but this was based on general floristic observations and personal knowledge rather than on quantitative surveys.

Subsequently numerous other botanists made important collections on Marojejy, and an impressive list of plants and herbarium specimens will soon be available (Miller et al., in prep.). However, prior to our work, no quantitative or structural sampling of the vegetation had been done on the massif. The biological inventory of the Parc National (PN) de Marojejy, conducted in 1996, provided an opportunity to fill this gap.

Humid forests are usually divided into altitudinally segregated vegetational belts based on floristic components and estimated quantitative characteristics (e.g., diameter at breast height [dbh], height). Our specific objectives were (1) to provide a quantitative floristic account of the various

study sites, (2) to compare the floristic composition of different habitats and habitats at different elevations on the massif, and (3) to document vegetational changes along an elevation gradient.

Methods

Vegetation surveys in the tropics have long suffered from the fact that the classic phytosociological approaches developed for use in temperate regions are not applicable because of the high species diversity and complexity of tropical ecosystems. A number of techniques have been devised to overcome this obstacle—almost as many techniques as there are groups of researchers working in this field. Whereas the high degree of floristic and structural variation between different types of tropical forests may warrant the use of different approaches, the lack of a common survey technique hampers comparisons among studies.

For tropical forests, 1 ha plots have been widely used, but they have a number of disadvantages: generally they take into account only individuals with dbh ≥ 10 cm, which leaves out herbs, shrubs, lianas, and most regenerating (i.e., young) tree species. They also do not provide precise results on vegetation structure. Establishing the plot itself is a time-consuming operation and generally damages part of the understory. In short, for several reasons the use of these plots in rapid inventory assessments is not ideal.

The methods used in rapid biodiversity assessment surveys should be simple but sufficiently comprehensive to allow characterization of critical aspects of the local flora and comparisons with other studies. To address these requirements, Gautier et al. (1994) have proposed a method that

combines sampling vegetation above 100 points regularly spaced along a line and sampling in small temporary plots. The linear sample provides an estimation of cover of the main species, which is a direct indication of their importance in the community. For tree species, the linear sample can be compared with the Importance Value Index of classic 1 ha plots. In addition, the linear sample gives detailed results on vegetation structure (vertical and horizontal distribution of vegetation). The small temporary plots are located along the line of the linear sample. They allow rapid measurement of main biometric parameters such as number of trees and basal areas. The combined technique of linear sampling and small plot sampling is relatively easily implemented in the field, even in difficult environments with a thick understory, such as in secondary regrowth. It is also suitable for steep and rapidly changing reliefs, where large surfaces for 1 ha plots often are not available. The time needed to establish and survey one linear sample and the associated temporary plot, including the collection of voucher specimens, is ca. 2.5–3 days in a dense forest with a relatively unknown flora.

Study Sites and Sampling Procedure

Fieldwork was conducted at five sites along an elevational gradient in the PN de Marojejy ranging from near 500 m to 1950 m. The study zones were centered on the five camps (at 450, 775, 1225, 1625, and 1875 m) and sampling was conducted within an elevational swath of ± 75 m. The precise localities of each camp and their georeferenced coordinates are given in Chapter 1 (pp. 5–6). Two habitats were studied in each of these sites, one on a slope (on a gradient intermediate between ridgetop and valley bottom) and one on a ridge (along the crest of a ridge). These two kinds of sites were chosen to better represent potential microhabitat variation within each elevational zone. The only exception was at 500 m, where, because of topographical features, flat plateaus rather than distinct ridges were found. In the highest elevational zone, only linear sampling was done.

An effort was made to choose floristically homogeneous sampling sites. The forest along the elevational gradient, however, had been partially disturbed by human activities. Indeed, in the first study zone, at 450 m, there were areas of disturbed forest, and selective logging was not rare.

In this elevational zone we chose sites for linear samples and plots in the least disturbed areas. In the second elevational zone, at 775 m, some evidence of selective cutting was also present. At higher altitudes, selective extraction of some tree species was noted, but there was no extensive perturbation.

Linear Samples

The linear sampling technique involved recording contacts of vegetation with a vertical line extending from 100 points set along a baseline at ground level. It is generally recommended that the length of the baseline be around 10 times the height of the canopy, but in our case, topographical features forced us to work along a 100 m line. Measurements were made at 100 points, 1 m apart. The height of contact and species encountered above each of the 100 points were recorded. To do so, we erected a vertical 8 m pole constructed out of 5 segments each 1.6 m long, the entirety demarcated in 20 cm increments. The heights at which all plants—trees, shrubs, lianas, herbaceous plants, and seedlings—came in contact with this pole were recorded for each of the sampled points. Heights of contacts above 8 m were estimated. When the vertical line passed through dense foliage, the lower and upper points of contact of this foliage mass were recorded. When plants could be unambiguously identified in the field, their scientific names were recorded on the data sheet. If the identity of a plant was in doubt, a voucher specimen was collected and the species was referred to as a “morphospecies” on the data sheet. These morphospecies were sequentially numbered or named independently for each altitudinal zone. If a voucher specimen could be unambiguously identified as identical to another specimen collected at the same site, it received the same binomial or morphospecies number and then the other specimen was discarded. Fertile individuals were also systematically collected.

The sterile material collected in the plots and along the linear samples was identified in the field at least to family level. After the material was dried, global morphospecies determinations were made in the herbarium of the Parc Botanique et Zoologique de Tsimbazaza (TAN), Antananarivo, and the herbarium of the Direction des Ressources Forestières et Piscicoles (= FO.FI.FA) (TEF), Antananarivo. In some cases binomial names could be assigned to these sterile specimens on the basis

of a fertile specimen represented in the general collections.

Plots

Temporary plots of 0.1 ha (100 × 10 m or 50 × 20 m) were marked, with the base of the linear sample used as the median line of each plot. Trees rooted within the plots and having a dbh ≥ 10 cm were recorded and their dbh was measured. Plots were not established in the highest elevational zone (1800–1950 m), which encompassed the ecotone between the upper lichen forest and high-elevation thicket, because in the lower portion of this zone the dwarf trees had less than the required dbh (≥ 10 cm).

General Collecting

Within each elevational zone, fertile specimens were collected from time to time outside the linear samples and plots but within the elevational swath of the site for additional floristic information. A maximum of seven specimens of each fertile individual were collected. The first specimen of each plant was deposited in the herbarium of TAN or TEF; the other specimens were sent to the herbaria of the Missouri Botanical Garden, St. Louis (MO), the Conservatoire et Jardin botaniques de la Ville de Genève (G), and the Muséum National d'Histoire Naturelle de Paris (P). For difficult groups, a specimen was also sent to a specialist for identification. Remaining duplicate specimens were designated to be sent to the Royal Botanic Gardens, Kew (K), and to the Agricultural University of Wageningen (WAG).

Data Analysis

Linear Samples

VEGETATION PROFILE—The data collected in the linear sample give a comprehensive view of a cross-section of the forest along a vertical plane above the baseline. Plotting all contacts on a graph with the length of the baseline as the *x*-axis and the height of the contacts as the *y*-axis gives an informative visual representation of the distribution of the vegetation. For a correct representation, the scales of both axes should be identical. In this representation, it is also possible to assign

specific symbols for the main species to give an idea of their distribution in the profile.

VERTICAL DISTRIBUTION OF VEGETATION—The contacts with vegetation can be separated vertically into height intervals. For each interval, the occurrence of vegetation above each of the 100 points of the baseline is summed to give a percent value of cover. The height of the interval can be even, or it can follow any other rule. We chose a first interval of 0–2 m for herbaceous and undergrowth vegetation, followed by a geometric two-fold progression: 0–2 m, 2–4 m, 4–8 m, 8–16 m, 16–32 m, >32 m. This height-array is often selected for tropical forests and has proved to be very informative. The data are then plotted on a vertical histogram where the length of each bar represents the cover of each interval. An interesting analysis of the shape of such histograms is presented in Chatelain (1996).

SPECIES COVER—Species cover is a direct indication of species' importance in the community. If the number of points is 100, as in our case, species cover can be directly inferred from the number of points above which the species is recorded, and expressed as a percentage. For tree species, a decreasing cover value generally reflects the ranking that can be obtained through more complicated procedures, such as calculating the Importance Value Index, at least for the prevalent species (Gautier et al., 1994). The number of individuals involved in these contacts is also derived from the data sheet and indicated beside the percentage cover value. Especially in our study plots, where topographical features limited the length of the baseline to 100 m, big tree species can exhibit percentage cover values that might be heavily dependent on this limitation and reach a nonrepresentative value, too low or too high. The latter artifact becomes obvious when a high percentage cover is associated with a small number of individuals, such as one or two.

SPECIES COVER PER HEIGHT INTERVAL—The same calculation can also be made after the information is first separated into height intervals as defined above. The percentage cover of the species in each interval is directly derived from the sum of the occurrences of the species above the 100 points of the baseline. It should be noted that for any species, the sum of the percentage cover in all intervals is generally higher than the global percentage cover because a species is often recorded in several intervals above a single point.

SPECIES-NUMBER OF POINTS ACCUMULATION CURVE—The cumulative number of species en-

countered along the sample can be plotted with respect to the number of points. The accumulation curve is similar to the classic species-area accumulation curves of surface plots and follows the same rules. Its shape and values are an indication of the homogeneity and the floristic richness of the sample. If the sample is homogeneous, a regular decrease in slope toward a horizontal asymptote is expected.

THE SHANNON-WEAVER DIVERSITY INDEX, H' —Species diversity can be quantified by means of a diversity index. For this survey we used the Shannon-Weaver diversity index, H' (Shannon & Weaver, 1949). This frequently used index takes into account not only the presence or absence of a species, but also its numerical importance. In this case the quantitative parameter used to calculate the index was the number of individuals censused along the lines of the linear samples. This diversity index increases with diversity. For two samples with an identical number of species, the index is lower if a few species are dominant than if the majority of species have a similar density.

THE HORN SIMILARITY INDEX, R_0 —The Horn similarity index, derived by comparing the Shannon-Weaver diversity indices of a number of plots, gives a useful measure of affinities in community composition (Brower et al., 1990). Its value ranges from 0 (no similarity) to 100%.

Temporary Plots

For the estimation of biometric parameters such as density and basal area of the community, it has been shown that when these values are plotted against an increasing sample area, the values at first fluctuate widely, and an accurate value can be reached only with plots of at least 0.16 ha (Gautier et al., 1994). Because of time constraints, it was possible to sample only 0.1 ha in each site, and this limitation should be remembered when one interprets the values obtained in this study.

DENSITY—The density defined here is the number of trees with a dbh ≥ 10 cm.

BASAL AREA—Basal area is the sum of the area of the cross-section of the trunk at 1.3 m of each tree with a dbh ≥ 10 cm. It is directly calculated from the diameter measurements of the trees (Centre Technique Forestier Tropical [CTFT], 1989).

DISTRIBUTION OF DBH—The distribution of number of trees according to diameter classes gives

additional information on a community's structure. Diameter classes are defined in 10 cm increments. The data are plotted as a histogram of the number of individuals according to increasing diameters. An inverted-J-shaped histogram is expected for mature forests.

Results

Description of the Samples

The results of the sampling are presented in detail in Appendix 3-1, along with a profile highlighting the species with a cover $>10\%$ in any height interval, the vertical distribution of the vegetation (% cover), the points-species accumulation curve, the number of stems ≥ 10 cm dbh, basal area, the number of species, and the Shannon diversity index, as well as a list of the species recorded, with cover values separated into height intervals. The samples themselves are briefly described below.

500 m, Slope Appendix 3-1a

The first sample was chosen in a rather dense lowland rain forest. All height intervals had a cover value $>60\%$, with the exception of the >32 m stratum, which included three emergent species (*Albizia* sp.1;* *Brochoneura acuminata* (Lam.) Warb.;† cf. *Deinbollia* sp.1). The maximum cover value (93%) occurred at the 16–32 m interval, with an important contribution from *Chrysophyllum boivinianum* (Pierre) Baehni, which also accounted for half of the cover of the 8–16 m interval. The 4–8 m interval was dominated by *Oncostemum* sp.1, *Diospyros* sp.2, and the epiphytic fern *Asplenium nidus* L. *Oncostemum* sp.1 was also important in the 2–4 m and 0–2 m intervals, together with two species of Rubiaceae and saplings of numerous species.

* Attribution of genera to families is given in Appendix 3-2.

† Authorities for species are given at the first mention of the species in the text.

490 m, Plateau

Appendix 3-1b

At the same altitude, this second sample also was a typical lowland rain forest. The emergent stratum was denser and comprised six species, including *Brochoneura acuminata* and *Canarium boivinii* Engl. The 8–16 m and 16–32 m intervals were dominated by *Chrysophyllum boivinianum*, along with Lauraceae sp.1, *Mallotus* sp.1, and *Macaranga* sp.3, the two latter species also dominating the 4–8 m interval. *Tabernaemontana* sp.1 and the tree fern *Cyathea decrescens* Mett. shared an important cover in the 4–8 m and 2–4 m intervals. The lower interval was broadly dominated by Poaceae sp.1. The profile gives the impression that the vegetation was rather loose, which was confirmed by the relatively low cover of the 16–32 m interval. Although no stumps were visible in the surroundings, this zone may have been selectively logged in the past.

800 m, Slope

Appendix 3-1c

At this altitude the forest was slightly lower than in the 500 m zone, and there were no emergent species above 32 m. The profile shows a rather discontinuous canopy around 25–30 m that is not reflected in the high cover value of the 16–32 m interval (74%) because of the contribution of some medium-sized trees below. However, there is a clear gap in the right-hand side of the profile, and the presence of secondary species (e.g., *Aframomum angustifolium* (Sonn.) K. Schum., *Ravenala madagascariensis* Sonn.) in the undergrowth indicated a past disturbance. In the other parts of the profile, important species included *Albizia* sp.1, *Cryptocarya* sp.3, *Chrysophyllum boivinianum*, and *Sloanea rhodantha* (Baker) Capuron in the 16–32 m interval, and *Deuteromallotus* sp.1 and *Symphonia* sp.4 in the 4–8 m and 8–16 m intervals.

800 m, Ridge

Appendix 3-1d

As in the preceding sample, there were no emergent species. The profile shows a very dense vegetation with a closed canopy dominated by *Uapaca* sp.2, *Canarium boivinii*, and two species of Lauraceae in the 16–32 m interval. In the 8–

16 m interval, *Uapaca* sp.2 was also important, together with *Mammea* sp.2 and *Eugenia* sp.1. Two species of *Pandanus*, one *Dypsis* sp., and one *Cyathea* sp. reached important cover values on the forest floor.

1200 m, Slope

Appendix 3-1e

The 1200 m slope sample had a continuous canopy that was included in the 16–32 m interval, except for a portion of the right-hand side of the profile, which was more open. Main species included *Ephippiandra* sp.2, an unidentified Rubiaceae, and *Brachylaena* sp.1. In the 8–16 m interval the vegetation was also relatively dense, with two species of *Mammea* and *Eugenia* sp.8. The 4–8 m interval included *Dypsis* sp.4 and the tree fern *Cyathea* sp.3. The 2–4 m interval has a relatively poor cover value; vegetation included *Tabernaemontana* sp.1, which was also important in the 500 m plateau sample. In turn, the lower interval reaches a high cover value with an unidentified pteridophyte species that accounted for half of the cover, and an unidentified Acanthaceae. With 103 species this sample exhibits the highest diversity value of the survey, with a still increasing species accumulation curve.

1200 m, Ridge

Appendix 3-1f

The ridge sample at 1200 m showed a much smaller forest: no contacts were recorded above 16 m. The forest was very dense below 10 m, with some emergents, including *Cryptocarya* sp.6, another unidentified Lauraceae, and *Eugenia* sp.4. The 4–8 m interval included the same species, together with *Canthium* sp.2 and *Elaeodendron* sp.1. In the 2–4 m interval there were numerous species with little species cover, except for *Dypsis* sp.4, which is worth mentioning here. The lower interval consisted mainly of lianescent bamboos, with two *Nastus* species accounting for more than half of the cover. The species accumulation curve displays a strong increase at the middle of the baseline corresponding to a slight change in slope along the ridge. The number of species encountered (97) was also very high.

TABLE 3-1. Distribution of diameters, density, and basal area for nine 0.1 ha plots in four different elevational zones in the PN de Marojejy.

Altitude (m)	Habitat	Number of trees per dbh (in cm) classes									Total no. of trees with dbh ≥ 10 cm	Basal area (m ²)
		10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100		
500	Slope	30	6	6	5	3	5	1	3	0	59	6.6
490	Plateau	34	12	6	2	1	1	2	1	0	59	3.8
800	Slope	46	19	4	3	0	1	1	2	0	76	4.4
800	Plateau	45	17	8	6	3	3	1	1	1	85	6.5
800	Ridge	90	33	11	4	1	3	0	0	1	143	6.7
1200	Slope	61	14	6	1	0	1	1	2	0	86	4.0
1200	Ridge	170	24	7	4	0	0	0	0	0	205	4.9
1600	Slope	116	40	6	1	0	0	0	0	0	163	4.6
1600	Ridge	7	2	0	1	0	0	0	0	0	10	0.3

1600 m, Slope Appendix 3-1g

Forest structure here was rather similar to the preceding sample, with almost no contacts above 16 m, a few emergents above 10 m (*Eugenia* sp.8 and *Eugenia* sp.4), and no clear stratification below. The 4-8 m interval was widely dominated by *Dypsis* sp.4 and *Polyscias* sp.5. The two lower intervals share a relatively low cover value (<70%), with numerous species.

1600 m, Ridge Appendix 3-1h

The ridge sample at this altitude showed a very dense dwarf forest structure with no stratification. Most of the contacts were below 8 m. Main species included *Calophyllum* sp.6, *Nastus* sp.2, and *Dypsis* sp.6. Asteraceae and Poaceae were rich in species and accounted for an important cover value. The number of species reached 98.

1850 m, Slope Appendix 3-1i

The structure of this sample was very similar to the preceding one, with a slightly denser 4-8 m interval that was dominated by *Calophyllum* sp.6 and *Cassinopsis* sp.4. The lower interval also included *Dichaetanthera* sp.8, an unidentified fern, and some lianescent bamboos (*Nastus* spp.).

1950 m, Ridge Appendix 3-1j

The vegetation at the highest altitude sampled was a dense ericoid thicket, with most contacts occurring below 2 m. The species with the highest cover value were *Nastus* sp.4, another unidentified Poaceae, and a species of *Weinmannia*. Among the shrubs species were also several Ericaceae (*Erica* spp.; *Agauria salicifolia* (Comm. ex Lam.) Hook. f. ex Oliv.) and Myrsinaceae. The herbaceous species included numerous Asteraceae.

Forest Structure

Table 3-1 summarizes the biometrical data extracted from the 0.1 ha plots nested in the linear surveys (number of trees per diameter classes, density, basal area). An additional plot was sampled at 800 m elevation on a plateau. No plots were established in the linear surveys at 1850 and 1950 m because of the lack of trees ≥ 10 cm dbh.

The density of trees ≥ 10 cm dbh ranged from 100 to 2,050 individuals per hectare. The lowest value was found on the ridge at 1600 m. The highest values occurred on the ridges at 800 and 1200 m and on the slope at 1600 m. They were mainly due to the contributions of the low-diameter vegetation classes (<30 cm dbh).

Figure 3-1 graphically expresses the distribution of dbh in 10-cm-increment classes for each plot. The dwarf structure of the 1600 m ridge sites is obvious, and for a clear interpretation of ligneous vegetation structure the smaller diameters should also have been sampled. All histograms fit

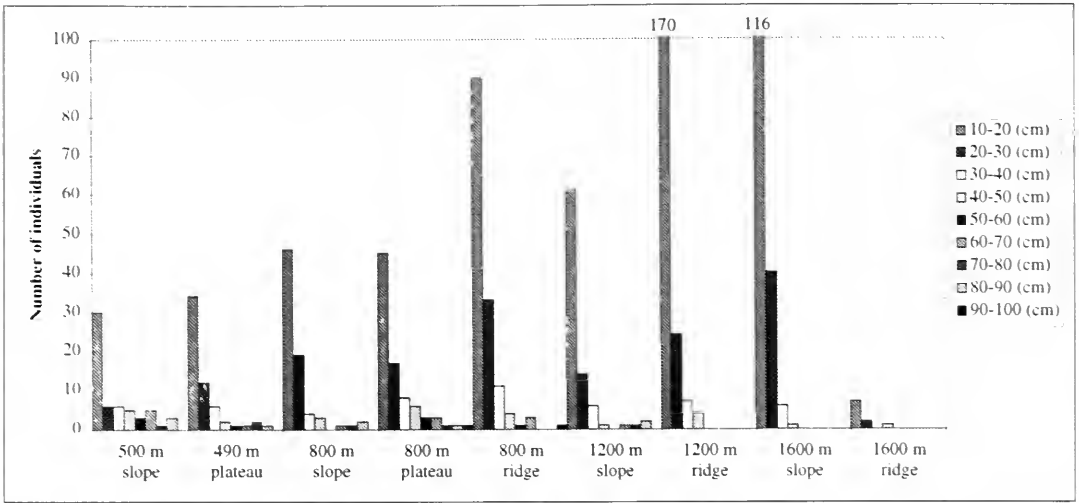


FIG. 3-1. Distribution of the individuals in 10-cm-increment dbh classes for nine 0.1 ha plots in four elevation zones in the PN de Marojejy. Within each plot, the order of the bars corresponds to the key read from top to bottom.

a classic inverted J curve, but some differences are noteworthy: the two 500 m plots share a relatively low number of individuals with dbh <20 cm. For >30 cm dbh, the plateau plot has low figures, which are reflected in the basal area value. The slope plot in turn has remarkably steady values in the >20 cm dbh classes: compared to the other histograms, the 20–30 cm class is very low and the >50 cm classes are high. The 1200 m ridge and 1600 m slope plots display a compression of the histogram toward the low values of diameter. The 1200 m ridge plot has two big trees in the 80–90 cm class, which is quite rare at this altitude. In the 800 m slope plot, there is a clear gap in the 50–60 cm class.

Basal area ranges from 3 to 67 m²/ha. The lowest value again occurred on the ridge at 1600 m. The highest values do not match the high values for density except for the 800 m ridge plot. The high basal area values of the 500 m slope and the 800 m plateau plots are mainly due to a relatively high number of trees with a dbh ≥30 cm.

The structural parameters extracted from the ten linear surveys are shown in Figures 3-2 (profiles) and 3-3 (cover per height interval histograms).

A few general observations on forest structure from the linear survey data were made in the brief descriptions of the samples, but combining all the data in a single figure adds new comparative information. Both samples at 500 m are quite similar, with the exception of the 16–32 m height in-

terval, which has more cover on the slope site. This finding is related to the high value of the >50 cm dbh classes and the high basal area mentioned earlier. At 800 m the slope site has lower cover values than the ridge site (especially below 16 m): this finding is again linked to the basal area and distribution of dbh classes.

From 800 m upward a gradual decrease in vegetation height is apparent. Also, within each altitude zone, vegetation on the slope site was systematically taller than vegetation on the ridge site. Furthermore, both the profiles and the cover per height interval histograms show that the forest structure of the ridge site is very similar to that of the slope site at the next higher altitude interval.

Forest Composition

Along the elevational transect, 3,011 angiosperm individuals representing 584 morphospecies in 73 families were censused (Appendices 3-2 and 3-3). In addition, 475 specimens of fertile plants were collected during the general collections, representing 64 families of angiosperms (Appendix 3-4). The list of the species present in each linear survey, along with their cover values, is given in Appendix 3-1 and was briefly commented on in the description of the samples.

The cover values of plant families along the ten linear samples is given in Appendix 3-3. For the

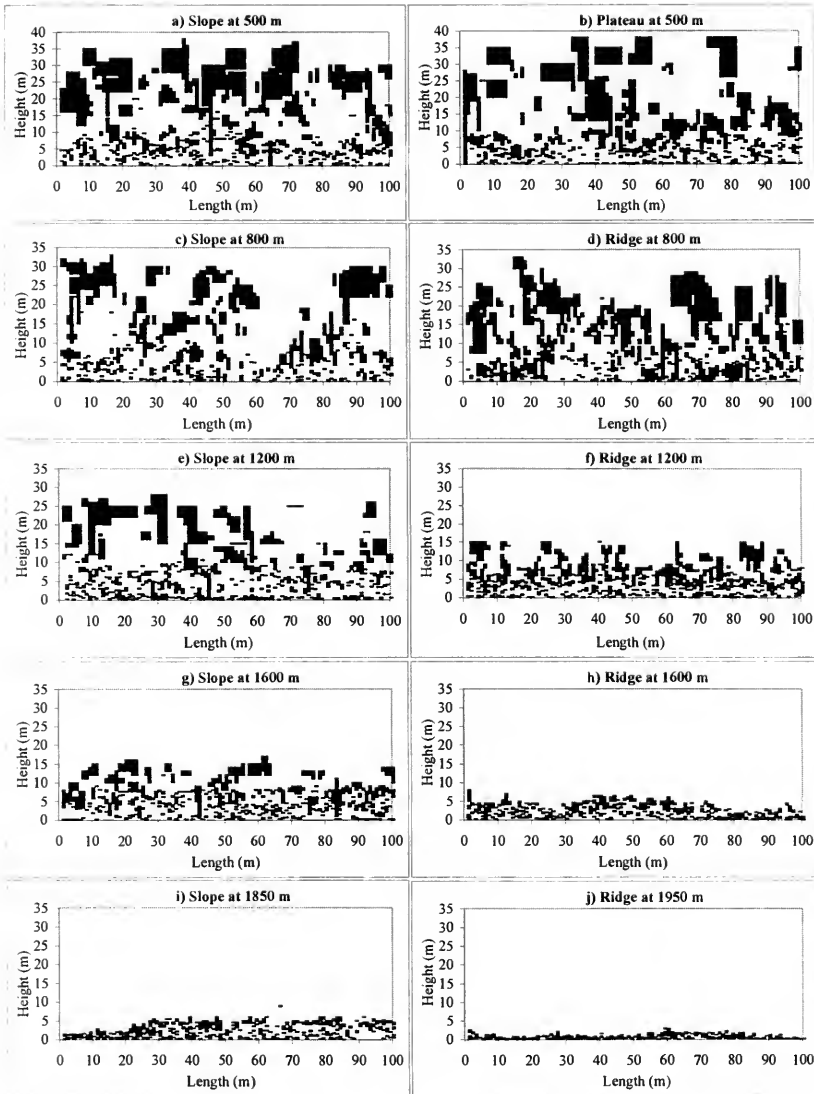


FIG. 3-2. Vegetation profile of the ten 100 m linear samples conducted in five elevation zones in the PN de Marojey. Data represent height of vegetation contacts measured or projected above the 100 points of the baseline linear sample.

main families the results are also expressed graphically in Figure 3-4. Some plant families were clearly restricted to low altitudes (Myristicaceae, Fabaceae, Annonaceae, Moraceae, Burseraceae, Apocynaceae) or, if represented at all altitudes, showed a clear preference for low elevation (Ebenaceae, Sapotaceae, Euphorbiaceae, Rubiaceae). Lauraceae were already dominant in the 500 m plots, but their cover values continued to increase up to 1200 m. Clusiaceae were responsible for an important percentage of cover at all altitudes. Poaceae were present in all samples and

reached important values in the highest plots as well as in the 500 m plateau plot. Myrsinaceae and Elaeocarpaceae also occurred at all altitudes, but with rather low cover values. Pandanaceae, Monimiaceae, Acanthaceae, Myrtaceae, Arecaeae, Melastomataceae, and Flacourtiaceae were likewise recorded at all altitudes, but their highest cover value occurred in the 1200–1600 m forests. Finally, Araliaceae, Asteraceae, Cunoniaceae, Balsaminaceae, and Ericaceae were seen mainly above 1200 m, and these families displayed an increasing affinity for high altitude.

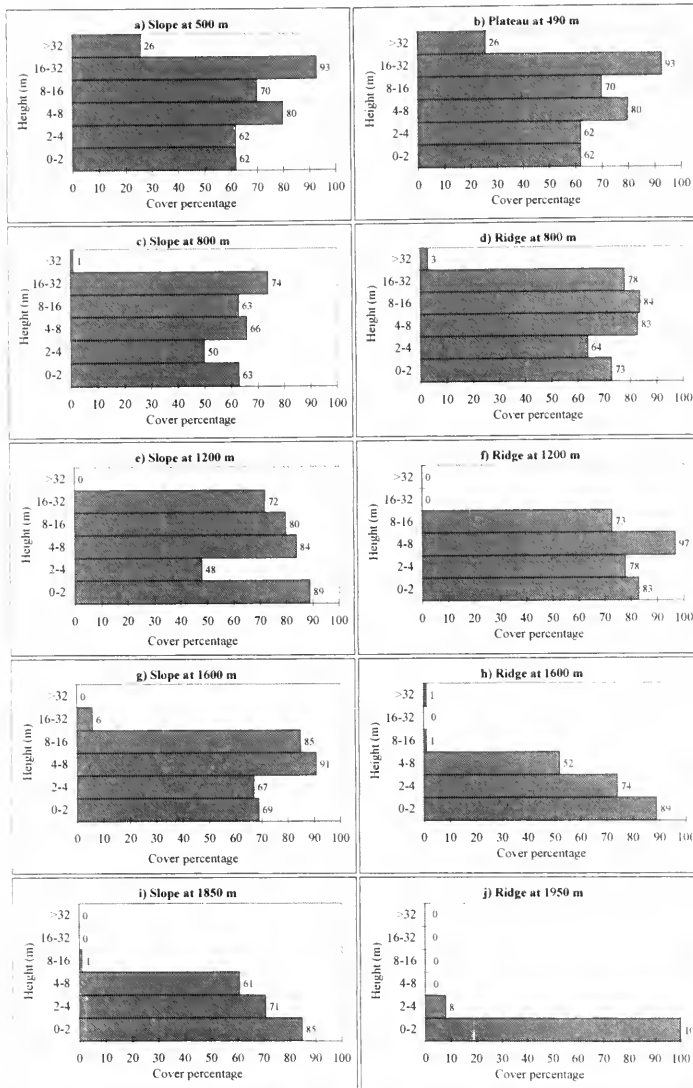


FIG. 3-3. Vertical distribution of vegetation (cover percentage in six height classes) for the ten 100 m linear samples surveyed in five elevational zones in the PN de Marojejy.

The number of species recorded in each linear survey is shown in Table 3-2, together with the Shannon-Weaver diversity index and the species/individual ratio. The highest numbers of species recorded occurred in the 1200 m samples. It should be noted that the species accumulation curves (Appendix 3-1) do not approach a saturation value at the end of 100 m of the baseline in all samples, with (perhaps) the exception of the two samples at highest elevation.

The values of the Shannon-Weaver diversity index (H') for species vary between 1.56 and 1.80 (for families, between 1.15 and 1.37) in the sam-

pled sites (Table 3-2). The degree of diversity quantified by this index is rather constant along the altitudinal transect, but the plots at low altitude and the 1950 m ridge have lower values. Taking into account what we said earlier regarding the species accumulation curves, this fact could be attributed to insufficient sampling at the two 500 m samples, but the 1950 m forest could in fact be less diverse.

The Horn similarity index values for species and families are presented in Table 3-3. The value calculated at the species or morphospecies level between ridge and slope sites of each elevational

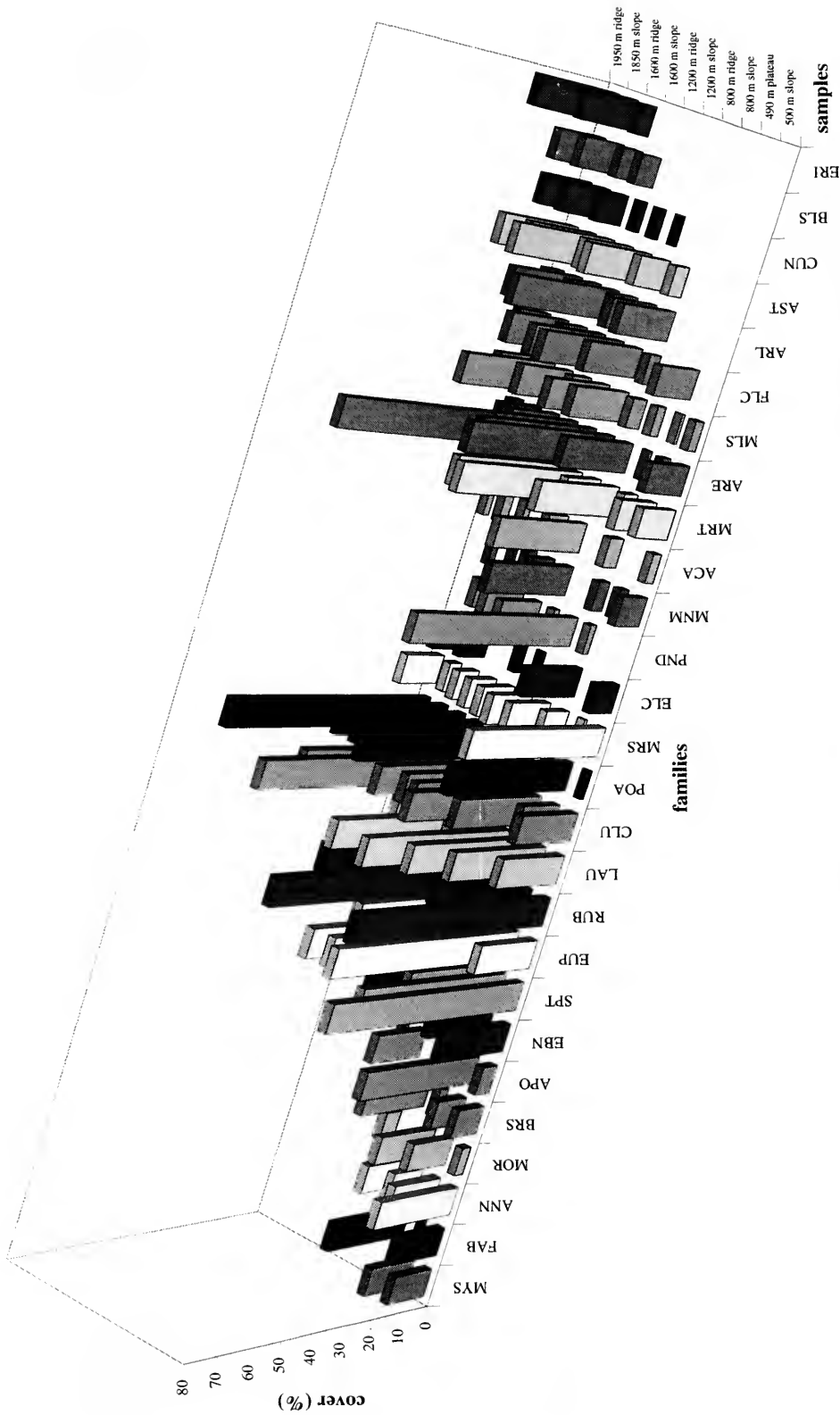


Fig. 3-4. Cover values of the 27 more important plant families in the ten 100 m linear samples surveyed in five elevation zones in the PN de Marojej. Abbreviations: MYS, Myrticaceae; FAB, Fabaceae; ANN, Annonaceae; MOR, Moraceae; BRS, Burseraceae; APO, Apocynaceae; EBN, Ebenaceae; SPT, Sapotaceae; EUP, Euphorbiaceae; RUB, Rubiaceae; LAU, Lauraceae; CLU, Clusiaceae; POA, Poaceae; MRS, Myrsinaceae; ELC, Elaeocarpaceae; PND, Pandanaceae; MNM, Monimiaceae; ACA, Acanthaceae; MRT, Myrtaceae; ARE, Araceae; MLS, Melastomataceae; FLC, Flacourtiaceae; ARL, Araliaceae; AST, Asteraceae; CUN, Cunoniaceae; BLS, Balsaminaceae; ERI, Ericaceae.

TABLE 3-2. Values of Shannon-Weaver diversity index for each linear transect in the PN de Marojejy.

Altitude (m)	Habitat	No. of Species	Shannon-Weaver diversity index		Species/No. of individuals ratio
			Species	Families	
500	Slope	66	1.56	1.29	0.29
490	Plateau	66	1.60	1.25	0.30
800	Slope	70	1.67	1.37	0.36
800	Ridge	78	1.73	1.35	0.27
1200	Slope	103	1.74	1.33	0.33
1200	Ridge	97	1.76	1.26	0.27
1600	Slope	82	1.67	1.28	0.26
1600	Ridge	98	1.80	1.29	0.24
1850	Slope	80	1.72	1.31	0.24
1950	Ridge	73	1.64	1.15	0.31

zone shows that important differences exist between the microhabitats within each elevational zone as well as between the altitudinal belts. None of these values shows more than 0.28 similarity. The index values at the species level would probably have been higher if the number of samples within each elevational zone had been increased. However, time was always a limiting factor in sur-

veying the numerous requisite samples. Even if the values of specific similarity are very low, the differences between these values still reveal sample clusters, which will be discussed later.

If the values for the 500 m samples, for which no ridge sample was available, are placed aside, the mean value of the similarity index for slope and ridge samples at the same altitude is 0.182. The mean value of the similarity index for a ridge sample and the slope sample at the next higher altitude is almost the same (0.187), whereas the mean value for a slope sample and the next higher slope sample is much lower (0.044). These figures further support the relation between the forests on ridges and slope plots at the next higher altitude and the intricateness of the forest types, as was noted earlier in the discussion of forest structure.

When comparisons are made at the family level the values of the Horn index are much higher, ranging from 0.35 to 0.88. The distribution of these values supports the trends observed in Figure 3-4.

Discussion

In his classic account of the vegetation types of Madagascar, Humbert (1965) described the east-

TABLE 3-3. Values of the Horn similarity index at the morphospecies level (above the diagonal in italics) and at the family level (below the diagonal) between the linear transects in the PN de Marojejy.

	Slope 500 m	Plateau 490 m	Slope 800 m	Ridge 800 m	Slope 1200 m	Ridge 1200 m	Slope 1600 m	Ridge 1600 m	Slope 1850 m	Ridge 1950 m
Slope 500 m	1.000	<i><u>0.277</u></i>	0.185	0.052	0.040	0.019	0.000	0.000	0.000	0.000
Plateau 490 m	0.673	1.000	<i><u>0.274</u></i>	0.091	0.035	0.020	0.004	0.000	0.000	0.012
Slope 800 m	0.721	0.795	1.000	0.121	0.040	0.015	0.008	0.018	0.004	0.000
Ridge 800 m	0.614	0.603	0.664	1.000	0.090	0.085	0.109	0.086	0.024	0.051
Slope 1200 m	0.523	0.648	0.687	0.682	1.000	0.188	0.177	0.080	0.055	0.102
Ridge 1200 m	0.662	0.589	0.617	<i><u>0.816</u></i>	0.757	1.000	<i><u>0.242</u></i>	0.095	0.032	0.006
Slope 1600 m	0.451	0.530	0.505	0.748	0.775	0.774	1.000	0.193	0.091	0.037
Ridge 1600 m	0.503	0.461	0.434	0.681	0.778	0.608	0.752	1.000	0.133	0.062
Slope 1850 m	0.480	0.429	0.445	0.636	0.748	0.666	0.743	<i><u>0.877</u></i>	1.000	<i><u>0.254</u></i>
Ridge 1950 m	0.456	0.354	0.364	0.502	0.703	0.560	0.639	0.769	<i><u>0.837</u></i>	1.000

Note: **Bold** entries represent medium index values (0.7–0.8 for families and 0.1–0.2 for species); **bold underscored** entries represent high index values (≥ 0.8 for families and ≥ 0.2 for species).

ern Malagasy humid forest and cited certain genera (or families) as abundant. In our study, *Chrysophyllum*, *Symphonia*, and the Lauraceae were indeed abundant, but *Dilobeia*, also cited as characteristic by Koechlin et al. (1974), was never recorded in this study. However, Humbert (1955) recorded *Dilobeia thouarsii* Roem. and Schult., but on Mt. de Beondroka, not on the main massif of Marojejy, and Miller (pers. commun.) noted that this species is common at some sites on Marojejy and Beondroka. To our knowledge, this species has never been recorded on the Tsaratanana or Manongarivo Massifs. It should also be mentioned that the genus *Podocarpus* was not found during our survey of the PN de Marojejy. Humbert (1955) did not observe this genus on the main slopes of Marojejy, although he found it in the foothills of the massif, for example on Mont d'Ambatosoratra, on Mont de Beondroka, and in the Ambatoharanana Valley (Laubenfels, 1972). At other surveyed mountain sites, such as the eastern slopes of the PN d'Andringitra, *Podocarpus* was one of the dominant taxa at 1600 m (Lewis et al., 1996). It is also present in the Réserve Spéciale de Manongarivo (pers. observ.) and on the Tsaratanana Massif, but absent in the PN d'Andohahela (Rakotomalaza & Messmer, 1999) and RS d'Ivohibe (pers. observ.). Given the uneven distribution of *Podocarpus*, it should no longer be considered one of the characteristic genera of eastern Malagasy forest from the littoral to high-altitude forests, as stated by Koechlin et al. (1974).

The eastern Malagasy humid forest contains a number of distinct vegetational communities that vary as a function of altitude. On the basis of the classification presented by Humbert (1955), which he later generalized to the whole eastern slope (1965), the eastern rain forest on the Marojejy Massif runs from the lower limit of the reserve to about 800 m. (The various classifications of these vegetation formations used by different researchers are given in Table 3-4.) Humbert's mid-elevation rain forest falls between 800 m and 1450 m; his lichen forest generally falls between 1450 m and 1800 m; and finally high-elevation thicket and grassland form a mosaic above 1800 m up to the summit at 2137 m. The results of our survey will now be compared with this classification.

In the lower portion of the lowland humid forest, the presence of *Mauloutchia humblotii* (H. Perrier) Capuron, *Chrysophyllum boivinianum*, *Sloanea rhodantha*, and *Canarium* sp. (not all these species were recorded in the samples, but

they were found in the surrounding forest) follows closely the characteristic floristic features of this formation as proposed by Humbert (1965). *Mauloutchia humblotii* is restricted to the lowest studied level, 500 m, and was not found at the 800 m site; the upper limit of this species is probably about 500–600 m. The upper limit of *Chrysophyllum boivinianum* stands at 1000 m.

The four samples around 500 m and 800 m altitude share a common structure, especially when the distribution of dbh is considered (Fig. 3-1). The profiles (Fig. 3-2) and vertical distribution of vegetation (Fig. 3-3) nevertheless show that the forests at 500 m are of a slightly taller stature. However, these forest structures fit well with Humbert's (1955) description of the eastern rain forest, with a canopy between 25 and 30 m high. The floristic composition of the slope sample at 800 m is an extension of that in the lowland humid forest as recorded at about 500 m (similarity index > 0.15; Table 3-3). The species composition of these three samples shows very little similarity (<0.05) with the samples at or above 1200 m. The ridge plot at 800 m has relatively low affinities with all other plots and may represent a transition in floristic composition although still related to the lowland rain forest in terms of structure.

The slope sample at 1200 m, with its 18–25 m canopy and a less important medium stratum, corresponds typically to the mid-elevation forests of Humbert. The presence of *Ephippiandra* and *Tambourissa* (Monimiaceae), two altitudinal indicator genera, supports this conclusion (Humbert, 1965; White, 1986). Lauraceae is also one of the dominant families, especially above 800 m, and this observation holds for most of the Malagasy humid forest (Lewis et al., 1996; Rabevoitra et al., 1996; Lowry et al., 1997; Rakotomalaza & Messmer, 1999).

In turn, the 1200 m ridge sample structure has more affinities with the description of the lichen forest (6–12 m canopy, intermingled with the shrub stratum), like the 1600 m slope sample. The change in forest composition between 1200 m and 1600 m is exemplified by the disappearance of *Canarium* sp. and *Sloanea rhodantha*, both species characteristic of lowland rain forest and mid-altitude rain forest up to 1200 m that were observed only in the slope habitats and not on the ridges at this altitude. Moreover, the appearance of bamboos and an increase in cover values for Clusiaceae such as *Symphonia* spp. support the observation. Indeed, bamboos and *Symphonia* are

TABLE 3-4. Synonyms for the different classifications of the vegetation formations.

Altitude (m) Perrier de la Bâthie (1921)	Altitude (m) Humbert (1955, 1965)	Altitude (m) Koechin et al. (1974)	Altitude (m) Cornet & Guillaumet (1976)	Altitude (m) White (1986)	Altitude (m) Du Puy & Moat (1996)
0-800 Eastern forest <i>Forêt orientale</i>	50-800 Eastern rain forest <i>Forêt dense ombrophil- le orientale</i>	0-800 Low-altitude sempervirent moist forest <i>Forêt dense humide semper- virente de basse altitude</i>	0-ca. 1100 Low-elevation moist evergreen forest and mid-elevation moist evergreen forest	0-800 Eastern rain forest	0-800 Evergreen, humid forest: low alti- tude
800-2000 Mid-elevation forest and lichen forest <i>Forêt à mousses et à sous-bois herbacés et forêt à lichens</i>	800-1450* Mid-elevation rain for- est <i>Forêt dense ombrophil- le de moyenne alti- tude</i>	800-1800 Moist montane forest <i>Forêt dense humide de mon- tagne</i>	ca. 1100-1800/2000 Mid-elevation subhu- mid evergreen for- est	800-1300 Eastern moist montane forest	800-1800 Evergreen, humid forest: mid-alti- tude
>2000 Ericoid thicket <i>Broussailles éricoides des hautes altitudes</i>	1450-1800† Mountain rain forest and Lichen forest <i>Forêt dense ombrophil- le de montagne et Sylve à lichen</i>	1800-2000 Sclerophyllous montane for- est <i>Forêt dense sclérophylle de montagne</i>	1300-2300 Eastern sclerophyllous montane forest	1800-2000 Evergreen, humid forest: lower mon- tane	>1800 Montane (<i>Erica</i>) scrubland

* Humbert (1965) delineates this zone as occurring between 800 and 1300 m.

† Humbert (1965) delineates this zone as occurring between 1300 and 2000 m.

‡ Humbert (1965) delineates this zone as occurring above 2000 m.

indicators of high-altitude and exposed formations such as ridges (Koechlin et al., 1974). The transition between mid-elevation rain forest and lichen forest would then occur between 1200 m and 1600 m (Table 3-3). The distinctly exposed position of the ridge sample at 1200 m, which shares 0.24 similarity with the 1600 m slope sample, would explain why this site can be categorized with the lichen forest formation.

The height of vegetation in the 1600 m ridge sample is still lower, like the 1850 slope sample. Both show a unique, dense stratum of vegetation with a maximum height of about 6–7 m. Structurally, these formations could be considered as belonging to the small-sized type of lichen forest. The small trees with reduced leaves and small-diameter, twisting trunks are also diagnostic of this formation (Koechlin et al., 1974). The floristic composition is also characteristic, as indicated by the presence of *Alberta* sp., *Symphonia* sp., *Weinmannia* spp., several species of Asteraceae, and a wide assortment of Myrtaceae, Lauraceae, and Araliaceae (*Schefflera* spp. and *Polyscias* spp.).

Above 1900 m the summital areas are subjected to high variations in humidity and temperature (Koechlin et al., 1974), conferring on the vegetation its particular aspect. The forest is reduced to high-elevation thicket, in which the ridge sample at 1950 m was established. It consists of a very low and dense thicket with Ericaceae woody plant genera *Erica* and *Agauria*, as well as *Cryptocarya* (Lauraceae). It corresponds to the ericoid thicket of Humbert (1965). Between the patches of this ericoid scrub, herbaceous high-altitude grassland rich in many Asteraceae, such as *Helichrysum*, *Vernonia*, and *Senecio*, dominates the landscape. The mosaic of these types of vegetation formations in the highest elevational zone essentially follows variations in topography, with high-elevation thicket on ridges and in valley bottoms and grassland on slopes.

A progressive change in vegetation was observed along the elevational transect in the PN de Marojejy. The family cover values in the samples (Fig. 3-4) show a clear shift in composition with altitude. However, as indicated by the Horn similarity index (Table 3-3), this change is gradual, and there is considerable overlap of families along the elevational transect. The high values for the Horn similarity index attest that the family taxonomic level is a too large an entity with which to characterize the different elevational vegetation zones. Forest classification should be based not on families but on species or morphospecies. Nev-

ertheless, some families are largely characteristic of a given altitude, especially when their importance value is taken into account.

The shifts from one type of vegetation formation to another were gradual but readily apparent. Furthermore, above 800 m floristic and structural similarities were noted between a ridge at a given elevation and the slope of the next highest zone (e.g., between the ridge at 1200 m and the slope sample at 1600 m). Hence, the distribution of vegetation types does not correlate with altitude alone. Moreover, as already noted by Humbert (1955), it is unlikely that the divisions will occur at the same elevation everywhere on the Marojejy Massif or along the same latitudinal gradient in Madagascar. Topography plays an important role in the scheme of demarcations between each altitudinal vegetation formation.

On a larger scale, a progressive downward shifting of elevational zonation toward the south of Madagascar may exist. We have already noted the downward shift of the botanical classification limits along the altitudinal gradient in the PN d'Andohahela (Rakotomalaza & Messmer, 1999). The results of the three 1.0 ha permanent plots established in the PN de Ranomafana (Lowry et al., 1997) also suggest that the altitudinal boundary between lowland rain forest and mid-altitude rain forest stands at 600 m instead of the classic 800 m. The plot at 1200 m, moreover, is different from the ones at 600 and 950 m, which are similar. The boundary, then, between mid-altitude rain forest and lichen forest should fall somewhere between 950 and 1200 m. These observations support a compression of the altitudinal vegetation zones along a latitudinal gradient from north to south.

To compare the biometric parameters determined during our study of the PN de Marojejy with other sites on Madagascar or elsewhere in the tropical world, we multiplied the 0.1 ha plots by 10 to bring them to the standard area of 1.0 ha. A comparison with other eastern humid forest sites in Madagascar shows overall similarities between these forests (Table 3-5). However, comparisons between Madagascar and tropical forests elsewhere in the world show that the number of trees with stems ≥ 10 cm dbh and basal area values are much higher in the PN de Marojejy than at sites in South America, Africa, and Asia (see Rakotomalaza & Messmer, 1999, for a review).

Regarding diversity, the fact that the number of species was highest at 1200 m could also be interpreted as an artifact of the length of the baseline

TABLE 3-5. Comparative plot data from other parts of Madagascar.

Sites	Plot size (ha)	Altitude (m)	Number of trees with dbh ≥ 10 cm per ha	Basal area (m ²) per ha	Shannon-Weaver diversity index—families	Shannon-Weaver diversity index—species
Miaranony, Ranomafana (Lowry et al., 1997)	1	600	769	49.9	—	—
Vatoharanana, Ranomafana (Lowry et al., 1997)	1	950	660	35.0	—	—
Vohiparara, Ranomafana (Lowry et al., 1997)	1	1200	1,092	25.6	—	—
Manombo (Rabevohitra et al., 1996)	1	80	787	—	—	—
Analalava-Marovony (Dumetz, 1993)	1	50	1,200	—	—	4.90
	1	50	840	—	—	4.60
	1	50	940	—	—	4.70
	1	50	1,280	—	—	5.00
Manatantely (Dumetz, 1993)	1	250	900	—	—	3.90
Andohahela (Rakotomalaza & Messmer, 1999)	1	440	739	34.1	1.32	1.76
	1	840	880	43.2	1.34	1.86
	1	1140	1,216	43.8	1.29	1.77
	1	1550	675	63.8	1.18	1.49
	1	1875	1,365	65.9	1.21	1.52
Marojejy, biological inventory of 1996	0.1	490	590	38.0	1.25	1.60
	0.1	500	590	66.0	1.29	1.56
	0.1	800	860	65.0	—	—
	0.1	800	760	44.0	1.37	1.67
	0.1	800	1,430	67.0	1.35	1.73
	0.1	1200	880	40.0	1.33	1.74
	0.1	1200	2,050	49.0	1.26	1.76
	0.1	1600	1,640	46.0	1.28	1.67
	0.1	1600	100	3.0	1.29	1.80
	—	1850	—	—	1.31	1.72
—	1950	—	—	1.15	1.64	

Note: The Shannon-Weaver diversity index values were calculated from the linear transect in the PN de Marojejy.

of the surveys (100 m), which is probably too short to allow adequate representation of the species, especially for the bigger trees in the lower-altitude samples. However, in 1 ha plots in the PN d'Andohahela, the same observation has been made for angiosperms (Rakotomalaza & Messmer, 1999) as well as for pteridophytes in the RS d'Anjanaharibe-Sud (Rakotondrainibe & Raharimalala, 1998), and thus the trend could be real. The species Shannon-Weaver diversity index value we measured in the PN de Marojejy is much lower than the ones calculated for other overseas tropical regions (reviewed by Rakotomalaza & Messmer, 1999). These values are nevertheless comparable to the ones calculated from the results obtained along the elevational transect in the PN d'Andohahela (Table 3-5), but the ratios of the number of species to the number of individuals are much higher in the PN de Marojejy. However, the

meaning of these low values is not yet elucidated, and the sample size might be implicated.

Because two different methods were used in the PN de Marojejy and the PN d'Andohahela, and owing to the insufficient amount of quantitative data along the latitudinal gradient in the eastern forests of the island, it would be premature to draw meaningful conclusions about clinal variation in species richness associated with latitudinal variation. This possibility, however, should be considered when subsequent data become available from the rain forests of Madagascar.

Conclusions

The field methods used during the 1996 inventory of the PN de Marojejy provided good quan-

titative measures and graphic representations of the structure, floristic composition, and variability of the vegetation along the elevational gradient. Regarding structure, the linear survey gives valuable information on forest structure even for dwarf forests, where trees ≥ 10 cm dbh are rare (1600 m ridge, 1800 m slope, and 1950 m ridge samples).

The linear sampling method has been used only in a few tropical forests (but see Chatelain, 1996), and comparisons with data obtained by other means from other sites are limited. More use of this method should be encouraged, because of its efficiency during rapid inventories under difficult conditions and the useful results it provides.

To allow a comparison of biometric parameters such as basal area, density, and the like, traditional plots are added to the linear sampling method. However, these plot data would be of greater value if their area is increased to 0.2 ha, as recommended by Gautier et al. (1994), and if the dbh lower limit is reduced to 2.5 cm instead of 10 cm in half of the plot.

The sampling method we used does not give a full account of the diversity of the richest sites, and problems in application of the diversity index still have to be solved. However, the compromise between the time devoted to each sample (ca. 2.5 days) and the data gathered renders the method very valuable for rapid assessment surveys.

Comparisons would have been easier if we would have applied the 0.1 ha transects (ten continuous transects, each 50 m \times 2 m), as proposed by Gentry (1982, 1988). Indeed, these 0.1 ha "Gentry" transects have been applied in the tropics at more sites than any other rapid assessment floristic evaluation technique. We did not, however, use this inventory method because it is often described more as a complement to 1.0 ha plots than as a survey method by itself (Phillips & Raven, 1996), aimed as it is toward capturing maximal diversity rather than accurate structural and floristic measurements. Moreover, a 0.1 ha "Gentry" transect probably traverses an area of approximately 2 or 3 ha (Phillips & Raven, 1996). To locate a homogeneous parcel of forest meeting this area requirement on the higher slopes of a mountain such as Marojejy would not be simple. Our aim was to describe two different habitats, slopes and ridges, in a restricted altitudinal interval. Thus, even if the 0.1 ha transect method is regarded as one of the favorite methods for floristic inventories, it was not adequate for our survey objectives.

The quantitative survey we made in the PN de Marojejy adds new data to that already recorded by the numerous collectors on the Marojejy Massif area during earlier botanical expeditions. The structural data add information about the elevational gradient in the northeastern forest of Madagascar. We have referred to Humbert's classification system in discussing our results obtained in the PN de Marojejy because it has a more precise basis than many other earlier schemes and because more recent classification systems are largely based on that of Humbert.

Generally, the structure and floristic composition of the forests along the altitudinal gradient agrees with Humbert's (1955, 1965) visual descriptions. The vegetation types he noted were readily encountered in our samples, but some shifts in altitude between slope and ridge vegetation types emphasized the influence of topography. Furthermore, the changes in vegetation types were gradual and the altitudinal gradient surveyed in this study encompassed an ecocline rather than clear-cut vegetation communities. Similar surveys in the Malagasy rain forests would help elucidate the relationship between altitudinal botanical zonation and latitudinal variation.

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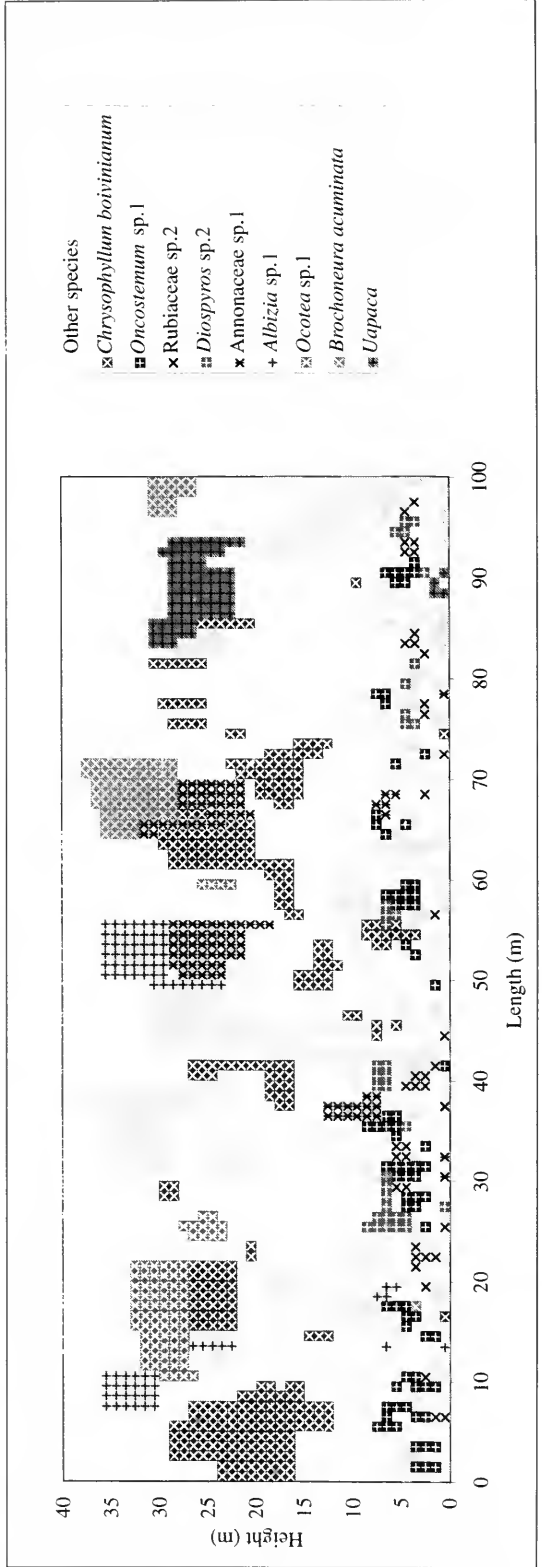
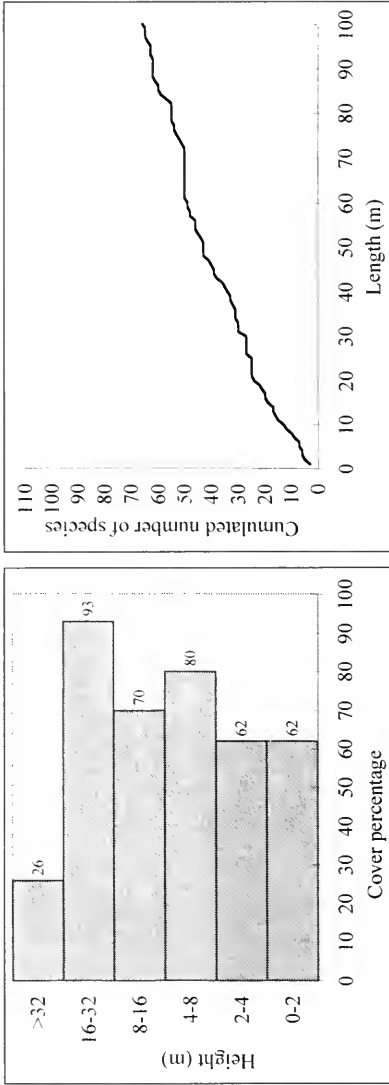
Literature Cited

- BROWER, J. E., J. H. ZAR, AND C. N. VON ENDE. 1990. *Field and Laboratory Methods for General Ecology*. 3rd ed. Brown Publishers, Dubuque, Iowa, 237 pp.
- CENTRE TECHNIQUE FORESTIER TROPICAL (CTFT). 1989. *Mémento du forestier: Techniques rurales en Afrique*. Ministère de la Coopération et du Développement (eds), Paris, 1266 pp.
- CHATELAIN, C. 1996. Possibilités d'application de l'imagerie satellitaire à haute résolution pour l'étude des transformations de la végétation en Côte d'Ivoire forestière. Thèse de doctorat, Université de Genève, Département de botanique et de biologie végétale, Genève.
- CORNET, A., AND J.-L. GUILLAUMET. 1976. Divisions floristiques et étages de végétation à Madagascar. *Cahier de l'ORSTOM (série Biologie)*, **11**: 35–42.
- DUMETZ, N. 1993. Mise en évidence de l'hétérogénéité floristique et structurale de la forêt orientale de basse altitude à Madagascar. Thèse de doctorat, Université de Paris VI, Paris.
- DU PUY, D. J., AND J. MOAT. 1996. A refined classification of the primary vegetation of Madagascar based on the underlying geology: Using GIS to map its distribution and to assess its conservation status, pp. 205–318. *In* Lourenço, W. R., ed. *Biogéographie de Madagascar*. Editions de l'ORSTOM, Paris.
- GAUTIER, L., C. CHATELAIN, AND R. SPICHTER. 1994. Presentation of a relevé method for vegetation studies based on fine-scale satellite imagery, pp. 1339–1350. *In* Seyani, J. H., and A. C. Chikuni, eds. *Proceedings of the XIII Plenary Meeting of the AETFAT, Malawi*, vol. 2.
- GENTRY, A. H. 1982. Patterns of neotropical plant species diversity, pp. 1–84. *In* Hecht, M. K., B. Wallace, and G. T. Prance, eds. *Evolutionary Biology*, vol. 15. Plenum Press, New York.
- . 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, **75**: 1–34.
- HUMBERT, H. 1955. Une merveille de la nature à Madagascar: Première exploration botanique du massif du Marojejy et de ses satellites. *Mémoires de l'Institut Scientifique de Madagascar, série B*, **6**: 1–271.
- . 1965. Description des types de végétation, pp. 46–78. *In* Humbert, H., and G. Cours Darne, eds. *Notice de la carte Madagascar. Extrait des travaux de la section scientifique et technique de l'Institut Français de Pondichéry, hors série no. 6*.
- KOECHLIN, J., J.-L. GUILLAUMET, AND P. MORAT. 1974. *Flore et Végétation de Madagascar*. Cramer, Vaduz, Liechtenstein, 687 pp.
- LAUBENFELS (DE), D. J. 1972. Podocarpacees. *Flore de Madagascar et des Comores*, **18**: 1–22.
- LEWIS, B. A., P. B. PHILLIPSON, M. ANDRIANARISATA, G. RAHAJASOA, P. J. RAKOTOMALAZA, M. RANDRIAMBOLOLONA, AND J. F. McDONAGH. 1996. A study of the botanical structure, composition, and diversity of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 24–72. *In* Goodman, S. M., ed. *A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation*. *Fieldiana: Zoology, n.s.*, no. 85.
- LOWRY, P. P., G. E. SCHATZ, AND P. B. PHILLIPSON. 1997. The classification of natural and anthropogenic vegetation in Madagascar, pp. 93–123. *In* Goodman, S. M., and B. D. Patterson, eds. *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington, D.C.
- MILLER, J. S., ET AL. In prep. A checklist of the vascular plants of Marojejy.
- PERRIER DE LA BÂTHIE, H. 1921. La végétation malgache. *Annales de l'Institut Botanico-géologique Colonial de Marseille (série 3)*, **9**: 1–226.
- PHILLIPS, O. L., AND P. H. RAVEN. 1996. A strategy for sampling neotropical forests, pp. 141–165. *In* Gibson, A. C., ed. *Neotropical Biodiversity and Conservation*. University of California Press, Berkeley and Los Angeles.
- RABEVOHITRA, R., P. P. LOWRY II, G. E. SCHATZ, H. RANDRIANJAFY, AND N. RAZAFINDRIANILANA. 1996. Assessment of plant diversity and conservation importance of east coast low elevation Malagasy rain forests: Rapport sur le projet. Centre National de la Recherche Appliquée au Développement Rural, Madagascar. Département de Recherches Forestières et Piscicoles, Madagascar, and Biodiversity Support Program, Missouri Botanical Garden, St. Louis.
- RAKOTOMALAZA, P. J., AND N. MESSMER. 1999. Structure and floristic composition of the vegetation of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, pp. 51–96. *In* Goodman, S. M., ed. *A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: with reference to elevational variation*. *Fieldiana: Zoology, n.s.*, no. 94.
- RAKOTONDRAINIBE, F., AND F. RAHARIMALALA. 1998. The pteridophytes of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: Floristic analysis and altitudinal distribution, pp. 17–38. *In* Goodman, S. M., ed. *A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: with reference to elevational variation*. *Fieldiana: Zoology, n.s.*, no. 90.
- SHANNON, C. E., AND W. WEAVER. 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, 117 pp.
- WHITE, F. 1986. La végétation de l'Afrique: Mémoire accompagnant la carte de végétation de l'Afrique UNESCO/AETFAT/UNSO. *Recherches sur les ressources naturelles XX*. ORSTOM-UNESCO, 384 pp.

(Appendices to Chapter 3 begin on the following page.)

APPENDIX 3-1a. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojejy: Slope at 500 m

a Marojejy, alt. 500 m, slope
 14°26.2'S - 49°46.5'E
 Density (≥ 10 cm dbh; 0.1
 ha plot) 590/ha
 Basal area (m²; 0.1 ha plot) 66/ha
 Number of species 66
 Shannon diversity index
 (linear survey data) 1.56



APPENDIX 3-1b. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojejy: Plateau at 490 m

b

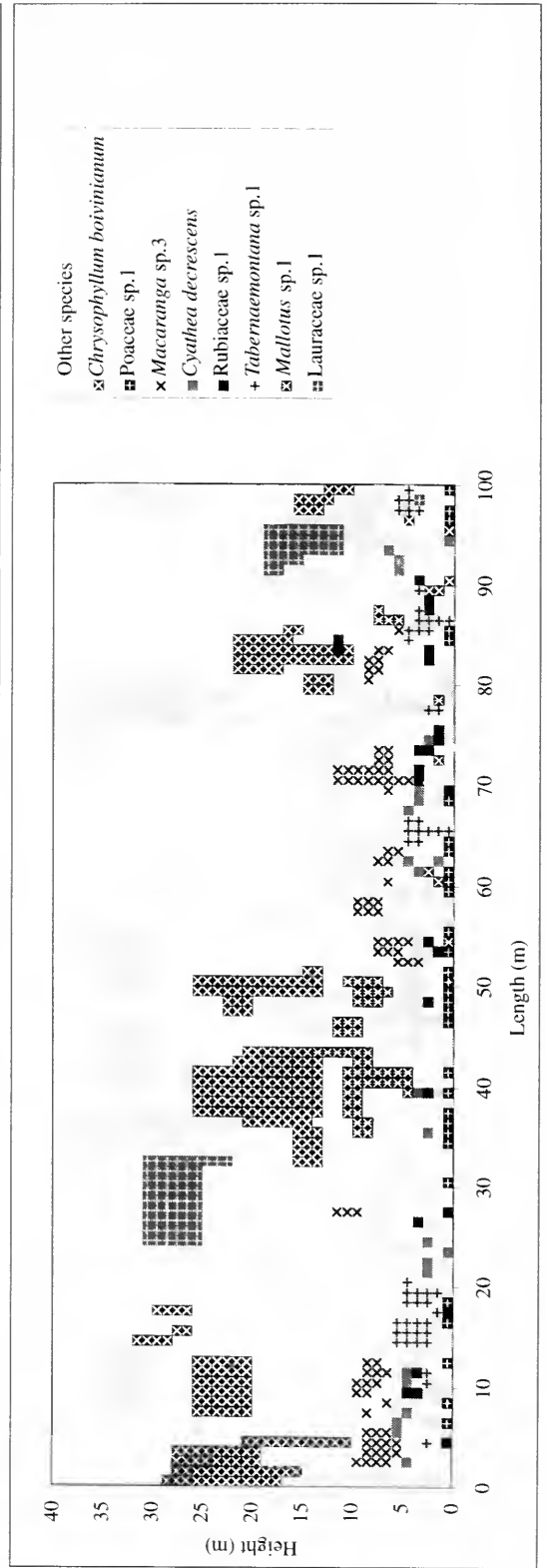
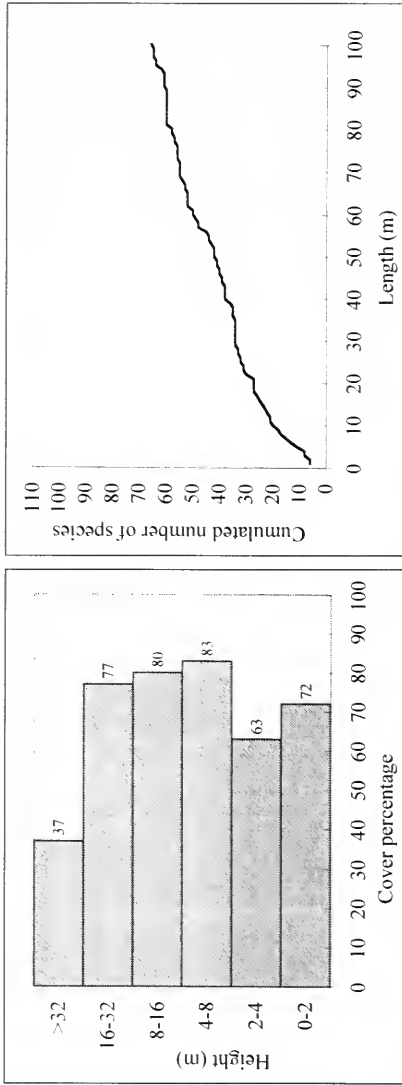
Marojejy, alt. 490 m, plateau
14°26.2' S - 49°46.5' E

Density (≥ 10 cm dbh: 0.1
ha plot) 590/ha

Basal area (m^2 : 0.1 ha plot) 38/ha

Number of species
(linear survey data) 66

Shannon diversity index
(linear survey data) 1.60



APPENDIX 3-1c. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojej: Slope at 800 m

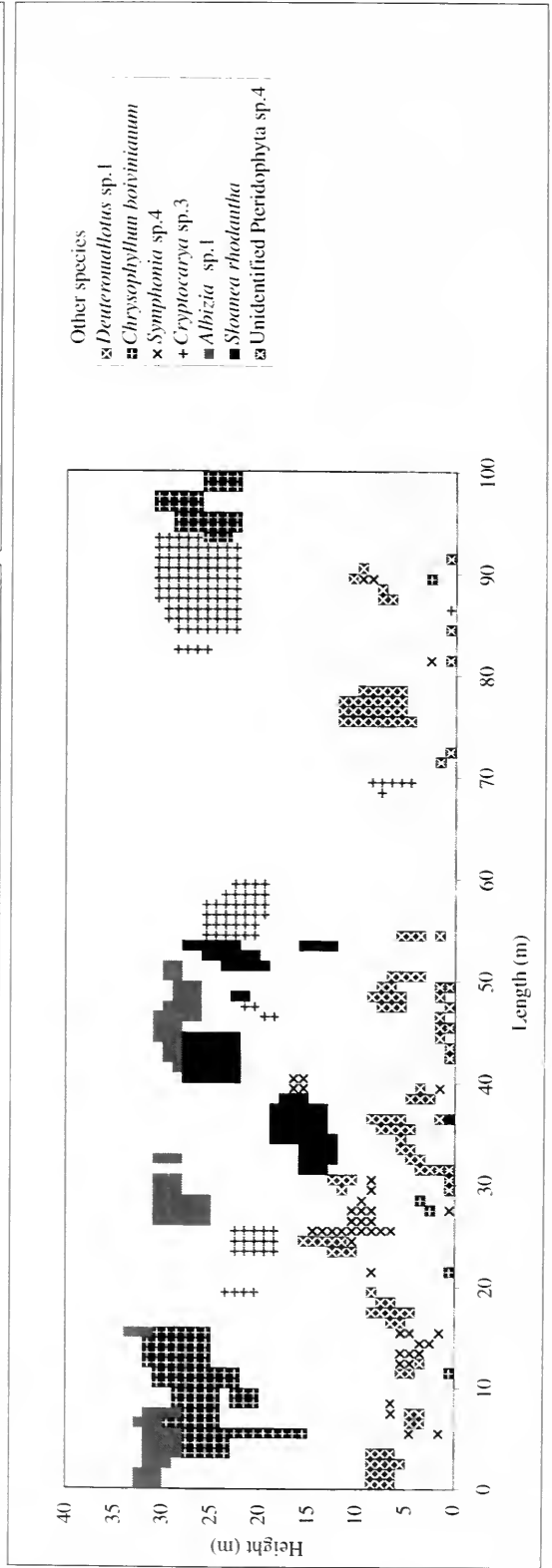
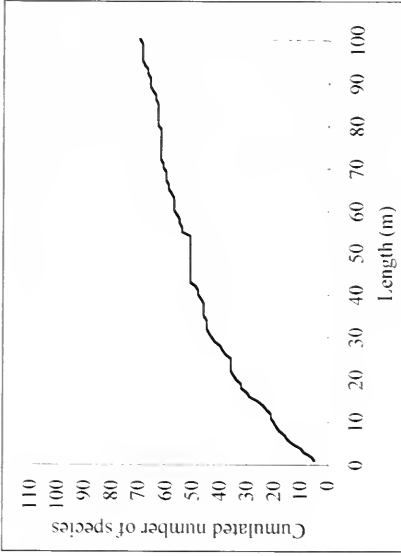
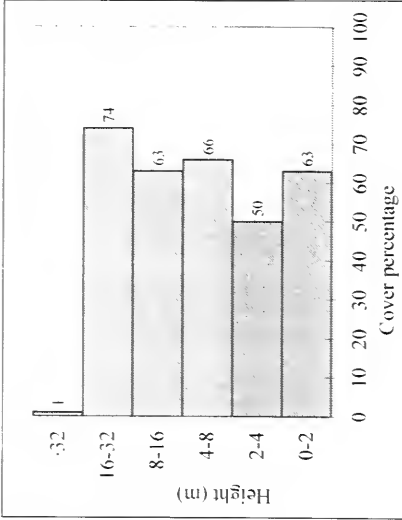
C Marojej, alt. 800 m, slope 14°26.0' S - 49°45.7' E

Density (≥ 10 cm dbh; 0.1 ha plot) 760/ha

Basal area (m²; 0.1 ha plot) 44/ha

Number of species (linear survey data) 70

Shannon diversity index (linear survey data) 1.67



APPENDIX 3-1d. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojejy: Ridge at 800 m

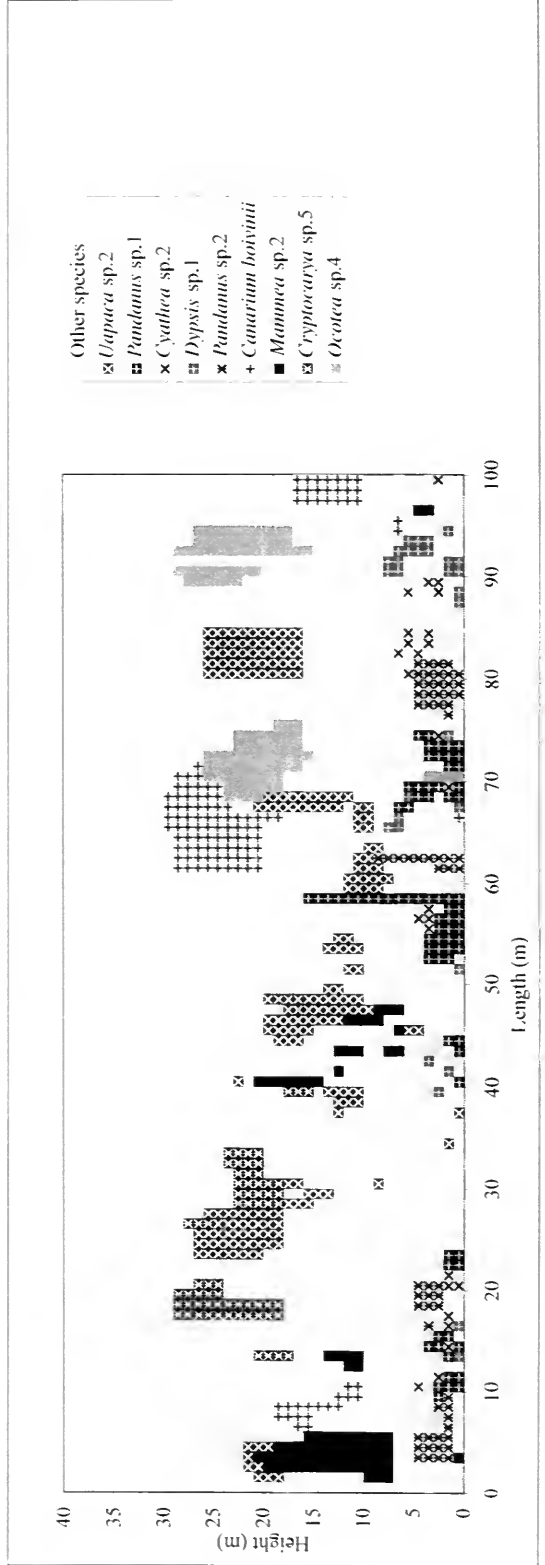
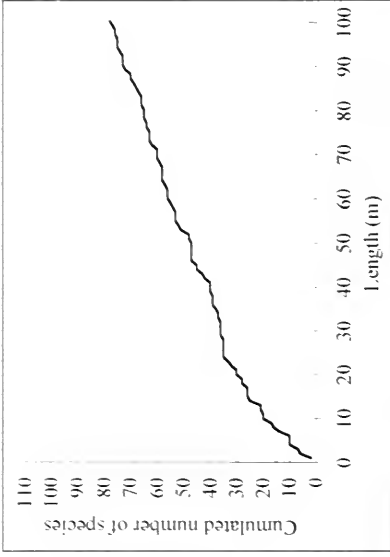
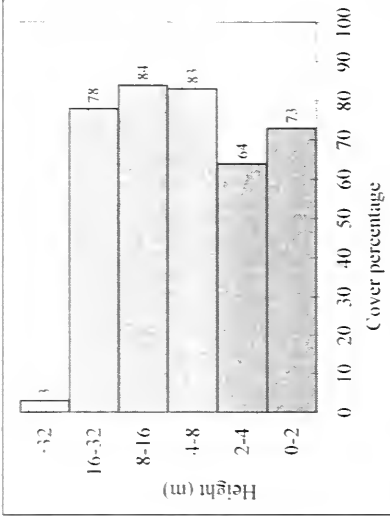
d Marojejy, alt. 800 m, ridge
14°26.0' S - 49°45.7' E

Density (≥ 10 cm dbh; 0.1 ha plot) 1430/ha

Basal area (m²; 0.1 ha plot) 67/ha

Number of species (linear survey data) 78

Shannon diversity index (linear survey data) 1.73



Species/morphospecies recorded	Cover value (%) by height interval†						Species/morphospecies recorded	Cover value (%) by height interval															
	0-2		2-4		8-16			16-32		>32		Global cover (No. of individuals)	0-2		2-4		8-16		16-32		>32		
	m	m	m	m	m	m		m	m	m	m		m	m	m	m	m	m	m	m	m	m	m
<i>Uapaca</i> sp. 2	47	(13)	3		7	<u>30</u>	<u>25</u>							1	3						3	(3)	
<i>Pandanus</i> sp. 1	34	(15)	<u>25</u>		4	1																3	(3)
<i>Cyathea</i> sp. 2	29	(17)	<u>9</u>	<u>11</u>	6																	3	(3)
<i>Dyopsis</i> sp. 1	22	(15)	<u>13</u>	3	7										2							3	(2)
<i>Pandanus</i> sp. 2	22	(7)	<u>18</u>	<u>13</u>	9																	3	(1)
<i>Canarium boivinii</i>	22	(4)	1		2	8	<u>14</u>															2	(2)
<i>Nastus</i> sp. 1	20	(7)	7	8	9																	2	(2)
<i>Polyscias</i> sp. 2	19	(11)		6	10	6																2	(2)
<i>Eugenia</i> sp. 1	18	(8)	3	4	4	9	7	3														2	(2)
<i>Mammea</i> sp. 2	15	(7)	1	1	9	<u>11</u>	4															2	(2)
<i>Cryptocarya</i> sp. 5	15	(5)			1	1	<u>13</u>															2	(1)
<i>Ocotea</i> sp. 4	15	(3)	1	1	1	6	<u>13</u>															2	(1)
<i>Ravenala madagascariensis</i>	12	(5)		4	8		1															2	(1)
<i>Calophyllum</i> sp. 1	11	(4)			2	6	8															2	(1)
<i>Erythroxylum</i> sp. 3	10	(2)	1	5	2	2	1															2	(1)
<i>Enterospermum</i> sp. 2	9	(6)	1	1	5	2	2															2	(1)
<i>Uapaca</i> sp. 1	8	(3)	1	1	1	5	2	2														2	(1)
<i>Eugenia</i> sp. 4	8	(3)	1	3	3	6																2	(1)
<i>Potamogetia crassifolia</i>	6	(5)	5	3																		2	(1)
<i>Potamogetia</i> sp. 2	6	(4)	1	1	3	2	2															2	(1)
<i>Noronhia</i> sp. 3	6	(3)	5	3	2																	2	(1)
<i>Oncostemum</i> sp. 3	6	(3)		1	4	2																2	(1)
<i>Calophyllum</i> sp. 4	6	(2)		2	4																	2	(1)
Unidentified Pteridophyta sp. 5	5	(5)	5		2	1																2	(1)
<i>Oncostemum</i> sp. 1	5	(4)	2		2																	1	(1)
Sapindaceae sp. 2	5	(1)																				1	(1)
<i>Diospyros</i> sp. 6	4	(4)	1	3	2																	1	(1)
<i>Vernonia</i> sp. 1	4	(4)	2	1	1																	1	(1)
<i>Anthocleista longifolia</i>	4	(3)	1	1	1	2																1	(1)
<i>Polyalthia perrieri</i>	4	(3)	1	2	2																	1	(1)
<i>Danais</i> sp. 1	4	(2)	1		3	3	2															1	(1)
<i>Dillenia</i> sp. 1	4	(2)		1	1	3																1	(1)
<i>Hugonia</i> sp. 1	4	(2)		1	1	1	1															1	(1)
<i>Mammea</i> sp. 1	4	(2)		3	3	3																1	(1)
<i>Protorhus</i> sp. 6	4	(2)		1	4	4																1	(1)
<i>Dillenia triquetra</i>	4	(1)		1	4	4																1	(1)
<i>Isolona</i> sp. 1	4	(1)		1	4	4	1															1	(1)
<i>Gravasia</i> sp. 3	3	(3)	3		2	1																1	(1)
<i>Homalium</i> sp. 6	3	(3)			1																	1	(1)

* Number of stems with dbh ≥ 10 cm, basal area, number of species, vertical distribution of vegetation, points-species accumulation curves, profiles highlighting species with cover value $> 10\%$ in any height interval, list of species recorded, and species cover values separated into height intervals.
† **Bold** entries represent cover values $\geq 5\%$ and **bold underlined** entries represent cover values $> 10\%$.

e APPENDIX 3-1e. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojejy:
Slope at 1200 m.

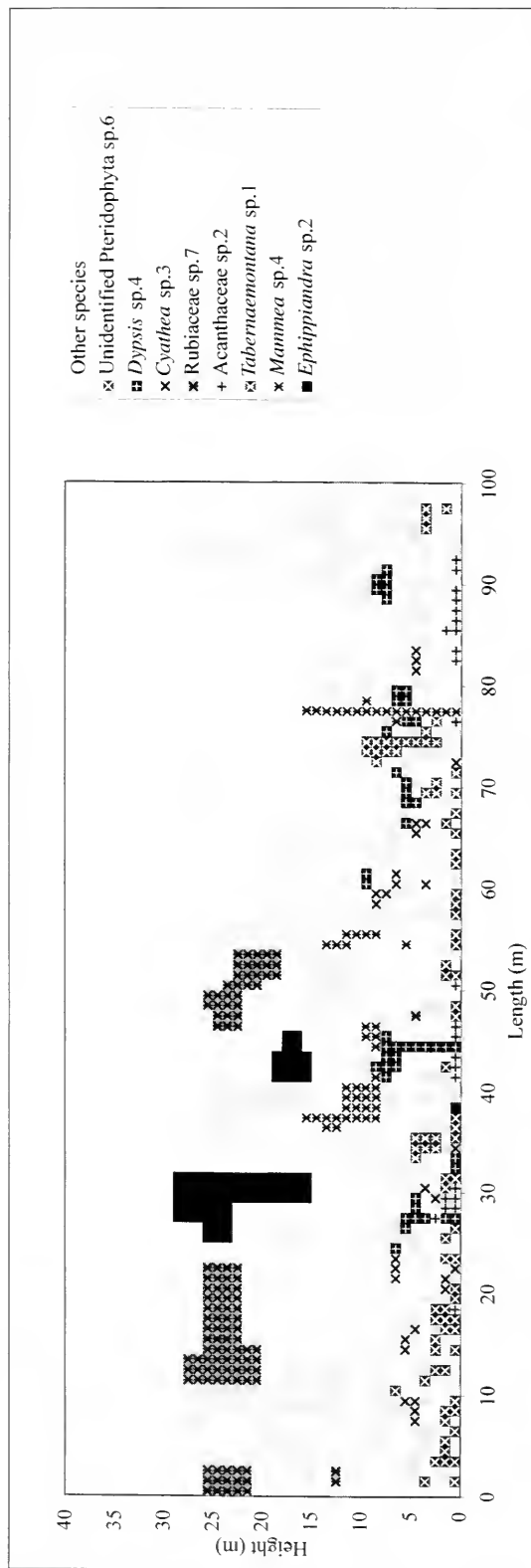
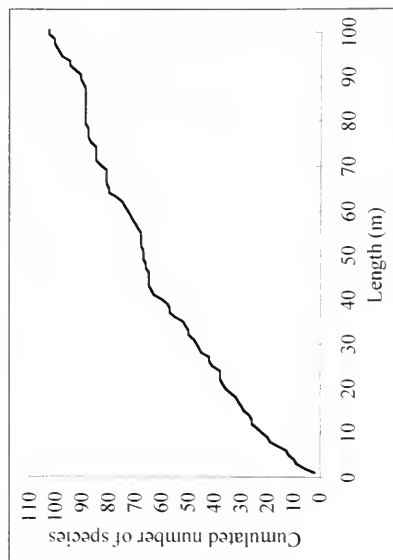
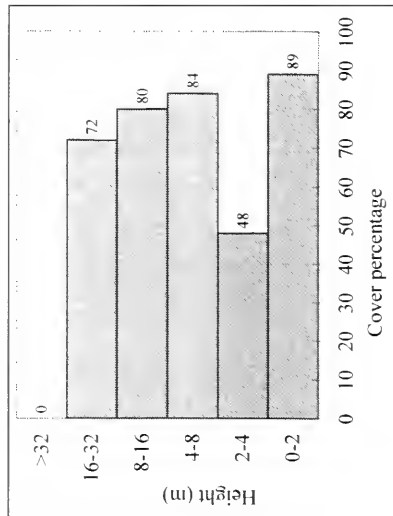
e Marojejy, alt. 1200 m, slope
14°26.2' S - 49°44.5' E

Density (≥ 10 cm dbh; 0.1
ha plot) 860/ha

Basal area (m²; 0.1 ha plot) 40/ha

Number of species
(linear survey data) 103

Shannon diversity index
(linear survey data) 1.74



Species/morphospecies recorded	Cover value (%) by height interval†					Global cover (No. of individuals)	Species/morphospecies recorded	Cover value (%) by height interval					Global cover (No. of individuals)	Species/morphospecies recorded	Cover value (%) by height interval				
	0-2	2-4	4-8	16	>32			0-2	2-4	4-8	16	>32			0-2	2-4	4-8	16	>32
	m	m	m	m	m			m	m	m	m	m			m	m	m	m	m
Unidentified Pteridophyta sp. 6	45	6	2			4 (1)	<i>Labramia</i> sp. 1	4					4 (1)	<i>cf. Schismatoclada</i> sp. 6	1				
<i>Dypsis</i> sp. 4	4	2	26	5		4 (1)	<i>Sapium</i> sp. 1					4	4 (1)	<i>Danais</i> sp. 3	1				
<i>Cyathea</i> sp. 3	26	13	5	16	1	3 (3)	<i>Begonia</i> sp. 1	3					3 (3)	<i>Dichaetanthera</i> sp. 9	1				
Rubiaceae sp. 7	23	3	1		23	3 (3)	<i>Gravasia</i> sp. 5	3					3 (3)	<i>Diospyros</i> sp. 11	1				1
Acanthaceae sp. 2	21	15	21	1		3 (3)	<i>Tambourissa</i> sp. 5	2	1				3 (3)	<i>Diospyros</i> sp. 6	1				
<i>Dypsis</i> sp. 3	19	5	7	9		3 (2)	<i>Canthium</i> sp. 5	1	2				3 (2)	<i>Diospyros</i> sp. 8	1				
<i>Mammea</i> sp. 3	17	8	2	4	3	3 (2)	<i>Potameia</i> sp. 4	1		2			3 (2)	<i>Dombeya</i> sp. 4	1				
<i>Tabernaemontana</i> sp. 1	17	7	4	11	5	3 (1)	<i>Canthium</i> sp. 3	1	2	3			3 (1)	<i>Dracaena reflexa</i>	1				
<i>Scolopia</i> sp. 2	16	9	1	3	4	3 (1)	<i>Canthium</i> sp. 6	1	2	3	2		3 (1)	<i>Elaphoglossum</i> sp. 1	1				
<i>Mammea</i> sp. 4	14	5	1	1	10	3 (1)	<i>Cryptocarya</i> sp. 3	1					3 (1)	<i>Eugenia</i> sp. 10	1				
<i>Ephippiandra</i> sp. 2	13	3	1		8	3 (1)	<i>Ocotea</i> sp. 7	1		5			3 (1)	<i>Eugenia</i> sp. 4	1				
<i>Pouridiana paucinervis</i>	12	6			10	2 (2)	Acanthaceae sp. 1	2		2			2 (2)	<i>Ficus</i> sp. 5	1				
<i>Enterospermum</i> sp. 4	12	5	3	10	3	2 (2)	Acanthaceae sp. 3	2		2			2 (2)	<i>Gaermera</i> sp. 5	1				
<i>Tambourissa</i> sp. 4	12	5	1	5	6	2 (2)	<i>Allophylus</i> sp. 1	2		2			2 (2)	<i>Gravasia</i> sp. 2	1				
<i>Eugenia</i> sp. 8	10	3			10	2 (2)	<i>Antidesma petiolare</i>	1		1			2 (2)	<i>Macaranga</i> sp. 5	1				
<i>Brachylaena</i> sp. 1	10	2			2	2 (2)	<i>Colea</i> sp. 1	1		1			2 (2)	<i>Melanophylla humbertiana</i>	1				
<i>Nastus</i> sp. 2	9	7	2	3	3	2 (2)	<i>Dypsis</i> sp. 1	1		2			2 (2)	<i>Memecylon</i> sp. 2	1				
Unidentified liana spp.	8	3	1	1	7	2 (2)	<i>Maesa</i> sp. 1	1		2			2 (2)	<i>Memecylon</i> sp. 3	1				
<i>Gravasia</i> sp. 1	7	7	7		1	2 (2)	<i>Oncostemum</i> sp. 16	1		2			2 (2)	<i>Olea</i> sp. 1	1				
<i>Oncostemum</i> sp. 6	7	5	1	2	4	2 (1)	<i>Scleria</i> sp. 1	1		3			2 (1)	<i>Oncostemum</i> sp. 11	1				
<i>Phyllarthron</i> sp. 1	7	1			7	2 (1)	<i>Asplenium nidus</i>	2		4			2 (1)	<i>Oncostemum</i> sp. 7	1				
<i>Cryptocarya</i> sp. 10	6	2			5	2 (1)	<i>Canthium</i> sp. 4	2		2			2 (1)	<i>Pandanus</i> sp. 1	1				
<i>Scheffera</i> sp. 2	6	2			6	2 (1)	<i>Ilex mitis</i>	2		2			2 (1)	<i>Pandanus</i> sp. 4	1				
<i>Canarium madagascariense</i>	6	1	1	4	6	2 (1)	<i>Pitiosporum</i> sp. 2	2		2			2 (1)	<i>Peperomia</i> sp. 1	1				
<i>Boehmeria</i> sp. 1	5	5			5	1 (1)	<i>Scheffera</i> sp. 9	1		4			1 (1)	<i>Pilea</i> sp. 1	1				
<i>Medinilla</i> sp. 7	5	4			5	1 (1)	Acanthaceae sp. 11	1		1			1 (1)	<i>Saldinia</i> sp. 1	1				
<i>Psychotria</i> sp. 1	5	4			5	1 (1)	Acanthaceae sp. 4	1		1			1 (1)	<i>Saldinia</i> sp. 1	1				
Unidentified Pteridophyta sp. 1	5	4	3	2	1	1 (1)	Acanthaceae sp. 5	1		1			1 (1)	<i>Sloanea rhodantha</i>	1				
<i>Ficus sorocooides</i>	5	4	3	2	1	1 (1)	Acanthaceae sp. 6	1		1			1 (1)	<i>Tambourissa</i> sp. 9	1				
<i>Oncostemum</i> sp. 1	4	4	1	2	1	1 (1)	Acanthaceae sp. 7	1		1			1 (1)	<i>Vepris</i> sp. 3	1				
<i>Diospyros</i> sp. 10	4	3	2	2		1 (1)	Acanthaceae sp. 8	1		1			1 (1)	<i>Weinmannia</i> sp. 11	1				
<i>Elaeodendron</i> sp. 1	4	2	2	2		1 (1)	Acanthaceae sp. 9	1		1			1 (1)						
<i>Polyscias</i> sp. 3	4	2	2	2		1 (1)	<i>Allophylus</i> sp. 3	1		1			1 (1)						
<i>Polyscias</i> sp. 4	4	2	2	2		1 (1)	<i>Aphoia theiformis</i>	1		1			1 (1)						
<i>Erythroxylum</i> sp. 3	4	2	3	1		1 (1)	<i>Aristolochia</i> sp. 1	1		1			1 (1)						
	4	2	3	1		1 (1)	Asteraceae sp. 8	1		1			1 (1)						
	4	2	4	4		1 (1)	<i>Begonia</i> sp. 1	1		1			1 (1)						
	4	1	4	4		1 (1)	<i>Canthium</i> sp. 2	1		1			1 (1)						

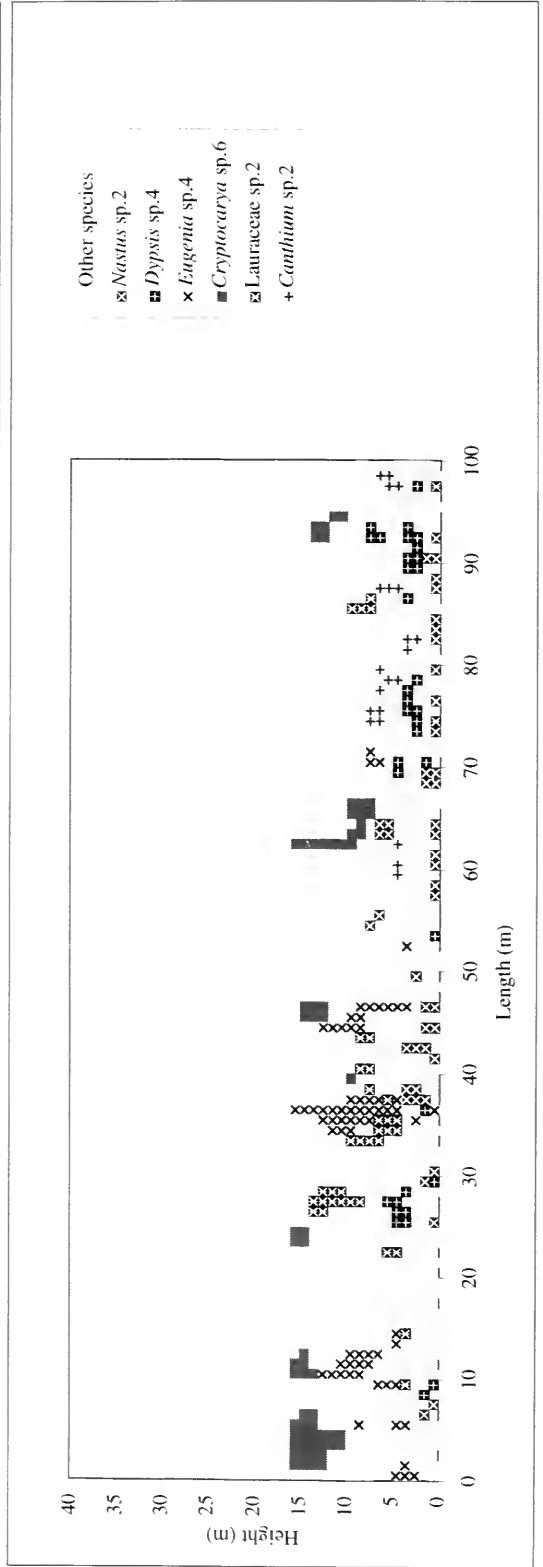
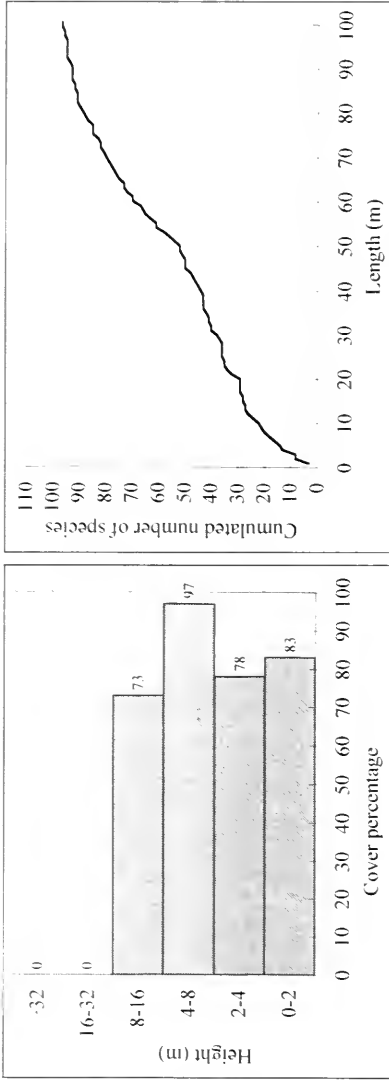
* Number of stems with dbh ≥10 cm, basal area, number of species, vertical distribution of vegetation, points-species accumulation curves, profiles highlighting species with cover value >10% in any height interval, list of species recorded, and species cover values separated into height intervals.
 † **Bold** entries represent cover values ≥5% and **bold underlined** entries represent cover values >10%.

f APPENDIX 3-1f. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojejy: Ridge at 1200 m

Marojejy, alt. 1200 m, ridge
 14°26.2' S - 49°44.5' E

Density (≥ 10 cm dbh): 2050/ha
 0.1 ha plot
 Basal area (m²; 0.1 ha plot) 49/ha

Number of species (linear survey data) 97
 Shannon diversity index (linear survey data) 1.76



Species/morphospecies recorded	Cover value (%) by height interval†						Global cover (No. of individuals)	Species/morphospecies recorded	Cover value (%) by height interval						Global cover (No. of individuals)	Species/morphospecies recorded				
	0-2		2-4		4-8				8-16		0-2		2-4				4-8		8-16	
	m	m	m	m	m	m			m	m	m	m	m	m			m	m	m	m
<i>Nastus</i> sp. 2	35	(31)	30	4	4	4	3	<i>Dichaeanthera</i> sp. 3	4	(3)	2	2	2	2	2	2	<i>Elaeocarpus</i> sp. 1			
<i>Dypsip</i> sp. 4	27	(14)	6	17	6	6	2	<i>Cassinopsis</i> sp. 2	4	(1)	4	4	4	4	4	4	<i>Phyllarthron</i> sp. 1			
<i>Eugenia</i> sp. 4	26	(16)	1	8	16	10	1	<i>Cassipourea</i> sp. 1	4	(1)	4	4	4	4	4	4	<i>Potameia</i> sp. 5			
<i>Cryptocarya</i> sp. 6	22	(7)	3	22	3	22	3	<i>Eugenia</i> sp. 8	4	(1)	4	4	4	4	4	4	<i>Tambourissa</i> sp. 3			
Lauraceae sp. 2	17	(12)	2	3	11	6	6	<i>Metanophylla humbertiana</i>	4	(1)	4	4	4	4	4	4	<i>Weinmannia</i> sp. 1			
<i>Elaeodendron</i> sp. 1	17	(11)	1	4	10	5	5	<i>Potameia</i> sp. 3	4	(1)	1	3	3	3	3	3	Acanthaceae sp. 10			
<i>Canthium</i> sp. 2	13	(7)	5	6	3	3	3	<i>Donnabeia</i> sp. 3	3	(3)	1	1	1	1	1	1	Angraecum sp. 1			
<i>Dypsip</i> sp. 3	13	(7)	5	6	3	3	3	<i>Donnabeia</i> sp. 3	3	(3)	1	1	1	1	1	1	<i>Glerodendron</i> sp. 2			
<i>Nastus</i> sp. 1	12	(12)	10	2	1	1	1	<i>Gaermera macrostipula</i>	3	(3)	3	2	2	2	2	2	<i>Cryptocarya</i> sp. 7			
<i>Mammea</i> sp. 4	12	(8)	1	6	8	1	1	<i>Gravasia</i> sp. 5	3	(3)	3	3	3	3	3	3	<i>Cyathia decrescens</i>			
<i>Bentibicia</i> sp. 1	11	(7)	6	3	1	8	5	<i>Oncostenium</i> sp. 9	3	(3)	1	2	1	1	1	1	<i>Danais</i> sp. 3			
Asteraceae sp. 1	9	(9)	6	3	1	8	5	<i>Polyscias</i> sp. 4	3	(3)	1	2	1	1	1	1	<i>Diospyros</i> sp. 8			
<i>Faucheria parvifolia</i>	9	(3)	2	9	5	5	5	<i>Smitax kraussiana</i>	3	(3)	1	1	1	1	1	1	<i>Gaermera</i> sp. 4			
<i>Ludia madagascariensis</i>	8	(4)	1	5	5	5	5	<i>Allophylus</i> sp. 2	3	(2)	1	2	1	1	1	1	<i>Ixora</i> sp. 2			
<i>Symphonia</i> sp. 5	8	(4)	1	1	6	1	1	<i>Enterospermum</i> sp. 3	3	(2)	1	2	1	1	1	1	<i>Landolphia</i> sp. 1			
<i>Dichaeanthera</i> sp. 2	8	(3)	4	5	5	5	5	<i>Ixora</i> sp. 1	3	(2)	1	2	1	1	1	1	<i>Macaranga</i> sp. 4			
Unidentified Pteridophyta sp. 6	7	(7)	6	1	6	1	1	<i>Memeylon</i> sp. 4	3	(2)	1	2	1	1	1	1	<i>Mapouria</i> sp. 3			
<i>Pandanus</i> sp. 3	7	(5)	1	3	4	4	4	<i>Polyscias</i> sp. 3	3	(2)	1	3	2	2	2	2	<i>Medinilla</i> sp. 7			
<i>Oliganthes</i> sp. 1	7	(4)	5	3	3	3	3	<i>Sapium</i> sp. 1	3	(2)	1	3	1	1	1	1	<i>Memeylon</i> sp. 2			
<i>Pandanus</i> sp. 2	7	(4)	6	1	1	1	1	<i>Schefflera</i> sp. 1	3	(2)	3	3	1	1	1	1	<i>Memeylon</i> sp. 3			
<i>Mammea</i> sp. 3	6	(6)	1	2	3	1	1	<i>Uapaca</i> sp. 3	3	(1)	3	3	3	3	3	3	<i>Mendoncia</i> sp. 1			
<i>Tambourissa</i> sp. 2	6	(5)	1	2	3	1	1	<i>Catophyllum</i> sp. 5	2	(2)	2	2	2	2	2	2	<i>Oncostenium</i> sp. 10			
<i>Eugenia</i> sp. 6	6	(4)	1	2	4	1	1	<i>Diospyros</i> sp. 7	2	(2)	2	2	2	2	2	2	<i>Oncostenium</i> sp. 16			
<i>Cyathia</i> sp. 1	6	(3)	2	2	2	2	2	<i>Enterospermum</i> sp. 4	2	(2)	2	2	2	2	2	2	<i>Oncostenium</i> sp. 7			
Acanthaceae sp. 12	5	(5)	5	5	5	5	5	<i>Eugenia</i> sp. 5	2	(2)	1	1	1	1	1	1	<i>Paederia</i> sp. 1			
<i>Oncostenium</i> sp. 8	5	(5)	5	5	5	5	5	<i>Filicium</i> sp. 1	2	(2)	2	2	2	2	2	2	<i>Plagioscyphus</i> sp. 2			
<i>Schismatoclada</i> sp. 1	5	(5)	2	2	2	2	2	<i>Grewia</i> sp. 3	2	(2)	1	1	1	1	1	1	<i>Protorhus</i> sp. 2			
<i>Casearia</i> sp. 1	5	(3)	2	3	1	1	1	<i>Psychotria</i> sp. 2	2	(2)	2	2	2	2	2	2	<i>Protorhus</i> sp. 4			
<i>Croton</i> sp. 4	5	(3)	4	2	2	2	2	<i>Vernonia</i> sp. 2	2	(2)	2	2	2	2	2	2	<i>Rubiaceae</i> sp. 13			
<i>Cyathia</i> sp. 3	5	(3)	2	3	2	2	2	<i>Vernonia</i> sp. 3	2	(2)	1	1	1	1	1	1	<i>Rubiaceae</i> sp. 14			
<i>Dracaena reflexa</i>	4	(4)	1	1	2	2	2	<i>Apodocephala</i> sp. 1	2	(1)	1	2	2	2	2	2	Unidentified Pterido-			
<i>Eugenia</i> sp. 7	4	(4)	3	1	3	1	1	<i>Cryptocarya</i> sp. 9	2	(1)	1	1	1	1	1	1	phyta sp. 9			
<i>Scolopia</i> sp. 1	4	(4)	3	1	3	1	1	<i>Diospyros</i> sp. 9	2	(1)	2	2	2	2	2	2	<i>Viscum</i> sp. 2			

* Number of stems with dbh ≥ 10 cm, basal area, number of species, vertical distribution of vegetation, points-species accumulation curves, profiles highlighting species with cover value $> 10\%$ in any height interval, list of species recorded, and species cover values separated into height intervals.
 † **Bold** entries represent cover values $\geq 5\%$ and **bold underlined** entries represent cover values $> 10\%$.

APPENDIX 3-1g. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojejy:
Slope at 1600 m

8

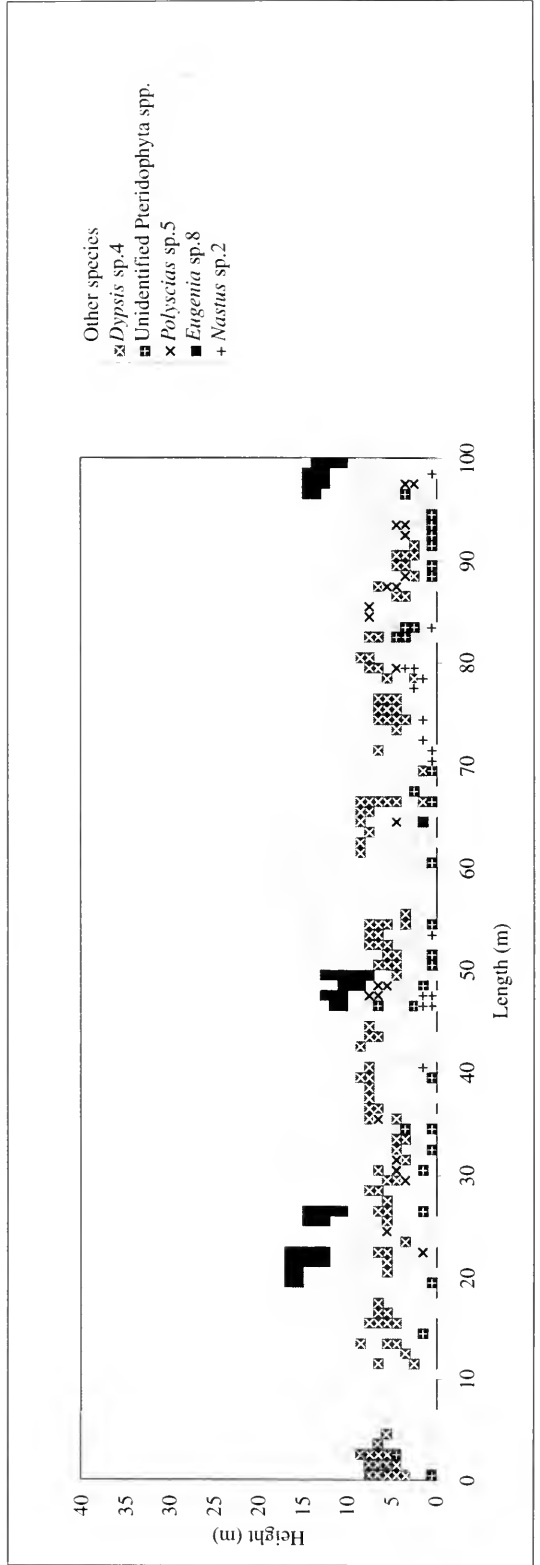
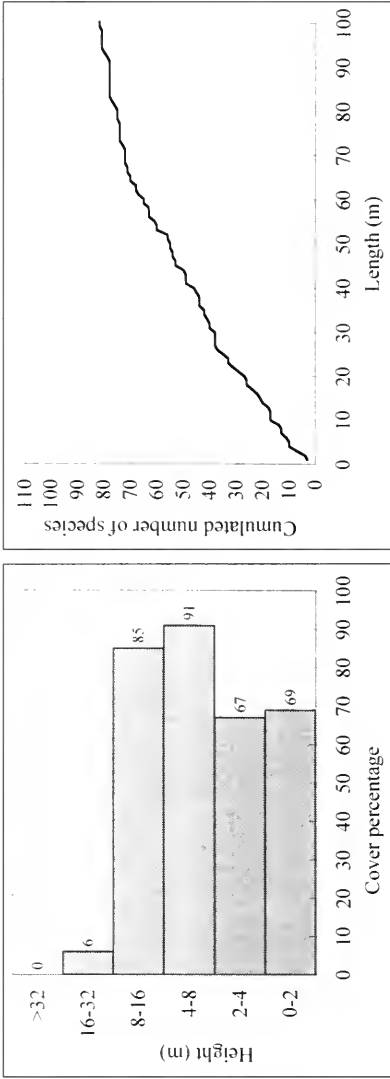
Marojejy, alt. 1600 m, slope
14°26.4' S - 49°44.5' E

Density (≥ 10 cm dbh): 1630/ha
0.1 ha plot

Basal area (m²; 0.1 ha plot) 46/ha

Number of species
(linear survey data) 82

Shannon diversity index
(linear survey data) 1.67



Species/morphospecies recorded	Cover value (%) by height interval†					Global cover (No. of individuals)	Cover value (%) by height interval					Species/morphospecies recorded	Global cover (No. of individuals)
	Cover value (%) by height interval†						Cover value (%) by height interval						
	0-2	2-4	4-8	8-16	16-32 >32		0-2	2-4	4-8	8-16	16-32 >32		
<i>Dypsis</i> sp. 4	3	<u>20</u>	<u>53</u>	1	1	2 (28)						<i>Angraecum</i> sp. 1	2 (2)
Unidentified Pteridophyta spp.	<u>23</u>	<u>5</u>	3			29 (28)						<i>Dypsis</i> sp. 3	2 (2)
<i>Polyscias</i> sp. 5	1	6	<u>11</u>			17 (11)						<i>Gravasia</i> sp. 5	2 (2)
<i>Homalium</i> sp. 4	1	1	<u>7</u>	<u>10</u>		16 (8)						<i>Impatiens</i> sp. 3	2 (2)
<i>Eugenia</i> sp. 8	1	2	<u>2</u>	<u>14</u>		16 (6)						<i>Noronhia</i> sp. 4	1 (1)
<i>Canthium</i> sp. 3	1	3	7	<u>6</u>		15 (9)						<i>Weinmannia</i> sp. 3	2 (2)
<i>Mammea</i> sp. 4	14	7	9			14 (9)						<i>Begonia</i> sp. 1	2 (1)
<i>Nastus</i> sp. 2	<u>11</u>	2				13 (10)						<i>Dombeya</i> sp. 6	2 (1)
<i>Eugenia</i> sp. 4	13	6	<u>8</u>	<u>10</u>		13 (6)						<i>Filicium</i> sp. 3	2 (1)
<i>Cyathea</i> sp. 4	9	8	3			9 (8)						<i>Isora</i> sp. 3	2 (1)
<i>Canthium</i> sp. 6	1	2	4	<u>5</u>		9 (6)						<i>Mapouria</i> sp. 4	2 (1)
<i>Schefflera</i> sp. 3	9	3	7	4		9 (3)						<i>Polyscias</i> sp. 4	2 (1)
<i>Cryptocarya</i> sp. 15	9	2	1	<u>8</u>		9 (2)						<i>Pyrostria</i> sp. 1	2 (1)
<i>Eugenia</i> sp. 19	8	5	<u>6</u>	<u>6</u>		8 (5)						<i>Tambourissa</i> sp. 6	2 (1)
<i>Polyscias</i> sp. 3	8	3	8	6		8 (3)						<i>Asplenium</i> sp. 1	1 (1)
<i>Vernonia</i> sp. 5	7	4	2	2	1	7 (4)						<i>Asteraceae</i> sp. 7	1 (1)
<i>Pittosporum</i> sp. 3	7	1	<u>5</u>			7 (1)						<i>Bulbophyllum</i> sp. 2	1 (1)
<i>Diospyros</i> sp. 13	6	6	3			6 (6)						<i>Celastraceae</i> sp. 1	1 (1)
<i>Peperomia</i> sp. 1	6	5	1	4		6 (5)						<i>Celastraceae</i> sp. 2	1 (1)
<i>Catophyllum</i> sp. 6	6	4	1	1	4	6 (4)						<i>Clerodendron</i> sp. 3	1 (1)
<i>Grewia</i> sp. 4	6	3	3	1	1	6 (3)						<i>Cryptocarya</i> sp. 11	1 (1)
<i>Ochrocarpos isaratananae</i>	6	3	<u>6</u>	<u>3</u>		6 (3)						<i>Cryptocarya</i> sp. 12	1 (1)
<i>Vernonia</i> sp. 4	6	3	2	2		6 (3)						<i>Cyathea bullata</i>	1 (1)
<i>Ilex mitis</i>	6	1	<u>6</u>	<u>2</u>		6 (1)						<i>Dichaeantha</i> sp. 1	1 (1)
<i>Oncostemum</i> sp. 13	5	5	2	6		5 (5)						<i>Diospyros</i> sp. 17	1 (1)
<i>Pandanus</i> sp. 3	5	2	1			5 (2)						<i>Flacourtiaceae</i> sp. 3	1 (1)
cf. <i>Schismatoclada</i> sp. 6	4	4	1	1		4 (4)						<i>Flacourtiaceae</i> sp. 4	1 (1)
<i>Impatiens</i> sp. 2	4	4	4	3		4 (4)						<i>Gaertnera</i> sp. 12	1 (1)
<i>Oncostemum</i> sp. 12	4	3	2	2		4 (4)						<i>Gaertnera</i> sp. 7	1 (1)
<i>Mammea</i> sp. 3	4	3	1	1		4 (3)						<i>Gravasia</i> sp. 4	1 (1)
<i>Pandanus</i> sp. 1	4	3	4			4 (3)						<i>Homalium</i> sp. 6	1 (1)
<i>Erythroxylum</i> sp. 9	4	2	1	3		4 (2)						<i>Impatiens</i> sp. 1	1 (1)
<i>Pandanus</i> sp. 2	4	2	2			4 (2)						<i>Malleastrum</i> sp. 2	1 (1)
<i>Aphloia theiformis</i>	3	3	1	2		3 (3)						<i>Medinilla</i> sp. 7	1 (1)
<i>Asteraceae</i> sp. 8	3	3	1	2		3 (3)						<i>Melastomataceae</i> sp. 2	1 (1)
<i>Viscum</i> sp. 3	3	3	1	1		3 (3)						<i>Mecynolon</i> sp. 5	1 (1)
<i>Anthocleista madagascariensis</i>	3	2	3	2		3 (2)						<i>Rubiaceae</i> sp. 14	1 (1)
<i>Macaranga</i> sp. 6	3	2	3	1		3 (2)						<i>Tambourissa</i> sp. 8	1 (1)
<i>Casearia</i> sp. 2	3	1	3	3		3 (1)						Unidentified "plantule"	1 (1)
<i>Gaertnera</i> sp. 6	3	1	2	3		3 (1)						Unidentified liana spp.	1 (1)
<i>Pittosporum</i> sp. 4	3	1	2	3	2	3 (1)							1 (1)

* Number of stems with dbh ≥ 10 cm, basal area, number of species, vertical distribution of vegetation, points-species accumulation curves, profiles highlighting species with cover value $> 10\%$ in any height interval, list of species recorded, and species cover values separated into height intervals.

† **Bold** entries represent cover values $\geq 5\%$ and **bold underlined** entries represent cover values $> 10\%$.

APPENDIX 3-1h. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojejy: Ridge at 1600 m

h

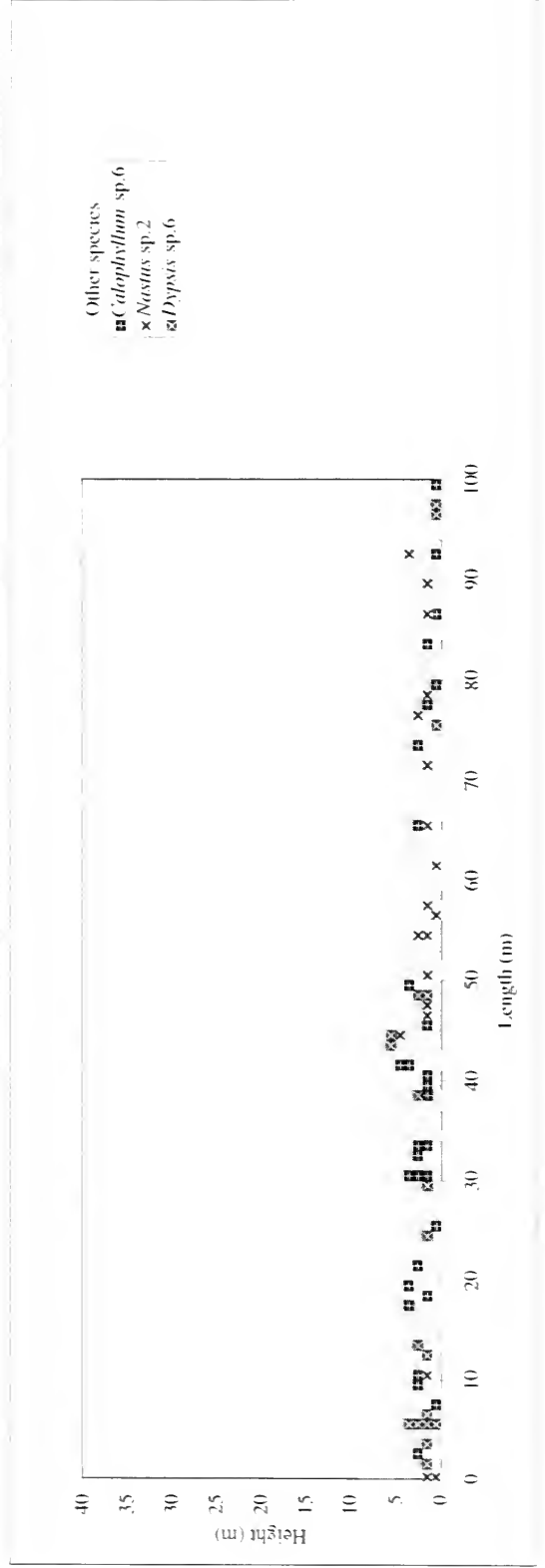
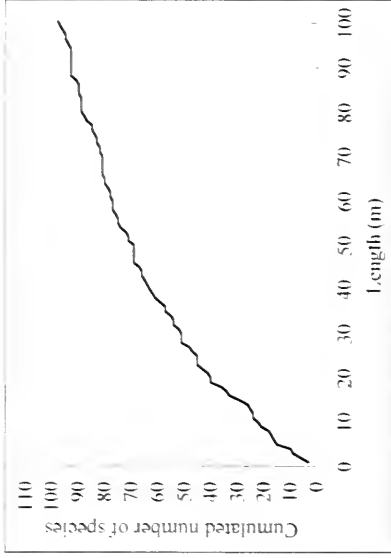
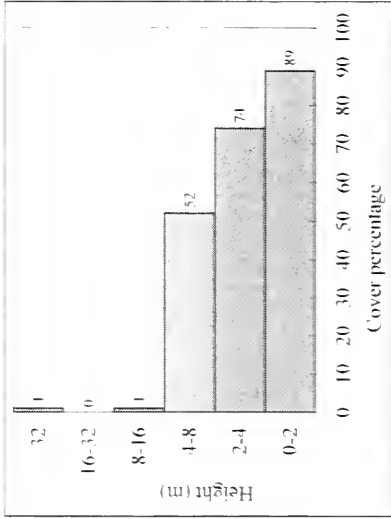
Marojejy, alt. 1600 m, ridge
14°26.4' S - 49°44.5' E

Density (≥ 10 cm dbh): 100/ha
0.1 ha plot

Basal area (m²; 0.1 ha plot): 3/ha

Number of species (linear survey data): 98

Shannon diversity index (linear survey data): 1.80



Species/morphospecies recorded	Cover value (%) by height interval†					Global cover (No. of individuals)	Cover value (%) by height interval					Global cover (No. of individuals)	Cover value (%) by height interval								
	Cover value (%) by height interval†						Global cover (No. of individuals)	Cover value (%) by height interval					Global cover (No. of individuals)	Cover value (%) by height interval							
	0-2	2-4	4-8	8-16	>32			0-2	2-4	4-8	8-16			>32	0-2	2-4	4-8	8-16	>32		
<i>Calophyllum</i> sp. 6	30	(30)	18	13	1	4	(4)	4	1	1	4	(4)	4	1	1	1	(1)	1	1	1	<i>Canthium</i> sp. 3
<i>Nastus</i> sp. 2	18	(18)	15	3		4	(4)	1	1	2	4	(4)	1	1	2	4	(4)	1	1	2	<i>Casearia</i> sp. 3
<i>Dypsis</i> sp. 6	16	(16)	12	2	2	4	(4)	3			4	(4)	3			4	(4)	3			Celastraceae sp. 2
<i>Mammea</i> sp. 5	14	(13)	10	5	2	4	(4)	4			4	(4)	4			4	(4)	4			<i>Cyathia bullata</i>
<i>Symphonia microphylla</i>	14	(12)	3	6	9	4	(3)	2	2		4	(3)	2	2		4	(3)	2	2		<i>Dypsis</i> sp. 5
<i>Myrica</i> sp. 1	10	(10)	3	6	1	4	(3)	1	1	2	4	(3)	1	1	2	4	(3)	1	1	2	<i>Erica</i> sp. 3
<i>Vernonia</i> sp. 6	10	(9)	8	2		4	(2)	1	1	2	4	(2)	1	1	2	4	(2)	1	1	2	<i>Eugenia</i> sp. 13
<i>Uapaca</i> sp. 6	10	(6)	5	6	3	4	(2)	1	1	2	4	(2)	1	1	2	4	(2)	1	1	2	<i>Eugenia</i> sp. 8
<i>Eugenia</i> sp. 12	9	(9)	2	2	5	4	(2)	1	1	2	4	(2)	1	1	2	4	(2)	1	1	2	Euphorbiaceae sp. 3
<i>Canthium</i> sp. 8	9	(6)	2	7	1	3	(3)	2			3	(3)	2			3	(3)	2			<i>Faucheria</i> sp. 3
Poaceae sp. 2	8	(8)	8			3	(3)	3			3	(3)	3			3	(3)	3			<i>Gaertnera</i> sp. 9
<i>Cassinopsis</i> sp. 3	7	(7)	1	4	3	3	(3)	3	1		3	(3)	3	1		3	(3)	3	1		<i>Gaertnera uniflora</i>
Sapotaceae sp. 4	7	(7)	2	4	3	3	(3)	1	1	2	3	(3)	1	1	2	3	(3)	1	1	2	Icacinaeae sp. 1
<i>Eugenia</i> sp. 1	7	(6)	2	6		3	(1)	1	3		3	(1)	1	3		3	(1)	1	3		Lauraceae sp. 4
<i>Medinilla</i> sp. 2	7	(5)	2	5		2	(2)	1			2	(2)	1			2	(2)	1			Liliaceae sp. 2
<i>Aphloia theiformis</i>	6	(6)	6			2	(2)	1	1		2	(2)	1	1		2	(2)	1	1		Mammea sp. 4
<i>Arundinaria</i> sp. 1	6	(6)		5	1	2	(2)	2			2	(2)	2			2	(2)	2			<i>Mammea</i> sp. 6
Asteraceae sp. 4	6	(6)	1	2	3	2	(2)	2			2	(2)	2			2	(2)	2			<i>Medinilla</i> sp. 7
Asteraceae sp. 7	6	(6)	6			2	(2)	2			2	(2)	2			2	(2)	2			<i>Pandanus</i> sp. 2
<i>Dichaeanthera</i> sp. 9	6	(6)	6			2	(2)	2			2	(2)	2			2	(2)	2			<i>Phyllanthus</i> sp. 1
<i>Scleria</i> sp. 2	6	(6)	6			2	(2)	2			2	(2)	2			2	(2)	2			<i>Phyllanthus</i> sp. 2
Acanthaceae sp. 13	6	(5)	4	1	2	2	(2)	2			2	(2)	2			2	(2)	2			<i>Polyscias</i> sp. 7
<i>Anthocleista madagascariensis</i>	6	(4)		1	6	2	(2)	2			2	(2)	2			2	(2)	2			Rubiaceae sp. 10
<i>Cassipourea</i> sp. 5	6	(4)	1	5	4	2	(2)	2			2	(2)	2			2	(2)	2			Rubiaceae sp. 13
Asteraceae sp. 3	5	(5)	3	2	1	2	(2)	2			2	(2)	2			2	(2)	2			Rubiaceae sp. 8
<i>Elaeocarpus</i> sp. 3	5	(5)	3	2	1	2	(2)	2			2	(2)	2			2	(2)	2			<i>Symphonia</i> sp. 6
<i>Erythroxylum</i> sp. 10	5	(5)	3	2	2	2	(2)	2			2	(2)	2			2	(2)	2			<i>Tambourissa</i> sp. 7
<i>Impatiens</i> sp. 9	5	(5)	5			2	(2)	2			2	(2)	2			2	(2)	2			<i>Uapaca</i> sp. 5
<i>Schismatoclada</i> sp. 3	5	(5)	5			2	(2)	2			2	(2)	2			2	(2)	2			Unidentified Iiana sp. 4
<i>Monoporus</i> sp. 2	5	(4)	3	1	2	2	(2)	1			2	(2)	1			2	(2)	1			<i>Viscum</i> sp. 3
<i>Diospyros</i> sp. 14	4	(4)	1	1	2	1	(1)	1			1	(1)	1			1	(1)	1			<i>Weinmannia humbertiana</i>
<i>Eugenia</i> sp. 11	4	(4)		3	1	1	(1)	1			1	(1)	1			1	(1)	1			
<i>Gaertnera macrostipula</i>	4	(4)	3	1		1	(1)	1			1	(1)	1			1	(1)	1			<i>Xyris</i> sp. 1

* Number of stems with dbh ≥ 10 cm, basal area, number of species, vertical distribution of vegetation, points-species accumulation curves, profiles highlighting species with cover value $> 10\%$ in any height interval, list of species recorded, and species cover values separated into height intervals.
 † **Bold** entries represent cover values $\geq 5\%$ and **bold underlined** entries represent cover values $> 10\%$.

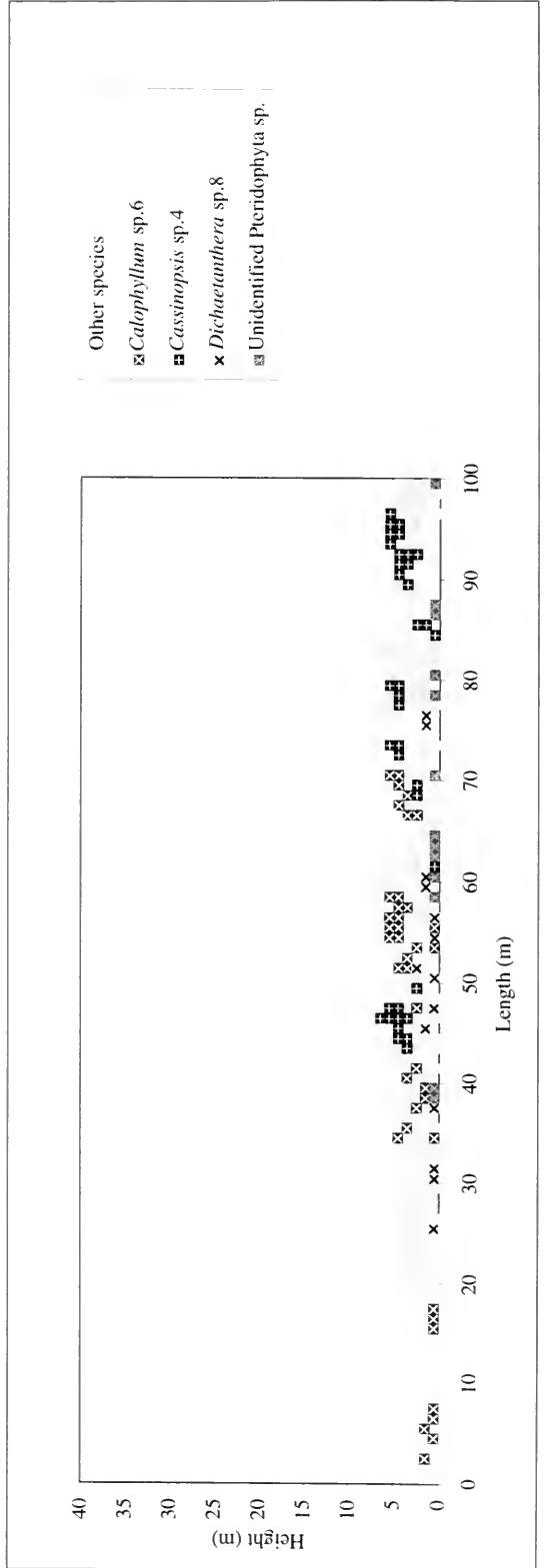
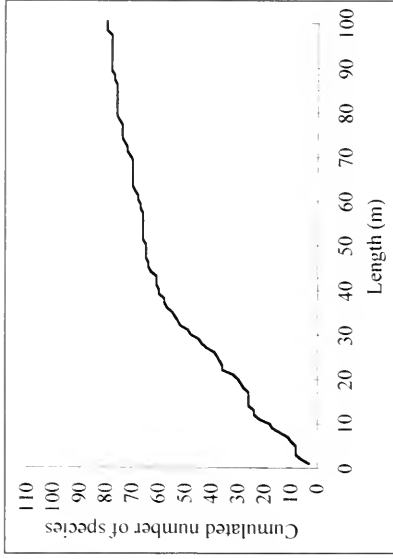
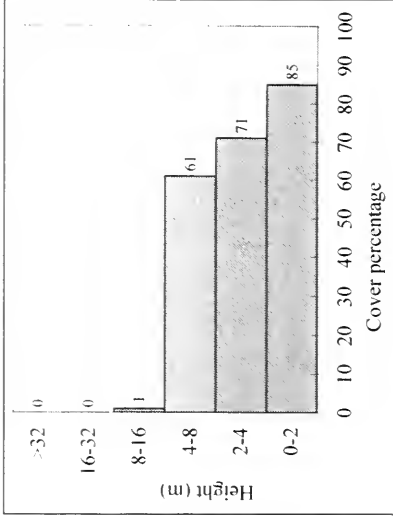
**APPENDIX 3-1i. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojejy:
Slope at 1850 m**

i Marojejy, alt. 1850 m, slope
14°26.8' S - 49°44.1' E

Density (≥ 10 cm dbh; 0.1
ha plot) -

Basal area (m^2 ; 0.1 ha plot) -

Number of species 80
(linear survey data)
Shannon diversity index 1.72
(linear survey data)



Species/morphospecies recorded	Global cover (No. of individuals)				Cover value (%) by height interval†				Cover value (%) by height interval				Global cover (No. of individuals)					
	0-2	2-4	4-8	8-16	16-32	>32	0-2	2-4	4-8	8-16	16-32	>32	0-2	2-4	4-8	8-16	16-32	>32
<i>Calophyllum</i> sp. 6	37 (30)	13	16	11									2	1				3 (3)
<i>Cassinopsis</i> sp. 4	24 (11)	4	15	15									1	2				3 (2)
<i>Nastus</i> sp. 4	17 (15)	5	10	8									2	3				3 (2)
<i>Dichaetanthera</i> sp. 8	16 (16)	15	1										2	2				3 (2)
Unidentified Pteridophyta sp. 8	14 (14)	14											3	3				3 (1)
<i>Dypsis</i> sp. 7	14 (11)	6	4	3									1	1				3 (1)
<i>Polyscias</i> sp. 8	13 (9)	6	5	2									1	1				2 (2)
<i>Nastus</i> sp. 2	10 (10)	7	3										2					2 (2)
<i>Elaeocarpus</i> sp. 2	10 (5)	2	3	5									2					2 (2)
<i>Impatiens</i> sp. 8	9 (9)	9											1	1				2 (2)
<i>Weinmannia</i> sp. 9	9 (9)	3	3	3									2	2				2 (2)
<i>Gaertnera</i> sp. 11	9 (8)	4	3	2									2	2				2 (2)
<i>Aphlotia theiformis</i>	8 (8)	8											2	2				2 (2)
Asteraceae sp. 6	8 (8)	6	2										2	2				2 (2)
<i>Erythroxylum</i> sp. 12	8 (5)	3	4	1	1								1	1				2 (2)
<i>Schefflera</i> sp. 8	8 (5)	2	7	2									1	1				2 (1)
<i>Ocotelepis</i> sp. 1	8 (3)	4	6	2									1	1				2 (1)
<i>Helichrysum</i> sp. 5	7 (7)	4	3										1	1				2 (1)
Poaceae sp. 4	6 (6)	6											1	1				2 (1)
<i>Weinmannia</i> sp. 10	6 (6)	1	5										1	1				1 (1)
Rubiaceae sp. 12	6 (5)	2	1	3									1	1				1 (1)
<i>Dichaetanthera</i> sp. 7	5 (5)	5											1	1				1 (1)
<i>Erica</i> sp. 8	5 (5)	3	1	1									1	1				1 (1)
<i>Impatiens</i> sp. 6	5 (5)	5											1	1				1 (1)
<i>Vaccinium</i> sp. 2	5 (4)	1	5										1	1				1 (1)
<i>Erica</i> sp. 9	5 (2)	4	4										1	1				1 (1)
<i>Clerodendron</i> sp. 6	4 (4)	3	1										1	1				1 (1)
Lauraceae sp. 6	4 (4)	1	3	2									1	1				1 (1)
<i>Medinilla</i> sp. 5	4 (4)	4											1	1				1 (1)
<i>Peperomia</i> sp. 1	4 (4)	4											1	1				1 (1)
<i>Phyllanthus</i> sp. 3	4 (4)	4											1	1				1 (1)
<i>Scolopia</i> sp. 3	4 (4)	3	1										1	1				1 (1)
<i>Eugenia</i> sp. 17	4 (3)	4											1	1				1 (1)
<i>Helichrysum</i> sp. 6	4 (3)	2	2										1	1				1 (1)
Acanthaceae sp. 16	3 (3)	3											1	1				1 (1)
<i>Agauria salicifolia</i>	3 (3)	1	1	2									1	1				1 (1)
<i>Eugenia</i> sp. 6	3 (3)	3		3									1	1				1 (1)
<i>Homalium</i> sp. 6	3 (3)	3	1										1	1				1 (1)
<i>Oncostemum</i> sp. 15	3 (3)	2	1										1	1				1 (1)
Sapotaceae sp. 3	3 (3)	1	2										1	1				1 (1)

* Number of stems with dbh ≥ 10 cm, basal area, number of species, vertical distribution of vegetation, points-species accumulation curves, profiles highlighting species with cover value $> 10\%$ in any height interval, list of species recorded, and species cover values separated into height intervals.
† **Bold** entries represent cover values $\geq 5\%$ and **bold underlined** entries represent cover values $> 10\%$.

APPENDIX 3-1j. Results* of Linear Sampling in Five Elevational Zones in the PN de Marojejy: Ridge at 1950 m

j

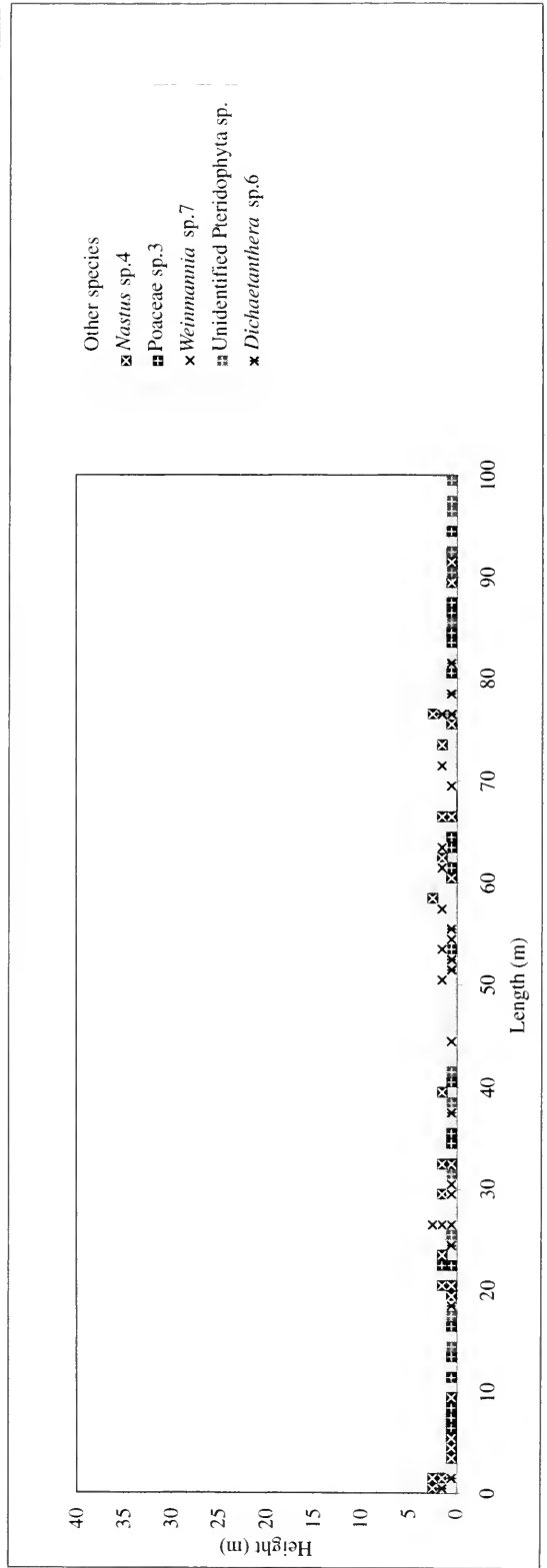
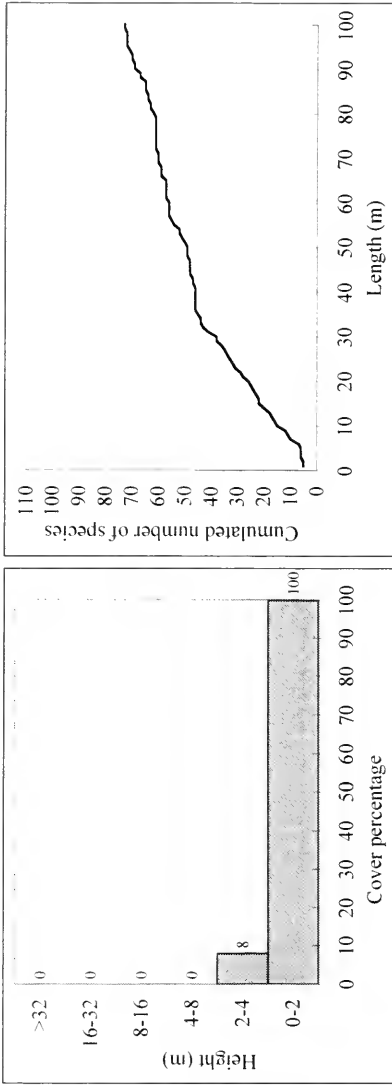
Marojejy, alt. 1950 m., ridge
 14°26.8' S - 49°44.1' E

Density (≥ 10 cm dbh; 0.1 ha plot) -

Basal area (m²; 0.1 ha plot) -

Number of species (linear survey data) 73

Shannon diversity index (linear survey data) 1.64



Species/morphospecies recorded	Global cover (No. of individuals)					Cover value (%) by height interval†					Species/morphospecies recorded	Global cover (No. of individuals)					
	0-2	2-4	4-8	8-16	>32	0-2	2-4	4-8	8-16	>32		0-2	2-4	4-8	8-16	>32	
<i>Nastus</i> sp. 4	32	(32)				29	3									2	(2)
Poaceae sp. 3	25	(25)				<u>25</u>										2	(2)
<i>Weinmannia</i> sp. 7	14	(14)				<u>14</u>	1									2	(2)
Unidentified Pteridophyta sp. 8	12	(12)				<u>12</u>										2	(2)
<i>Dichaetanthera</i> sp. 6	11	(11)				<u>11</u>										2	(2)
Gleicheniaceae sp. 1	11	(11)				<u>11</u>										2	(2)
<i>Symphonia</i> sp. 7	11	(11)				<u>11</u>	2									2	(2)
<i>Scleria</i> sp. 3	10	(10)				10										2	(2)
<i>Eugenia</i> sp. 14	9	(9)				9										2	(2)
<i>Erica</i> sp. 5	8	(8)				8										2	(2)
<i>Impatiens</i> sp. 5	8	(8)				8										1	(1)
Asteraceae sp. 2	8	(8)				8										1	(1)
<i>Clerodendron</i> sp. 6	7	(7)				7										1	(1)
<i>Impatiens</i> sp. 6	7	(7)				7										1	(1)
<i>Erica</i> sp. 6	7	(6)				7										1	(1)
<i>Aphloia theiformis</i>	6	(6)				6										1	(1)
Poaceae sp. 4	6	(6)				6										1	(1)
<i>Agauria salicifolia</i>	5	(5)				5										1	(1)
<i>Scolopia</i> sp. 3	5	(5)				5										1	(1)
<i>Cassinopsis</i> sp. 4	4	(4)				3	1									1	(1)
<i>Dypsis</i> sp. 7	4	(4)				4										1	(1)
<i>Embelia</i> sp. 1	4	(4)				4										1	(1)
<i>Helichrysum</i> sp. 4	4	(4)				4										1	(1)
<i>Phyllanthus</i> sp. 3	4	(4)				4										1	(1)
<i>Senecio</i> sp. 2	4	(4)				4										1	(1)
<i>Vaccinium</i> sp. 2	4	(4)				4										1	(1)
<i>Monoporus</i> sp. 1	4	(3)				2	2									1	(1)
<i>Bulbophyllum</i> sp. 3	3	(3)				3										1	(1)
Celastraceae sp. 3	3	(3)				3										1	(1)
<i>Lycopodium</i> sp. 1	3	(3)				3										1	(1)
<i>Mapouria</i> sp. 5	3	(3)				3										1	(1)
<i>Nematostylis</i> sp. 1	3	(3)				3										1	(1)
<i>Oncostemum</i> sp. 14	3	(3)				3										1	(1)
<i>Schefflera</i> sp. 6	3	(3)				3										1	(1)
Acanthaceae sp. 15	2	(2)				2										1	(1)
Araliaceae sp. 1	2	(2)				2										1	(1)
Asteraceae sp. 7	2	(2)				2										1	(1)

* Number of stems with dbh ≥ 10 cm, basal area, number of species, vertical distribution of vegetation, points-species accumulation curves, profiles highlighting species with cover value $> 10\%$ in any height interval, list of species recorded, and species cover values separated into height intervals.
 † **Bold** entries represent cover values $\geq 5\%$ and **bold underlined** entries represent cover values $> 10\%$.

APPENDIX 3-2. Plant Species/Morphospecies Censused in the Ten Linear Samples in Five Elevational Zones in PN de Marojejy, with Their Cover Value (%)

Family	Species/morphospecies	500 m Slope	490 m Plateau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1850 m Ridge	1950 m Slope	1950 m Ridge
Acanthaceae	<i>Mendoncia</i> sp.1					1							
Acanthaceae	sp.1	3		5		2							
Acanthaceae	sp.2					21							
Acanthaceae	sp.3					2							
Acanthaceae	sp.4					1							
Acanthaceae	sp.5					1							
Acanthaceae	sp.6					1							
Acanthaceae	sp.7					1							
Acanthaceae	sp.8					1							
Acanthaceae	sp.9					1							
Acanthaceae	sp.10					1							
Acanthaceae	sp.11					1							
Acanthaceae	sp.12						5						
Acanthaceae	sp.13							6					
Acanthaceae	sp.14							1					
Acanthaceae	sp.15											2	
Acanthaceae	sp.16												
Agavaceae	<i>Dracaena reflexa</i> Lam.	6		2	2	1	4			3		2	
Anacardiaceae	<i>Protortus</i> sp.2												
Anacardiaceae	<i>Protortus</i> sp.4												
Anacardiaceae	<i>Protortus</i> sp.6				4								
Anacardiaceae	sp.1				1								
Anisophylleaceae	<i>Anisophyllea fallax</i> Scott-Elliott	5											
Annonaceae	<i>Artabotrys</i> sp.1	3	1	3	2								
Annonaceae	<i>Isolona</i> sp.1				4								
Annonaceae	<i>Polyalthia perrieri</i> Cavaco & Keraudren			3	4								
Annonaceae	sp.1	21	13										
Annonaceae	sp.2												
Annonaceae	sp.3												
Annonaceae	sp.4			1	1								
Annonaceae	<i>Xylopia</i> sp.1	3		3									
Annonaceae	<i>Xylopia</i> sp.2				2								
Apiaceae	sp.1												1
Apocynaceae	<i>Carissa</i> sp.1		1										
Apocynaceae	<i>Landolphia</i> sp.1	5	10	3			1						
Apocynaceae	<i>Landolphia</i> sp.2												
Apocynaceae	<i>Landolphia</i> sp.3		2										
Apocynaceae	<i>Landolphia</i> sp.4		2	1									
Apocynaceae	sp.1			2									
Apocynaceae	<i>Tabernaemontana</i> sp.1		23										17

APPENDIX 3-2. Continued

Family	Species/morphospecies	500 m Slope	490 m Plateau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Aquifoliaceae	<i>Ilex mitis</i> (L.) Radlk.	3						6			
Araceae	<i>Pothos scandens</i> L.	2	4	7	19						
Araliaceae	<i>Polyscias</i> sp.2								2		
Araliaceae	<i>Polyscias</i> sp.3					4	3	8			
Araliaceae	<i>Polyscias</i> sp.4					4	3	2			
Araliaceae	<i>Polyscias</i> sp.5							17			
Araliaceae	<i>Polyscias</i> sp.6								4		
Araliaceae	<i>Polyscias</i> sp.7								1		
Araliaceae	<i>Polyscias</i> sp.8									13	
Araliaceae	<i>Schefflera</i> sp.1						3				
Araliaceae	<i>Schefflera</i> sp.2					6					
Araliaceae	<i>Schefflera</i> sp.3							9			
Araliaceae	<i>Schefflera</i> sp.4								2		1
Araliaceae	<i>Schefflera</i> sp.5										3
Araliaceae	<i>Schefflera</i> sp.6										
Araliaceae	<i>Schefflera</i> sp.7									3	
Araliaceae	<i>Schefflera</i> sp.8									8	
Araliaceae	<i>Schefflera</i> sp.9					2					2
Araliaceae	sp.1										
Araliaceae	sp.2								2		
Areaceae	<i>Dypsis</i> sp.1	8	1	1	22	2					
Areaceae	<i>Dypsis</i> sp.2	6	2		2						
Areaceae	<i>Dypsis</i> sp.3					19	13	2			
Areaceae	<i>Dypsis</i> sp.4					29	27	77			
Areaceae	<i>Dypsis</i> sp.5								1		
Areaceae	<i>Dypsis</i> sp.6								16	14	4
Areaceae	<i>Dypsis</i> sp.7										
Aristolochiaceae	<i>Aristolochia</i> sp.1					1					
Asteraceae	<i>Apodocephala</i> sp.1						2				
Asteraceae	<i>Brachylaena merana</i> (Baker) Humbert					10			3		
Asteraceae	<i>Brachylaena</i> sp.1										
Asteraceae	<i>Camposperma</i> sp.1								1		
Asteraceae	<i>Helichrysum adhaerens</i> (DC.) R. Vig. & Humbert										1
Asteraceae	<i>Helichrysum</i> sp.1								2		
Asteraceae	<i>Helichrysum</i> sp.2										1
Asteraceae	<i>Helichrysum</i> sp.3										1
Asteraceae	<i>Helichrysum</i> sp.4										4
Asteraceae	<i>Helichrysum</i> sp.5									7	
Asteraceae	<i>Helichrysum</i> sp.6									4	
Asteraceae	<i>Helichrysum</i> sp.7										1

Family	Species/morphospecies	500 m Slope	490 m Plateau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Asteraceae	<i>Helicrysum</i> sp.8									1	
Asteraceae	<i>Oliganthus</i> sp.1					7					
Asteraceae	<i>Senecio</i> sp.1										1
Asteraceae	<i>Senecio</i> sp.2									1	4
Asteraceae	<i>Senecio</i> sp.3						9				2
Asteraceae	sp.1									1	8
Asteraceae	sp.2								5		
Asteraceae	sp.3								6		
Asteraceae	sp.4										1
Asteraceae	sp.5										
Asteraceae	sp.6									8	
Asteraceae	sp.7							1	6		2
Asteraceae	sp.8			1	1			3	1		
Asteraceae	<i>Vernonia</i> sp.1			4							
Asteraceae	<i>Vernonia</i> sp.2					2					
Asteraceae	<i>Vernonia</i> sp.3					2				1	
Asteraceae	<i>Vernonia</i> sp.4							6			
Asteraceae	<i>Vernonia</i> sp.5							7			
Asteraceae	<i>Vernonia</i> sp.6								10		
Asteraceae	<i>Impatiens</i> sp.1							1			
Balsaminaceae	<i>Impatiens</i> sp.2							4			
Balsaminaceae	<i>Impatiens</i> sp.3							2			
Balsaminaceae	<i>Impatiens</i> sp.4								2		
Balsaminaceae	<i>Impatiens</i> sp.5										8
Balsaminaceae	<i>Impatiens</i> sp.6									5	7
Balsaminaceae	<i>Impatiens</i> sp.7										1
Balsaminaceae	<i>Impatiens</i> sp.8										
Balsaminaceae	<i>Impatiens</i> sp.9								5		
Begoniaceae	<i>Begonia</i> sp.1					3		2			
Bignoniaceae	<i>Colca</i> sp.1					2					
Bignoniaceae	<i>Phyllarthron</i> sp.1					7					
Burseraeae	<i>Canarium boivinit</i> Engl.						2				
Burseraeae	<i>Canarium madagascariense</i> Engl.		6	10	3						
Canellaceae	<i>Cinnamosma</i> sp.1					6					
Celastraceae	sp.1			2							
Celastraceae	sp.2							1			
Celastraceae	sp.3							1	1		
Chloranthaceae	sp.1										3
Clusiaceae	<i>Calophyllum</i> sp.1		2								
Clusiaceae	<i>Calophyllum</i> sp.2										
Clusiaceae	<i>Calophyllum</i> sp.4										

APPENDIX 3-2. *Continued*

Family	Species/morphospecies	500 m		800 m		800 m		1200 m		1600 m		1850 m		1950 m	
		Slope	Plateau	Slope	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge	
Clusiaceae	<i>Calophyllum</i> sp.5						2								
Clusiaceae	<i>Calophyllum</i> sp.6									6	30				37
Clusiaceae	<i>Mannaea bongoi</i> (R. Vig. & Humbert) Kosterm.			2											
Clusiaceae	<i>Mannaea</i> sp.1	9	2	1		4									
Clusiaceae	<i>Mannaea</i> sp.2					15									
Clusiaceae	<i>Mannaea</i> sp.3							17	6	4					
Clusiaceae	<i>Mannaea</i> sp.4							14	12	14					1
Clusiaceae	<i>Mannaea</i> sp.5														14
Clusiaceae	<i>Mannaea</i> sp.6														1
Clusiaceae	<i>Mannaea</i> sp.8														2
Clusiaceae	<i>Ochrocarpos orthocladus</i> (Baker) H. Perrier														3
Clusiaceae	<i>Ochrocarpos</i> sp.1	11	1												1
Clusiaceae	<i>Ochrocarpos</i> sp.2									6					
Clusiaceae	<i>Ochrocarpos tsaratananae</i> H. Perrier														
Clusiaceae	<i>Psorospermum</i> sp.1														2
Clusiaceae	<i>Symphonia microphylla</i> (Cambess.) Vesque										14				
Clusiaceae	<i>Symphonia</i> sp.1		8												
Clusiaceae	<i>Symphonia</i> sp.4				26										
Clusiaceae	<i>Symphonia</i> sp.5								8						
Clusiaceae	<i>Symphonia</i> sp.6														1
Clusiaceae	<i>Symphonia</i> sp.7														11
Clusiaceae	<i>Symphonia</i> sp.8														1
Connaraceae	<i>Agelaea pentagyna</i> (Lam.) Baill.														
Convolvulaceae	sp.1	4	4		1										
Cunoniaceae	<i>Weinmannia humbertiana</i> Bernardi														
Cunoniaceae	<i>Weinmannia</i> sp.1									2					1
Cunoniaceae	<i>Weinmannia</i> sp.3														
Cunoniaceae	<i>Weinmannia</i> sp.5									2					4
Cunoniaceae	<i>Weinmannia</i> sp.6														1
Cunoniaceae	<i>Weinmannia</i> sp.7														14
Cunoniaceae	<i>Weinmannia</i> sp.8														1
Cunoniaceae	<i>Weinmannia</i> sp.9														
Cunoniaceae	<i>Weinmannia</i> sp.10														9
Cunoniaceae	<i>Weinmannia</i> sp.11														6
Cyperaceae	<i>Scleria</i> sp.1							1							
Cyperaceae	<i>Scleria</i> sp.2							2							
Cyperaceae	<i>Scleria</i> sp.3														3
Dilleniaceae	<i>Dillenia triquetra</i> (Rottb.) Gilg														4
Dilleniaceae	<i>Dillenia</i> sp.1														4
Ebenaceae	<i>Diospyros</i> sp.1														7

Family	Species/morphospecies	500 m	490 m	800 m	800 m	1200 m	1200 m	1600 m	1600 m	1850 m	1950 m
		Slope	Plateau	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge
Ebenaceae	<i>Diospyros</i> sp.2	21	4	11							
Ebenaceae	<i>Diospyros</i> sp.3	1									
Ebenaceae	<i>Diospyros</i> sp.4	1									
Ebenaceae	<i>Diospyros</i> sp.5			3							
Ebenaceae	<i>Diospyros</i> sp.6				4						
Ebenaceae	<i>Diospyros</i> sp.7					2					
Ebenaceae	<i>Diospyros</i> sp.8					1					
Ebenaceae	<i>Diospyros</i> sp.9						2				
Ebenaceae	<i>Diospyros</i> sp.10				4						
Ebenaceae	<i>Diospyros</i> sp.11					1					
Ebenaceae	<i>Diospyros</i> sp.13							6			
Ebenaceae	<i>Diospyros</i> sp.14								4		
Ebenaceae	<i>Diospyros</i> sp.17						2				
Elaeocarpaceae	<i>Elaeocarpius</i> sp.1										
Elaeocarpaceae	<i>Elaeocarpius</i> sp.2								10		
Elaeocarpaceae	<i>Elaeocarpius</i> sp.3						5				
Elaeocarpaceae	<i>Elaeocarpius</i> sp.4								1		
Elaeocarpaceae	<i>Elaeocarpius</i> sp.5										
Elaeocarpaceae	<i>Sloanea rhodantha</i> (Baker) Capuron sp.1	8		19				4			
Ericaceae	<i>Agauria salicifolia</i> (Lam.) Oliv.									3	5
Ericaceae	<i>Erica</i> sp.1							2			1
Ericaceae	<i>Erica</i> sp.2								1		
Ericaceae	<i>Erica</i> sp.3										1
Ericaceae	<i>Erica</i> sp.4										8
Ericaceae	<i>Erica</i> sp.5										7
Ericaceae	<i>Erica</i> sp.6										2
Ericaceae	<i>Erica</i> sp.7									5	
Ericaceae	<i>Erica</i> sp.8									5	
Ericaceae	<i>Erica</i> sp.9										
Ericaceae	<i>Vaccinium</i> sp.1										
Ericaceae	<i>Vaccinium</i> sp.2								2		
Erythroxylaceae	<i>Erythroxylum</i> sp.1		2								
Erythroxylaceae	<i>Erythroxylum</i> sp.3				10	4					
Erythroxylaceae	<i>Erythroxylum</i> sp.4				2						
Erythroxylaceae	<i>Erythroxylum</i> sp.5				2						
Erythroxylaceae	<i>Erythroxylum</i> sp.9										
Erythroxylaceae	<i>Erythroxylum</i> sp.10										
Erythroxylaceae	<i>Erythroxylum</i> sp.11										
Erythroxylaceae	<i>Erythroxylum</i> sp.12										
Erythroxylaceae										5	1
Erythroxylaceae										8	

APPENDIX 3-2. *Continued*

Family	Species/morphospecies	500 m Slope	490 m Plateau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Euphorbiaceae	<i>Antidesma petiolare</i> Tul.					2					
Euphorbiaceae	<i>Antidesma</i> sp.1	3									
Euphorbiaceae	<i>Bridelia</i> sp.1	1									
Euphorbiaceae	<i>Bridelia</i> sp.2			6							
Euphorbiaceae	<i>Bridelia</i> sp.3				1						
Euphorbiaceae	<i>Croton</i> sp.1			3							
Euphorbiaceae	<i>Croton</i> sp.4						5				
Euphorbiaceae	<i>Deuteromallotus</i> sp.1	5	11	46		4	17				
Euphorbiaceae	<i>Elaeodendron</i> sp.1			1							
Euphorbiaceae	<i>Macaranga cuspidata</i> Baill.			1							
Euphorbiaceae	<i>Macaranga</i> sp.2										
Euphorbiaceae	<i>Macaranga</i> sp.3										
Euphorbiaceae	<i>Macaranga</i> sp.5								3		
Euphorbiaceae	<i>Macaranga</i> sp.6										
Euphorbiaceae	<i>Macaranga</i> sp.7				1						
Euphorbiaceae	<i>Mallotus</i> sp.1		19								
Euphorbiaceae	<i>Phyllanthus</i> sp.1										1
Euphorbiaceae	<i>Phyllanthus</i> sp.2										1
Euphorbiaceae	<i>Phyllanthus</i> sp.3									4	4
Euphorbiaceae	<i>Sapium</i> sp.1					4	3				
Euphorbiaceae	sp.2				1						
Euphorbiaceae	sp.3										1
Euphorbiaceae	<i>Uapaca</i> sp.1										
Euphorbiaceae	<i>Uapaca</i> sp.2	11	2		8						
Euphorbiaceae	<i>Uapaca</i> sp.3				47						
Euphorbiaceae	<i>Uapaca</i> sp.5						3				
Euphorbiaceae	<i>Uapaca</i> sp.6									1	10
Euphorbiaceae	<i>Uapaca</i> sp.6										
Fabaceae	<i>Albizia</i> sp.1	16	1	26							
Flacourtiaceae	<i>Aphloia theiformis</i> (Vahl) Benn.					1					
Flacourtiaceae	<i>Bembicia</i> sp.1										
Flacourtiaceae	<i>Casearia</i> sp.1						11				
Flacourtiaceae	<i>Casearia</i> sp.2						5				
Flacourtiaceae	<i>Casearia</i> sp.3							3			2
Flacourtiaceae	<i>Homalium</i> sp.1		9								
Flacourtiaceae	<i>Homalium</i> sp.4										
Flacourtiaceae	<i>Homalium</i> sp.6								16		2
Flacourtiaceae	<i>Ludia madagascariensis</i> Clos				3				1		3
Flacourtiaceae	<i>Scolopia</i> sp.1										
Flacourtiaceae	<i>Scolopia</i> sp.2										
Flacourtiaceae	<i>Scolopia</i> sp.3										
Flacourtiaceae					1	16					
Flacourtiaceae										4	5

Family	Species/morphospecies	500 m Slope	490 m Plateau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Lauraceae	sp.6										4
Lauraceae	sp.7										2
Lauraceae	sp.10										1
Liliaceae	sp.1		1								
Liliaceae	sp.2								1		
Linaceae	<i>Hugonia</i> sp.1				4						
Loganiaceae	<i>Anthocleista longifolia</i> (Lam.) Boiteau			4							
Loganiaceae	<i>Anthocleista madagascariensis</i> Baker				4						
Loranthaceae	<i>Bakerella</i> sp.1							3	6	1	
Loranthaceae	<i>Viscum</i> sp.1	5				1					
Loranthaceae	<i>Viscum</i> sp.2						1		1		
Loranthaceae	<i>Viscum</i> sp.3							3	1	2	
Maranthaceae	sp.1	1									
Melanophyllaceae	<i>Melanophylla humbertiana</i> Keraudren					1	4				
Melastomataceae	<i>Dichaeatanthera</i> sp.1							1			
Melastomataceae	<i>Dichaeatanthera</i> sp.2						8				
Melastomataceae	<i>Dichaeatanthera</i> sp.3						4				
Melastomataceae	<i>Dichaeatanthera</i> sp.5								2		
Melastomataceae	<i>Dichaeatanthera</i> sp.6										
Melastomataceae	<i>Dichaeatanthera</i> sp.7										11
Melastomataceae	<i>Dichaeatanthera</i> sp.8									5	
Melastomataceae	<i>Dichaeatanthera</i> sp.9					1			6	16	
Melastomataceae	<i>Gravesia</i> sp.1	2			1	7					
Melastomataceae	<i>Gravesia</i> sp.2				1						
Melastomataceae	<i>Gravesia</i> sp.3				3						
Melastomataceae	<i>Gravesia</i> sp.4							1			
Melastomataceae	<i>Gravesia</i> sp.5					3	3	2			
Melastomataceae	<i>Medimilla</i> sp.1	1									
Melastomataceae	<i>Medimilla</i> sp.2								7		
Melastomataceae	<i>Medimilla</i> sp.3									2	2
Melastomataceae	<i>Medimilla</i> sp.4									1	
Melastomataceae	<i>Medimilla</i> sp.5									4	
Melastomataceae	<i>Medimilla</i> sp.6										1
Melastomataceae	<i>Medimilla</i> sp.7					5	1	1	1		
Melastomataceae	<i>Medimilla</i> sp.8			1							
Melastomataceae	<i>Memecylon</i> sp.1		2								
Melastomataceae	<i>Memecylon</i> sp.2				1	1					
Melastomataceae	<i>Memecylon</i> sp.3				1						
Melastomataceae	<i>Memecylon</i> sp.4						3				
Melastomataceae	<i>Memecylon</i> sp.5							1			

APPENDIX 3-2. *Continued*

Family	Species/morphospecies	500 m		800 m		800 m		1200 m		1600 m		1850 m		1950 m	
		Slope	Plateau	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge		
Melastomataceae	sp.1	1													
Melastomataceae	sp.2				1						2				
Melastomataceae	sp.3		3												
Meliaceae	<i>Malleastrum</i> sp.1	2								1					
Meliaceae	<i>Malleastrum</i> sp.2									1					
Meliaceae	<i>Trichilia</i> sp.1	2	1												
Monimiaceae	<i>Ephippiandra</i> sp.1		3	4											
Monimiaceae	<i>Ephippiandra</i> sp.2							13							
Monimiaceae	<i>Tambourissa</i> sp.1	1													
Monimiaceae	<i>Tambourissa</i> sp.2								6						
Monimiaceae	<i>Tambourissa</i> sp.3								2						
Monimiaceae	<i>Tambourissa</i> sp.4							12							
Monimiaceae	<i>Tambourissa</i> sp.5							3							
Monimiaceae	<i>Tambourissa</i> sp.6									2					
Monimiaceae	<i>Tambourissa</i> sp.7										1				
Monimiaceae	<i>Tambourissa</i> sp.8							1							
Monimiaceae	<i>Tambourissa</i> sp.9														
Monimiaceae	sp.1	8													
Monimiaceae	sp.2													2	
Moraceae	<i>Ficus lutea</i> Vahl		4	7											
Moraceae	<i>Ficus soroceoides</i> Baker							4							
Moraceae	<i>Ficus</i> sp.2														
Moraceae	<i>Ficus</i> sp.3														
Moraceae	<i>Ficus</i> sp.4														
Moraceae	<i>Ficus</i> sp.5														
Moraceae	<i>Streblus</i> sp.1														
Moraceae	<i>Treculia</i> sp.1														
Moraceae	<i>Trilepisium madagascariense</i> DC.														
Moraceae	sp.1	2	2	1											
Moraceae	sp.2														
Moraceae	sp.2	1													
Myricaceae	<i>Myrica</i> sp.1													10	1
Myricitaceae	<i>Brochoneura acuminata</i> (Lam.) Warb.														
Myrsinaceae	<i>Embelia</i> sp.1	13	15												4
Myrsinaceae	<i>Maesa</i> sp.1							2							
Myrsinaceae	<i>Monoporus</i> sp.1														4
Myrsinaceae	<i>Monoporus</i> sp.2														
Myrsinaceae	<i>Oncostemum</i> sp.1														5
Myrsinaceae	<i>Oncostemum</i> sp.2	47	1	8				4							
Myrsinaceae	<i>Oncostemum</i> sp.3														6
Myrsinaceae	<i>Oncostemum</i> sp.4														2

APPENDIX 3-2. Continued

Family	Species/morphospecies	500 m		800 m		800 m		1200 m		1600 m		1600 m		1850 m		1950 m	
		Slope	Plateau	Slope	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge	
Myrsinaceae	<i>Oncostemum</i> sp.6							7									
Myrsinaceae	<i>Oncostemum</i> sp.7							1									
Myrsinaceae	<i>Oncostemum</i> sp.8							5									
Myrsinaceae	<i>Oncostemum</i> sp.9							3									
Myrsinaceae	<i>Oncostemum</i> sp.10							1									
Myrsinaceae	<i>Oncostemum</i> sp.11							1									
Myrsinaceae	<i>Oncostemum</i> sp.12									4							
Myrsinaceae	<i>Oncostemum</i> sp.13									5							
Myrsinaceae	<i>Oncostemum</i> sp.14																3
Myrsinaceae	<i>Oncostemum</i> sp.15													3			
Myrsinaceae	<i>Oncostemum</i> sp.16																
Myrsinaceae	sp.2								2								
Myrsinaceae	sp.3								2								2
Myrtaceae	<i>Eugenia emimensis</i> Baker																
Myrtaceae	<i>Eugenia</i> sp.1																
Myrtaceae	<i>Eugenia</i> sp.2								18								
Myrtaceae	<i>Eugenia</i> sp.3	5	6	5					2								
Myrtaceae	<i>Eugenia</i> sp.4	7	4						8								
Myrtaceae	<i>Eugenia</i> sp.5																
Myrtaceae	<i>Eugenia</i> sp.6																
Myrtaceae	<i>Eugenia</i> sp.7																
Myrtaceae	<i>Eugenia</i> sp.8																
Myrtaceae	<i>Eugenia</i> sp.10																
Myrtaceae	<i>Eugenia</i> sp.11																
Myrtaceae	<i>Eugenia</i> sp.12																
Myrtaceae	<i>Eugenia</i> sp.13																
Myrtaceae	<i>Eugenia</i> sp.14																
Myrtaceae	<i>Eugenia</i> sp.15																
Myrtaceae	<i>Eugenia</i> sp.16																
Myrtaceae	<i>Eugenia</i> sp.17																
Myrtaceae	<i>Eugenia</i> sp.19																
Myrtaceae	<i>Syzygium</i> sp.1																
Oleaceae	<i>Noronhia</i> sp.1	1															
Oleaceae	<i>Noronhia</i> sp.2																
Oleaceae	<i>Noronhia</i> sp.3																
Oleaceae	<i>Noronhia</i> sp.4																
Oleaceae	<i>Olea</i> sp.1																
Orchidaceae	<i>Angraecum</i> sp.1																
Orchidaceae	<i>Bulbophyllum</i> sp.1																
Orchidaceae	<i>Bulbophyllum</i> sp.2																

APPENDIX 3-2. Continued

Family	Species/morphospecies	500 m Slope	490 m Plateau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Orechidaceae	<i>Bulbophyllum</i> sp.3										3
Orehidaceae	<i>Cynorchis</i> sp.1									1	
Pandanaceae	<i>Pandanus</i> sp.1		1	34	1			4		3	
Pandanaceae	<i>Pandanus</i> sp.2			22			7	4	1		
Pandanaceae	<i>Pandanus</i> sp.3		1				7	5			
Pandanaceae	<i>Pandanus</i> sp.4				1						
Piperaceae	<i>Peperomia</i> sp.1				1			6		4	
Piperaceae	<i>Peperomia</i> sp.2										1
Piperaceae	<i>Peperomia</i> sp.3										1
Pittosporaceae	<i>Pittosporum</i> sp.1										
Pittosporaceae	<i>Pittosporum</i> sp.2	3			2			7			
Pittosporaceae	<i>Pittosporum</i> sp.3										
Pittosporaceae	<i>Pittosporum</i> sp.4							3			
Poaceae	<i>Arundinaria</i> sp.1								6		
Poaceae	<i>Nastus</i> sp.1	1	9		20		12				
Poaceae	<i>Nastus</i> sp.2				3	9	35	13	18	10	
Poaceae	<i>Nastus</i> sp.3								4		
Poaceae	<i>Nastus</i> sp.4									17	32
Poaceae	<i>Panicum</i> sp.1										1
Poaceae	<i>Panicum</i> sp.2									2	1
Poaceae	sp.1		33	2					8		
Poaceae	sp.2										
Poaceae	sp.3									1	25
Poaceae	sp.4									6	6
Poaceae	sp.5										1
Pteridophyta	<i>Angiopteris</i> sp.1				6						
Pteridophyta	<i>Asplenium nidus</i> L.	16	9	9	2						
Pteridophyta	<i>Asplenium</i> sp.1							1			
Pteridophyta	<i>Blechnum</i> sp.1								1		2
Pteridophyta	<i>Cyathea bullata</i> (Baker) Domin										
Pteridophyta	<i>Cyathea costularis</i> Bonap.	5	24	3			1				
Pteridophyta	<i>Cyathea decrescens</i> Mett.			2							
Pteridophyta	<i>Cyathea hildebrandtii</i> Kuhn										
Pteridophyta	<i>Cyathea</i> sp.4							9		1	1
Pteridophyta	<i>Cyathea</i> sp.1										
Pteridophyta	<i>Cyathea</i> sp.2	4		6	29		6				
Pteridophyta	<i>Cyathea</i> sp.3										
Pteridophyta	<i>Diplazium</i> sp.1	2				26	5				
Pteridophyta	<i>Elaphoglossum</i> sp.2										
Pteridophyta	<i>Elaphoglossum</i> sp.1					1				1	2

Family	Species/morphospecies	500 m Slope	490 m Plateau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Pteridophyta	Gleicheniaceae sp.1										11
Pteridophyta	<i>Lycopodium</i> sp.1										3
Pteridophyta	<i>Nephrolepis</i> sp.1	2								1	
Pteridophyta	<i>Pleopeltis</i> sp.1									14	12
Pteridophyta	sp.8										
Pteridophyta	sp.9	3					1				
Pteridophyta	sp.1					5					
Pteridophyta	sp.2			4							
Pteridophyta	sp.3			2							
Pteridophyta	sp.4			12							
Pteridophyta	sp.5				5						
Pteridophyta	sp.6					52	7				
Pteridophyta	sp.7	3									
Pteridophyta	spp.							29	4		
Pteridophyta	<i>Stenochlaena tenuifolia</i> (Desv.) Moore	8					4				
Rhizophoraceae	<i>Cassipourea</i> sp.1								2		
Rhizophoraceae	<i>Rhizophora</i> sp.4								6		
Rhizophoraceae	<i>Cassipourea</i> sp.5								2		
Rubiaceae	<i>Albertya minor</i> Baill.										1
Rubiaceae	<i>Albertya</i> sp.1										
Rubiaceae	<i>Bertiera</i> sp.1	2									
Rubiaceae	<i>Bertiera</i> sp.2	1									
Rubiaceae	<i>Canephora</i> sp.1			2							
Rubiaceae	<i>Canthium</i> sp.1				1						
Rubiaceae	<i>Canthium</i> sp.2						13				
Rubiaceae	<i>Canthium</i> sp.3				1						
Rubiaceae	<i>Canthium</i> sp.4				3			15	1		
Rubiaceae	<i>Canthium</i> sp.5				2						
Rubiaceae	<i>Canthium</i> sp.6				3						
Rubiaceae	<i>Canthium</i> sp.7				3			9	3		
Rubiaceae	<i>Canthium</i> sp.8								9		
Rubiaceae	<i>Canthium</i> sp.9									1	
Rubiaceae	<i>Canthium</i> sp.10										2
Rubiaceae	<i>Canthium</i> sp.11										1
Rubiaceae	cf. <i>Schismatochlada</i> sp.6										
Rubiaceae	<i>Danais</i> sp.1					1		4			
Rubiaceae	<i>Danais</i> sp.2				4						
Rubiaceae	<i>Danais</i> sp.3				1					1	
Rubiaceae	<i>Enterospermum</i> sp.1				1		1				
Rubiaceae	<i>Enterospermum</i> sp.2				1						
Rubiaceae					9						

APPENDIX 3-2. *Continued*

Family	Species/morphospecies	500 m		800 m		800 m		1200 m		1600 m		1850 m		1950 m	
		Slope	Plateau	Slope	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge	Slope	Ridge	
Rubiaceae	<i>Enterosperrum</i> sp.3							3							
Rubiaceae	<i>Enterosperrum</i> sp.4			12				2							
Rubiaceae	<i>Gaertnera macrostipula</i> Baker							3		4					
Rubiaceae	<i>Gaertnera uniflora</i> ined.									1					
Rubiaceae	<i>Gaertnera</i> sp.1	3													
Rubiaceae	<i>Gaertnera</i> sp.4							1							
Rubiaceae	<i>Gaertnera</i> sp.5			1											
Rubiaceae	<i>Gaertnera</i> sp.6								3						
Rubiaceae	<i>Gaertnera</i> sp.7							1							
Rubiaceae	<i>Gaertnera</i> sp.9										1				
Rubiaceae	<i>Gaertnera</i> sp.10													2	
Rubiaceae	<i>Gaertnera</i> sp.11														
Rubiaceae	<i>Gaertnera</i> sp.12								1						
Rubiaceae	<i>Ixora</i> sp.1							3							
Rubiaceae	<i>Ixora</i> sp.2							1							
Rubiaceae	<i>Ixora</i> sp.3								2						
Rubiaceae	<i>Mapouria</i> sp.2	7	1												
Rubiaceae	<i>Mapouria</i> sp.3														
Rubiaceae	<i>Mapouria</i> sp.4							1							
Rubiaceae	<i>Mapouria</i> sp.5								2						
Rubiaceae	<i>Nematostylis</i> sp.1													3	
Rubiaceae	<i>Pucceria</i> sp.1													3	
Rubiaceae	<i>Pouridiantlia paucinervis</i> (Hiern) Bremek.														
Rubiaceae	<i>Psychotria</i> sp.1			12											
Rubiaceae	<i>Psychotria</i> sp.2			5				2							
Rubiaceae	<i>Psychotria</i> sp.1									2					
Rubiaceae	<i>Rothmannia</i> sp.1	14													
Rubiaceae	<i>Saldinia</i> sp.1														
Rubiaceae	<i>Schismatochлада</i> sp.1														
Rubiaceae	<i>Schismatochлада</i> sp.2														
Rubiaceae	<i>Schismatochлада</i> sp.3											3			
Rubiaceae	<i>Schismatochлада</i> sp.4											5			1
Rubiaceae	<i>Schismatochлада</i> sp.5													3	
Rubiaceae	sp.1	8	23												
Rubiaceae	sp.2	32													
Rubiaceae	sp.3	1													
Rubiaceae	sp.5														
Rubiaceae	sp.7														23

APPENDIX 3-2. *Continued*

Family	Species/morphospecies	500 m Slope	490 m Plateau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Rubiaceae	sp.8								1		
Rubiaceae	sp.9								2		
Rubiaceae	sp.10								1		
Rubiaceae	sp.11									1	
Rubiaceae	sp.12										6
Rubiaceae	sp.13				2		1		1		
Rubiaceae	sp.14						1	1			
Rutaceae	<i>Vepris</i> sp.1	2			2						
Rutaceae	<i>Vepris</i> sp.2										
Rutaceae	<i>Vepris</i> sp.3					1					
Rutaceae	<i>Vepris</i> sp.4										
Rutaceae	<i>Zanthoxylum madagascariense</i> Baker	2	1							1	
Rutaceae	sp.1			1							
Sapindaceae	<i>Allophylus</i> sp.1					2					
Sapindaceae	<i>Allophylus</i> sp.2						3				
Sapindaceae	<i>Allophylus</i> sp.3					1					
Sapindaceae	<i>Begonia</i> sp.1			1		1					
Sapindaceae	cf. <i>Deinbollia</i> sp.1			1							
Sapindaceae	cf. <i>Deinbollia</i> sp.2										
Sapindaceae	<i>Filicium</i> sp.1						2				
Sapindaceae	<i>Filicium</i> sp.3							2			
Sapindaceae	<i>Plagioscyphus</i> sp.1	2		1							
Sapindaceae	<i>Plagioscyphus</i> sp.2						1				
Sapindaceae	sp.1	6									
Sapindaceae	sp.2				5						
Sapotaceae	<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	65	49	27							
Sapotaceae	<i>Faucheria hexandra</i> (Lecomte) Lecomte				2						
Sapotaceae	<i>Faucheria parvifolia</i> Lecomte						9		1		
Sapotaceae	<i>Faucheria</i> sp.3										
Sapotaceae	<i>Labramia</i> sp.1					4					
Sapotaceae	sp.3										
Sapotaceae	sp.4										
Smilacaceae	<i>Smilax kraussiana</i> Meisn.								7		
Sterculiaceae	<i>Byttneria</i> sp.1	2	3	4			3				
Sterculiaceae	<i>Dombeya</i> sp.1		8		2						
Sterculiaceae	<i>Dombeya</i> sp.2										
Sterculiaceae	<i>Dombeya</i> sp.3			1			3				
Sterculiaceae	<i>Dombeya</i> sp.4										
Sterculiaceae	<i>Dombeya</i> sp.6					1				2	

APPENDIX 3-2. *Continued*

Family	Species/morphospecies	500 m Slope	490 m Plateau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Sireliaceae	<i>Ravenala madagascariensis</i> Sonn.			3	12				4		
Thymelaeaceae	<i>Atemossiphon</i> sp.1									8	
Thymelaeaceae	<i>Octolepis</i> sp.1			5	1						
Tiliaceae	<i>Grewia</i> sp.2					2					
Tiliaceae	<i>Grewia</i> sp.3							6			
Tiliaceae	<i>Grewia</i> sp.4										
Urticaceae	<i>Boehmeria</i> sp.1			1	5						
Urticaceae	<i>Pilea</i> sp.1			2	1						
Urticaceae	sp.1										
Verbenaceae	<i>Clerodendron</i> sp.1	1									
Verbenaceae	<i>Clerodendron</i> sp.2				1						
Verbenaceae	<i>Clerodendron</i> sp.3										
Verbenaceae	<i>Clerodendron</i> sp.5							3			
Verbenaceae	<i>Clerodendron</i> sp.6								1	4	7
Xyridaceae	<i>Xyris</i> sp.1										2
Zingiberaceae	<i>Aframomum angustifolium</i> (Sonn.) K. Schum.			7							
Unidentified	"Plantule"							1			
Unidentified	liana sp.1		6								
Unidentified	liana sp.2	4	1								
Unidentified	liana sp.3		1								
Unidentified	liana sp.4								1		
Unidentified	liana spp.		8	15	8			1			
Unidentified	sp.1										
Unidentified	sp.2										
Unidentified	sp.3			1					3		
Unidentified	sp.4										2

APPENDIX 3-3. Plant Families Censused in the Ten Linear Samples in Five Elevational Zones in PN de Marojejy, with Their Cover Value (%)

Family	490 m									
	500 m Slope	Pla-teau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Acanthaceae	3		5		31	7		2	3	2
Agavaceae	6		2	2	1	4			2	
Anacardiaceae				5		2		5		
Anisophylleaceae	5									
Annonaceae	27	16	10	13						
Apiaceae										1
Apocynaceae	5	39	6		17	1				
Aquifoliaceae	3				2		6			
Araceae	2	4	7							
Araliaceae				19	16	9	36	11	24	6
Arecaceae	14	3	1	24	50	40	79	17	14	4
Aristolochiaceae					1					
Asteraceae				5	11	22	17	34	23	26
Balsaminaceae							7	7	14	16
Begoniaceae					3		2			
Bignoniaceae					9	2				
Burseraceae	9	10	3	22	6					
Canellaceae				2						
Celastraceae							2	1		3
Chloranthaceae									1	
Clusiaceae	20	13	29	39	31	28	31	63	44	13
Convolvulaceae			1							
Cunoniaceae	4				1	2	2	9	15	16
Cyatheaceae				29				1		
Cyperaceae				3	2			6		10
Dilleniaceae				8						
Ebenaceae	23	11	14	4	7	5	7	4		
Elaeocarpaceae	8		19		1	2		9	12	
Ericaceae								5	18	28
Erythroxylaceae				14	4		4	5	8	1
Euphorbiaceae	20	62	57	58	9	30	3	14	4	4
Fabaceae	16	1	26							
Flacourtiaceae		14		4	19	28	25	9	20	11
Icacinaceae		2	1			4		8	24	4
Lauraceae	22	32	40	49	15	47	11	3	7	
Liliaceae		1						1		
Linaceae				4						
Loganiaceae				4			3	6		
Loranthaceae	5					1			3	
Maranthaceae	1									
Melanophyllaceae					1	4				
Melastomataceae	3	1	3	5	19	21	7	18	31	13
Meliaceae	4	4					1			
Menispermaceae		4								
Monimiaceae	9	3	4		29	8	3	1	2	
Moraceae	3	14	19		5					
Myricaceae								10		1
Myristicaceae	13	15								
Myrsinaceae	47	1	8	14	14	11	9	7	4	13
Myrtaceae	12	13	5	28	12	42	37	26	13	9
Oleaceae	1		4	7	1		2			
Orchidaceae				1		1	3	1	1	3
Pandanaceae			2	56	2	14	13	1	3	
Piperaceae					1		6		4	2
Pittosporaceae					2		10			
Poaceae	1	42	2	23	9	47	13	36	36	66
Pteridophyta excl. Cyatheaceae	38	38	44	5	88	20	50	4	17	31

APPENDIX 3-3. *Continued*

Family	490 m									
	500 m Slope	Pla-teau	800 m Slope	800 m Ridge	1200 m Slope	1200 m Ridge	1600 m Slope	1600 m Ridge	1850 m Slope	1950 m Ridge
Rhizophoraceae						4		8		
Rubiaceae	66	26	27	20	68	38	40	34	21	13
Rutaceae	4	1	1	2	1				1	
Sapindaceae	18		3	5	4	6	2			
Sapotaceae	65	49	27	2	4	9		8	3	
Smilacaceae	2	3	4							
Sterculiaceae		8	1	2	1	3	2			
Strelitziaceae			3	12						
Thymeleaceae								4	8	
Tiliaceae			5	1		2	6			
Urticaceae			3		6					
Verbenaceae	1					1	1	3	4	7
Viscaceae							3	1		
Xyridaceae								1		2
Zingiberaceae			7							

APPENDIX 3-4. Fertile Plant Specimens Collected During the General Collections Along the Altitudinal Gradient in PN de Marojejy

Family	Genus and species	Collector* and number	Altitude (m)†
Acanthaceae	cf. <i>Ruellia</i> sp.	PJ 746	450 ± 75
Acanthaceae		NM 257	775 ± 75
Acanthaceae		NM 334	1625 ± 75
Acanthaceae		NM 413	1875 ± 75
Acanthaceae		NM 414	1875 ± 75
Acanthaceae		PJ 776	775 ± 75
Acanthaceae		PJ 895	1625 ± 75
Anacardiaceae	<i>Camposperma</i> sp.	NM 314	1225 ± 75
Anacardiaceae	<i>Camposperma</i> sp.	PJ 800	1225 ± 75
Anacardiaceae	<i>Camposperma</i> sp.	PJ 871	1625 ± 75
Anacardiaceae	<i>Protorhus</i> sp.	NM 235	450 ± 75
Anacardiaceae	<i>Protorhus</i> sp.	NM 305	1225 ± 75
Anacardiaceae	<i>Protorhus</i> sp.	PJ 728	450 ± 75
Anacardiaceae	<i>Protorhus</i> sp.	PJ 752	450 ± 75
Anacardiaceae	<i>Protorhus</i> sp.	PJ 806	1225 ± 75
Anacardiaceae	<i>Sorindeia madagascariensis</i> DC.	NM 238	450 ± 75
Annonaceae	cf. <i>Isolona</i> sp.	NM 263	775 ± 75
Annonaceae	<i>Isolona</i> sp.	NM 215	450 ± 75
Annonaceae	<i>Isolona</i> sp.	NM 227	450 ± 75
Annonaceae	<i>Isolona</i> sp.	PJ 761	775 ± 75
Annonaceae	<i>Monanthes</i> sp.	PJ 827	1225 ± 75
Annonaceae	<i>Polyalthia emarginata</i> Diels	NM 281	1225 ± 75
Annonaceae	<i>Polyalthia emarginata</i> Diels	PJ 836	1225 ± 75
Annonaceae	<i>Polyalthia emarginata</i> Diels	PJ 859	1625 ± 75
Annonaceae	<i>Polyalthia</i> sp.	PJ 725	450 ± 75
Annonaceae	<i>Xylopia</i> sp.	NM 312	1225 ± 75
Apiaceae	<i>Enteromorpha</i> sp.	PJ 902	1875 ± 75
Apocynaceae	<i>Landolphia</i> sp.	NM 223	450 ± 75
Apocynaceae	<i>Tabernaemontana eusepala</i> Aug. DC.	PJ 748	450 ± 75
Apocynaceae	<i>Tabernaemontana</i> sp.	PJ 820	1225 ± 75
Aquifoliaceae	<i>Ilex mitis</i> (L.) Radlk.	NM 306	1225 ± 75
Aquifoliaceae	<i>Ilex mitis</i> (L.) Radlk.	NM 350	1625 ± 75
Aquifoliaceae	<i>Ilex mitis</i> (L.) Radlk.	PJ 849	1625 ± 75
Araliaceae	<i>Polyscias</i> sp.	NM 385	1875 ± 75
Araliaceae	<i>Polyscias</i> sp.	NM 408	1875 ± 75
Araliaceae	<i>Polyscias</i> sp.	PJ 726	450 ± 75
Araliaceae	<i>Polyscias</i> sp.	PJ 757	775 ± 75
Araliaceae	<i>Polyscias</i> sp.	PJ 787	1225 ± 75
Araliaceae	<i>Polyscias</i> sp.	PJ 944	1875 ± 75
Araliaceae	<i>Schefflera</i> sp.	PJ 798	1225 ± 75
Araliaceae	<i>Schefflera</i> sp.	PJ 874	1625 ± 75
Araliaceae	<i>Schefflera</i> sp.	PJ 938	1875 ± 75
Araliaceae		NM 344	1625 ± 75
Arecaceae	<i>Dypsis</i> sp.	NM 211	450 ± 75
Asclepiadaceae		PJ 919	1875 ± 75
Asclepiadaceae?		PJ 914	1875 ± 75
Asteraceae	<i>Apodocephala</i> sp.	PJ 768	775 ± 75
Asteraceae	<i>Brachylaena merana</i> (Baker) Humbert	NM 310	1225 ± 75
Asteraceae	<i>Helichrysum adhaerens</i> (DC.) R. Vig. & Humbert	NM 384	1875 ± 75
Asteraceae	<i>Helichrysum adhaerens</i> (DC.) R. Vig. & Humbert	PJ 925	1875 ± 75
Asteraceae	<i>Helichrysum</i> sp.	NM 337	1625 ± 75
Asteraceae	<i>Helichrysum</i> sp.	NM 343	1625 ± 75
Asteraceae	<i>Helichrysum</i> sp.	NM 375	1875 ± 75
Asteraceae	<i>Helichrysum</i> sp.	NM 382	1875 ± 75
Asteraceae	<i>Helichrysum</i> sp.	NM 383	1875 ± 75
Asteraceae	<i>Helichrysum</i> sp.	NM 422	1875 ± 75
Asteraceae	<i>Helichrysum</i> sp.	NM 429	1875 ± 75
Asteraceae	<i>Helichrysum</i> sp.	PJ 855	1625 ± 75
Asteraceae	<i>Helichrysum</i> sp.	PJ 924	1875 ± 75

APPENDIX 3-4. *Continued*

Family	Genus and species	Collector* and number	Altitude (m)†
Asteraceae	<i>Helichrysum</i> sp.	PJ 926	1875 ± 75
Asteraceae	<i>Helichrysum</i> sp.	PJ 934	1875 ± 75
Asteraceae	<i>Rochonia</i> sp.	PJ 935	1875 ± 75
Asteraceae	<i>Senecio</i> sp.	NM 332	1625 ± 75
Asteraceae	<i>Senecio</i> sp.	NM 391	1875 ± 75
Asteraceae	<i>Senecio</i> sp.	NM 412	1875 ± 75
Asteraceae	<i>Senecio</i> sp.	NM 428	1875 ± 75
Asteraceae	<i>Senecio</i> sp.	PJ 765	775 ± 75
Asteraceae	<i>Senecio</i> sp.	PJ 865	1625 ± 75
Asteraceae	<i>Senecio</i> sp.	PJ 909	1875 ± 75
Asteraceae	<i>Senecio</i> sp.	PJ 922	1875 ± 75
Asteraceae	<i>Vernonia</i> sp.	NM 346	1625 ± 75
Asteraceae	<i>Vernonia</i> sp.	NM 374	1875 ± 75
Asteraceae	<i>Vernonia</i> sp.	PJ 863	1625 ± 75
Asteraceae	<i>Vernonia</i> sp.	PJ 923	1875 ± 75
Asteraceae	<i>Vernonia</i> sp.	PJ 955	1875 ± 75
Asteraceae		NM 365	1875 ± 75
Asteraceae		NM 370	1875 ± 75
Asteraceae		PJ 819	1225 ± 75
Asteraceae		PJ 850	1625 ± 75
Asteraceae		PJ 870	1625 ± 75
Asteraceae		PJ 873	1625 ± 75
Asteraceae		PJ 932	1875 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	NM 256	775 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	NM 356	1625 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	NM 376	1875 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	NM 387	1875 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	NM 388	1875 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	NM 410	1875 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	PJ 774	775 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	PJ 821	1225 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	PJ 868	1625 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	PJ 896	1625 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	PJ 899	1625 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	PJ 921	1875 ± 75
Balsaminaceae	<i>Impatiens</i> sp.	PJ 950	1875 ± 75
Begoniaceae	<i>Begonia</i> sp.	NM 288	1225 ± 75
Bignoniaceae	<i>Colea</i> sp.	NM 237	450 ± 75
Bignoniaceae	<i>Phyllarthron</i> sp.	NM 317	1625 ± 75
Bignoniaceae	<i>Phyllarthron</i> sp.	NM 345	1625 ± 75
Bignoniaceae	<i>Phyllarthron</i> sp.	PJ 811	1225 ± 75
Burseraceae	<i>Canarium madagascariense</i> Engl.	NM 220	450 ± 75
Burseraceae	<i>Canarium madagascariense</i> Engl.	PJ 733	450 ± 75
Burseraceae	<i>Canarium</i> sp.	NM 294	1225 ± 75
Burseraceae	<i>Protium</i> sp.	PJ 734	450 ± 75
Canellaceae	<i>Cinnamosma madagascariensis</i> Danguy	NM 247	775 ± 75
Celastraceae		NM 396	1875 ± 75
Celastraceae		PJ 841	1225 ± 75
Chloranthaceae	<i>Ascarina</i> sp.	PJ 898	1625 ± 75
Clusiaceae	<i>Calophyllum drouhardi</i> H. Perrier	NM 407	1875 ± 75
Clusiaceae	<i>Calophyllum</i> sp.	NM 214	450 ± 75
Clusiaceae	<i>Mammea</i> sp.	NM 323	1625 ± 75
Clusiaceae	<i>Mammea</i> sp.	PJ 790	1225 ± 75
Clusiaceae	<i>Mammea</i> sp.	PJ 797	1225 ± 75
Clusiaceae	<i>Mammea</i> sp.	PJ 852	1625 ± 75
Clusiaceae	<i>Mammea</i> sp.	PJ 904	1875 ± 75
Clusiaceae	<i>Ochrocarpos</i> sp.	NM 242	450 ± 75
Clusiaceae	<i>Ochrocarpos</i> sp.	NM 248	775 ± 75
Clusiaceae	<i>Ochrocarpos</i> sp.	NM 250	775 ± 75
Clusiaceae	<i>Ochrocarpos</i> sp.	NM 404	1875 ± 75

APPENDIX 3-4. *Continued*

Family	Genus and species	Collector* and number	Altitude (m)†
Clusiaceae	<i>Ochrocarpos</i> sp.	PJ 723	450 ± 75
Clusiaceae	<i>Psorospermum</i> sp.	NM 277	1225 ± 75
Clusiaceae	<i>Psorospermum</i> sp.	PJ 872	1625 ± 75
Clusiaceae	<i>Psorospermum</i> sp.	PJ 930	1875 ± 75
Clusiaceae	<i>Symphonia microphylla</i> (Cambess.) Vesque	PJ 890	1625 ± 75
Clusiaceae	<i>Symphonia</i> sp.	NM 216	450 ± 75
Clusiaceae	<i>Symphonia</i> sp.	NM 361	1875 ± 75
Clusiaceae	<i>Symphonia</i> sp.	PJ 727	450 ± 75
Clusiaceae	<i>Symphonia</i> sp.	PJ 801	1225 ± 75
Clusiaceae	<i>Symphonia</i> sp.	PJ 808	1225 ± 75
Clusiaceae		NM 303	1225 ± 75
Cunoniaceae	<i>Weinmannia</i> sp.	NM 380	1875 ± 75
Cunoniaceae	<i>Weinmannia</i> sp.	NM 381	1875 ± 75
Cunoniaceae	<i>Weinmannia</i> sp.	NM 394	1875 ± 75
Cunoniaceae	<i>Weinmannia</i> sp.	NM 402	1875 ± 75
Cunoniaceae	<i>Weinmannia</i> sp.	NM 423	1875 ± 75
Cunoniaceae	<i>Weinmannia</i> sp.	PJ 837	1225 ± 75
Cunoniaceae	<i>Weinmannia</i> sp.	PJ 897	1625 ± 75
Cunoniaceae	<i>Weinmannia</i> sp.	PJ 959	1875 ± 75
Cyperaceae	<i>Cyperus</i> sp.	PJ 908	1875 ± 75
Cyperaceae		NM 369	1875 ± 75
Droseraceae	<i>Drosera</i> sp.	NM 363	1875 ± 75
Droseraceae	<i>Drosera</i> sp.	PJ 916	1875 ± 75
Ebenaceae	<i>Diospyros</i> sp.	NM 268	1225 ± 75
Ebenaceae	<i>Diospyros</i> sp.	NM 287	1225 ± 75
Ebenaceae	<i>Diospyros</i> sp.	NM 302	1225 ± 75
Ebenaceae	<i>Diospyros</i> sp.	NM 316	1225 ± 75
Ebenaceae	<i>Diospyros</i> sp.	NM 354	1625 ± 75
Ebenaceae	<i>Diospyros</i> sp.	PJ 722	450 ± 75
Ebenaceae	<i>Diospyros</i> sp.	PJ 754	450 ± 75
Ebenaceae	<i>Diospyros</i> sp.	PJ 770	775 ± 75
Ebenaceae	<i>Diospyros</i> sp.	PJ 778	775 ± 75
Ebenaceae	<i>Diospyros</i> sp.	PJ 782	1225 ± 75
Ebenaceae	<i>Diospyros</i> sp.	PJ 812	1225 ± 75
Ebenaceae	<i>Diospyros</i> sp.	PJ 826	1225 ± 75
Ebenaceae		PJ 843	1225 ± 75
Elaeocarpaceae	<i>Elaeocarpus</i> sp.	NM 333	1625 ± 75
Elaeocarpaceae	<i>Sloanea rhodantha</i> (Baker) Capuron	PJ 789	1225 ± 75
Ericaceae	<i>Agauria</i> sp.	NM 386	1875 ± 75
Ericaceae	<i>Agauria</i> sp.	PJ 840	1225 ± 75
Ericaceae	<i>Erica</i> sp.	NM 362	1875 ± 75
Ericaceae	<i>Erica</i> sp.	NM 378	1875 ± 75
Ericaceae	<i>Erica</i> sp.	NM 427	1875 ± 75
Ericaceae	<i>Erica</i> sp.	PJ 799	1225 ± 75
Ericaceae	<i>Erica</i> sp.	PJ 903	1875 ± 75
Ericaceae	<i>Erica</i> sp.	PJ 958	1875 ± 75
Ericaceae	<i>Erica</i> sp.	PJ 967	1875 ± 75
Ericaceae	<i>Erica</i> sp.	PJ 969	1875 ± 75
Ericaceae	<i>Vaccinium</i> sp.	NM 340	1625 ± 75
Ericaceae	<i>Vaccinium</i> sp.	NM 411	1875 ± 75
Ericaceae	<i>Vaccinium</i> sp.	NM 421	1875 ± 75
Ericaceae	<i>Vaccinium</i> sp.	PJ 942	1875 ± 75
Eriocaulaceae	<i>Eriocaulus</i> sp.	NM 377	1875 ± 75
Erythroxylaceae	<i>Erythroxylum</i> sp.	NM 260	775 ± 75
Erythroxylaceae	<i>Erythroxylum</i> sp.	PJ 767	775 ± 75
Erythroxylaceae	<i>Erythroxylum</i> sp.	PJ 794	1225 ± 75
Erythroxylaceae	<i>Erythroxylum</i> sp.	PJ 945	1875 ± 75
Euphorbiaceae	<i>Alchornea</i> or <i>Suregada</i> sp.	PJ 941	1875 ± 75
Euphorbiaceae	<i>Antidesma</i> sp.	PJ 721	450 ± 75
Euphorbiaceae	<i>Antidesma</i> sp.	PJ 740	450 ± 75

APPENDIX 3-4. *Continued*

Family	Genus and species	Collector* and number	Altitude (m)†
Euphorbiaceae	<i>Antidesma</i> sp.	PJ 741	450 ± 75
Euphorbiaceae	<i>Bridelia</i> sp.	PJ 736	450 ± 75
Euphorbiaceae	<i>Croton</i> sp.	NM 359	1875 ± 75
Euphorbiaceae	<i>Croton</i> sp.	NM 379	1875 ± 75
Euphorbiaceae	<i>Croton</i> sp.	PJ 793	1225 ± 75
Euphorbiaceae	<i>Croton</i> sp.	PJ 804	1225 ± 75
Euphorbiaceae	<i>Croton</i> sp.	PJ 953	1875 ± 75
Euphorbiaceae	<i>Drypetes</i> sp.	NM 270	1225 ± 75
Euphorbiaceae	<i>Drypetes</i> sp.	NM 273	1225 ± 75
Euphorbiaceae	<i>Fluggea</i> sp.	PJ 717	450 ± 75
Euphorbiaceae	<i>Macaranga cuspidata</i> Baill.	NM 234	450 ± 75
Euphorbiaceae	<i>Macaranga</i> sp.	NM 213	450 ± 75
Euphorbiaceae	<i>Macaranga</i> sp.	NM 221	450 ± 75
Euphorbiaceae	<i>Macaranga</i> sp.	NM 292	1225 ± 75
Euphorbiaceae	<i>Macaranga</i> sp.	PJ 885	1625 ± 75
Euphorbiaceae	<i>Mallotus</i> sp.	PJ 730	450 ± 75
Euphorbiaceae	<i>Phyllanthus</i> sp.	NM 239	450 ± 75
Euphorbiaceae	<i>Phyllanthus</i> sp.	NM 298	1225 ± 75
Euphorbiaceae	<i>Phyllanthus</i> sp.	PJ 779	775 ± 75
Euphorbiaceae	<i>Uapaca</i> sp.	NM 254	775 ± 75
Euphorbiaceae	<i>Uapaca</i> sp.	NM 279	1225 ± 75
Euphorbiaceae	<i>Uapaca</i> sp.	NM 313	1225 ± 75
Euphorbiaceae	<i>Uapaca</i> sp.	NM 330	1625 ± 75
Euphorbiaceae		PJ 743	450 ± 75
Fabaceae	<i>Strongylodon</i> sp.	NM 264	775 ± 75
Fabaceae	<i>Strongylodon</i> sp.	PJ 751	450 ± 75
Flacourtiaceae	<i>Aphloia theiformis</i> (Vahl) Benn.	PJ 857	1625 ± 75
Flacourtiaceae	<i>Casearia</i> sp.	PJ 759	775 ± 75
Flacourtiaceae	<i>Scolopia</i> sp.	PJ 894	1625 ± 75
Flacourtiaceae	<i>Scolopia</i> sp.	PJ 928	1875 ± 75
Gentianaceae	<i>Exacum</i> sp.	NM 274	1225 ± 75
Gentianaceae	<i>Exacum</i> sp.	NM 390	1875 ± 75
Gentianaceae		PJ 920	1875 ± 75
Gesneriaceae	<i>Streptocarpus</i> sp.	PJ 745	450 ± 75
Icacinaceae	<i>Cassinopsis</i> sp.	NM 358	1875 ± 75
Icacinaceae	<i>Cassinopsis</i> sp.	PJ 817	1225 ± 75
Icacinaceae		PJ 829	1225 ± 75
Icacinaceae		PJ 844	1225 ± 75
Juncaceae		PJ 907	1875 ± 75
Juncaceae?		NM 401	1875 ± 75
Lauraceae	<i>Appolonias</i> sp.	NM 397	1875 ± 75
Lauraceae	<i>Appolonias</i> sp.	PJ 951	1875 ± 75
Lauraceae	<i>Cryptocarya</i> sp.	NM 276	1225 ± 75
Lauraceae	<i>Cryptocarya</i> sp.	NM 319	1625 ± 75
Lauraceae	<i>Cryptocarya</i> sp.	PJ 758	775 ± 75
Lauraceae	<i>Cryptocarya</i> sp.	PJ 785	1225 ± 75
Lauraceae	<i>Cryptocarya</i> sp.	PJ 882	1625 ± 75
Lauraceae	<i>Ocotea</i> sp.	NM 236	450 ± 75
Lauraceae	<i>Ocotea</i> sp.	NM 311	1225 ± 75
Lauraceae	<i>Potameia</i> sp.	NM 284	1225 ± 75
Lauraceae	<i>Potameia</i> sp.	NM 326	1625 ± 75
Lauraceae	<i>Potameia</i> sp.	PJ 946	1875 ± 75
Lauraceae		NM 285	1225 ± 75
Lauraceae		PJ 825	1225 ± 75
Lauraceae		PJ 845	1225 ± 75
Lauraceae		PJ 867	1625 ± 75
Loganiaceae	<i>Anthocleista madagascariensis</i> Baker	PJ 851	1625 ± 75
Loganiaceae	<i>Anthocleista madagascariensis</i> Baker	PJ 948	1875 ± 75
Loranthaceae	<i>Bakerella</i> sp.	NM 297	1225 ± 75
Loranthaceae	<i>Bakerella</i> sp.	NM 395	1875 ± 75

APPENDIX 3-4. *Continued*

Family	Genus and species	Collector* and number	Altitude (m)†
Loranthaceae	<i>Bakerella</i> sp.	NM 406	1875 ± 75
Loranthaceae		PJ 863	1625 ± 75
Loranthaceae		PJ 956	1875 ± 75
Melanophyllaceae	<i>Melanophylla humbertiana</i> Keraudren	PJ 732	450 ± 75
Melastomataceae	<i>Dichaetanthera</i> sp.	NM 251	775 ± 75
Melastomataceae	<i>Dichaetanthera</i> sp.	NM 336	1625 ± 75
Melastomataceae	<i>Dichaetanthera</i> sp.	PJ 773	775 ± 75
Melastomataceae	<i>Dionycha</i> sp.	PJ 940	1875 ± 75
Melastomataceae	<i>Memecylon</i> sp.	NM 241	450 ± 75
Melastomataceae	<i>Memecylon</i> sp.	PJ 744	450 ± 75
Melastomataceae		NM 348	1625 ± 75
Melastomataceae		NM 416	1875 ± 75
Meliaceae	<i>Malleastrum</i> sp.	NM 212	450 ± 75
Meliaceae	<i>Malleastrum</i> sp.	PJ 756	775 ± 75
Monimiaceae	<i>Decarydendron</i> sp.	PJ 839	1225 ± 75
Monimiaceae	<i>Ephippiandra madagascariensis</i> (Cavaco) Lorence	PJ 818	1225 ± 75
Monimiaceae	<i>Ephippiandra perrieri</i> (Cavaco) Lorence	PJ 905	1875 ± 75
Monimiaceae	<i>Tambourissa</i> cf. <i>parvifolia</i> Baker	PJ 884	1625 ± 75
Monimiaceae	<i>Tambourissa</i> cf. <i>purpurea</i> (Tul.) A. DC.	NM 249	775 ± 75
Monimiaceae	<i>Tambourissa purpurea</i> (Tul.) A. DC.	NM 307	1225 ± 75
Monimiaceae	<i>Tambourissa</i> sp.	NM 301	1225 ± 75
Monimiaceae	<i>Tambourissa</i> sp.	PJ 731	450 ± 75
Monimiaceae	<i>Tambourissa</i> sp.	PJ 772	775 ± 75
Monimiaceae	<i>Tambourissa</i> sp.	PJ 788	1225 ± 75
Monimiaceae	<i>Tambourissa</i> sp.	PJ 810	1225 ± 75
Monimiaceae	<i>Tambourissa thouvenotii</i> Danguy	PJ 747	450 ± 75
Moraceae	<i>Dorstenia</i> sp.	PJ 775	775 ± 75
Moraceae	<i>Ficus politoria</i> Lam.	NM 261	775 ± 75
Moraceae	<i>Ficus politoria</i> Lam.	PJ 777	775 ± 75
Moraceae	<i>Ficus</i> sp.	NM 226	450 ± 75
Moraceae	<i>Ficus</i> sp.	NM 230	450 ± 75
Moraceae	<i>Ficus</i> sp.	NM 233	450 ± 75
Moraceae	<i>Ficus</i> sp.	PJ 724	450 ± 75
Moraceae	<i>Ficus tiliaefolia</i> Baker	PJ 755	450 ± 75
Moraceae	<i>Trilepisium madagascariense</i> DC.	NM 222	450 ± 75
Myricaceae	<i>Myrica</i> cf. <i>spathulata</i> Mirb.	PJ 876	1625 ± 75
Myricaceae	<i>Myrica phillyreaefolia</i> Baker	PJ 802	1225 ± 75
Myricaceae	<i>Myrica phillyreaefolia</i> Baker	PJ 875	1625 ± 75
Myricaceae	<i>Myrica</i> sp.	PJ 929	1875 ± 75
Myrsinaceae	<i>Embelia</i> sp.	PJ 834	1225 ± 75
Myrsinaceae	<i>Embelia</i> sp.	PJ 939	1875 ± 75
Myrsinaceae	<i>Maesa</i> sp.	PJ 816	1225 ± 75
Myrsinaceae	<i>Monoporus</i> sp.	PJ 856	1625 ± 75
Myrsinaceae	<i>Monoporus</i> sp.	PJ 947	1875 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	NM 224	450 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	NM 244	775 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	NM 339	1625 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	NM 393	1875 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	NM 403	1875 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	NM 409	1875 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	NM 415	1875 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	NM 420	1875 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	NM 425	1875 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	PJ 718	450 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	PJ 760	775 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	PJ 780	775 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	PJ 792	1225 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	PJ 803	1225 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	PJ 832	1225 ± 75
Myrsinaceae	<i>Oncostemum</i> sp.	PJ 891	1625 ± 75

APPENDIX 3-4. *Continued*

Family	Genus and species	Collector* and number	Altitude (m)†
Myrsinaceae	<i>Oncostemum</i> sp.	PJ 937	1875 ± 75
Myrsinaceae		PJ 860	1625 ± 75
Myrsinaceae		PJ 957	1875 ± 75
Myrtaceae	<i>Eugenia</i> sp.	PJ 918	1875 ± 75
Myrtaceae	<i>Syzygium</i> sp.	NM 282	1225 ± 75
Myrtaceae	<i>Syzygium</i> sp.	NM 304	1225 ± 75
Myrtaceae	<i>Syzygium</i> sp.	NM 329	1625 ± 75
Myrtaceae	<i>Syzygium</i> sp.	NM 424	1875 ± 75
Myrtaceae	<i>Syzygium</i> sp.	PJ 858	1625 ± 75
Myrtaceae	<i>Syzygium</i> sp.	PJ 933	1875 ± 75
Myrtaceae	<i>Syzygium</i> sp.	PJ 960	1875 ± 75
Myrtaceae	<i>Syzygium</i> sp.	PJ 961	1875 ± 75
Myrtaceae	<i>Syzygium</i> sp.	PJ 962	1875 ± 75
Myrtaceae	<i>Syzygium</i> sp.	PJ 963	1875 ± 75
Oleaceae	<i>Noronhia</i> sp.	PJ 720	450 ± 75
Oleaceae	<i>Noronhia</i> sp.	PJ 729	450 ± 75
Orchidaceae	<i>Angraecum</i> sp.	NM 228	450 ± 75
Orchidaceae	<i>Angraecum</i> sp.	NM 229	450 ± 75
Orchidaceae	<i>Angraecum</i> sp.	NM 255	775 ± 75
Orchidaceae	<i>Angraecum</i> sp.	PJ 889	1625 ± 75
Orchidaceae	<i>Bulbophyllum</i> sp.	PJ 831	1225 ± 75
Orchidaceae	<i>Bulbophyllum</i> sp.	PJ 906	1875 ± 75
Orchidaceae	<i>Calanthes</i> sp.	PJ 886	1625 ± 75
Orchidaceae	<i>Cynorchis</i> sp.	NM 266	775 ± 75
Orchidaceae	<i>Cynorchis</i> sp.	NM 372	1875 ± 75
Orchidaceae		NM 352	1625 ± 75
Orchidaceae		NM 364	1875 ± 75
Orchidaceae		PJ 887	1625 ± 75
Orchidaceae		PJ 910	1875 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 210	450 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 218	450 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 219	450 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 243	450 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 259	775 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 289	1225 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 295	1225 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 308	1225 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 309	1225 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 353	1625 ± 75
Piperaceae	<i>Peperomia</i> sp.	NM 360	1875 ± 75
Piperaceae	<i>Piper</i> sp.	NM 231	450 ± 75
Piperaceae	<i>Piper</i> sp.	NM 240	450 ± 75
Piperaceae	<i>Piper</i> sp.	NM 296	1225 ± 75
Pittosporaceae	<i>Pittosporum ambrense</i> Cufod.	PJ 815	1225 ± 75
Pittosporaceae	<i>Pittosporum ambrense</i> Cufod.	PJ 833	1225 ± 75
Pittosporaceae	<i>Pittosporum</i> cf. <i>verticillatum</i> Bojer	NM 291	1225 ± 75
Pittosporaceae	<i>Pittosporum humbertii</i> Cufod.	PJ 968	1875 ± 75
Pittosporaceae	<i>Pittosporum polyspernum</i> Tul.	PJ 719	450 ± 75
Pittosporaceae	<i>Pittosporum polyspernum</i> Tul.	PJ 781	775 ± 75
Pittosporaceae	<i>Pittosporum</i> sp.	NM 217	450 ± 75
Pittosporaceae	<i>Pittosporum verticillatum</i> Bojer	PJ 880	1625 ± 75
Poaceae		NM 280	1225 ± 75
Poaceae		PJ 749	450 ± 75
Poaceae		PJ 912	1875 ± 75
Poaceae		PJ 913	1875 ± 75
Poaceae		PJ 915	1875 ± 75
Proteaceae	<i>Faurea forficuliflora</i> Baker var. <i>elliptica</i> Humbert	PJ 864	1625 ± 75
Rhizophoraceae	<i>Cassipourea</i> sp.	NM 278	1225 ± 75
Rhizophoraceae	<i>Cassipourea</i> sp.	NM 322	1625 ± 75
Rhizophoraceae	<i>Cassipourea</i> sp.	PJ 828	1225 ± 75

APPENDIX 3-4. *Continued*

Family	Genus and species	Collector* and number	Altitude (m)†
Rhizophoraceae	<i>Cassipourea</i> sp.	PJ 881	1625 ± 75
Rhizophoraceae	<i>Macarisia</i> sp.	PJ 854	1625 ± 75
Rhizophoraceae		PJ 805	1225 ± 75
Rubiaceae	<i>Alberta minor</i> Baill.	NM 318	1625 ± 75
Rubiaceae	<i>Alberta minor</i> Baill.	NM 331	1625 ± 75
Rubiaceae	<i>Alberta minor</i> Baill.	NM 426	1875 ± 75
Rubiaceae	<i>Alberta sambiranensis</i> Cavaco	NM 293	1225 ± 75
Rubiaceae	<i>Canthium</i> sp.	NM 246	775 ± 75
Rubiaceae	<i>Canthium</i> sp.	NM 269	1225 ± 75
Rubiaceae	<i>Canthium</i> sp.	NM 290	1225 ± 75
Rubiaceae	<i>Canthium</i> sp.	PJ 764	775 ± 75
Rubiaceae	<i>Canthium</i> sp.	PJ 807	1225 ± 75
Rubiaceae	<i>Canthium</i> sp.	PJ 842	1225 ± 75
Rubiaceae	<i>Canthium</i> sp.	PJ 892	1625 ± 75
Rubiaceae	cf. <i>Chapelieria</i> sp.	NM 347	1625 ± 75
Rubiaceae	cf. <i>Chapelieria</i> sp.	PJ 813	1225 ± 75
Rubiaceae	cf. <i>Chapelieria</i> sp.	PJ 846	1625 ± 75
Rubiaceae	cf. <i>Chapelieria</i> sp.	PJ 847	1625 ± 75
Rubiaceae	<i>Danais</i> cf. <i>tsaratananensis</i> Homolle	NM 341	1625 ± 75
Rubiaceae	<i>Gaertnera macrostipula</i> Baker	PJ 796	1225 ± 75
Rubiaceae	<i>Gaertnera</i> sp.	NM 245	775 ± 75
Rubiaceae	<i>Gaertnera</i> sp.	NM 338	1625 ± 75
Rubiaceae	<i>Gaertnera</i> sp.	NM 405	1875 ± 75
Rubiaceae	<i>Gaertnera</i> sp.	PJ 742	450 ± 75
Rubiaceae	<i>Gaertnera</i> sp.	PJ 809	1225 ± 75
Rubiaceae	<i>Gaertnera</i> sp.	PJ 848	1625 ± 75
Rubiaceae	<i>Gaertnera uniflora</i> ined.	NM 300	1225 ± 75
Rubiaceae	<i>Hyperacanthus</i> sp.	PJ 762	775 ± 75
Rubiaceae	<i>Ixora</i> sp.	NM 252	775 ± 75
Rubiaceae	<i>Ixora</i> sp.	NM 267	1225 ± 75
Rubiaceae	<i>Ixora</i> sp.	NM 349	1625 ± 75
Rubiaceae	<i>Ixora</i> sp.	PJ 735	450 ± 75
Rubiaceae	<i>Ixora</i> sp.	PJ 883	1625 ± 75
Rubiaceae	<i>Lemyrea</i> sp.	PJ 784	1225 ± 75
Rubiaceae	<i>Mapouria pyrrotricha</i> Bremek.	NM 299	1225 ± 75
Rubiaceae	<i>Morinda</i> sp.	PJ 769	775 ± 75
Rubiaceae	<i>Mussaenda erectiloba</i> Wernham	NM 325	1625 ± 75
Rubiaceae	<i>Nematostylis anthophylla</i> (A. Rich.) Baill.	NM 367	1875 ± 75
Rubiaceae	<i>Nematostylis anthophylla</i> (A. Rich.) Baill.	NM 399	1875 ± 75
Rubiaceae	<i>Pauridiantha paucinervis</i>	NM 225	450 ± 75
Rubiaceae	<i>Payera beondrokensis</i> (Humbert) Buchner & Puff	PJ 900	1875 ± 75
Rubiaceae	<i>Payera</i> sp.	PJ 822	1225 ± 75
Rubiaceae	<i>Psychotria</i> cf. <i>ankafinensis</i> (K. Schum.) Bremek.	NM 400	1875 ± 75
Rubiaceae	<i>Psychotria lokohensis</i> Bremek.	PJ 716	450 ± 75
Rubiaceae	<i>Psychotria</i> sp.	NM 272	1225 ± 75
Rubiaceae	<i>Psychotria</i> sp.	NM 355	1625 ± 75
Rubiaceae	<i>Psychotria</i> sp.	NM 417	1875 ± 75
Rubiaceae	<i>Psychotria</i> sp.	NM 418	1875 ± 75
Rubiaceae	<i>Psychotria</i> sp.	PJ 715	450 ± 75
Rubiaceae	<i>Psychotria</i> sp.	PJ 738	450 ± 75
Rubiaceae	<i>Psychotria</i> sp.	PJ 814	1225 ± 75
Rubiaceae	<i>Psychotria</i> sp.	PJ 824	1225 ± 75
Rubiaceae	<i>Psychotria</i> sp.	PJ 949	1875 ± 75
Rubiaceae	<i>Sabicea diversifolia</i> Pers.	NM 258	775 ± 75
Rubiaceae	<i>Saldinia</i> sp.	PJ 739	450 ± 75
Rubiaceae	<i>Schismatoclada</i> cf. <i>farahimpensis</i> Homolle	PJ 737	450 ± 75
Rubiaceae	<i>Schismatoclada</i> sp.	NM 342	1625 ± 75
Rubiaceae	<i>Schismatoclada</i> sp.	NM 392	1875 ± 75
Rubiaceae	<i>Schismatoclada</i> sp.	PJ 965	1875 ± 75
Rubiaceae	<i>Schismatoclada</i> sp.	PJ 966	1875 ± 75

APPENDIX 3-4. *Continued*

Family	Genus and species	Collector* and number	Altitude (m)†
Rubiaceae	<i>Tarenna</i> sp.	PJ 766	775 ± 75
Rubiaceae	<i>Tarenna</i> sp.	PJ 835	1225 ± 75
Rubiaceae		NM 324	1625 ± 75
Rubiaceae		PJ 931	1875 ± 75
Rubiaceae		PJ 943	1875 ± 75
Rubiaceae		PJ 964	1875 ± 75
Rutaceae	<i>Citrus</i> sp.	NM 232	450 ± 75
Rutaceae	<i>Evodia</i> or <i>Ivodea</i> sp.	PJ 877	1625 ± 75
Rutaceae	<i>Evodia</i> or <i>Ivodea</i> sp.	PJ 878	1625 ± 75
Rutaceae	<i>Evodia</i> sp.	NM 398	1875 ± 75
Rutaceae	<i>Vepris</i> sp.	NM 286	1225 ± 75
Rutaceae		PJ 879	1625 ± 75
Sapindaceae	<i>Tina</i> sp.	NM 275	1225 ± 75
Sapindaceae	<i>Tina</i> sp.	NM 315	1225 ± 75
Sapindaceae	<i>Tina</i> sp.	NM 320	1625 ± 75
Sapindaceae	<i>Tina</i> sp.	NM 327	1625 ± 75
Sapindaceae	<i>Tina</i> sp.	PJ 791	1225 ± 75
Sapindaceae	<i>Tina</i> sp.	PJ 823	1225 ± 75
Sapindaceae	<i>Tina striata</i>	PJ 786	1225 ± 75
Sapotaceae	<i>Faucherea</i> sp.	NM 253	775 ± 75
Sapotaceae	<i>Faucherea</i> sp.	NM 271	1225 ± 75
Sapotaceae	<i>Faucherea</i> sp.	NM 335	1625 ± 75
Sapotaceae	<i>Faucherea thouvenotii</i> Lecomte	PJ 838	1225 ± 75
Sapotaceae	<i>Faucherea thouvenotii</i> Lecomte	NM 283	1225 ± 75
Scrophulariaceae		NM 351	1625 ± 75
Sterculiaceae	<i>Dombeya</i> sp.	NM 373	1875 ± 75
Sterculiaceae	<i>Dombeya</i> sp.	NM 419	1875 ± 75
Sterculiaceae	<i>Dombeya</i> sp.	PJ 763	775 ± 75
Sterculiaceae	<i>Dombeya</i> sp.	PJ 893	1625 ± 75
Thymeleaceae	<i>Atemmosiphon coriaceus</i> Léandri	NM 321	1625 ± 75
Thymeleaceae	<i>Atemmosiphon coriaceus</i> Léandri	PJ 795	1225 ± 75
Thymeleaceae	<i>Octolepis</i> sp.	PJ 853	1625 ± 75
Tiliaceae	<i>Grewia</i> sp.	PJ 753	450 ± 75
Ulmaceae		PJ 750	450 ± 75
Urticaceae		NM 265	775 ± 75
Urticaceae		PJ 888	1625 ± 75
Urticaceae?		NM 262	775 ± 75
Verbenaceae	<i>Clerodendron</i> sp.	NM 389	1875 ± 75
Verbenaceae	<i>Clerodendron</i> sp.	PJ 783	1225 ± 75
Verbenaceae	<i>Clerodendron</i> sp.	PJ 901	1875 ± 75
Verbenaceae	<i>Clerodendron</i> sp.	PJ 927	1875 ± 75
Verbenaceae	<i>Clerodendron</i> sp.	PJ 954	1875 ± 75
Verbenaceae		NM 328	1625 ± 75
Verbenaceae		NM 357	1875 ± 75
Verbenaceae		PJ 830	1225 ± 75
Verbenaceae		PJ 861	1625 ± 75
Viscaceae	<i>Viscum</i> sp.	PJ 771	775 ± 75
Xyridaceae	<i>Xyris</i> sp.	NM 366	1875 ± 75
Xyridaceae	<i>Xyris</i> sp.	NM 371	1875 ± 75
Xyridaceae	<i>Xyris</i> sp.	PJ 869	1625 ± 75
Xyridaceae	<i>Xyris</i> sp.	PJ 917	1875 ± 75
		NM 368	1875 ± 75
		PJ 866	1625 ± 75
		PJ 911	1875 ± 75
		PJ 936	1875 ± 75
		PJ 952	1875 ± 75

* Collectors: NM, Nathalie Messmer; PJ, Pierre Jules Rakotomalaza.

† The altitudes refer to the five elevational zones.

Chapter 4

The First *Beckeriella* Williston from the Afrotropical Region: Two New Species from Madagascar (Diptera: Ephydriidae)

Wayne N. Mathis¹ and David A. Grimaldi²

Abstract

Two new species of the shore-fly genus *Beckeriella* are described from specimens collected on the island of Madagascar. These are the first species of *Beckeriella* from the Afrotropical Region, and aside from *B. filipina* (from the Philippines), they are the first species of the genus to be described from regions outside of the New World tropics, where the genus has its greatest diversity.

Résumé

Deux nouvelles espèces du Madagascar du genre "la mouche de la plage" *Beckeriella* sont décrites. Ce sont les premières espèces du genre *Beckeriella* récoltées dans la région afrotropicale. Hors *B. filipina* (des Philippines) les espèces décrites ici sont les premières qui proviennent des régions autres que les néotropiques, où ce genre a actuellement la plus grande diversité.

Introduction

Beckeriella Williston is an uncommonly collected genus of shore flies that, until recently, was represented by 10 New World species (Mathis & Zatzwornicki, 1995). Four years ago, however, Lizzaralde de Grosso (1994) described *B. filipina* from the Philippines, which substantively and somewhat anomalously increased the known distribution for the genus. Such an apparent disjunct distribution between the Philippines and the tropical neotropics was unknown among the Ephydriidae. Here we extend even further the known worldwide distribution and describe two new species from Madagascar, the first of this genus from

the Afrotropical Region. This further expands the known distribution of *Beckeriella* and alters our ideas about the historical origins and phylogeny of the genus.

Methods

The terminology and methods used in this study were explained previously (Mathis, 1990). Because of the small size of the specimens, study and illustration of the male terminalia required the use of a compound microscope. To ensure effective communication about structures of the male terminalia, we have adopted the terminology of other workers in Ephydriidae (see references in Mathis, 1986). Usage of these terms, however, should not be taken as an endorsement of them from a theoretical or morphological view over alternatives that have been proposed (Cumming et

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al., 1995; Griffiths, 1972; McAlpine, 1981). Rather, we are deferring to tradition until the morphological issues are better resolved.

Three ratios (one cephalic, two venational) are commonly used in the descriptions and are defined here for the convenience of the user (ratios are ranges based on three specimens): 1. Gena-to-eye ratio is the genal height measured at the maximum eye height divided by the eye height. 2. Costal vein ratio is the straight-line distance between the apices of veins R_{2+3} and R_{4+5} /distance between the apices of veins R_1 and R_{2+3} . 3. M vein ratio is the straight-line distance along M between crossveins dm-cu and r-m/distance apicad of crossvein dm-cu.

Tribe Gastropini Cresson

Gastropini Cresson, 1949:250 (as Gastropsini).

TYPE GENUS—*Gastrops* Williston, 1897 (Zatwarnicki, 1995:127–130 [world catalog]).

DISCUSSION—Williston (1897) described both genera, *Beckeriella* and *Gastrops*, that now make up the tribe Gastropini, which until recently was placed in the subfamily Parydrinae (Cresson, 1949; Lizarralde de Grosso, 1989; Wirth, 1968). Currently the tribe is placed in the subfamily Gymnomyzinae, based on Zatwarnicki's (1992) assessment of characters of the male terminalia. Although the tribe is undoubtedly monophyletic (Mathis, 1977), other aspects concerning the phylogenetic relationships of the tribe, such as identification of the tribe's sister group and the monophyly of the two included genera, are unresolved. Two colleagues, Stark (pers. comm.) and Lizarralde de Grosso (pers. comm.), are now studying these phylogenetic issues as part of more comprehensive research on the tribe. Thus, we defer comment on the phylogeny and taxonomic status of the included genera and recognize *Beckeriella* as described previously and diagnosed herein.

Genus *Beckeriella* Williston

Beckeriella Williston, 1897:2.

TYPE SPECIES—*Ephydra bispinosa* Thomson, 1868 (= *Scatophaga bispinosa* Fabricius, 1805), monotypy. (Cresson, 1934:201–205 [review]; Wirth, 1968:20 [Neotropical catalog]; Lizarralde de Grosso, 1986:133–137 [species description];

1990:143–146 [species description]; 1991a:39–42 [species description]; 1991b:45–48 [species description]; 1992:229–233 [species description]; 1994:57–59 [species description, Philippines]; Mathis & Zatwarnicki, 1995:27–129 [world catalog]).

DIAGNOSIS—A tribe of the subfamily Gymnomyzinae that is distinguished from other tribes by the following combination of characters: moderately small to large shore flies, length 2.5–5.5 mm.

Head—Frons rectangular, wider than long, vertex at level beyond posterior margin of posterior ocelli; pseudopostocellar setae greatly reduced or lacking; ocellar seta well developed, subequal to outer vertical seta, proclinate, slightly divergent; fronto-orbital seta 2, both proclinate, only anterior setae usually well developed, oriented anterolaterally, posterior seta much smaller or lacking; outer vertical seta well developed; inner vertical seta weakly developed to lacking, if present much smaller than outer seta and with medioproclinate orientation. Scape and pedicel comparatively long and semiporrect; flagellomere 1, comparatively long, greatly elongate and pendulous in some species, apex rounded; pedicel lacking a well-developed dorsoapical seta; flagellum long, bearing 6–12 dorsal rays along length. Face in profile usually concave, sometimes with dorsal half shallowly tumescent, usually with a transverse crease near midheight, usually bare of microtomentum, shiny, bearing a single seta and smaller setulae laterally near margin with parafacial, rarely bearing a 2nd seta ventrad from larger seta. Eye somewhat projected laterally, bulbous, horizontally ovate (bluntly rounded anteriorly in lateral view, more narrowly rounded posterodorsally) or vertically ovate. Anterior oral margin more or less straight; clypeus wide, bandlike, short, partially to mostly concealed by ventral margin of face and gena; genal seta 1, frequently reduced in size.

Thorax—Generally dark-colored; scutellum usually moderately flat, rectangular to trapezoidal, only apical scutellar seta well developed, these sometimes arising from small tubercles; acrostichal setulae minute, usually in 2 rows; only the posteriormost dorsocentral seta well developed, slightly displaced laterally; no presutural or postsutural supra-alar seta; postalar seta 1; propronotum setulose but lacking a large seta; notoplueron usually with 2 setae near ventral margin, posterior seta stronger, anterior seta sometimes lacking; anepisternum bearing 1 large seta along posterior margin; katepisternum bearing 1 large seta and

with anterior $\frac{2}{3}$ usually bare of microtomentum, similar to anteroventral corner of anepisternum, shiny; otherwise pleuron thinly microtomentose. Wing usually infusate, sometimes very dark, to maculate; vein R_{2+3} curved anteriorly at apex rather abruptly, often bearing a subapical stump vein; frequently with some veins sinuous, especially veins R_{2+3} , R_{4+5} , and M. Halter with knob blackish brown. Femora usually brown to black; fore- and especially hind femora sometimes swollen; fore-femur bearing numerous long setae along posteroventral surface; midfemur bearing numerous long setae along anteroventral surface; basal tarsomeres yellow, apical 2–3 brownish black.

Abdomen—Strongly convex, domelike, thinly to moderately invested with microtomentum, sometimes more so toward posterior margin, to nearly bare, subshiny to shiny, often with some metallic luster; tergites with lateroventral margins sharply defined, often with cuticular microsculpturing, surface appearing shallowly wrinkled or puckered; 2nd tergite with patch of dorsoerect setulae laterally.

DISTRIBUTION—With the exception of the two species described here and *B. filipina* (from the Philippines), *Beckeriella* is known only from the New World tropics, where the genus currently has its greatest diversity, with 10 species. Many undescribed species are already known and available in collections (Stark, pers. comm.), and undoubtedly numerous others remain to be discovered. Although the shore flies of the Afrotropical Region have not been well collected, we find it somewhat anomalous that the first species of *Beckeriella* were found on Madagascar and not in continental Africa. On Madagascar, the two species were collected at higher elevation, above 1000 m, and from the same province (Antsiranana).

DISCUSSION—*Beckeriella* is apparently of ancient origin and is the only identified genus of shore flies that is represented by fossils in amber (Evenhuis, 1994). The fossils, which are from Dominican amber of unknown provenance, represent a few species and date from the Oligocene/Miocene epochs. Stark (pers. comm.) is now studying and describing these species.

Beckeriella fasciata, new species

Figures 4-1, 4-2a,b

DESCRIPTION—A large shore fly (Fig. 4-1), length 5.2 mm; head generally yellow; thorax and

abdomen black, subshiny to shiny; wing generally dark brown with subapical transverse white band.

Head (Fig. 4-2a)—Generally yellow; mesofrons rectangular, longer than wide, brown; fronto-orbits brown. Inner vertical seta greatly reduced or lacking; fronto-orbital setae 2, posterior seta short, much less than half length of anterior seta, anterior seta slightly longer than outer vertical seta. Scape yellowish brown basally becoming brown apically, length distinctly shorter than pedicel; pedicel brown with some gray microtomentum dorsally; flagellomere 1 dark brown on dorsal half, yellow on ventral half both laterally and medially, length about $2.5\times$ height; flagellomere bearing 11 dorsal rays. Face concave in lateral view, yellow except for wide stripe just ventrad of antennal bases and a thinner stripe at midheight of facial concavity. Eye transversely ovate, anterior margin bluntly rounded, tapered posteriorly to more narrowed posterior margin. Gena yellow, moderately high, gena-to-eye ratio 0.39. Clypeus yellow, wide, short, largely concealed in oral cavity. Mouthparts yellow.

Thorax—Generally black; scutum subshiny, thinly invested with brown microtomentum anteromedially, anterior and anterolateral margins of scutum lightly gray microtomentose, microtomentum becoming sparser and appearing shinier posteriorly until just before posterior margin, which is narrowly but more densely microtomentose, brown; scutellum very sparsely and uniformly brown microtomentose, rectangular (Fig. 4-2b), wider than long, with posterior margin broadly truncate, apical scutellar setae arising from short tubercles at posterolateral corners of scutellum, about as long as length of scutellum; pleuron black, mostly uniformly sparsely microtomentose except for shiny, bare anteroventral corner of anepisternum and anterior $\frac{2}{3}$ of katepisternum. Wing mostly brown, slightly darker basally, with irregular (basal and apical margins) subapical transverse white band at level of apex of vein R_{2+3} and continued posteriorly just apical of crossvein dm-cu; crossvein r-m slightly whitened medially; vein R_{2+3} sinuous, curved sharply toward costa at apex, short, making costal section III as long as section II; vein R_{4+5} sinuous; crossvein dm-cu longer than apex of vein CuA_1 , apical of crossvein dm-cu; costal vein ratio 0.87; M vein ratio 0.60; alula short and wide, fringing setulae as long as alular height; knob of halter blackish brown. Legs mostly brownish black to black, sometimes with shiny surfaces, only foretibia and basal 3 tarsomeres

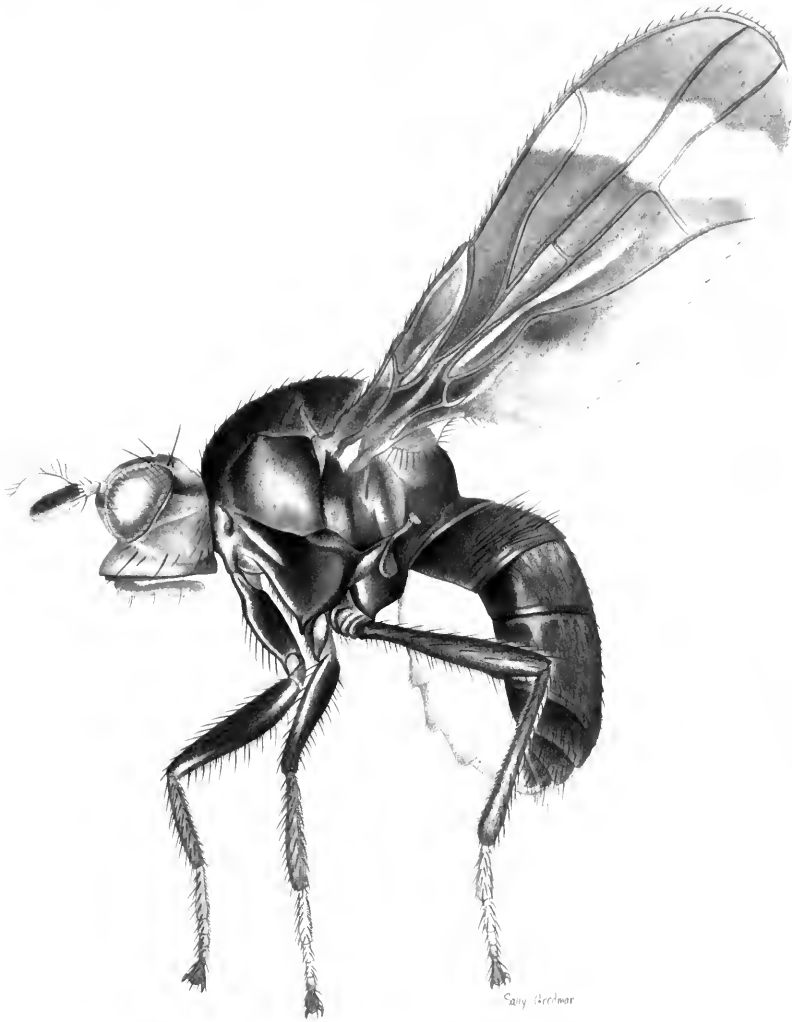


FIG. 4-1. *Beckeriella fasciata*. Habitus, lateral view.

yellow; apices of mid- and hind tibiae brown, slightly lighter in color than femora.

Abdomen—Appearing domelike, generally black, subshiny, thinly microtomentose; 2nd tergite with lateral patches of dorsoerect setae; lateral margins of tergites sharply defined.

TYPE MATERIAL—The holotype female is labeled “Madagascar-Est dct. Sambava R.N. [now Parc National de Marojejy] XII Marojejy-Ouest 1140 m XI-59 [Nov 1959] P.Soga/INSTITUT SCIENTIFIQUE MADAGASCAR [blue; black margin].” The holotype is double-mounted (minuten in rectangular block or pith), is in good condition (right flagellomere 1 missing, left wing torn apically, some tarsi missing, an-

tennae lost soon after illustrating), and is deposited in the Natal Museum (Pietermaritzburg, South Africa).

DISTRIBUTION—Afrotropical: Madagascar (Antsiranana).

ETYMOLOGY—The specific epithet, *fasciata*, refers to the subapical white fascia or band on an otherwise brown to dark brown wing.

DIAGNOSIS—This species is distinguished from congeners, especially *B. maculata*, by its large size (5.2 mm), the largely brown wing with a subapical white transverse band, and its body coloration (see description).

REMARKS—This species is represented by a single female.

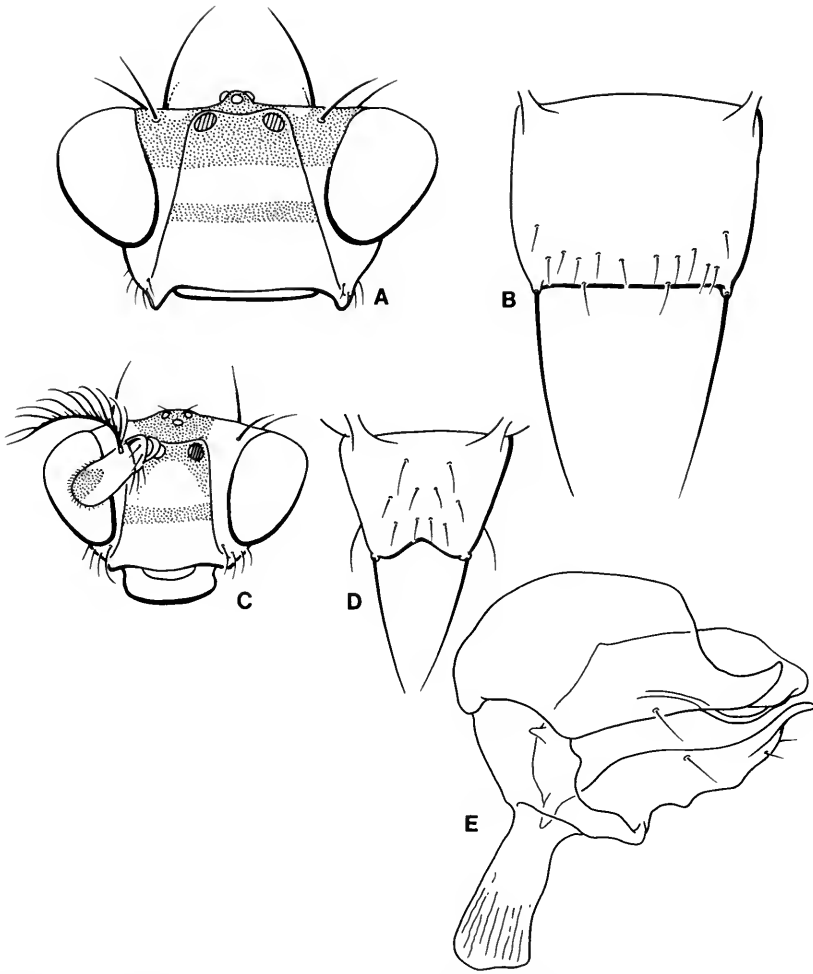


FIG. 4-2. a, b: *Beckeriella fasciata*. a, Head, anterior view. b, Scutellum, dorsal view. c-e: *Beckeriella maculata*. c, Head, anterior view. d, Scutellum, dorsal view. e, Male genitalia, lateral view.

***Beckeriella maculata*, new species**

Figures 4-2c-e, 4-3 to 4-5

DESCRIPTION—Moderately small shore fly, length 2.5–2.70 mm; head generally yellow; thorax and abdomen black, subshiny to shiny; wing generally dark brown on basal half, apical half white with maculate pattern.

Head (Fig. 4-2c)—Generally yellow; mesofrons rectangular, slightly wider than long; fronto-orbits yellow. Inner vertical seta well developed, equal in length to fronto-orbital seta; fronto-orbital setae 2, posterior seta very short, much less than half length of anterior seta, anterior seta slightly longer than outer vertical seta. Scape and pedicel yellow with some grayish microtomentum dorsally; length of scape distinctly shorter than

pedicel; flagellomere 1 mostly yellow, lateral surface with brown stripe extended from anterodorsal corner to base, yellow on dorsal and ventral sides of stripe, median surface with only anterodorsal corner brown, otherwise yellow, length about twice height; flagellomere bearing 9–10 dorsal rays. Face shiny, bare of microtomentum, concave in lateral view with distinct transverse crease at midheight, with a transverse brown stripe at crease, otherwise whitish yellow. Eye transversely ovate, anterior margin bluntly rounded, tapered posteriorly to more narrowed posterior margin. Gena yellow, moderately low, gena-to-eye ratio 0.26–0.30. Clypeus yellow, wide, short, largely concealed in oral cavity. Mouthparts yellow.

Thorax—Generally black; scutum subshiny, anterior and anterolateral margins of scutum light-

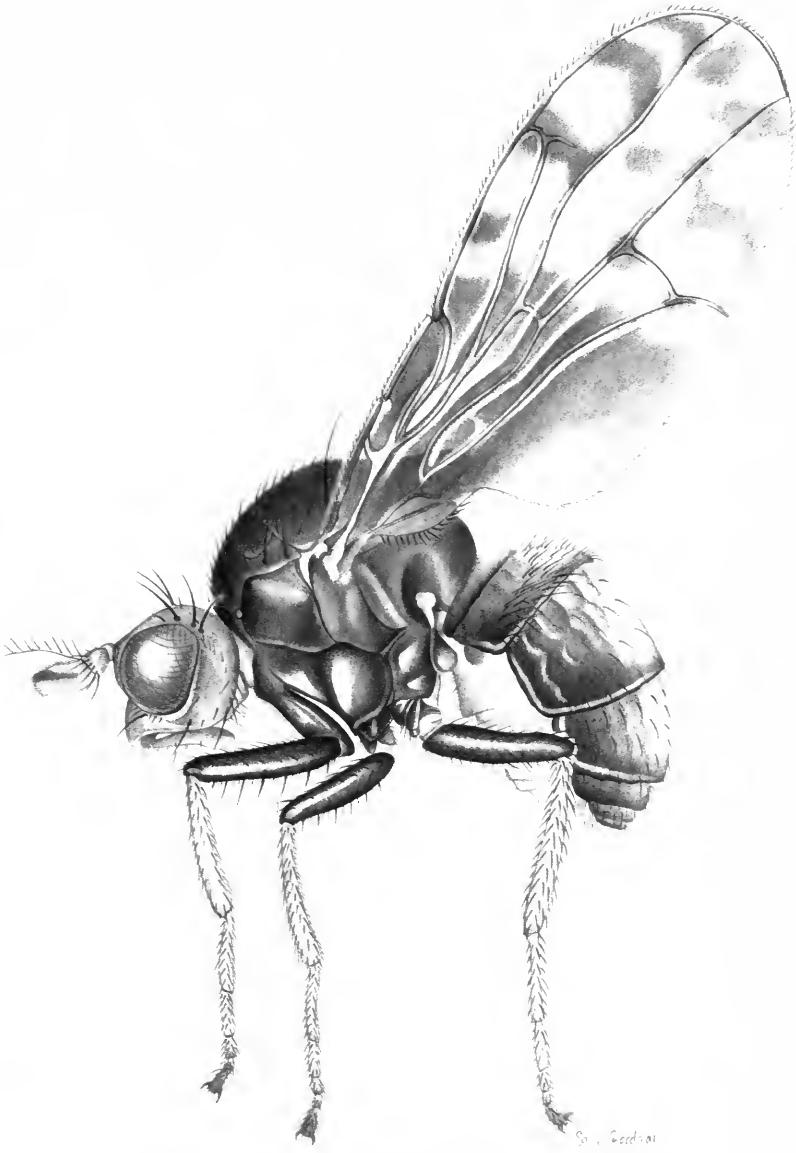


FIG. 4-3. *Beckeriella maculata*. Habitus, lateral view.

ly gray microtomentose, posterior half to $\frac{2}{3}$ of scutum mostly with brown microtomentum, with long gray linear spot on median side of dorsocentral track that extends from anterior margin posteriorly for $\frac{2}{3}$ length of scutum and 2 linear spots laterally on either side of transverse suture; scutellum with dorsal surface finely granulose, mostly black with some bluish black reflections, very sparsely brown microtomentose, trapezoidal (Fig. 4-2d), about as long as wide, gradually tapered posteriorly, with posterior margin emarginate me-

dially, apical scutellar setae arising from postero-lateral corners, without tubercles at base, subapical scutellar setae about $\frac{1}{2}$ length of apical setae, inserted laterally at apical $\frac{2}{3}$. Wing mostly brown on basal half, dark brown basally, becoming slightly and gradually lighter toward apical half; apical half of wing maculate, mostly hyaline with dark brown irregular spots and zigzag and C-shaped bands; vein R_{2+3} sinuous, curved sharply toward costa at apex, bearing a subapical stump vein that is oriented posteriorly, vein R_{2+3} short,

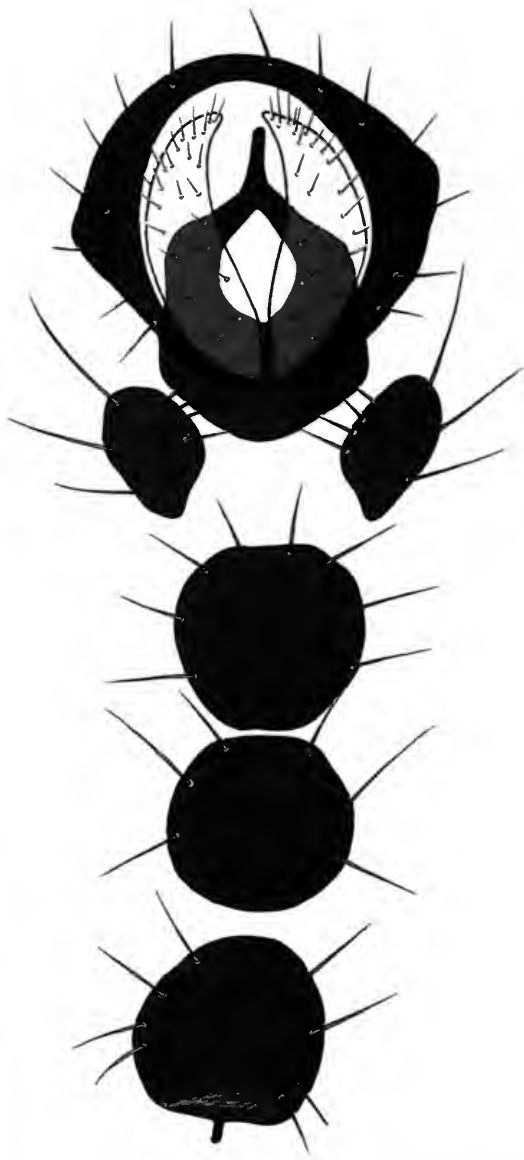


FIG. 4-4. *Beckeriella maculata*. Male terminalia, ventral view, including epandrium, cerci, and sternites 2-5 (5th divided).

making costal section III as long as section II; vein R_{4+5} sinuous; crossvein dm-cu longer than apex of vein CuA_1 apicad of crossvein dm-cu; costal vein ratio 1.15-1.18; M vein ratio 0.55-0.57; alula short and wide, fringing setulae black, longer than alular height; knob of halter blackish brown. Legs with coxae, trochanters, and femora black; tibiae mostly yellow, with dorsal surfaces of mid- and hind tibiae partially dark brown; basal 3 tarsomeres yellow, apical 2 blackish brown; api-

ces of mid- and hind tibiae brown, slightly lighter in color than femora.

Abdomen—Generally black, subshiny to shiny, with some dark blue reflections; generally sparsely gray microtomentose, especially on anterior $\frac{2}{3}$ of tergites, microtomentum becoming denser submarginally along posterior margin of tergites. Male abdomen (Fig. 4-4): sternites 2-4 rounded, bearing setulae along lateral margins; sternite 2 with small anteromedial papilla; 5th sternite subdivided; epandrium in ventral view widest at midheight, angulate laterally at greatest width; cerci in ventral view subelliptical, medial margin sinuous, wider anteriorly; aedeagus (Fig. 4-2e) tubular; aedeagal apodeme (Fig. 4-2e) with long, narrow keel; granite (Fig. 4-2e) with apex recurved, pointed; hypandrium a somewhat rectangular sclerite with anterior margin shallowly rounded. Female abdomen (Fig. 4-5): Tergites generally wide, 2-4 comparatively long, tergites 5-8 short, 4th with 2 narrow patches of microtomentum toward posterior margin on either side of median; sternites 2-4 subquadrate, angles rounded; sternites 5-7 conspicuously wider than long, width of 7th about $\frac{1}{2}$ 5th, 8th sternite subdivided, each sclerite circular; female ventral receptacle (Fig. 4-5) with operculum bell-shaped, higher than wide, extended process J-shaped, as long as height of operculum.

TYPE MATERIAL—The holotype male is labeled "MADAGASCAR: Antsiranana, Marojejy, 11 km NW Manantenina, X.25-XI.3.1996 1,225 m, E. Quinter." The holotype is double mounted (glued to a paper triangle), is in good condition, and is deposited in the American Museum of Natural History (AMNH). Thirteen paratypes bear the same locality label data as the holotype (9 AMNH, 4 United States National Museum [USNM]). All specimens of the type series were collected in pan traps set at the side of a stream.

DISTRIBUTION—Afrotropical: Madagascar (Antsiranana).

ETYMOLOGY—The specific epithet, *maculata*, refers to the dappled or maculate apical half of the wing.

Key to Malagasy Species of *Beckeriella*

1. Wing mostly brown with irregular subapical transverse white band; scutellum rectangular, wider than long, posterior margin broadly truncate; inner vertical seta greatly reduced, length

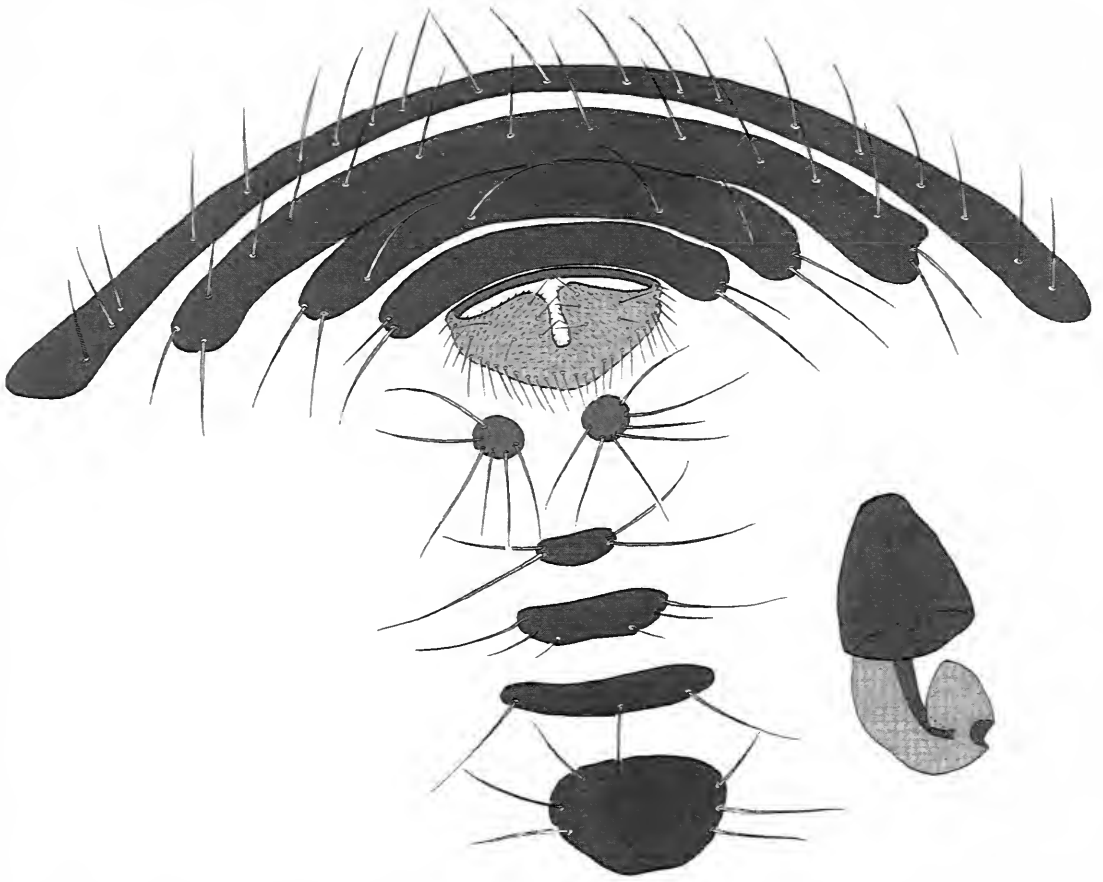


FIG. 4-5. *Beckeriella maculata*. Female terminalia. posterior view, showing apical tergites and sternites, and ventral receptacle. lateral view.

much less than half that of outer vertical seta
 *B. fasciata*, new species

1. Wing with basal half brown and apical half maculate, mostly hyaline with dark brown spots; scutellum trapezoidal, about as long as wide, tapered posteriorly, posterior margin emarginate medially; inner vertical seta well developed, equal in length to fronto-orbital seta *B. maculata*, new species

AMNH. The holotype of *B. fasciata* was loaned to us by the Natal Museum, Pietermaritzburg, South Africa (David A. Barraclough). Sally Goodman made the habitus illustrations and helped with line drawings. For critically reviewing a draft of this paper, we thank Volker Hollmann-Schirmacher and Julian Stark.

Acknowledgments

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Literature Cited

- CRESSON, B. T. JR. 1934. Descriptions of new genera and species of the dipterous family Ephydriidae.—XI. Transactions of the American Entomological Society, **60**: 199–222.
- . 1949. A systematic annotated arrangement of the genera and species of the North American Ephydriidae (Diptera). IV. The Subfamily Napaenae. Transactions of the American Entomological Society, **74**: 225–260.
- CUMMING, J. M., B. J. SINCLAIR, AND D. M. WOOD. 1995.

- Homology and phylogenetic implications of male genitalia in Diptera—Eremoneura. *Entomologica Scandinavica*, **26**: 120–151.
- EVENHUIS, N. L. 1994. Catalogue of the Fossil Flies of the World (Insecta: Diptera). Backhuys Publishers, Leiden, 600 pp.
- GRIFFITHS, G. C. D. 1972. The phylogenetic classification of Diptera Cyclorrhapha with special reference to the structure of the male postabdomen. *Series Entomologica*, **8**: 1–340. W. Junk, The Hague.
- LIZARRALDE DE GROSSO, M. S. 1986. Dos nuevas especies de *Beckeriella* Williston (Diptera Ephydriidae). *Acta Zoologica Lilloana*, **38**(2): 133–137, 14 figs.
- . 1989. Ephydriidae de la Republica Argentina (Insecta—Diptera). Serie Monografica y Didactica No. 3. Facultad de Ciencias Naturales e Instituto Miguel Lillo Universidad Nacional de Tucumán. 93 pp.
- . 1990. Aportes al conocimiento del género *Beckeriella* Williston, I. Descripción de *B. longiventris* sp. nov. y redescipción de *B. bispinosa* (Diptera-Ephydriidae). *Revista de la Sociedad de Entomológica Argentina*, **48**(1–4)1990(89): 143–147.
- . 1991a. Aportes al conocimiento del género *Beckeriella* Williston. II. Descripción de *B. paragipas* sp. nov. y redescipción de *B. schildi*. (Diptera-Ephydriidae). *Acta Zoologica Lilloana*, **40**(1): 39–42.
- . 1991b. Aportes al conocimiento del género *Beckeriella* Williston. III. Descripción de *B. pseudoclypeata*, sp. n. y redescipción de *B. magnicornis* Cresson (Diptera, Ephydriidae). *Revista Brasileira de Entomologia*, **35**(1): 45–48.
- . 1992. Aportes al conocimiento del género *Beckeriella* Williston. IV. Redescipción de *B. pendicornis* y descripción de *B. parapendicornis* sp. n. (Diptera, Ephydriidae). *Revista Brasileira de Entomologia*, **36**(1): 229–233.
- . 1994. Aportes al conocimiento del género *Beckeriella* Williston. Descripción de *B. filipina* sp. nov. (Diptera: Ephydriidae). *Neotropica*, **40**(103–104): 57–59.
- MATHIS, W. N. 1977. Key to the Neotropical genera of Parydrinae with a revision of the genus *Eleleides* Cresson (Diptera: Ephydriidae). *Proceedings of the Biological Society of Washington*, **90**(3): 553–565.
- . 1986. Studies of Psilopinae (Diptera: Ephydriidae), I: A revision of the shore fly genus *Placopsidella* Kertész. *Smithsonian Contributions to Zoology*, **430**: 1–30.
- . 1990. A revision of the shore-fly genus *Diphuia* Cresson (Diptera: Ephydriidae). *Proceedings of the Entomological Society of Washington*, **92**(4): 746–756.
- MATHIS, W. N., AND T. ZATWARNICKI. 1995. A world catalog of the shore flies (Diptera: Ephydriidae). *Memoirs on Entomology, International*, **4**: vi+423 pp.
- MCALPINE, J. F. 1981. Morphology and terminology—Adults, pp. 9–63. *In* McAlpine, J. F., et al., eds., *Manual of Nearctic Diptera*. Ottawa. [Volume 1 is Monograph 27 of Research Branch Agriculture Canada.]
- WILLISTON, S. W. 1897. *Diptera Brasiliana*. Part IV. *Kansas University Quarterly, series A*, **6**: 1–12.
- WIRTH, W. W. 1968. 77. Family Ephydriidae, pp. 1–43. *In* Papavero, N., ed., *A catalogue of the Diptera of the Americas south of the United States*. Departamento de Zoologia, Secretaria de Agricultura, São Paulo.
- ZATWARNICKI, T. 1992. A new classification of Ephydriidae based on phylogenetic reconstruction (Diptera: Cyclorrhapha). *Genus*, **3**(2): 65–119.

Chapter 5

The Tracheline Spider Genus *Paccius* (Araneae, Corinnidae) in the Parc National de Marojejy, Madagascar

Norman I. Platnick¹

Abstract

Five new species of the tracheline spider genus *Paccius* Simon are described from the Parc National de Marojejy, Madagascar, including the first known females of the genus. Males have extraordinarily modified setae on the palpal tibia that may serve to disperse pheromones or a secretion that forms an epigynal plug in mated females. All five species found at Marojejy appear to be endemic to the area as well as altitudinally segregated: *P. angulatus* at 450 m, *P. griswoldi* and *P. scharffi* (belonging to different species groups) at 700–800 m, *P. quinteri* at 1625 m, and *P. elevatus* at 1875 m.

Résumé

Cinq nouvelles espèces d'araignée tracheline genre *Paccius* Simon ont été décrites à partir des spécimens collectés dans le Parc National de Marojejy, Madagascar. Parmi elles se trouvait le premier individu de sexe femelle connu appartenant à ce genre. Chez les mâles, les barbillons du tibia sont extraordinairement modifiés et sont remplacés par des poils raides qui doivent leur servir pour disperser les phéromones ou la sécrétion qui forme le bouchon épigynal des femelles avec lesquelles ils viennent de s'accoupler. Toutes les cinq espèces trouvées à Marojejy paraissent être endémiques de l'aire en question de même qu'elles semblent être réparties selon l'altitude: *P. angulatus* à 450 m, *P. griswoldi* et *P. scharffi* (appartenant à différents groupes d'espèces) à 700–800 m, *P. quinteri* à 1625 m, et *P. elevatus* à 1875 m.

Introduction and Background

The spider genus *Paccius* Simon 1898 is an obscure taxon. The type species was originally described as *Trachelas madagascariensis* by Simon (1889) on the basis of a single male, in poor condition, from an unspecified locality on the island. In his famous *Histoire naturelle des araignées*, Simon originally (1897: 180) retained the species in *Trachelas* L. Koch 1872, a genus that served (then and now) as a "wastebasket" group for relatively unmodified trachelines. In a supplement to

that consideration, however, Simon (1898a, p. 216) indicated that he had recently had the opportunity to study additional specimens, and established the genus *Paccius*, with *T. madagascariensis* as its type. Simon also included two additional species, *P. quadridentatus* from the Seychelles (subsequently described by Simon, 1898b, p. 384) and *P. mucronatus*. Bonnet (1958, p. 3273) considered *P. mucronatus* a nomen nudum, but Simon's (1898a) discussion provides putatively diagnostic information (and even a type locality, "Sainte-Marie de Madagascar"), and the name is unquestionably available.

Simon published no illustrations of any of the three species, however, and the genus has (perhaps therefore) remained in obscurity. Benoit

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(1978) reported on *P. quadridentatus* from the Seychelles, illustrating a male and describing the female, but his specimens are clearly just misidentified members of the widespread, synanthropic corinnid genus *Oedignatha* Thorell 1881. In other words, males of three species of *Paccius* were very briefly described a century ago, females of the genus remain unknown, and no illustrations have appeared in the literature. Through the courtesy of Dr. Christine Rollard of the Muséum National d'Histoire Naturelle (MNHN), Paris, types of all three Simon species have been available for comparison with the material described below.

The absence of modern information on *Paccius* is especially remarkable, for at least two reasons. First, available collections, fragmentary as they are, nevertheless indicate that the genus has radiated extensively on Madagascar; there may be as many as 25 species on the island (as well as others from the Comoro Islands, La Réunion, and Mauritius). All the species seem to be narrowly endemic, so that the genus has great promise as a subject for cladistic biogeography. Second, the male palpal morphology is very unusual. The tibial apophysis bears highly modified setae, one of which is enormously enlarged and elaborated into a scooped-out channel (Figs. 5-1, 5-2). Because the channel appears to open into the interior of the segment, it may be used for dispersing pheromones or the secretions that are used to produce the epigynal plugs frequently found in (presumably mated) females.

Here I describe just those specimens of *Paccius* that have been taken in the Parc National (PN) de Marojejy, Madagascar, where there appear to be at least five species, all of which are new to science and which are in large part altitudinally separated (the only two species that have been taken at the same altitude, *P. griswoldi* and *P. scharffi*, belong to different species groups within the genus). The collections studied include both those of the recent expedition (currently housed in the American Museum of Natural History, AMNH) as well as those made by Dr. J. Coddington and colleagues in 1993 and housed in the National Museum of Natural History, Smithsonian Institution (USNM).

Paccius angulatus, new species (Figures 5-1, 5-2)

TYPE—Male holotype taken in a Malaise trap at 450 m on a tributary of the Manantenina River,

8.0 km NW of Manantenina, in the Parc National de Marojejy, 14°26.2'S, 49°46.5'E, Antsiranana Province, Madagascar (13–24 October 1996; E. Quinter, T. Nguyen), deposited in AMNH.

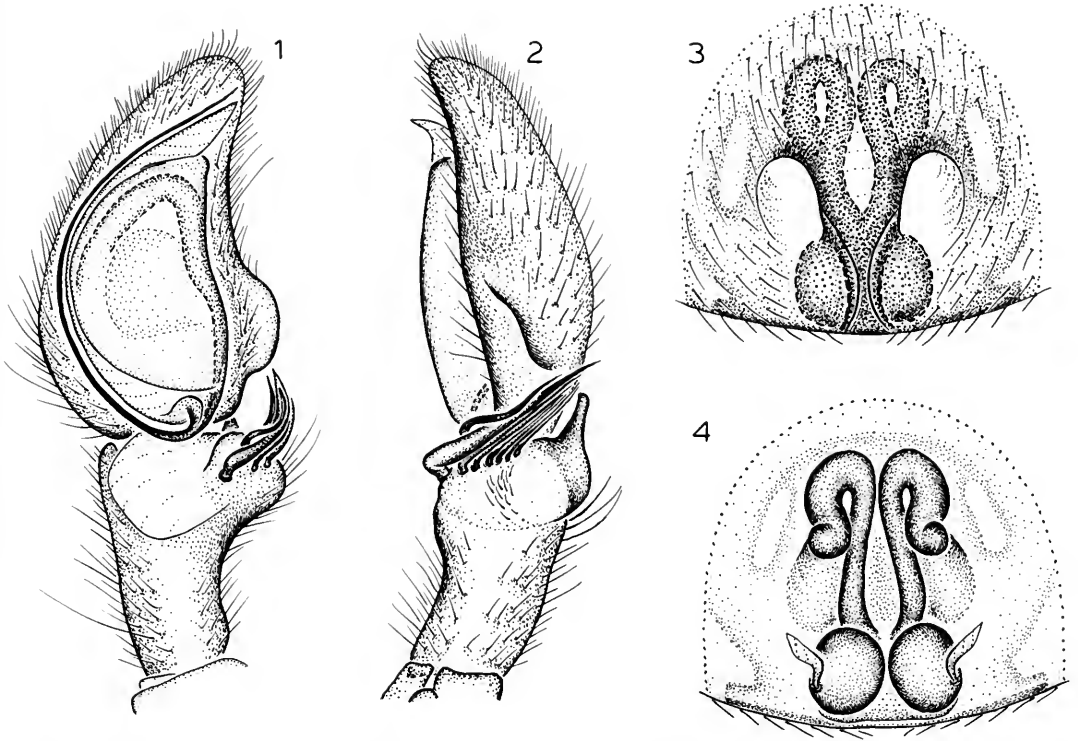
ETYMOLOGY—The species name refers to the shape of the base of the male retrolateral tibial apophysis.

DIAGNOSIS—Males resemble those of *P. madagascariensis* but have a much smaller retrolateral expansion on the cymbium (Fig. 5-1), only one (rather than two) modified tibial seta dorsal of, and overlapping, the large channelized seta (Fig. 5-2), and in having a dorsally expanded base on the tibial apophysis itself (Fig. 5-2).

MALE—Total length, not including chelicerae, 8.6 mm. Carapace dark red, entire surface covered with procurved rows of tubercles. From above, both eye rows almost straight, posterior row wider than anterior; from front, both rows slightly procurved; anterior median eyes largest, posterior medians smallest, lateral subequal; anterior medians separated by less than their diameter, farther from anterior laterals; posterior medians separated by twice their diameter, by three times their diameter from posterior laterals; lateral eyes of each side separated by their diameter; median ocular quadrangle wider than long, wider in back than long. Clypeal height less than anterior median eye diameter; chilum large, triangular, pointed and protuberant medially. Chelicerae dark red, protuberant, with four teeth on each margin; retromargin with lobe-shaped extension at base of fang. Labium and endites dark red; labium narrowed at about one-fourth its length, truncate distally; endites depressed along medial edges but without distinct median grooves. Sternum dark orange, sides granulate, with triangular extensions to and between coxae, not fused with epimeric sclerites, which extend around fourth coxae, separating them from pedicel.

Abdomen long, white, with orange epigastric scutum encircling pedicel and occupying anterior surface of dorsum; large, orange dorsal scutum covering almost all of dorsum anteriorly, all of dorsum posteriorly; venter with four irregular, longitudinal rows of small, orange sclerites. Epigastric scutum with arm-shaped posterolateral extensions extending around booklung openings, which are bordered posteriorly by pair of rectangular, sclerotic strips. Anterior lateral spinnerets two-segmented, approximate, well removed from tracheal spiracle; posterior median spinnerets short, tubular; posterior lateral two-segmented.

Leg formula 1423; leg I orange, other legs yellow.



FIGS. 5-1 to 5-4. 1, 2, *Paccius angulatus*, new species. 3, 4, *P. elevatus*, new species. 1, left male palp, ventral view; 2, same, retrolateral view; 3, epigynum, ventral view; 4, same, dorsal view.

low; spines absent, metatarsi and tarsi I, II scopulate, with two ventral rows of black denticles; metatarsi III, IV with distal preening brushes; two dentate claws accompanied by dense claw tufts; trochanters unnotched.

Palpal tibia distally expanded, ventral portion of expanded area unsclerotized, bearing three enlarged setae; median seta boat-shaped, with interior channel; distal seta sinuous, crossing over into channel of median seta at about half its length; retrolateral tibial apophysis with large, expanded, angular base (Fig. 5-2); cymbium with retrolateral expansion occupying only about one-fifth of cymbial length (Fig. 5-1); embolar base slightly excavated.

FEMALE—Unknown.

OTHER MATERIAL EXAMINED—None.

***Paccius elevatus*, new species**

(Figures 5-3, 5-4)

TYPE—Female holotype taken beating vegetation at 1875 m at the source of the Andranomifototra River, 11.0 km NW of Manantenina, in the

Parc National de Marojejy, 14°26.8'S, 49°44.1'E, Antsiranana Province, Madagascar (13–19 November 1996; E. Quinter), deposited in AMNH.

ETYMOLOGY—The specific name refers to the relatively high altitude at which the species was taken.

DIAGNOSIS—Females can easily be recognized by the large lateral epigynal openings and elevated, longitudinal, median epigynal ridge (Fig. 5-3). MALE—Unknown.

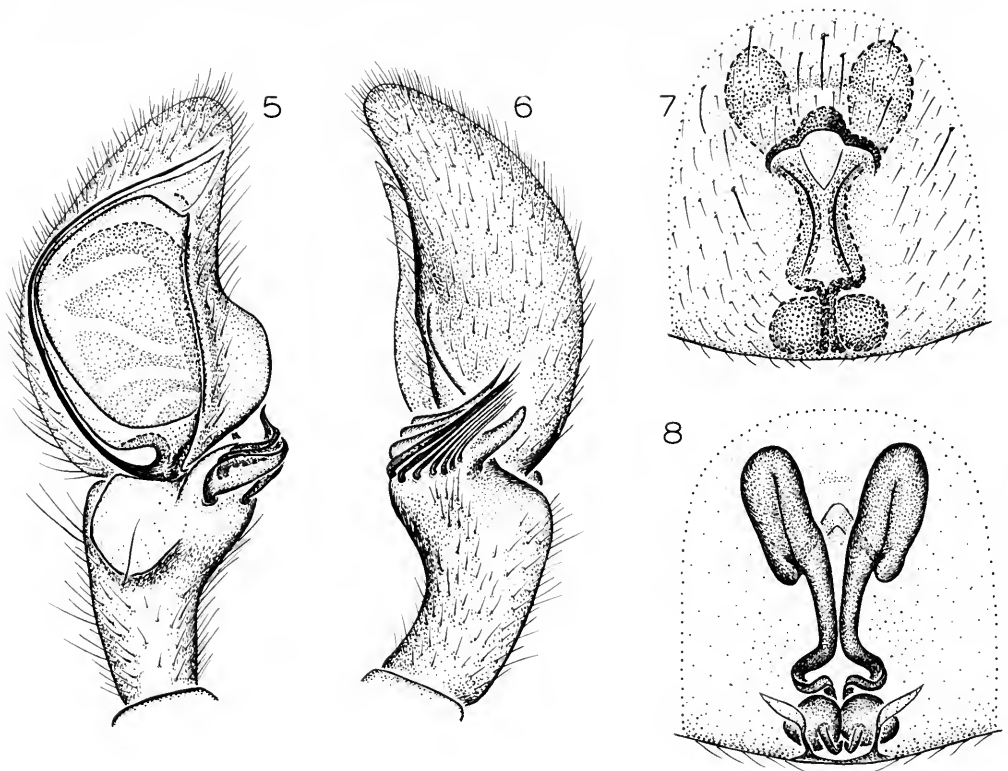
FEMALE—Total length, not including chelicerae, 8.8 mm. As in *P. griswoldi*, except for the following. Cheliceral promargin with four or five teeth. Epigynum with large, lateral openings and elevated, longitudinal median ridge (Fig. 5-3); ducts not curled posteriorly (Fig. 5-4).

OTHER MATERIAL EXAMINED—One female taken with the holotype (AMNH).

***Paccius griswoldi*, new species**

(Figures 5-5 to 5-8)

TYPES—Male holotype and female allotype taken on the forest floor at night at 700–800 m in



FIGS. 5-5 to 5-8. *Paccius griswoldi*, new species. 5, Left male palp, ventral view; 6, same, retrolateral view; 7, epigynum, ventral view; 8, same, dorsal view.

the Parc National de Marojejy, 8.4 km NNW of Manantenina, 14°26'S, 49°45'E, Antsiranana Province, Madagascar (12 November 1993; C. Griswold), deposited in USNM.

ETYMOLOGY—The specific name is a patronym in honor of the collector of the types.

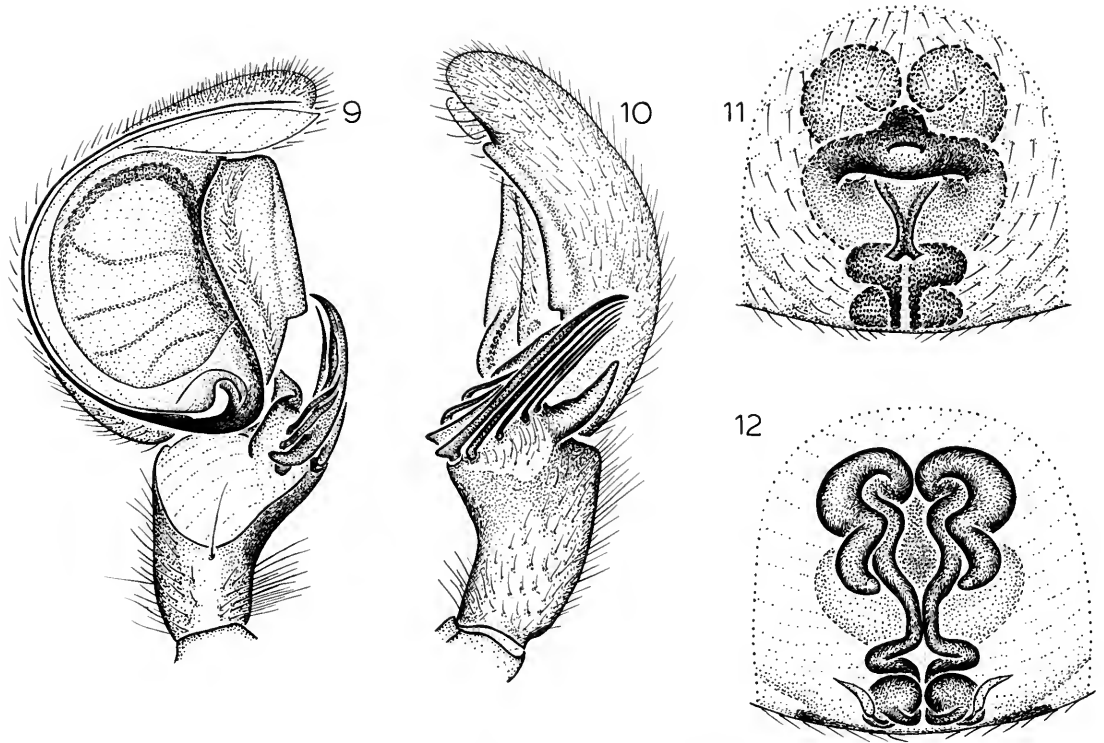
DIAGNOSIS—Males resemble those of *P. madagascariensis* but have a much smaller retrolateral expansion on the cymbium (Fig. 5-5) and have the tip of the tibial apophysis well removed from (rather than touching) the modified setae (Fig. 5-6). Females resemble those of *P. quinteri* in having long, straight median epigynal ducts, but differ in having those ducts curled posteriorly (Fig. 5-8).

MALE—Total length, not including chelicerae, 9.3 mm. As in *P. angulatus*, except for the following. Cheliceral promargin with five teeth. Abdominal venter with longitudinal rows of sclerites completely encased within large, orange ventral scutum. All setae associated with retrolateral tibial apophysis enlarged; median boat-shaped seta crossed by two more distal setae, more proximal setae forming thick white brush well separated

from digitiform tip of tibial apophysis (Fig. 5-6); cymbium with retrolateral expansion occupying only about one-fourth of cymbial length (Fig. 5-5); embolar base distinctly excavated.

FEMALE—As in male *P. angulatus*, except for the following. Total length, not including chelicerae, 10.9 mm. Cheliceral promargin with five teeth. Epigastric scutum restricted to sides and venter; dorsal scutum restricted to small sclerite above pedicel, on anterior surface of abdomen; abdominal dorsum pale gray, with two pairs of darker cardiac spots; venter pale gray, with two longitudinal rows of few dark spots. Posterior median and posterior lateral spinnerets each with two and one cylindrical gland spigots, respectively, but posterior medians shaped as in male. Palpal tibia and tarsus with elongated setae but without spines; tarsal claw long, apparently smooth. Epigynum with small hood and long, depressed atrium (Fig. 5-7); ducts recurved anteriorly, curled posteriorly (Fig. 5-8).

OTHER MATERIAL EXAMINED—MADAGASCAR: Antsiranana: PN de Marojejy, 8.4 km NNW of Manantenina, 14°26'S, 49°45'E, 700–800 m,



FIGS. 5-9 to 5-12. *Paccius scharffi*, new species. 9, Left male palp, ventral view; 10, same, retrolateral view; 11, epigynum, ventral view; 12, same, dorsal view.

11-14 November 1993, beating foliage, on forest floor and foliage at night (C. Griswold, N. Scharff, USNM), 1♂, 4♀; tributary, Manantenina River, PN de Marojejy, 10.0 km NW of Manantenina, 14°26.0'S, 49°45.7'E, 15-22 October 1996, beating vegetation, 750 m (E. Quinter, T. Nguyen, AMNH), 1♀.

***Paccius scharffi*, new species**
(Figures 5-9 to 5-12)

TYPE—Male holotype and female allotype taken on foliage at 700-800 m in the Parc National de Marojejy, 8.4 km NNW of Manantenina, 14°26'S, 49°45'E, Antsiranana Province, Madagascar (12-14 November 1993; N. Scharff, J. Coddington), deposited in USNM.

ETYMOLOGY—The specific name is a patronym in honor of the collector of the holotype.

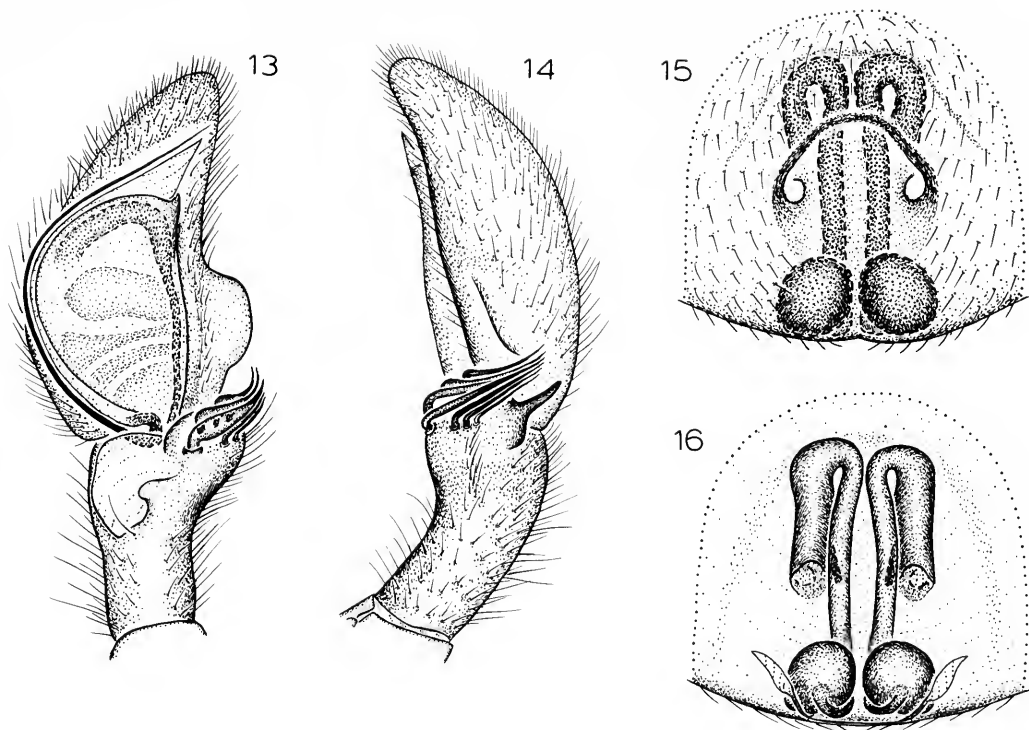
DIAGNOSIS—Males resemble those of *P. mucronatus* in having a relatively large cymbial expansion (Fig. 5-9), but they can be distinguished by the angular proximal corner of the cymbial expansion (Fig. 5-9) and the longer tip of the retro-

lateral tibial apophysis (Fig. 5-10). Females can be recognized by the transverse epigynal hood (Fig. 5-11) and anteriorly expanded epigynal ducts (Fig. 5-12).

MALE—Total length, not including chelicerae, 6.8 mm. As in *P. angulatus*, except for the following. Abdominal venter with longitudinal rows of sclerites completely encased within large, orange ventral scutum. All setae associated with retrolateral tibial apophysis enlarged; median boat-shaped seta crossed by two more distal setae, more proximal setae forming thick white brush, well separated from elongate, granulate tip of tibial apophysis (Fig. 5-10); cymbium with retrolateral expansion occupying over half of cymbial length, situated more distally than in other species (Fig. 5-9); embolar base elongated, excavated.

FEMALE—Total length, not including chelicerae, 6.6 mm. As in *P. griswoldi*, except for the following. Cheliceral promargin with four teeth. Epigynum with small anterior pocket, transverse hood, and wide, deeply depressed atrium (Fig. 5-11); ducts thickened, recurved anteriorly, curled posteriorly (Fig. 5-12).

OTHER MATERIAL EXAMINED—None.



FIGS. 5-13 to 5-16. *Paccius quinteri*, new species. **13**, Left male palp, ventral view; **14**, same, retrolateral view; **15**, epigynum, ventral view; **16**, same, dorsal view.

Paccius quinteri, new species

(Figures 5-13 to 5-16)

TYPES—Male holotype and female allotype taken in a yellow pan trap set at 1625 m along a tributary at head of Andranomifototra River, 10.5 km NW of Manantenina, in the Parc National de Marojejy, 14°26.4'S, 49°44.5'E, Antsiranana Province, Madagascar (6–12 November 1996; E. Quinter), deposited in AMNH.

ETYMOLOGY—The specific name is a patronym in honor of the collector of the types.

DIAGNOSIS—Males resemble those of *P. madagascariensis* but have a much smaller retrolateral expansion on the cymbium (Fig. 5-13) and a sharply narrowed tip of the retrolateral tibial apophysis (Fig. 5-14). Females can be recognized by the small anterolateral epigynal openings (Fig. 5-15) and long straight epigynal ducts (Fig. 5-16).

MALE—Total length, not including chelicerae, 8.0 mm. As in *P. angulatus*, except for the following. Abdominal venter with longitudinal rows of sclerites completely encased within large orange ventral scutum. All setae associated with retrolateral tibial apophysis enlarged; median boat-

shaped seta crossed by two more distal setae, more proximal setae forming thick white brush, well separated from subdistally sharply narrowed tip of tibial apophysis (Fig. 5-14); cymbium with retrolateral expansion occupying about one-fourth of cymbial length (Fig. 5-13); embolar base excavated, recessed behind soft tissue of tibial tip.

FEMALE—Total length, not including chelicerae, 5.3 mm. As in *P. griswoldi*, except for the following. Cheliceral promargin with four teeth. Only two or three denticles on metatarsi I, none on tarsi I or leg II. Epigynum with small anterolateral openings (Fig. 5-15); ducts long, straight, recurved anteriorly, not curled posteriorly (Fig. 5-16).

OTHER MATERIAL EXAMINED—None.

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Literature Cited

- BENOIT, P. L. G. 1978. Contributions à l'étude de la faune terrestre des îles granitiques de l'archipel des Séchelles (Mission P. L. G. Benoit—J. J. Van Mol 1972). Clubionidae, Ctenidae et Pisauridae (Araneae). *Revue de Zoologie Africaine*, **92**: 940–946.
- BONNET, P. 1958. *Bibliographia Araneorum*, tome II. Douladoure, Toulouse, pp. 3027–4230.
- SIMON, E. 1889. Descriptions d'espèces et de genres nouveaux de Madagascar et de Mayott. *Annales de la Société Entomologique de France*, série 6, **8**: 223–236.
- . 1897. *Histoire Naturelle des Araignées*, tome 2. Roret, Paris, pp. 1–192.
- . 1898a. *Histoire Naturelle des Araignées*, tome 2. Roret, Paris, pp. 193–380.
- . 1898b. Arachnides recueillis en 1895 par M. le Dr A. Brauer (de l'Université de Marburg) aux îles Séchelles. *Annales de la Société Entomologique de France*, **66**: 370–388.

Chapter 6

Fruit Flies as Ecological Indicators: Species Diversity and Abundance of Drosophilidae (Diptera) Along an Altitudinal Transect in the Parc National de Marojejy, Madagascar

David A. Grimaldi,¹ Eric L. Quinter,¹ and Tam Nguyen¹

Abstract

Fifty-eight species of drosophilid flies were collected along an altitudinal transect ranging from 450 m to 1875 m in the Parc National de Marojejy, northeastern Madagascar. Over a 6-week period flies were collected at five stations (450, 750, 1225, 1625, and 1875 m) along the altitudinal transect by means of Malaise traps, yellow pan traps, fruit-baited traps, and sweeping. At least 70% of the species collected by each method were obtained exclusively by that method, indicating that any one method will yield only a small fraction of the total fauna of drosophilids. Greatest species diversity occurred between (and including) 750 m and 1625 m; the proportion of species found at only one of the five stations was also highest between (and including) 750 m and 1625 m. Thirty-six (62%) of the species were represented by five or fewer specimens, which can seriously complicate analyses of relative abundance. However, the faunal composition dramatically reflected altitude, with an average of 50% species replacement between adjacent stations. Given the speciose nature of drosophilids (3,200 world species), their ecological diversity, their abundance, and the abundance of cosmopolitan tramp species in disturbed habitats, this is an extremely useful group to use in the rapid assessment of ecological conditions and habitat differences.

Résumé

Cinquante-huit espèces de mouches drosophiles ont été collectées le long d'un transect altitudinal allant de 450 m à 1875 m dans le Parc National de Marojejy, dans le Nord-Est de Madagascar. Les mouches ont été collectées dans cinq stations (450, 750, 1225, 1625, et 1875 m) pendant six semaines, le long d'un transect altitudinal, en utilisant des trappes "Malaise," des "yellow pan traps," des pièges appâtés avec des fruits et des balayures. 70% et plus des espèces collectées à partir de chaque technique n'étaient pas capturés par les autres systèmes de piégeage, ce qui indique que n'importe laquelle de ces méthodes contribuera à l'inventaire d'une petite partie du total des drosophiles recensés. La plus haute diversité d'espèces était trouvée entre 750 et 1625 m. Trente-six (62%) des espèces sont représentés par cinq spécimens ou moins ce qui complique sérieusement les analyses au niveau de l'abondance relative. Cependant, la composition faunistique reflète dramatiquement l'altitude, avec une moyenne de 50% de remplacement d'espèces entre des stations adjacentes. Les drosophiles, avec une diversité spécifique assez élevée (3,200 espèces mondiales), une diversité écologique et une

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abondance importantes ainsi qu'une abondance d'espèces vagabondes cosmopolites dans les habitats perturbés, constituent un groupe extrêmement utile pour un inventaire rapide des conditions écologiques et des différences pouvant exister entre les habitats.

Introduction

The family Drosophilidae is renowned largely on the basis of a species that is one of the three most intensively studied laboratory eukaryotes: *Drosophila melanogaster* Meigen. As of 1986, 2,822 species had been described for the family (Wheeler, 1981, 1986), and several hundred more have been described since then. Species diversity is overwhelmingly circumtropical, and hundreds of species have yet to be formally described and even discovered. Largely because of the frugivorous habits of many species in *Drosophila*, for which the family is best known, the actual ecological diversity in the family is rarely appreciated. Indeed, the drosophilids are among the most ecologically diverse of all families of Diptera (reviewed by Ashburner, 1981). Species and entire lineages exist that also breed: in fungi, including dangerously toxic mushrooms (Jaenike et al., 1983); as miners of stems and leaves; in living flowers (Brcic, 1983); in the nephric exudates of land crabs (Carson, 1974); as probable parasites of spittle bug nymphs (Grimaldi & Nguyen, 1999); as inquilines in bee nests (Juillard, 1947, 1948); and as larval predators of black fly and chironomid larvae and eggs (Tsacas & Disney, 1974), sessile homopterans (such as scale insects and "white flies") (Grimaldi, 1988), spider eggs (Swezey, 1929), and even the embryos of centrolenellid glass frogs (Grimaldi, 1994). Given such species diversity and disparate ecology, Drosophilidae would presumably have been used routinely for habitat assessment, but they have not, perhaps because of the taxonomic skills required for separating and identifying tropical species.

In October and November 1996, a team of biologists funded by the World Wide Fund for Nature and the American Museum of Natural History (AMNH) explored the biodiversity of the Parc National (PN) de Marojejy, with the aim of determining biotic composition along an altitudinal transect close to the highest summit in the reserve. Besides various vertebrates and plants, invertebrates studied included arthropods such as spiders and various kinds of flies (see other chapters in this volume). Faunistic treatment of Afro-tropical drosophilids is quite advanced, based for-

unately on the excellent descriptive taxonomy of Tsacas, Chassagnard, and co-workers (i.e., Chassagnard et al., 1997; Tsacas, 1990; Tsacas & Lachaise, 1979; Tsacas et al., 1988). The drosophilid fauna of Madagascar, however, is poorly known, with only 37 species having been recorded as of 1981, of which 10 were known only from that island (Tsacas et al., 1981). According to these authors, 15 of the Malagasy species were shared with mainland Africa, 8 with the Mascarene Islands, and 5 with the Comoro Islands. Since the publication of the Tsacas et al. 1981 review, several expeditions by the Laboratoire de Biologie et Génétique Evolutives of the Centre National de la Recherche Scientifique (CNRS) and the Muséum National d'Histoire Naturelle (Paris) have been conducted specifically to survey the Malagasy drosophilids. Publication of the results of those surveys is in progress (e.g., Chassagnard & McEvey, 1992). Given that the much smaller and more distant Mascarene Islands harbor 39 known species, it would be reasonable to expect Madagascar to have a fauna of 200 or more species. Although the focus of our particular study is ecological assessment, the results and specimens resulting from this survey contribute to larger, long-term systematic studies of the unique drosophilid fauna of Madagascar.

Materials and Methods

Collection methods involved Malaise traps, yellow pan traps, fruit-baited *Drosophila* traps, and sweep netting. For ideal or maximal comparisons between collection sites, it is critical that the collection techniques used be standardized as closely as possible ("constant-effort trapping"; Southwood, 1980). However, as thoroughly discussed by Southwood (1980), this is rarely achievable. Even the most seemingly constant-effort methods, such as Malaise traps and yellow pan traps, differ in their effectiveness, depending on variations in the microhabitats in which they are placed. The effectiveness of fruit baiting varies with microhabitat location and with the type, age, and quantity of the bait. Nonetheless, all methods com-

bined give a reasonable approximation of proportional differences in species abundance.

The Malaise traps were made from white "no-see-um" netting, approximately 2×3 m in size, and were customized for compact storage by use of a "head" made of the netting, from which was suspended a Whirl-pak bag of 80% ethanol (this head obviates the use of larger, heavier plastic or glass collecting heads). The netting head was sprayed with a contact insecticide; when insects that were funneled into the head touched the netting, they dropped into the bag of alcohol below. Malaise traps are a passive collection device that intercept flying insects, particularly Diptera and Hymenoptera (Southwood, 1980). Their effectiveness is greatest at the edge of a forest, particularly on a steep hill opposite or close to the canopy. One or two Malaise traps were used at each station and were left in place for the duration of the survey. Each bag was emptied of its contents just before we ascended to the next camp and on the return trip to the base of the mountain.

Yellow pan traps are routinely used for collecting parasitoid Hymenoptera (Southwood, 1980) and are often used for some families of Diptera, such as Empididae and Dolichopodidae. They have never been used for collecting Drosophilidae, but they proved to be very useful here. Bright yellow plastic bowls filled with soapy water were placed in clusters of three at numerous favorable sites (near streams, in mossy vegetated spots) within each station or camp. These were emptied every other day and the contents transferred to alcohol. Yellow pan traps are an active collection device, in that the yellow color appears to attract certain insects, which then become caught in the fluid.

Fruit-baited traps were based on a design first developed by Grimaldi (1985) and used to study seasonal changes in population densities of *Drosophila*. The traps are made of two plastic, bowl-like containers screwed together at the mouths. The bottom container has holes in it for the flies to enter; the interior of the bottom container is painted black, to facilitate the flies' movement to the upper container (drosophilids are phototactic). The upper container has a fine-screened funnel in it, and the mashed and yeasted bait is applied to the sides of the container. Flies attracted to the bait and the light cannot escape through the small hole at the end of the mesh funnel. This device actively collects large numbers of fruit-breeding species, which are attracted to the aromatics produced by fermentation. Yeasted, mashed oranges

and/or bananas were used for bait, and the traps were hung in shaded locations and emptied periodically.

Sweep nets were successful only at the first two stations because the terrain and understory vegetation at the higher sites prevented use of this technique. It is a very effective method for collecting drosophilid species not normally bait-trapped, such as species that congregate on rotting wood or in leaf litter.

Collection Sites

Collection sites were in areas surrounding each camp. E. L. Quinter and T. Nguyen did the fieldwork at the 450 and 750 m stations; Quinter continued the fieldwork alone at the higher stations. Floristic details of each station are provided in Chapters 1 and 3 of this volume and are only summarized here. Representative habitats at stations 2–5 are shown in Figs. 6-1 to 6-4.

STATION 1—Elevation approximately 450 m, location approximately 8 km NW of Manantenina (GPS coordinates $14^{\circ}26.2'S$, $49^{\circ}46.5'E$). Surveys conducted 5–13 October. The station was established at the edge of a tributary of the Manantenina River, surrounded on all sides by mountains covered with dense tropical vegetation, some of which consisted of adventitious species indicative of former human occupation, mixed with the original indigenous rain forest flora.

STATION 2—Elevation approximately 750 m, location approximately 10 km NW of Manantenina (GPS coordinates $14^{\circ}26.0'S$, $49^{\circ}45.7'E$). Surveys conducted 15–22 October. The station was situated along a different tributary of the Manantenina River, again surrounded by rugged, mountainous terrain, this time featuring sheer rock faces as well as open areas in dense forest (Fig. 6-1) created by wet, moss-covered rock slides.

STATION 3—Elevation approximately 1225 m, location approximately 11 km NW of Manantenina (GPS coordinates $14^{\circ}26.2'S$, $49^{\circ}44.5'E$). Surveys conducted 25 October–3 November. The station was located on a ridge surrounded by higher ridges and peaks. Vegetation was considerably different from that of the two previous sites, the most conspicuous difference being the presence of many scrubby trees luxuriantly encrusted with lichens, especially trees along the ridgetops (Fig. 6-2).

STATION 4—Elevation approximately 1625 m, location approximately 10.5 km NW of Manan-



FIG. 6-1. Habitat at 750 m station. (Photograph by Eleanor Sterling.)

tenina (GPS coordinates $14^{\circ}26.4'S$, $49^{\circ}44.5'E$). Surveys conducted 6–12 November. The camp was located in a swale between two ridges, along a tributary at the head of the Andranomifototra River. Vegetation at this site was similar to that at the 1225 m station (Fig. 6-3).

STATION 5—Elevation approximately 1875 m, approximately 11 km NW of Manantenina (GPS coordinates $14^{\circ}26.8'S$, $49^{\circ}44.1'E$). Surveys were conducted 13–19 November. This station was above timberline but approximately 250 m below the summit of Marojejy. The camp itself was situated on a grass- and shrub-covered slope devoid

of all but a few shrubby trees encrusted with lichens (Fig. 6-4). The terrain was granitic, carpeted by a very thick, spongy mat of moss, lichens, and ericaceous shrubs, with very little soil. Even the bamboos were dwarfed in size, being at most 2–3 m high. The summit was windy, rocky, and barren.

Specimen Handling

Drosophilid specimens were stored in vials of 70% ethanol and were prepared at the AMNH.



FIG. 6-2. Habitat (left) at 1225 m station, and Malaise trap in situ. (Photographs by Eleanor Sterling.)

They were critical point-dried and then mounted onto pinned paper points (a standard procedure for acalyptate fly specimens); then they were sorted carefully by genus and species on the basis of external features of males and females. No dissections were made; these will be done later, for systematic reports in which more accurate species identifications are required and new species will be described. It is traditional in drosophilid systematics to base species definitions on males only; as a result, female specimens are often ignored. This approach does stabilize nomenclature, since species are usually more easily separated on the basis of males. However, as a result of this, a plethora of female characters (e.g., Grimaldi, 1990; Grimaldi & Nguyen, 1999) have been ignored. External features of colors and patterns, wing vein ratios, number and position of arisal branches, and other features often allow a reliable association of males and females. We used the classification of drosophilid genera presented by Grimaldi (1990), in particular the placement of *Scaptodrosophila* and *Hirtodrosophila* as separate genera, not subgenera within *Drosophila*.

Results

Table 6-1 presents the data on numbers of individual flies of each sex collected at each station and by each technique. They are identified as sp. 1, sp. 2, and so on, within each genus. The three *Zaprionus* species, however, represent identifiable, described species as based on revisions of this genus by Tsacas and Chassagnard (1990), Chassagnard and McEvey (1992), Chassagnard and Tsacas (1993), and other works by these authors. Tables 6-2 and 6-3 summarize the species diversity among sites and among trapping methods, respectively. Table 6-4 is a summary of the number of species shared among the five altitudinal stations.

Fifty-eight species of Madagascar Drosophilidae were collected (Table 6-1), based on 723 identified specimens, which is approximately 15 more species than had been recorded from the island thus far. This is also 25 more species than were collected in a geographical transect across Kenya by means of bait traps (Escher et al., 1997). Nevertheless, the sampling for our survey was still



FIG. 6-3. Malaise trap situated near 1625 m station, and in situ *Drosophila* bait trap. (Photographs by Eleanor Sterling.)



FIG. 6-4. In situ Malaise trap near 1875 m station. (Photograph by Eleanor Sterling.)

incomplete, as illustrated by the lack of specimens for 12 genera—represented by some 60 described species in the African Region—that are either recorded or suspected to be in Madagascar: *Amiota*, *Apenthecia*, *Cacoxenus*, *Erima*, *Gitona*, *Hirtodrosophila*, *Paraleucophenga*, *Dettopsomyia*, *Jennealopsis*, *Lissocephala*, *Luzonimyia*, and *Zygothrica*. Some of these are restricted to specific hosts, such as fleshy fungi (*Hirtodrosophila* and *Zygothrica*) and decaying tree trunks (*Amiota*, *Erima*, and *Gitona*). Some of these genera may be restricted to the African mainland, such as *Jennealopsis* and *Apenthecia*, the latter closely associated with *Aloe* and similar plants (Chassag-

nard et al., 1997). Unless one systematically swept over blooms of fungi and up and down the trunks of trees, large components of the fauna would be (and apparently have been) missed. Less explainable, however, is the absence from our collections of *Lissocephala*, the virtual absence of *Leucophenga*, and poor species representation of *Zaprionus*, which are speciose genera in the Afrotropics. There are approximately 10 species of *Leucophenga* in Madagascar alone and 60 species from the mainland; they are presumably associated with, but almost certainly not restricted to, fungi. *Lissocephala* has 17 Afrotropical species, although none are apparently recorded from Mad-

TABLE 6-1. Numbers of Drosophilidae Specimens Collected Along Altitudinal Transect by All Collection Methods.

Taxon	No. and sex of flies (method of capture) in each altitudinal zone						Total
	450 m	750 m	1225 m	1625 m	1850 m		
<i>nr. Calodrosophila</i>	0	0	0	4 ♂ (yp)	0	4 ♂	
<i>Chynomyza</i>							
sp. 1	0	2 ♂ (1 bt, 1 mt)	0	0	0	2 ♂	
sp. 2	0	1 ♀ (mt)	0	0	0	1 ♀	
<i>Dichaetophora</i>							
sp. 1	0	1 ♂, 2 ♀ (yp)	9 ♂, 4 ♀ (yp)	8 ♂, 4 ♀ (yp)	0	18 ♂, 10 ♀	
sp. 2	0	0	1 ♂, 1 ♀ (yp)	1 ♀ (yp)	0	1 ♂, 2 ♀	
sp. 3	0	0	0	1 ♀ (yp)	0	1 ♀	
sp. 4	0	1 ♀ (yp)	1 ♀ (yp)	0	0	2 ♀	
sp. 5	0	0	1 ♂, 1 ♀ (yp)	2 ♂, 1 ♀ (yp)	0	3 ♂, 2 ♀	
<i>Drosophila (Drosophila)</i>							
sp. 1	0	0	1 ♂ (yp)	11 ♂, 11 ♀ (yp)	4 ♀ (yp)	12 ♂, 15 ♀	
sp. 2	0	0	1 ♂, 1 ♀ (yp)	1 ♀ (yp)	0	1 ♂, 2 ♀	
sp. 3	5 ♂, 5 ♀ (bt)	9 ♂, 7 ♀ (bt)	3 ♂, 2 ♀ (bt)	0	0	17 ♂, 14 ♀	
sp. 4	0	0	1 ♂, 2 ♀ (bt)	4 ♀ (bt)	8 ♂, 16 ♀ (bt)	9 ♂, 22 ♀	
sp. 5	0	0	1 ♂, 1 ♀ (bt)	9 ♂, 16 ♀ (bt)	20 ♂, 10 ♀ (bt)	30 ♂, 27 ♀	
sp. 6	0	1 ♂, 1 ♀ (mt)	0	0	0	1 ♂, 1 ♀	
sp. 7	0	0	0	1 ♀ (mt)	0	1 ♀	
sp. 8	0	0	0	0	1 ♀ (bt)	1 ♀	
sp. 9	0	0	1 ♂ (bt)	0	0	1 ♂	
sp. 10	0	1 ♀ (bt)	2 ♀ (bt)	0	0	3 ♀	
sp. 11	0	0	0	0	1 ♀ (bt)	1 ♀	
<i>Drosophila (Sophophora)</i>	8 ♂, 11 ♀ (bt)	0	0	0	0	8 ♂, 11 ♀	
sp. 12							
<i>montium</i> grp. sp. 13	9 ♂, 8 ♀ (bt)	7 ♂, 1 ♀ (bt)	1 ♂ (bt)	0	0	17 ♂, 9 ♀	
<i>melanogaster</i> grp.							
sp. 14	1 ♂ (bt)	2 ♂, 1 ♀ (bt)	32 ♂, 10 ♀ (bt)	11 ♂, 10 ♀ (bt)	4 ♂, 4 ♀ (bt)	50 ♂, 25 ♀	
sp. 15	0	6 ♂, 13 ♀ (bt)	1 ♂, 1 ♀ (bt)	0	0	7 ♂, 14 ♀	
sp. 16	39 ♂, 18 ♀ (bt)	37 ♂, 17 ♀ (bt)	8 ♂, 5 ♀ (bt)	0	0	84 ♂, 40 ♀	
sp. 17	0	4 ♂, 1 ♀ (bt)	0	0	0	4 ♂, 1 ♀	
<i>Leucophenga</i> sp.	1 ♀ (mt)	0	0	0	0	1 ♀	
<i>Liodesophila</i>							
sp. 1	0	0	0	1 ♂, 2 ♀ (yp)	0	1 ♂, 2 ♀	
sp. 2	1 ♂, 1 ♀ (bt)	0	0	0	0	1 ♂, 1 ♀	
sp. 3	1 ♀ (m)	1 ♀ (yp)	0	0	0	2 ♀	
sp. 4	0	0	0	1 ♀ (yp)	2 ♂ (yp)	2 ♂, 1 ♀	
sp. 5	0	0	0	1 ♂, 1 ♀ (yp)	0	1 ♂, 1 ♀	

TABLE 6-1. Continued.

Taxon	No. and sex of flies (method of capture) in each altitudinal zone					Total
	450 m	750 m	1225 m	1625 m	1850 m	
<i>Microdrosophila</i>						
sp. 1	1 ♂, 2 ♀ (mt)	18 ♂, 13 ♀ (3yp, 28mt)	0	0	0	19 ♂, 15 ♀
sp. 2	1 ♂ (mt)	2 ♂, 10 ♀ (5yp, 7mt)	2 ♂, 2 ♀ (yp)	2 ♀ (yp)	0	5 ♂, 14 ♀
sp. 3	0	3 ♂ (2mt, 1yp)	0	0	0	3 ♂
sp. 4	0	1 ♂ (mt)	0	0	0	1 ♂
<i>Mycodrosophila</i>						
sp. 1	0	2 ♂ (mt)	0	0	0	2 ♂
sp. 2	1 ♀ (n)	0	0	0	0	1 ♀
<i>Neotanygastrella</i> sp.	0	2 ♂, 3 ♀ (4mt, 1bt)	0	0	0	2 ♂, 3 ♀
<i>Paraleucopenga</i> sp.	0	0	0	1 ♂ (yp)	0	1 ♂
<i>Scaptodrosophila</i>						
sp. 1	0	0	0	1 ♀ (mt)	1 ♀ (mt)	2 ♀
sp. 2	0	1 ♂, 1 ♀ (mt)	0	0	0	1 ♂, 1 ♀
sp. 3	0	0	0	1 ♂ (mt)	0	1 ♂
sp. 4	6 ♂, 6 ♀ (n)	0	0	0	0	6 ♂, 6 ♀
sp. 5	4 ♂, 2 ♀ (n)	0	1 ♂, 1 ♀ (n)	0	0	5 ♂, 3 ♀
sp. 6	5 ♂ (n)	0	0	0	0	5 ♂
sp. 7	0	0	1 ♀ (yp)	4 ♂, 2 ♀ (yp)	0	4 ♂, 3 ♀
sp. 8	0	2 ♂ (yp)	1 ♂, 1 ♀ (yp)	0	0	3 ♂, 1 ♀
sp. 9	0	0	0	0	0	1 ♂, 3 ♀
sp. 10	0	8 ♀ (bt)	14 ♂, 36 ♀ (bt)	1 ♂, 3 ♀ (yp)	0	17 ♂, 45 ♀
sp. 11	3 ♂, 2 ♀ (n)	5 ♂ (yp)	1 ♂, 3 ♀ (yp)	1 ♂ (bt)	2 ♂, 1 ♀ (bt)	9 ♂, 5 ♀
sp. 12	0	0	0	3 ♂, 5 ♀ (bt)	0	3 ♂, 5 ♀
sp. 13	1 ♂ (n)	0	0	0	0	1 ♂
sp. 14	0	0	0	1 ♀ (bt)	1 ♀ (bt)	2 ♀
sp. 15	0	0	0	0	1 ♂, 1 ♀ (bt)	1 ♂, 1 ♀
<i>Scaptomyza</i> sp.	0	0	0	1 ♂, 3 ♀ (mt)	0	1 ♂, 3 ♀
<i>Siegana</i> sp.	0	1 ♀ (mt)	0	0	0	1 ♀
<i>Zaprionus</i>						
sp. 1	0	2 ♂, 14 ♀ (bt)	12 ♂, 6 ♀ (bt)	0	0	14 ♂, 20 ♀
sp. 2	1 ♀	6 ♂, 2 ♀ (bt)	1 ♂, 1 ♀ (bt)	0	0	7 ♂, 4 ♀
sp. 3	0	0	5 ♂, 3 ♀ (bt)	1 ♂, 1 ♀ (bt)	0	6 ♂, 4 ♀

NOTE: yp = yellow pan trap; bt = bait trap; mt = Malaise trap; n = net.

TABLE 6-2. Species Diversity Along Altitudinal Transect.

Variable	No. of species at altitude					
	450 m	750 m	1225 m	1625 m	1875 m	
No. of species	17	25	24	25	11	
No. of exclusive species	4	8	1	10	3	
Coefficient of Similarity*						
C_j	0.31		0.40	0.32	0.28	
C_s	0.47		0.32	0.31	0.43	

* C_j = Jaccard's coefficient; C_s = modified Sørensen's coefficient.

agascar; this genus breeds extensively in figs (*Ficus*) (Lachaise, 1977; Lachaise & Tsacas, 1983).

Zaprionus has been the subject of revisionary studies and currently consists of 53 species, with 14 species alone known from Madagascar (Chassagnard & McEvey, 1992; Chassagnard & Tsacas, 1993). They are large, conspicuously colored flies often abundant on decaying fruits, but only three species were collected in bait traps in our study: *Zaprionus kolodkinae* Chassagnard and Tsacas, 1987 (*Zaprionus* sp. 1 in Table 6-1); *Z. mascariensis* Tsacas and David, 1975 (*Zaprionus* sp. 2); and *Z. spinipilus* Chassagnard and McEvey, 1992 (*Zaprionus* sp. 3). *Zaprionus kolodkinae* is endemic to Madagascar (throughout the country); *Z. mascariensis* occurs on Madagascar, the Comores, Mauritius, and Réunion islands; and *Z. spinipilus* is known from Madagascar and the African mainland (Cameroon and Malawi).

In contrast to the several aspects of incomplete sampling in this study are several genera for which our sampling is apparently better than would be expected on the basis of the 1981 review by Tsacas et al. For example, two species of *Chymomyza* were found, where none were known to exist from Madagascar; five *Dichaetophora* species were collected, with only one previously reported; 15 *Scaptodrosophila* species were collected, with only three recorded from Madagascar previously; four to five *Liodyrosophila* (generic identity of the fifth awaits confirmation), where only three were known; and four *Microdrosophila*

were found where only one was previously recorded.

An unexpected result was the success of yellow pan traps, which collected 108 specimens belonging to 19 species; three-fourths of these species were collected only in this manner. Groups collected predominantly by yellow pan traps were *Dichaetophora*, *Liodyrosophila*, a species in or near the genus *Calodyrosophila*, and several species of *Drosophila* s.s. (spp. 1, 2) and *Scaptodrosophila* (spp. 7, 8, 9, 11). The capture by Malaise traps is as expected on the basis of previous experiences in the Neotropics, with a respectable species diversity based on relatively small samples. Fifteen species were collected with Malaise traps, based on just 64 specimens. Groups collected predominantly with Malaise traps were *Chymomyza* and *Neotanygastrella* (they have similar habits), several species of *Scaptodrosophila* (sp. 1-3), the only species of *Scaptomyza* found, and the four species of *Microdrosophila*. Approximately three-fourths of the species found in Malaise traps were collected only in this manner. The number of specimens collected by hand netting is meager (only 28) and reflects the inexperience of the collectors; experienced collectors of drosophilids usually acquire their most diverse samples this way, relying on knowledge of breeding sites. Interestingly, seven species were collected by hand netting, five of which were acquired only in this manner. Also expected is the abundance of specimens collected with bait traps: 523 identified

TABLE 6-3. Drosophilid Diversity by Collection Method.

Variable	No. collected by means of			
	Fruit bait traps	Malaise traps	Yellow pan traps	Netting
Total no. of species	23	15	19	7
No. (%) exclusive	19 (82)	11 (73)	15 (78)	5 (71)
No. of specimens	523	64	108	28

TABLE 6-4. Drosophilid Species Shared by Altitude.

Altitude	No. of shared species by altitude				
	450 m	750 m	1225 m	1625 m	1875 m
450 m	17	16	8	2	1
750 m	—	25	14	4	2
1225 m	—	—	24	12	5
1625 m	—	—	—	25	8
1875 m	—	—	—	—	11

specimens in 23 species, the highest diversity of the four methods used. Since fruit-breeding species tend to be abundant and ubiquitous, it is interesting that 82% of the species found at fruit baits were collected only in this way. Clearly, relying on just one collection technique would give a very incomplete sample of the fauna.

Species number did not vary significantly among stations, the greatest difference being 11 species at 1875 m, with 17–25 species at the lower stations. Species composition, however, varied dramatically. As shown in Table 6-2, the number of species unique to a particular station was highest at 750 and 1625 m (eight and ten, respectively; the 1225 m station was apparently anomalous, with only one species unique to it). Two coefficients of similarity were used to quantify similarities in species compositions: Jaccard's coefficient and a modified Sørensen's coefficient (Southwood, 1980). Jaccard's coefficient is defined as

$$C_j = j/(a + b) - j,$$

where j is number of species common to two stations and a and b are the total number of species at each station. Unfortunately, this coefficient gives equal weight to all species regardless of abundance and rarity, and rare species can greatly skew indices of similarity, since they are often intercepted by chance. This is a particularly important consideration here, since 36 (62%) of the drosophilid species were represented by five or fewer specimens. Although a coefficient in which similarity is weighted by the relative abundance of shared species is preferable, it too is biased by the sampling techniques used (an "active" method such as bait trapping gives a yield that is disproportionately high compared with, say, Malaise trapping). The modified Sørensen coefficient takes relative abundance into account:

$$C_N = 2j_N/(aN + bN),$$

where aN and bN are the total numbers of individuals sampled in habitats a and b , and jN is the

sum of lesser values for species common to both stations. As shown in Table 6-2, differences among stations for the two indices is minor, the most substantial difference being that the Jaccard coefficient ranks the similarity between stations 2 and 3 as relatively high and the modified Sørensen coefficient ranks the similarity between these two stations as relatively low. This is probably because each of these stations has 12 species that are represented by five or fewer specimens.

Table 6-4 reveals that, as expected, adjacent stations have the most species in common. *As one goes to the next higher station, approximately half the number of species, or fewer, remain in common.* None of the stations can be identified as more faunally distinct than another; they all show a progressive and accumulated transformation of the drosophilid fauna along the altitudinal transect and are clearly distinct from the lowlands (<450 m) fauna. Since moisture, cold tolerance, and plant hosts are all known to influence drosophilids, all of these factors probably affect species diversity and abundance of these flies.

An interesting observation is the absence of cosmopolitan "tramp" drosophilid species in the samples. This result stands in contrast to the finding of cosmopolitan tramp noctuid moth species, present at all stations (E. L. Quinter, pers. observ.) but most abundant at the highest stations, where the level of endemism of the native noctuids is also highest. This may reflect a greater vagility of noctuids, combined with hilltopping behavior. Species recognized for their ability to colonize and thrive in areas highly disturbed by humans are *Drosophila melanogaster*, *D. simulans* (these two are native to central Africa), *D. hydei* (native to the New World), *D. immigrans* (native to Asia), *D. funebris* (native to Europe), *D. busckii* (native to Asia), and most recently *D. malerkotliana* (native to Asia). These and other anthrophilic species are highly tolerant of cool temperatures, desiccation, and high concentrations of ethanol (a product of fermentation in breeding sites), accept a range

of hosts in which to breed, and have excellent dispersal ability and reproductive capacity (Parsons & Stanley, 1981). Although some of our bait-trapped species were abundant enough to be considered tramps (e.g., *D. melanogaster* grp. spp. 14 and 16), a lack of the common cosmopolitan species in our bait traps indicates that this area of the PN de Marojejy is a relatively pristine environment as yet unaffected by human encroachment.

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Literature Cited

- ASHBURNER, M. 1981. Entomophagous and other bizarre *Drosophilidae*, pp. 395–429. In Ashburner, M., et al., eds., *The Genetics and Biology of Drosophila*, vol. 3a. Academic Press, London.
- BRNCIC, D. 1983. The ecology of flower-breeding *Drosophila*, pp. 333–382. In Ashburner, M., et al., eds., *The Genetics and Biology of Drosophila*, vol. 3e. Academic Press, London.
- CARSON, H. L. 1974. Three flies and three islands: Parallel evolution in *Drosophila*. Proceedings of the National Academy of Sciences, USA, **71**: 3517–3521.
- CHASSAGNARD, M.-T., AND S. F. McEVEY. 1992. The *Zaprionus* of Madagascar, with descriptions of five new species (Diptera: Drosophilidae). *Annals de la Société Entomologique de France*, **28**: 317–335.
- CHASSAGNARD, M.-T., AND L. TSACAS. 1993. Le sous-genre *Zaprionus* s.str. définition de groupes d'espèces et révision du sous-groupe *vittiger* (Diptera: Drosophilidae). *Annals de la Société Entomologique de France*, **29**: 173–194.
- CHASSAGNARD, M.-T., L. TSACAS, AND D. L. LACHAISE. 1997. *Drosophilidae* (Diptera) of Malawi. *Annals of the Natal Museum*, **38**: 61–131.
- ESCHER, S. A., K. ERIKSSON, AND G. BÄCHLI. 1997. Collection of *Drosophilidae* (Diptera) along a transect in Kenya. *Bulletin de la Société Entomologique Suisse*, **70**: 1–14.
- GRIMALDI, D. 1985. Niche separation and competitive coexistence in mycophagous *Drosophila* (Diptera: Drosophilidae). *Proceedings of the Entomological Society of Washington*, **87**: 498–511.
- . 1988. Relicts in the Drosophilidae, pp. 183–213. In Liebherr, J. K., ed., *Zoogeography of Caribbean Insects*. Cornell University Press, Ithaca.
- . 1990. A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). *Bulletin of the American Museum of Natural History*, **197**: 1–139.
- . 1994. Description and immature stages of *Hirtodrosophila batracida* sp.n. (Diptera: Drosophilidae), a predator of frog embryos. *Entomologica Scandinavica*, **25**: 129–136.
- GRIMALDI, D., AND T. NGUYEN. 1999. Monograph of the spittle-bug flies, genus *Cladochaeta* (Diptera: Drosophilidae: Cladochaetini). *Bulletin of the American Museum of Natural History*, **241**: 1–326.
- JAENIKE, J., D. A. GRIMALDI, A. E. SLUDER, AND A. L. GREENLEAF. 1983. Alpha-amanitin tolerance in mycophagous *Drosophila*. *Science*, **221**: 165–167.
- JUILLARD, C. 1947. *Cacoxenus indagator* Loew (Dipt., Drosophilidae). Contribution à la biologie d'une parasite d'*Osmia rufa* L. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **20**: 567–593.
- . 1948. Le comportement des larves de *Cacoxenus indagator* dans les nids de l'*Osmia rufa*. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **21**: 547–554.
- LACHAISE, D. 1977. Niche separation of African *Lissocephala* within the *Ficus* drosophilid community. *Oecologia*, **31**: 201–214.
- LACHAISE, D., AND L. TSACAS. 1983. Breeding sites in tropical African drosophilids, pp. 221–332. In Ashburner, M., et al., eds., *The Genetics and Biology of Drosophila*, vol. 3e. Academic Press, London.
- PARSONS, P. A., AND S. M. STANLEY. 1981. Domesticated and widespread species, pp. 349–393. In Ashburner, M., et al., eds., *The Genetics and Biology of Drosophila*, vol. 3a. Academic Press, London.
- SOUTHWOOD, T. R. E. 1980. *Ecological Methods*, With Particular Reference to the Study of Insect Populations, second ed. Chapman and Hall, London.
- SWEZEY, O. H. 1929. Notes on the egg parasites of insects in Hawaii. *Proceedings of the Hawaiian Entomological Society*, **7**: 282–292.
- TSACAS, L. 1990. *Drosophilidae* de l'Afrique Australe (Diptera). *Annals of the Natal Museum*, **31**: 103–161.
- TSACAS, L., AND M.-T. CHASSAGNARD. 1990. Les espèces du genre *Zaprionus* à fémur antérieurs spinuleux (Diptera: Drosophilidae). *Annals de la Société Entomologique de France*, **26**: 461–487.
- TSACAS, L., AND R. H. L. DISNEY. 1974. Two new African species of *Drosophila* (Diptera, Drosophilidae) whose larvae feed on *Simulium* larvae (Dipt., Simuliidae). *Tropenmedizin Parasitologie*, **25**: 360–377.
- TSACAS, L., AND D. LACHAISE. 1979. La radiation africaine des *Lissocephala* inféodés aux *Ficus* (Diptera: Drosophilidae). *Annals de la Société Entomologique de France*, **15**: 589–603.
- TSACAS, L., M.-T. CHASSAGNARD, AND J. R. DAVID. 1988. Un nouveau groupe d'espèces afrotropicales anthophiles dans le sous-genre *Scaptodrosophila* du genre

Drosophila (Diptera: Drosophilidae). *Annals de la Société Entomologique de France*, **24**: 181–202.

TSACAS, L., D. LACHAISE, AND J. R. DAVID. 1981. Composition and biogeography of the Afrotropical drosophilid fauna, pp. 197–259. *In* Ashburner, M., et al., eds., *The Genetics and Biology of Drosophila*, vol. 3a. Academic Press, London.

WHEELER, M. R. 1981. The Drosophilidae: A taxonomic overview, pp. 1–97. *In* Ashburner, M., et al., eds., *The Genetics and Biology of Drosophila*, vol. 3a. Academic Press, London.

———. 1986. Additions to the catalogue of the world's Drosophilidae, pp. 395–409. *In* Ashburner, M., et al., eds., *The Genetics and Biology of Drosophila*, vol. 3e. Academic Press, London.

Chapter 7

Parasitic and Commensal Arthropods of Some Birds and Mammals of the Parc National de Marojejy, Madagascar

Barry M. OConnor¹

Abstract

Examination of 80 specimens representing 15 species of mammals and 8 specimens representing 7 species of birds collected in the Parc National de Marojejy yielded numerous collections of parasitic and commensal arthropods. All host species and all host individuals harbored arthropod associates. Preliminary identifications of 17 families of mites (Acari) as well as parasitic insects belonging to the orders Siphonaptera (fleas) and Phthiraptera (lice) are reported. A species of the flower-inhabiting mite family Ameroseiidae is reported phoretic in the nares of the yellow-bellied sunbird-asity, *Neodrepanis hypoxantha*, for the first time. A species of Pseudoscorpionida is reported phoretic on *Eliurus grandidieri*, the first record of mammal-phoretic pseudoscorpions from Madagascar. The ectoparasite fauna of the Parc National de Marojejy is generally similar in its overall makeup to those of the Parc National d'Andringitra and the Réserve Spéciale d'Anjanaharibe-Sud.

Résumé

L'examen de 80 spécimens représentant 15 espèces de mammifères et de 8 spécimens représentant 7 espèces d'oiseaux, collectés dans le Parc National de Marojejy, a permis de disposer de plusieurs collections d'arthropodes parasites et commensaux. Toutes les espèces et les individus hôtes recèlent des associations d'arthropodes. Des identifications préliminaires de 17 familles de mites (Acari) ainsi que d'insectes parasites appartenant aux ordres de Siphonaptera (puces) et de Phthiraptera (poux) sont rapportées. Une espèce de mites qui habite les fleurs (famille des Ameroseiidae) est rapportée d'être phorétique dans les narines de *Neodrepanis hypoxantha* (Philépitte faux-souimanga de Salomonsen) pendant un premier temps. Puis, une espèce de Pseudoscorpionida est rapportée d'être phorétique sur *Eliurus grandidieri*, le premier cas d'association mammifères-pseudoscorpions enregistré à Madagascar. La faune ectoparasite du Parc National de Marojejy est généralement similaire dans son ensemble avec celles du Parc National d'Andringitra et de la Réserve Spéciale d'Anjanaharibe-Sud.

Introduction

This chapter continues the study of parasitic and commensal arthropods associated with Mad-

agascar's unique vertebrate fauna on the basis of specimens collected during faunal surveys led by Steven M. Goodman. I have previously reviewed the literature summarizing this parasite fauna and provided preliminary lists of families and genera of mites and orders of insects associated with birds and mammals of the Réserve Naturelle In-

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tégrale d'Andringitra (subsequently reclassified as a Parc National [PN]) (OConnor, 1996) and the Réserve Spéciale (RS) d'Anjanaharibe-Sud (OConnor, 1998). The present contribution reports the results of a similar survey conducted in the PN de Marojejy in 1996.

Methods and Materials

A total of 80 specimens representing 15 species of mammals and 8 specimens representing 7 species of birds collected in the PN de Marojejy were examined for arthropod parasites. Specimens were collected by S. M. Goodman and his associates during the survey of this area in 1996. Specimens to be examined for parasites were collected and processed, and information was entered into a database as described in the previous studies (OConnor, 1996, 1998).

The following list is a preliminary report of the results of this sampling. Because final identifications and descriptions of new taxa for most collections are still pending, I report here the parasite/commensal faunas for each host species generally at the level of family or, occasionally, genus or species. For each host species, the number of individuals examined is indicated after the species name, and the number of host individuals harboring a particular arthropod taxon is listed after the taxon name if more than one host was examined. Host specimens are vouchered in the Field Museum of Natural History (FMNH), Chicago; FMNH museum catalog numbers for each specimen examined follow the host name. The bird classification used here follows that presented in Chapter 10.

Results

Class Mammalia

Order Lipotyphla

Family Tenrecidae

Microgale cowani (N = 7)

159522, 159529–31, 159533–4, 159659

Acari: Parasitiformes

Ixodidae (5)

Laelapidae (6)

Acari: Acariformes

Trombiculidae (7)

Myobiidae:

Microgalobia (3)

Madamyobia (2)

Glycyphagidae (3)

Atopomelidae:

Listrophoroides (*Alistrophoroides*) (7)

Listrophoroides (*Madlistrophoroides*) (6)

Microgale dobsoni (N = 1)

159541

Acari: Parasitiformes

Ixodidae

Acari: Acariformes

Trombiculidae

Atopomelidae:

Listrophoroides (*Alistrophoroides*)

Listrophoroides (*Madlistrophoroides*)

Microgale gymnorhyncha (N = 2)

159544, 159547

Acari: Parasitiformes

Ixodidae (1)

Laelapidae (1)

Acari: Acariformes

Trombiculidae (1)

Atopomelidae:

Listrophoroides (*Alistrophoroides*) (2)

Listrophoroides (*Madlistrophoroides*) (1)

Microgale longicaudata (N = 1)

159546

Acari: Acariformes

Trombiculidae

Glycyphagidae

Atopomelidae:

Listrophoroides (*Alistrophoroides*)

Listrophoroides (*Madlistrophoroides*)

Microgale monticola (N = 9)

159529, 159549–53, 159556, 159569, 159676

Acari: Parasitiformes

Ixodidae (5)

Laelapidae (9)

Acari: Acariformes

Trombiculidae (8)

Myobiidae:

Microgalobia (4)

Glycyphagidae (1)

Atopomelidae:

Listrophoroides (*Alistrophoroides*) (9)

Listrophoroides (*Madlistrophoroides*) (6)

Microgale parvula (N = 3)

159560–1, 159680

Acari: Parasitiformes

Ixodidae (2)

Laelapidae (2)
Acari: Acariformes
Trombiculidae (3)
Glycyphagidae (1)
Atopomelidae:
 Listrophoroides (Alistrophoroides) (2)
 Listrophoroides (Madlistrophoroides) (3)
Sarcoptidae:
 Notoedres (1)

Microgale principula (N = 1)
159547

Acari: Acariformes
Myobiidae:
 Microgalobia
Demodicidae
Trombiculidae
Atopomelidae:
 Listrophoroides (Alistrophoroides)
 Listrophoroides (Madlistrophoroides)
Sarcoptidae:
 Notoedres (1)

Microgale soricoides (N = 3)
159554–5, 159564

Acari: Parasitiformes
Ixodidae (1)
Laelapidae (3)
Acari: Acariformes
Myobiidae:
 Microgalobia (2)
Trombiculidae (2)
Atopomelidae:
 Listrophoroides (Alistrophoroides) (2)
 Listrophoroides (Madlistrophoroides) (3)

Microgale talazaci (N = 3)
159537, 159571, 159576

Acari: Parasitiformes
Ixodidae (2)
Laelapidae (2)
Acari: Acariformes
Trombiculidae (3)
Myobiidae:
 Microgalobia (2)
Atopomelidae:
 Listrophoroides (Alistrophoroides) (2)
 Listrophoroides (Madlistrophoroides) (3)

Oryzoricetes hova (N = 1)
159578

Acari: Parasitiformes
Ixodidae:
 Ixodes
 Haemaphysalis
Laelapidae

Acari: Acariformes
Glycyphagidae
Atopomelidae:
 Listrophoroides (Alistrophoroides)
 Listrophoroides (Madlistrophoroides)

Order Rodentia

Family Muridae

Eliurus grandidieri (N = 22)

Acari: Parasitiformes
Ixodidae (1)
Laelapidae (17)
Acari: Acariformes
Trombiculidae (22)
Demodicidae:
 Demodex (3)
Glycyphagidae (1)
Atopomelidae:
 Listrophoroides (Eulistrophoroides) (7)
 Listrophoroides (Pallistrophoroides) (22)

Pseudoscorpionida

Probably Chernetidae (3)
Insecta: Phthiraptera: Anoplura
Unidentified family (19)
Insecta: Siphonaptera
Unidentified family (2)

Eliurus majori (N = 10)

159624–8, 159630, 159632, 159634, 159637–8

Acari: Parasitiformes
Laelapidae (7)
Pachylaelapidae (1)
Acari: Acariformes
Trombiculidae (10)
Demodicidae:
 Demodex (1)
Atopomelidae:
 Listrophoroides (Eulistrophoroides) (3)
 Listrophoroides (Pallistrophoroides) (9)
Insecta: Phthiraptera: Anoplura
Unidentified family (8)

Eliurus minor (N = 2)

159639–40

Acari: Parasitiformes
Laelapidae (2)
Acari: Acariformes
Trombiculidae (2)
Demodicidae:
 Demodex (2)
Atopomelidae:
 Listrophoroides (Pallistrophoroides) (2)
Insecta: Phthiraptera: Anoplura

Unidentified family (2)

Eliurus webbi (N = 5)

Acari: Parasitiformes

Ixodidae (1)

Laelapidae (4)

Pachylaelapidae (1)

Acari: Acariformes

Trombiculidae (5)

Demodicidae:

Demodex (2)

Glycyphagidae (2)

Atopomelidae:

Listrophoroides (Eulistrophoroides) (1)

Listrophoroides (Pallistrophoroides) (5)

Insecta: Phthiraptera: Anoplura

Unidentified family (1)

Voalavo gymnocaudus (2)

Acari: Parasitiformes

Laelapidae (2)

Acari: Acariformes

Trombiculidae (2)

Demodicidae:

Demodex (2)

Atopomelidae:

Listrophoroides (Eulistrophoroides) (2)

Listrophoroides (Pallistrophoroides) (2)

Class Aves

Order Passeriformes

Family Eurylaimidae

Neodrepanis coruscans (N = 1)

Acari: Acariformes

Proctophyllodidae

Trouessartiidae

Neodrepanis hypoxantha (N = 2)

Acari: Parasitiformes

Rhinonyssidae (1)

Ameroseiidae (1)

Acari: Acariformes

Proctophyllodidae (2)

Trouessartiidae (2)

Family Ploceidae

Foudia omissa (N = 1)

Acari: Acariformes

Proctophyllodidae

Avenzoariidae

Trouessartiidae

Family Pycnonotidae

Berneria zosterops (N = 1)

Acari: Acariformes

Analgidae

Proctophyllodidae

Avenzoariidae

Trouessartiidae

Insecta: Phthiraptera: Mallophaga

Unidentified family

Family Timaliidae

Oxylabes madagascariensis (N = 1)

Acari: Acariformes

Analgidae

Proctophyllodidae

Avenzoariidae

Trouessartiidae

Insecta: Phthiraptera: Mallophaga

Unidentified family

Family Turdidae

Copsychus albospectularis (N = 1)

Acari: Acariformes

Trombiculidae

Ereynetidae

Analgidae

Proctophyllodidae

Trouessartiidae

Xolalgidae

Monticola sharpei (N = 1)

Acari: Acariformes

Analgidae

Proctophyllodidae

Trouessartiidae

Discussion

Comparison of the parasite fauna (compound parasite communities) of the PN de Marojejy with those of the PN d'Andringitra and RS d'Anjanaharibe-Sud (OConnor, 1996, 1998) reveals a strong similarity at the ordinal, familial, and generic levels, suggesting that these parasite communities are similar throughout the forested regions of the country. The collection of a specimen of the family Ameroseiidae from *Neodrepanis hypoxantha* marks the first record of this family in association with this group of birds. Other ameroseiid species have been reported from nectarivorous birds in Australia (Halliday, 1997). Like other bird-phoretic ameroseiid mites, this

specimen was recovered from the intranasal cavity. Most flower-inhabiting Ameroseiidae disperse on nectarivorous insects such as bees and butterflies. Haitlinger (1987) described *Afrocypholaelaps ranomafanaensis* phoretic on an unidentified butterfly from Madagascar. Phoretic pseudoscorpions are reported here for the first time from the rodent *Eliurus grandidieri*. Several individuals of this species harbored these symbionts; numerous individuals were attached by their pedipalpal chelae to hairs of the hind legs. The pseudoscorpions shared this attachment site with large laelapid mites of the genus *Androlaelaps*. Since no other mammalian host carried these organisms, some specificity may be indicated.

Acknowledgments

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Literature Cited

- HAITLINGER, R. 1997. *Afrocypholaelaps ranomafanaensis* sp. n. (Acari, Mesostigmata, Ameroseiidae) from butterfly from Madagascar. *Polskie Pismo Entomologiczne*, **57**: 531–533.
- HALLIDAY, R. B. 1997. Revision of the Australian Ameroseiidae (Acarina: Mesostigmata). *Invertebrate Taxonomy*, **10**: 179–201.
- OCONNOR, B. M. 1996. Parasitic and commensal arthropods of some birds and mammals of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 136–141. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **85**: 1–319.
- . 1998. Parasitic and commensal arthropods of some birds and mammals of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, pp. 73–78. *In* Goodman, S. M., ed., A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **90**: 1–246.

Chapter 8

Notes on a Small Collection of Fishes from the Parc National de Marojejy, Northeastern Madagascar, with a Description of a New Species of the Endemic Genus *Bedotia* (Atherinomorpha: Bedotiidae)

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Abstract

A small collection of fishes from the Manantenina River in northeastern Madagascar is reported. Included in the collection are six native species, two Malagasy endemics, and one introduced species. One of the endemic taxa is a new species of the endemic rainbow fish genus *Bedotia*. The new species, *B. marojejy*, described herein, is readily distinguished from all congeners by a characteristic pigmentation pattern and low vertebral count.

Résumé

Une petite collection de poissons provenant de la Rivière Manantenina (nord-est de Madagascar) est rapportée. Six espèces natives, deux endémiques de Madagascar et une introduite sont incluses dans la collection. L'un des taxons endémiques est une espèce nouvelle qui appartient au genre *Bedotia*. La nouvelle espèce, *B. marojejy*, décrite ici se distingue de ses congénères par des pigmentations caractéristiques et un faible nombre de vertèbres.

Introduction

In a recent summary of the freshwater fishes of Madagascar, Stiassny and Raminosoa (1994) provide an annotated listing of the native fishes of the island. Although the continental waters of Madagascar are relatively depauperate in terms of overall species richness, there is a high-level of endemism (84%) in the freshwater ichthyofauna. Particularly striking is the fact that many of these endemic taxa are basal representatives of their respective clades (Stiassny, 1992; Stiassny & Raminosoa, 1994). Despite the pronounced threat to the island's freshwater ecosystems and the evolutionary

importance of many of these taxa, Madagascar's freshwater fish fauna remains relatively poorly documented and is often overlooked in conservation efforts. Benstead et al. (2000) have noted that if the criteria of the United States Endangered Species Act were applied to the fishes of the island, 10 species would be considered critically endangered and 12 would be considered threatened; insufficient data preclude accurate determination of the status of most of the remainder. There is clearly a strong impetus to continue with ongoing attempts to assess the taxonomic composition, range, and conservation status of the Malagasy ichthyofauna (Benstead et al., 2000; Reinthal & Stiassny, 1991, 1997; Stiassny & Raminosoa, 1994; Stiassny & Reinthal, 1992).

There have been few collections of fishes from the region of the Parc National (PN) de Marojejy,

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and with the exception of the description of a single taxon, *Rheocloides pellegrini* Nichols and LaMonte, 1931 (= *Rheocles pellegrini*; see Stiassny, 1990), collected during the Mission Zoologique Franco-Anglo-Américaine (Rand, 1936) from a locality "one day west of Andapa," no records of freshwater fishes from this area occur in the literature. In addition to the type of *R. pellegrini*, a number of other fishes collected during the Mission Zoologique Franco-Anglo-Américaine are deposited in the Ichthyology Department of the American Museum of Natural History (AMNH), and where appropriate these have been consulted as comparative materials. So too has a small collection of fishes from the Lokoho River, downstream of Belaoko, made by Patrick De Rham in October 1993 and deposited at the AMNH.

During the 1996 faunal survey of the PN de Marojejy a small collection of fishes from a locality at the banks of the Manantenina River at the southeastern boundary of the reserve (Fig. 8-1), about 28 km NE of the town of Andapa, was obtained. In view of the general paucity of material from this region and the pressing need for baseline taxonomic and distributional data for Malagasy fishes, a taxonomic report on the collection is presented here. Included among the material is a new species of rainbow fish of the endemic genus, *Bedotia* Regan, 1903, which is described herein.

Abbreviations

AMNH, American Museum of Natural History; BMNH, Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; RMNH, Nationaal Natuurhistorisch Museum, Leiden; SL, standard length; TL, total length.

Taxonomic Review

1. Family Bedotiidae

The endemic Malagasy family Bedotiidae comprises the genera *Bedotia* Regan, 1903, and *Rheocles* Jordan and Hubbs 1919. Although *Rheocles* has been the subject of recent revision (Stiassny, 1990; Stiassny & Reinthal, 1992), the rainbow fishes of the genus *Bedotia* have received considerably less attention recently. Currently, the tax-

onomy of *Bedotia* is confused and greatly in need of modern revisional study (Arnoult, 1959; Kiener, 1963; Catala, 1975). We have begun this process, and preliminary findings recognize five taxa (*B. madagascariensis* Regan 1903, *B. longianalis* Pellegrin 1914, and three undescribed species). The specimens of *Bedotia* from the Manantenina River are quite distinct from any of these other nominal forms and are readily diagnosable on the basis of a unique color pattern. Given the highly distinctive nature of the Manantenina specimens and the long-term nature of a comprehensive generic revision, the Manantenina species will be described herein and subsequently incorporated into a broader revisional study.

Bedotia marojejy, new species

(Figure 8-2)

HOLOTYPE—AMNH 224647, female, 46.6 mm SL. Banks of the Manantenina River (Lokoho River basin) at the SE boundary of the PN de Marojejy (approximate coordinates 14°28'S, 49°49'E), some 28 km NE of the town of Andapa. Collected by local fisherwoman using traditional dipnets. October–November 1996.

PARATYPES—AMNH 224648, two alcohol specimens, one male, 47.7 mm SL, one undetermined sex, 33.9 mm SL, one cleared and double-stained specimen, undetermined sex, 45.3 mm SL. Same data as holotype.

DIAGNOSIS—*Bedotia marojejy* is readily distinguished from all other nominal *Bedotia* by a distinctive color pattern characterized by a series of dark blotches arrayed along the lateral midline. In all other *Bedotia* species the lateral markings are dominated by a broad midlateral band of pigmentation, and similar blotching is never evident. *B. marojejy* is further distinguished from other *Bedotia* by a low total vertebral count of 34 (including the terminal, hypural-bearing half centrum), compared to 35–37 (very rarely 34) in the other species.

DESCRIPTION—Morphological measurements and meristic counts are given in Table 8-1. Measurement of standard length, head length, snout length, eye diameter, and caudal peduncle length and depth follows Kottelat (1990). Body depth is measured at the deepest part of the body, at the origin of the pelvic fins. The distance from the snout to the first or second dorsal fin is measured straight from the tip of the snout to a vertical through the base of the first fin ray in each fin

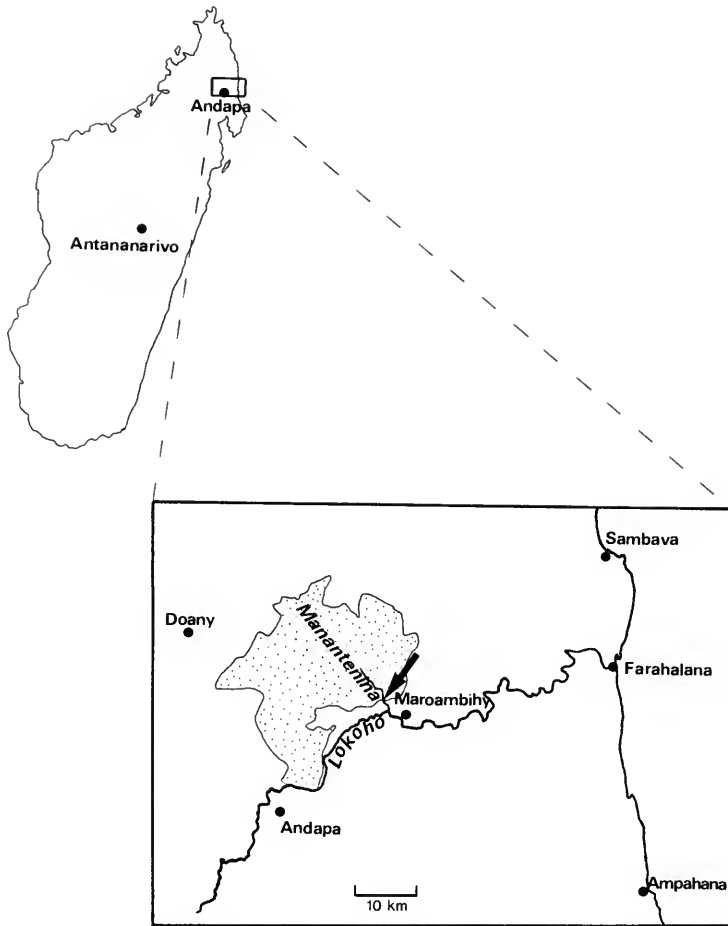


FIG. 8-1. Location of the PN de Marojejy (stippled area) in Madagascar. Arrow points to approximate locality in which fishes were collected.

respectively. Anal length is measured from the base of the first anal-fin ray to the base of the last fin ray. Lower jaw length is measured from the dentary symphysis to the posterior tip of the corner of the mouth. Currently the largest known specimen of *B. marojejy* is a 47.7 mm SL male.

Bedotia marojejy are robust, relatively short-bodied fishes somewhat deep-bodied anteriorly and with moderate belly curvature. Dorsum of head and nape broadly flatten to first dorsal fin. Origin of first dorsal is well behind vertical through pelvic-fin insertion, and origin of second dorsal is well behind vertical through origin of anal fin.

Snout is strongly indented behind prominent premaxillary pedicels. Lower jaw is prognathous and angled at about 30–35° to horizontal when mouth is closed. Premaxilla and maxilla reach

vertical through anterior margin of orbit. Premaxillae with deep lateral “bedotia notch” are characteristic of the genus (Stiassny, 1990).

Teeth—Anteriorly both upper and lower jaws bear two to three rows of numerous small, strongly recurved unicuspid teeth. The inner and outer rows of teeth are poorly differentiated. The lower jaw and the premaxilla posterior to the bedotia notch each have a single row of teeth. A single row of teeth is present along the anteroventral face of vomer, and a tiny patch of endopterygoid teeth is also present. No palatine or ectopterygoid teeth are present, at least in individuals of sizes available for examination.

Gill Rakers—Two or three stout hypobranchial rakers and eight or nine elongate ceratobranchial rakers are present on the lower limb of the first branchial arch. All rakers are strongly denticulate.

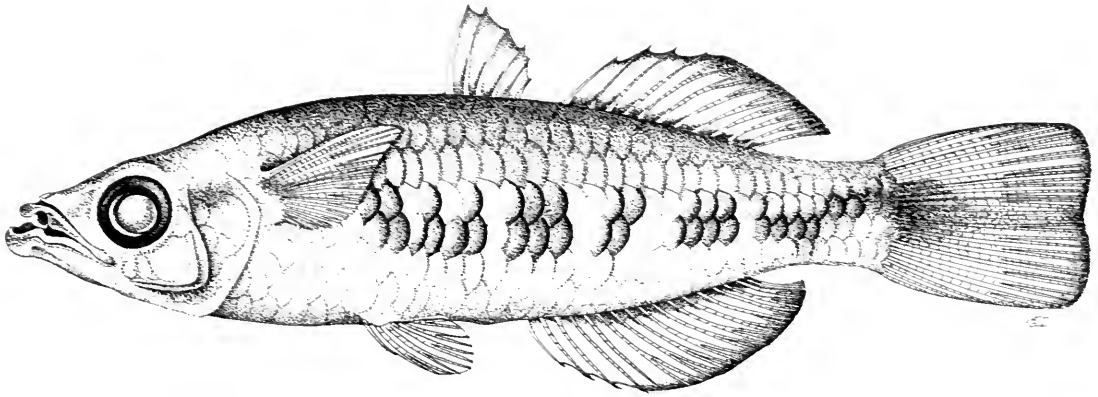


FIG. 8-2. Holotype of *Bedotia marojejy* sp. nov., AMNH 224647, female, 46.6 mm SL.

Scales—Body is covered with large, regularly imbricate, cycloid scales. Predorsal scales number 16 or 17 along the dorsal midline. Thirty-two or 33 scales occur along the midlateral axis from just behind the operculum, above the pectoral fin, to the end of the hypural plate. Ten scales in transverse series are located between the anal fin and the second dorsal fin (including a very small scale adjacent to each fin). One or two scales separate the first and second dorsal fins. Twelve or 13 scales in transverse series are located entirely around the caudal peduncle (circumpeduncular series). Dorsal, anal, and caudal scale sheaths and

axillary pelvic scales are absent. The body is fully scaled.

Fins—First dorsal fin bears six weak spines. Second dorsal fin bears 12 or 13 rays, with the first 3 or 4 unbranched. Anal fin bears 17 rays, usually with the first 5 unbranched. Pectoral fin bears 14 rays that are high set and relatively short, the longest upper rays extending only a little beyond the vertical from the pelvic-fin insertion. The pelvic fin has one weak spine and five strongly bifurcate, branched rays. The caudal fin is weakly emarginate.

Vertebrae—Total vertebral count (taken from

TABLE 8-1. *Bedotia marojejy*, new species.

Character Evaluated	Holotype	Paratypes (N)	Min.*	Max.	Mean
Standard length	46.6	3	33.9	47.7	43.4
Head length (% SL)	30.6	3	27.0	30.0	29.1
Snout length (% HL)	32.9	3	30.7	31.3	31.7
Eye diameter (% HL)	27.3	3	26.9	30.7	28.3
Body depth (% SL)	23.3	3	23.7	24.0	23.7
Caudal peduncle length (% HL)	54.5	3	54.6	57.5	55.5
Caudal peduncle depth (% HL)	33.6	3	34.6	36.0	34.7
Snout—first dorsal origin (% SL)	54.4	3	52.1	52.8	52.9
Snout—second dorsal origin (% SL)	65.3	3	63.9	65.4	65.0
Anal length (% SL)	28.3	3	27.0	29.7	28.1
Lower jaw length (% HL)	51.0	3	48.7	53.0	50.9

Character Evaluated	Holotype	Paratypes (N)	Range	Distribution
Longitudinal scales	33	3	32–33	32 (1) 33 (3)
Gill rakers (lower arch)	11	3		11 (4)
Anal rays	17	3		17 (4)
Second dorsal rays	12	3	12–13	12 (3) 13 (1)
Vertebrae—total	34	3		34 (4)
(Precaudal + caudal + terminal half centrum)	(17 + 16 + 1)			(17 + 16 + 1)(4)

*Min. and max. are the ranges only for the paratypical series, whereas the mean represents the entire sample.

radiographs and directly from the cleared and double-stained specimen), 34: 17 precaudal vertebrae (haemal arch not fused), 16 caudal vertebrae (haemal arch fused), and terminal, hypural-bearing half centrum. As noted in the diagnosis, a total vertebral count of 34 is rarely encountered in other *Bedotia* species. However, the sample size for *B. marojejy* is small compared with the number of specimens available for the five nominal congeneric species, and intraspecific variation within *B. marojejy* may be underestimated.

Preserved Coloration—Ground color in both male and female specimens is a pale creamy yellow. Dorsum of snout, nape, and body is darkly pigmented. A black bar passes from the symphysis of the lower jaw through the eye to the posterodorsal border of the opercle. A dark crescentic patch occurs at the pectoral-fin base. A series of 6 to 8 darkly pigmented blotches is arrayed along the lateral midline. The ventrum of head, chest, and body is pale creamy yellow. A broad wedge of pigment occurring at the caudal-fin base extends as a narrow median stripe to the caudal margin. The caudal margin and ventral and dorsal edges are darkly pigmented. The bases of the second dorsal and anal fins are darkly pigmented, and both fins have distal margins, also darkly pigmented. No data on live coloration are currently available.

Viscera and Diet—Gut extremely short, intestinal length only about one-third body length. In all four specimens the intestines are almost empty, containing nothing but a few partially disarticulated insects. In all individuals the remains of both aquatic (larvae) and terrestrial insects were found, suggesting that this species is probably essentially insectivorous, opportunistically feeding on both autochthonous and allochthonous sources.

DISTRIBUTION—Currently the species is known only from the type locality in the Manantenina River. In view of the paucity of collections from this region, however, it is probable that additional populations of *B. marojejy* are present in similar habitats throughout the surrounding area.

ETYMOLOGY—The specific epithet was made in reference to the locality in which the type series was collected.

2. Family Anguillidae

Anguilla marmorata Quoy and Gaimard, 1824 (See Castle (1984) for synonymies)

One specimen of *Anguilla marmorata* was collected at the Manantenina River site (AMNH

226649, 570 mm TL). It accords well with descriptions of the species by Bauchot and Bianchi (1984) and Skelton (1993) in having the dorsal-fin origin nearer to the gill slit than to the anus, the maxillary toothbands with distinctive longitudinal grooves, and in being heavily mottled brownish black. These features readily distinguish *A. marmorata* from the three other anguillids currently recognized in Malagasy freshwaters: *A. mossambica* (Peters, 1852), *A. bicolor* McClelland, 1844, and *A. bengalensis labiata* (Peters, 1852).

Anguilla marmorata, commonly called the giant mottled eel, attains lengths of up to 185 cm TL (Skelton, 1993). It is widespread in fresh and brackish waters from sea level up to altitudes of 300–900 m throughout Madagascar (Kiener, 1963). Outside of Madagascar *A. marmorata* is widespread from Western Cape Province to Kenya in Africa (Skelton, 1993), the Comoros (Teugels et al., 1985), and east to Polynesia and the Ryukus, Japan.

COMPARATIVE MATERIAL—*Anguilla marmorata*: AMNH 88113, 460 mm TL, Toamasina (Tamatave), main marketplace in town center, Madagascar, 15-VII-1988, M. L. J. Stiassny, P. N. Reinthal; AMNH 88125, 400 mm TL, Toamasina (Tamatave), main marketplace in town center, Madagascar, 15-VII-1988, M. L. J. Stiassny, P. N. Reinthal; AMNH 58991, 62.4 mm, 170 mm, 175 mm TL, creek crossing N coast road ca. 4.5 km N of Bogia, Madang drainage, New Guinea, 19-X-1987, L. R. Parenti, G. R. Allen, D. Coates.

Anguilla mossambica (Peters, 1852) (See Castle (1984) for synonymies)

One specimen of *Anguilla mossambica* was collected at the Manantenina River site (AMNH 226650, 320 mm TL). It too accords well with descriptions of the species by Bauchot and Bianchi (1984) and Skelton (1993). Like *A. marmorata*, *A. mossambica* has the dorsal-fin origin nearer to the gill slit than to the anus, and this readily distinguishes it from the other two Malagasy anguillids. *A. mossambica* lacks the mottled coloration, and its maxillary toothbands lack the longitudinal grooves characteristic of *A. marmorata*.

Anguilla mossambica, commonly called the African longfin eel, attains lengths of up to 120 cm TL (Skelton, 1993). It is the most widespread of all Malagasy freshwater eels and is found from sea level up to altitudes of over 900 m throughout

the island (Kiener, 1963). Outside of Madagascar *A. mossambica* is commonly encountered on the African mainland in east coast rivers from Kenya south to Cape Agulhas, Republic of South Africa, and it occurs on other western Indian Ocean islands (Skelton, 1993).

COMPARATIVE MATERIAL—*Anguilla mossambica*: AMNH 88114, 295 mm TL, Toamasina (Tamatave), main marketplace in town center, Madagascar, 15-VII-1988, M. L. J. Stiassny, P. N. Reinthal; AMNH 88010, 490 mm TL, town of Ranomafana, Namorona River in shallow pools cut off from mainstream by rocky outcrops, Madagascar, 26-VI-1988, M. L. J. Stiassny, P. N. Reinthal; AMNH 11686, 399 mm TL, Madagascar, 1931, Archibold Expedition (= Mission Zoologique Franco-Anglo-Américaine), A. L. Rand, W. H. du Mont.

3. Family Mugilidae

Agonostomus telfairii Bennett, 1831

(See Thomson (1986) for synonyms)

A single specimen of *Agonostomus telfairii* was collected (AMNH 226651, 191 mm SL). Thomson (1997) recognized two Indian Ocean species of *Agonostomus* in his revision of the Mugilidae, namely *A. catalai* Pellegrin, 1932, with a thick upper lip, and *A. telfairii*, with a thinner lip. In the holotype of *A. catalai*, collected from the Haute Mananano, Sahasinaka District, Madagascar, the mid-height of the upper lip is 21% of the head length; in the holotype of *A. telfairii*, collected from Mauritius, the upper lip thickness is 10% of the head length. The specimen from the Manantenina River has an upper lip thickness of 17% head length. Examinations of comparative material indicate a complete range of lip thickness; for example, a collection from the Nosivolo River (Mangoro drainage), Madagascar, includes 11 specimens of *Agonostomus* (AMNH 97100) with lip thickness graded from 11% to 18% of head length. Ingham (1952) and Thomson (1997) stated that the thick-lipped species, *A. catalai*, could be distinguished by having only a single row of teeth in the lower jaw; however, collections examined in this study include specimens of *Agonostomus* with thick lips and up to three irregularly arranged rows of teeth in the lower jaw. Other distinguishing features for *A. catalai* given by Thomson (1997) include the relative position on the head of the upper part of the preorbital and

posterior tip of the upper jaw, relative position of the pelvic fin, and number of gill rakers. However, it is not possible to satisfactorily distinguish between the two species using these features.

Agonostomus telfairii (here including *A. catalai*) is known from rivers of Madagascar, Anjouan (Comoros), and the Mascarene islands of Réunion and Mauritius (Thomson, 1980). According to Catala (1975), in Madagascar *A. catalai* (= *A. telfairii*) is restricted to the upper reaches of fast-flowing, rocky streams where it feeds exclusively on algae. Kiener (1963) suggested that, in Madagascar, *A. telfairii* would be unable to ascend the rapids and waterfalls of the fast-flowing hill streams.

Besides *A. telfairii* (including *A. catalai*), Ingham (1952) and Thomson (1997) recognized only one other species of *Agonostomus*, *A. monticola*, which is insectivorous and inhabits the upper reaches of torrential, rocky rivers in Central and South America (Cruz, 1987; Phillip, 1993). However, *A. monticola* is thought to migrate during the rainy season down to coastal waters, where it spawns before immediately returning upstream. After a short period at sea, the prejuveniles return to the rivers and migrate upstream (Cruz, 1987; Ditty & Shaw, 1996). Hill streams and rivers comprising isolated pools separated by small waterfalls may not present a barrier to upstream migration because *A. monticola* is an accomplished leaper (K. Lazara, pers. comm.). *A. telfairii* might show a similar, catadromous ecology to *A. monticola*. *A. telfairii* can reach ca. 36 cm SL; it is taken in subsistence fisheries but not commercially (Thomson, 1980).

The global distribution of *Agonostomus* is remarkably disjunct; *A. monticola* is restricted to rivers of Central America, northern South America, and the Galapagos Islands (Harrison, 1995, Thomson, 1978, 1997), and *A. telfairii* is restricted to rivers of the aforementioned islands of the western Indian Ocean. There is not sufficient information to provide any well-supported explanation for this distribution of *Agonostomus*. However, two possible scenarios would benefit from further analysis. One explanation is that this is the relict of a former Tethyan distribution, with extension into the eastern Pacific during the Oligocene and Miocene. This distribution would have been disrupted by two vicariance processes: Miocene closure of the Mediterranean, with the associated Messinian salinity crisis of that region, and development of the current Panamanian isthmus during the Pliocene. A former Tethyan con-

nection between Indo-Pacific and Atlantic relatives has been discussed for various taxa; for example, cods (Howes, 1991), gobies (Harrison, 1993; McKay & Miller, 1997), and anguillid eels (Tagliavini et al., 1996; Tsukamoto & Aoyama, 1998). Anguillid eels, like species of *Agonostomus*, have a catadromous lifestyle (McDowall, 1997). Vicariance biogeography of the Caribbean and eastern Pacific regions has been discussed by various authors (e.g., Coates & Obando, 1996; Iturralde-Vinent & MacPhee, 1999; Rosen, 1975; White, 1986).

An alternative hypothesis is that the current distribution of *Agonostomus* is a relict of a prolonged Gondwanan link between Indo-Madagascar and South America, via Antarctica, that may have lasted until ca. 80 million years ago (Sampson et al., 1998). This scenario requires *Agonostomus* to be at least twice as old as the oldest known fossil mugilid, dated to 30–40 MYBP (Patterson, 1993). This may be possible, considering information for other smegmamorphs (*sensu* Johnson & Patterson, 1993). White (1986) discusses Cretaceous ancestral antherinids, although the earliest fossil material is from the early Eocene, and the minimum age of cyprinodontiforms is estimated to be late Triassic, although the oldest described fossil cyprinodontiform is from the Oligocene (Parenti, 1981; Patterson, 1993). Contemporary distribution of *Agonostomus* through South America would, according to this scenario, be related to the very complex processes of Andean orogeny, associated changes in South American riverine drainages, and periodic marine transgressions, through the late Cretaceous and Tertiary (for discussion see Harrington, 1962; Lundberg, 1997; Lundberg et al., 1998; Schaefer, 1997; Webb, 1995; Weitzman & Weitzman, 1982).

COMPARATIVE MATERIAL—*Agonostomus telfairii*: BMNH 1861.8.14.9, holotype, 108.5 mm SL, Mauritius, Gerrard; AMNH 215499, 2 specimens, 79.3 mm and 84.7 mm SL, Lokoho River, Andapa region, downstream Belaoko, northeast Madagascar, P. De Rham, 21-X-1993. *Agonostomus telfairii* var. *catalai*: MNHN 1932-162, holotype, 129.8 mm SL, Haute Mananano, Madagascar, Catala; BMNH 1865.9.21.4-5, 2 specimens, 175 and 195 mm SL, Johanna (?Anjouan); presented by Col. Playfair; BMNH (no register no.), 126.5 mm SL, Madagascar, Dr. S. E. Gray; AMNH 97100, 11 specimens, 136.5–227 mm SL, Tamatave Province, Nosivolo River, below Zule's Village, deep pools, Madagascar, M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 23-IX-1990; AMNH

97112, 132 mm SL, Toamasina (Tamatave) Province, Nosivolo River, 10 km upstream from Marolambo, Madagascar, M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 23-IX-1990. *Nestis cyprinoides*: MNHN 5553, syntype, 207.5 mm SL, Île de France (Île Maurice), Désjardins; MNHN A.963, 2 syntypes, 163 mm and 146.2 mm SL, Île de France (Île Maurice), Dussumier; MNHN A.4318, 2 syntypes, 67.8 mm and 65.8 mm SL, Île Bourbon (La Réunion), Leschenault. *Nestis dobulooides*: MNHN A.4650, holotype, 360 mm SL, Île de France (Île Maurice), Lamarre Piquot.

4. Family Cichlidae

Paratilapia polleni Bleeker, 1868

(See Maréchal and Gosse (1991) for synonymies)

Three specimens of the endemic cichlid genus, *Paratilapia*, were collected at the Manantenina River site (AMNH 226652; 54.7 mm SL, 50.6 mm SL, 33.0 mm SL). Although most contemporary authors follow Pellegrin's (1904) synonymy of *Paracara typus* Bleeker, 1878, and *Paratilapia bleekeri* Sauvage, 1891, with *P. polleni* Bleeker, 1868, several field biologists have noted the existence of distinct local phenotypes (Loiselle, 1995). In a preliminary taxonomic note on the genus, Loiselle and Stiassny (1993) resurrected Sauvage's *P. bleekeri*, noting, among other features, the large size of the spots and spangling of this species when compared with the small spots of *P. polleni*. However, Loiselle and Stiassny (1993) accepted the synonym *Paracara typus* with *Paratilapia polleni*, mainly because of a paucity of comparative material and the extremely poor state of the single type specimen of *P. typus*. In the absence of a thorough revision there remains considerable confusion regarding the species-level taxonomy of *Paratilapia*. The problem of a definitive identification of the Manantenina material is compounded by the fact that the specimens lack the diagnostic coloration and patterning of adult fish. However, based on a morphometric appraisal, the Manantenina specimens appear to approximate the more gracile, longer-jawed *P. polleni* phenotype than the deeper-bodied, shorter-jawed *P. bleekeri*. Interestingly, although the Manantenina specimens exhibit a typical juvenile *Paratilapia* patterning of 8–9 narrow, closely spaced vertical bars and a large ocellated tilapia-spot in the soft dorsal fin (Stiassny & Ger-

stner, 1992), the largest individual is a male with advanced testicular development. According to Kiener (1963), *P. polleni* are sexually mature at about 12 cm on the Central High Plateau, compared to 8 cm in the nutrient-poor acid waters of the coastal plain where growth rates are retarded. The Manantenina populations apparently are attaining sexual maturity at a notably smaller size.

Prior to the extensive deforestation of the island and the introduction of predatory exotic species, *Paratilapia polleni* was the most widespread of all Malagasy endemic cichlids, being recorded from most regions of the island (Kiener, 1963; Kiener & Maugé, 1966). However, because the species cannot survive temperatures lower than 12–15°C, it has always been absent from areas much above 1500 m (Kiener, 1963). *P. polleni* has been eradicated from much of its original range by habitat alteration and introduced exotic species. Today, although both *P. polleni* and *P. bleekeri* are still widely distributed in eastern coastal regions, they are nowhere abundant. *P. polleni* is recorded as attaining sizes of 30 cm, although individuals of that size are rarely encountered today.

COMPARATIVE MATERIAL—*Paratilapia polleni*: RMNH 4.483, syntype, 119.3 mm SL, “Ambassuana” Madagascar septentrionalis in fluviis (Nosy-bé), 1864; RMNH 6.690, syntypes, 104.4 mm SL, 60.1 mm SL, “Ambassuana” Madagascar septentrionalis in fluviis (Nosy-bé), 1864; RMNH 3.994, syntype, 117.5 mm SL, “Ambassuana” Madagascar septentrionalis in fluviis (Nosy-bé), 1864; AMNH 18842, Region d’Ankarana, Waterlot; AMNH 11689, Madagascar, Mission Zoologique Franco-Anglo-Américaine (= Archibold Expedition), 28-IX-1931; AMNH 97002, Bay Lake behind first dune, ca. 100 m from sea, east of road by Salehy Village, 1 km S of turnoff from Marolambo-Mananjary Road, Toamasina (Tamatave) Province, Madagascar, 16-IX-1990, M. L. J. Stiassny, P. N. Reinthal, G. J. P. Naylor; AMNH 97030, Mouth of Mangoro River, opposite camp by Salehy Village, Toamasina (Tamatave) Province, Madagascar, 17-IX-1990, M. L. J. Stiassny, P. N. Reinthal, G. J. P. Naylor. *Paracara typus*: RMNH holotype, Madagascar orientalis in fluviis (rivière de Mananara, à l’entrée de la baie d’Antongil), specimen disarticulated. *Paratilapia bleekeri*: MNHN A.4195, syntypes, 90.3 mm SL, 88.0 mm SL, 84.4 mm SL, marais et rizières de l’Imerina, près d’Antananarivo.

Oreochromis mossambicus (Peters, 1852)

(See Trewavas and Teugels (1991) for synonymies)

Four juvenile specimens of the introduced African cichlid *Oreochromis mossambicus* were collected at the Manantenina River site (AMNH 226653; 63.6 mm SL, 56.2 mm SL, 52.6 mm SL, 34.1 mm SL). They conform to the descriptions of the species (e.g., Trewavas, 1983; Skelton, 1993) and exhibit numerous vertical bars and a characteristic series of 2–5 midlateral blotches and some blotches of a more dorsal series. Apparently *O. mossambicus* was introduced into Madagascar from Mozambique in 1956 by the Forestry Service for use in “rizipisciculture” (the culture of fishes in flooded rice fields; Kiener, 1963). The species is now widespread throughout the island.

5. Family Eleotridae

Eleotris fusca (Schneider, 1801)

(See Maugé (1986b) for synonymies)

Four specimens of *Eleotris* were collected at the Manantenina River site (AMNH 226654; 2 males, 121.7 mm and 94 mm SL, and 2 females, 119.3 mm and 89 mm SL). They generally accord with Akihito’s (1967) and Hoese’s (1986) descriptions of *E. fusca*, having 8 or more gill rakers on the first epibranchial, 61–66 scales in a longitudinal series, infraorbital transverse rows 2, 4, and 6 penetrating below longitudinal row d, and 9 transverse infraorbital rows anterior to row b (the last two characters are ambiguous in the smallest specimen). These features distinguish *E. fusca* from the very similar *E. melanosoma* Bleeker. However, examination of comparative material indicates that infraorbital papillae patterns are variable. For example, specimens with high scale counts (indicative of *E. fusca*) have an *E. melanosoma* type papillae patterning, or intermediate papillae patterns. It will not be possible to resolve the taxonomy of Malagasy species of *Eleotris* more precisely until a detailed review of the 13 nominal Indo-West Pacific species (Miller, 1998) has been conducted.

Eleotris fusca attains 26 cm (Hoese, 1986). It is currently reported as a widespread, epibenthic species, found in fresh, brackish, and littoral waters throughout much of Madagascar and from the east African coast eastward to Polynesia (Catala,

1982; Maugé, 1986b). However, this distribution requires confirmation through a taxonomic review of the species.

COMPARATIVE MATERIAL—*Eleotris fusca*: AMNH 215521, male, 121 mm SL, Nosy-bé, Djabala River, near Ampombilava village, Madagascar, P. Loiselle, 18-IX-1990. *Eleotris melanosoma*: AMNH 96904, male, 53.9 mm SL, Toamasina (Tamatave Province), main market place in town center, caught nearby, Madagascar, local fishermen, M. L. J. Stiassny, P. N. Reinthal, 15-XII-1988. *Eleotris* cf. *melanosoma*: AMNH 051509, male, 102.8 mm SL, 1 day W of Andapa, northern Madagascar, Mission Zoologique Franco-Anglo-Américaine (= Archibold Expedition), A. L. Rand, W. H. du Mont, 2-X-1931; AMNH 097039, 7 specimens, 17.9–41.3 mm SL; Toamasina (Tamatave) Province, small affluent tributary, River Mangoro, ca. 1 km upstream of Mangoro ferry crossing, Madagascar, M. L. J. Stiassny, P. N. Reinthal and G. J. P. Naylor, 17-IX-1990; AMNH 97048, 1 male, 154 mm SL, 3 females, 64.6–102.2 mm SL, Toamasina (Tamatave) Province, small stream ca. 20 km from Mangoro ferry crossing on road to Marolambo, through banana plantation, Madagascar, M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 18-IX-1990.

6. Family Gobiidae

Awaous aeneofuscus (Peters, 1852)
(See Maugé (1986a) for synonymies)

Two specimens of *Awaous* were collected at the Manantenina River site (AMNH 226655; 1 female, 178 mm SL, and 1 male, 121.8 mm SL). Both specimens conform to descriptions of *A. aeneofuscus* (for example, Catala, 1982; e.g., with 26–36 small predorsal scales extending anteriorly to a vertical through the preopercular canal, scales absent on the opercle and preopercle, 55–60 scales in longitudinal series, and the mouth not extending beyond the anterior of the eye. There are two dark bands running anteroventrally from the eye toward the mouth, and the body has a series of dark brown patches just dorsal to the midline (see Teugels et al., 1985, fig. 7). The pigmentation features are more distinct in the smaller male specimen than in the large female. For a general comparison, see photographs in Schmidt et al. (1996, p. 34); the female appears similar to the large specimen shown in photograph 2, and

the smaller male is slightly darker than the specimen in photograph 10.

Awaous aeneofuscus inhabits fresh and brackish waters of South Africa, Mozambique, Madagascar, and the Comoros (Teugels et al., 1985; Maugé, 1986a). Kiener (1963) reports that the species may be found at altitudes up to 950 m. It may attain 35 cm SL (Catala, 1982), although larger specimens tend to be found not as far upriver (Kiener, 1963).

COMPARATIVE MATERIAL—*Awaous aeneofuscus*: AMNH 215496, 2 males, 85.8 mm and 91.2 mm SL, Lokoho River, Andapa region, downstream of Belaoko, northeast Madagascar, P. De Rham, 2-X-1993; AMNH 88093, 1 male (from collection of 14 specimens), 134 mm SL, Pangalanes north of Mangoro River, Mahanoro town behind Hotel de la Pangalane, Madagascar, M. L. J. Stiassny, P. N. Reinthal, 9-VII-1988; AMNH 097055, 3 females, 76.4–148 mm SL, Toamasina (Tamatave) Province, Savalany River (small stream) by Ambodivovoka village, bridge over road to Marolambo, Madagascar, M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 18-IX-1990.

Subfamily Sicydiinae

Catala (1982) listed five sicydiine species from Madagascar or neighboring islands, incorrectly placing them all within the genus *Sicydium* Valenciennes. These were: *S. acutipinnis* (Guichenot), *S. franouxi* Pellegrin, *S. fasciatum* Day, *S. laticeps* Valenciennes, and *S. lagocephalum* (Pallas). Maugé (1986a) reassigned the species *acutipinnis* Guichenot to its original genus, *Cotylopus* Guichenot, 1863, and noted that reports of this species from Madagascar are doubtful. Watson's (1995) review of the genus and species concurred, and he listed *acutipinnis* as known only from Réunion. Additionally, Catala's (1982) description of *S. acutipinnis* is inaccurate, citing a very high scale count: 75 in longitudinal series, compared to 46–63 cited by Watson (1995). The remaining Malagasy species are all assigned to the genus *Sicyopterus* Gill, 1861 (Maugé, 1986a). *S. laticeps* has been synonymized with *S. lagocephalum* (Smith, 1959; Maugé, 1986a).

Sicyopterus fasciatus and *S. franouxi* are very similar, and Maugé (1986a) listed *Sicydium franouxi* (= *Sicyopterus franouxi*) as a possible synonym of *Sicyopterus fasciatus*. Pellegrin (1935) and Catala (1982) refer to the absence of scales on the median part of the nape of the neck and

median part of the abdomen in *S. franouxi* as a character differentiating it from *S. fasciatus*. Examination of comparative material indicates that differences in scalation of the nape are difficult to detect and perhaps subjective. However, comparison of similar-sized specimens of *S. franouxi* and *S. fasciatus* (114 mm SL, AMNH 097149; and 115 mm SL, AMNH 215495, respectively) indicates that the abdomen of *S. fasciatus* is entirely scaled, whereas that of *S. franouxi* is less well-scaled ventromedially. Smaller specimens of *S. franouxi* also usually have the ventromedial part of the abdomen less well-scaled, or naked, compared to the ventrolateral parts of the abdomen, although this is slightly variable. Pellegrin (1935) referred to the coloration of *S. franouxi* as being diagnostic, and this seems to be the most reliable feature for differentiating it from *S. fasciatus*. In most specimens of *S. franouxi* the anterior of the snout, just above the upper lip, is dark brown and continues as a dark brown band that runs beneath the eye and over the mid part of the preopercle towards its dorsoposterior margin. A prominent, longitudinal dark brown band extends along the midline of the body from the pectoral axilla to the anterior half of the caudal fin. The rest of the body is usually a lighter brown. This background pigmentation is darker in some specimens, however, such that the longitudinal band, although still visible, is less distinct. Some of the lighter specimens show traces of four or five dark brown, transverse bars on the body, and Pellegrin's (1935) original description refers to these. These transverse bands

may be more prominent in fresh specimens, as suggested by a photograph, labeled as "*Sicyopterus pranouxi*" [sic] in Schmidt et al. (1996, p. 34, photograph 5). The base of the pectoral fin is dark brown dorsally, at the same level as the longitudinal band on the body. The pectoral fin rays are darkish brown near their bases but paler distally, producing a crescent-shaped band of dark pigmentation over the fin. In comparative material of *Sicyopterus fasciatus* the snout and sides of the head are dark brown or dark gray, but this species lacks the distinctive longitudinal band of dark brown pigmentation that runs the length of the body in *S. franouxi*. Day's (1876, p. 299) description and figure (pl. 54) of *S. fasciatus* give no indication of a dark brown longitudinal bar. The body coloration in *S. fasciatus* appears to be more of a gray-brown than the light brown seen in *S. franouxi*. The available comparative material of *S. fasciatus* shows only vague traces of transverse bands of dark brown pigment on the body, but Day's description and figure indicate that the bands are quite distinct. The pectoral fins of *S. fasciatus* have a more uniform dark gray-brown pigmentation than those of *S. franouxi*.

The possibility of conspecificity between *S. fasciatus* and *S. franouxi* should not be discounted. However, until a more detailed review of western Indian Ocean sicydiines has been completed it seems reasonable to distinguish between the *S. fasciatus* and *S. franouxi* according to the squamation and pigmentation features described above. A provisional key for Malagasy species of *Sicyopterus* follows:

- 1a. Scales on nape and ventral part of abdomen much smaller than those on flanks; 58–63 scales in longitudinal series (excluding scales on caudal fin) 2
- 1b. Scales on nape and ventral part of abdomen more or less equal in size to those on flanks; usually 52 or fewer scales in longitudinal series (excluding scales on caudal fin) *Sicyopterus lagocephalus*
- 2a. Distinct, longitudinal, dark brown bar along midline of body; body otherwise lightish brown; pectoral fin darkish brown near base and on mid-part of fin but paler distally, producing a crescent-shaped band of dark pigmentation over the fin; ventromedial part of abdomen usually lacking scales *Sicyopterus franouxi*
- 2b. No dark brown longitudinal bar along midline of body; body grayish brown; pectoral fin uniform dark gray-brown; ventromedial part of abdomen entirely scaled *Sicyopterus fasciatus*

***Sicyopterus lagocephalus* (Pallas, 1774)**
(See Maugé (1986a) for synonymies)

One sicydiine collected at the Manantenina River site (AMNH 226656, 1 female, 109.0 mm

SL) is identified as *Sicyopterus lagocephalus* according to the above key. This species is darkish gray-brown, with traces of five or six transverse, darker brown, bands on the body and a longitudinal, dark brown band running along the midline.

The pectoral fins have a uniform dark brown pigmentation. The collected specimen (AMNH 226656) is slightly darker brown than other comparative material. Catala's (1982) scale count for *S. lagocephalus* (57–65) is high according to the available comparative material.

Sicyopterus lagocephalus inhabits swift-flowing streams of Madagascar, Réunion, Mauritius, and the Comoros (Maugé, 1986a; Teugels et al., 1985; Watson, 1995). *S. lagocephalus* attains ca. 120 mm total length and is presumably amphidromous like other sicydiine gobies; the adults reproduce in freshwater, and the larvae are carried down to the sea, where they remain for some time before returning to freshwater to mature and reproduce (Harrison, 1993; McDowall, 1997; Watson, 1998). The ascent of enormous numbers of postlarval *S. lagocephalus* up rivers of Réunion and Madagascar has been reported by Valenciennes in Cuvier and Valenciennes (1837) and Kiener (1963). The migratory return of postlarvae to freshwater more or less coincides with each new moon; the more significant migrations in Madagascar occur between April and September (Kiener, 1963). The postlarvae are fished by local people and eaten fresh or dried.

COMPARATIVE MATERIAL—*Sicyopterus lagocephalus*: AMNH 215498, 3 males, 76.4–104.0 mm SL, Lokoho River, Andapa region, downstream of Belaoko, northeast Madagascar, P. De Rham, 21-X-1993. *S. fasciatus*: AMNH 215495, 1 male, 134 mm SL, and 1 female, 115.2 mm SL, Lokoho River, Andapa region, downstream of Belaoko, NE Madagascar, P. De Rham, 21-X-1993. *S. franouxi*: AMNH 097149, 4 females?, 77.1–113.6 mm SL, Toamasina (Tamatave) Province, Nosivolo River below Ambatomasina village, ca. 16 km E-NE of Marolambo, in large pool, Madagascar, M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 21-IX-1990; AMNH 097071, 2 females, 52.6 mm and 83.6 mm SL, and one specimen of undetermined sex, 54.6 mm SL, Toamasina (Tamatave) Province, Sahala River, near Andranavolo, Madagascar, M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 19-IX-1990; AMNH 097080, 4 females, 73.8–98.5 mm SL, 1 male, 63.7 mm SL, and 2 specimens of undetermined sex, 67.8 mm and 95.5 mm SL, Toamasina (Tamatave) Province, Nosivolo River, below Ampasimaniona village, 26 km E-NE of Marolambo, large side pool below rapids, Madagascar, M. L. J. Stiassny, P. N. Reinthal and G. J. P. Naylor, 20-IX-1990; AMNH 097068, 1 specimen of undetermined sex, 38.6 mm SL, Toamasina (Tamatave)

Province, stream by Ambinanindrano, Madagascar, M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 19-IX-1990.

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Literature Cited

- AKIHITO, PRINCE. 1967. On four species of the gobiid fishes of the genus *Eleotris* found in Japan. *Japanese Journal of Ichthyology*, 14(4/6): 135–166.
- ARNOULT, J. 1959. Faune de Madagascar. X. Poissons des eaux douces. L'Institut de Recherche Scientifique, Tananarive, 155 p.
- BAUCHOT, M.-L., AND G. BIANCHI. 1984. Fiches FAO d'identification des Guide des espèces pour les besoins de la pêches. Guides des poissons commerciaux de Madagascar (espèces marines et d'eaux saumâtres). Avec le support du Programme des Nations Unies pour le Développement (Projet RAF/79/065). Rome, FAO, 135 p.
- BENSTEAD, J. P., M. L. J. STIASSNY, P. V. LOISELLE, K. R. RISENG, AND N. RAMINOSOA. 2000. River conservation in Madagascar, pp. 203–229. *In* Boon, P. J., B. R. Davies, and G. E. Petts, eds., *Global Perspectives on River Conservation: Science, Policy and Practice*. Wiley, New York.
- CASTLE, P. H. J. 1984. Anguillidae, pp. 134–137. *In* Daget, J., J.-P. Gosse, and D. F. E. Thys van den Audenaerde, eds., *Check-list of the freshwater fishes of Africa*. Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), Paris and Musée Royal de l'Afrique Centrale (MRAC), Tervuren.
- CATALA, R. 1975. Poissons d'eau douce de Madagascar.

- Revue française d'Aquariologie et Herpetologie, **1**: 29–32.
- . 1982. Poissons d'eau douce de Madagascar. *Revue française d'Aquariologie et Herpetologie*, **9**(2): 57–64.
- COATES, A. G., AND J. A. OBANDO. 1996. The geologic evolution of the Central American isthmus, pp. 21–56. *In* Jackson, J. B. C., A. F. Budd, and A. G. Coates, eds., *Evolution and Environment in Tropical America*. University of Chicago Press, Chicago, IL.
- CRUZ, G. A. 1987. Reproductive biology and feeding habits of cuyamel, *Joturus pichardi* and tepemehín, *Agonostomus monticola* (Pisces; Mugilidae) from Rio Plátano, Mosquitia, Honduras. *Bulletin of Marine Science*, **40**(1): 63–72.
- CUVIER, G., AND A. VALENCIENNES. 1837. *Histoire naturelle des poissons*, **12**. xxix + 507 pp., pl. 344–368. Paris, Strasbourg.
- DAY, F. 1876. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma and Ceylon. Part **2**: 169–368, pl. 41–78. Wm. Dawson and Sons, London.
- DITTY, J. G., AND SHAW, R. F. 1996. Spatial and temporal distribution of larval striped mullet (*Mugil cephalus*) and white mullet (*M. curema*, family: Mugilidae) in the northern Gulf of Mexico, with notes on mountain mullet, *Agonostomus monticola*. *Bulletin of Marine Science*, **59**(2): 271–288.
- HARRINGTON, H. J. 1962. Paleographic development of South America. *Bulletin of the American Association of Petroleum Geologists*, **46**(10): 1773–1814.
- HARRISON, I. J. 1993. The West African sicydiine fishes, with notes on the genus *Lentipes* (Teleostei: Gobiidae). *Ichthyological Exploration of Freshwaters*, **4**(3): 201–232.
- . 1995. Mugilidae, pp. 1293–1298. *In* Fischer, W., F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds., *Guia FAO para la identificación de especies para los fines de la pesca. Pacífico Centro-Oriental*, **3**. FAO, Rome.
- HOESE, D. F. 1986. Eleotridae, pp. 807–811. *In* Smith, M. M., and P. C. Heemstra, eds., *Smith's Sea Fishes*. Springer-Verlag, Berlin.
- HOWES, G. J. 1991. Biogeography of gadoid fishes. *Journal of Biogeography*, **18**: 595–622.
- INGHAM, S. E. 1952. The biology and taxonomy of the Mugilidae. Unpublished manuscript in Library of Natural History Museum, London.
- ITURRALDE-VINENT, M. A., AND R. D. E. MACPHEE. 1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, **238**: 1–95.
- JOHNSON, G. D., AND C. PATTERSON. 1993. Percomorph phylogeny: A survey of acanthomorphs and a new proposal. *Bulletin of Marine Science*, **52**(1): 554–626.
- KIENER, A. 1963. Poissons, pêche et pisciculture à Madagascar. Centre Technique Forestier Tropical, Nogent sur Marne, **24**: 244 p.
- KIENER, A., AND M. MAUGÉ. 1966. Contributions à l'étude systématique et écologique des poissons Cichlidae endémiques de Madagascar. *Mémoires du Muséum National d'Histoire Naturelle, Série A, Zoologie*, **XL**(2): 4–99.
- KOTTELAT, M. 1990. Sailfin silversides (Pisces: Telmattherinidae) of Lakes Towuti, Mahalona and Wawontoa (Sulawesi, Indonesia) with descriptions of two new genera and two new species. *Ichthyological Exploration of Freshwaters*, **1**(3): 35–54.
- LOISELLE, P. V. 1995. The cichlids of Jurassic Park. Part 1. *Cichlid News*, **4**(3): 18–23.
- LOISELLE, P. V., AND M. L. J. STIASSNY. 1993. How many marakely? *Journal of the American Cichlid Association*, **15**(7): 2–8.
- LUNDBERG, J. G. 1997. Freshwater fishes and their paleobiotic implications, pp. 67–91. *In* Kay, R. F. R. H. Madden, R. L. Cifelli, and J. J. Flynn, eds., *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D.C.
- LUNDBERG, J. G., L. G. MARSHALL, J. GUERRERO, B. HORTON, M. C. MALABARBA, AND F. WESSELENGH. 1998. The stage for Neotropical fish diversification: A history of tropical South American rivers, Chapter 1. *In* Malabarba, L. R., R. E. Reis, R. P. Vari, C. A. S. Lucena, and Z. M. S. Lucena, eds., *Phylogeny and Classification of Neotropical Fishes*. Museu de Ciências e Tecnologia, PUCRS. Porto Alegre, Brazil.
- MARÉCHAL, C., AND J.-P. GOSSE. 1991. *Paratilapia*, pp. 358. *In* Daget, J., J.-P. Gosse, G. G. Teugels, and D. F. E. Thys van den Audenaerde, eds., *Check-list of the freshwater fishes of Africa*, **4**. Institut Royal des Sciences Naturelles de Belgique (ISNB), Bruxelles, Musée Royal de l'Afrique Centrale (MRAC), Tervuren, Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), Paris.
- MAUGÉ, A. L. 1986a. Gobiidae, pp. 358–388. *In* Daget, J., J.-P. Gosse, and D. F. E. Thys van den Audenaerde, eds., *Check-list of the freshwater fishes of Africa*, **2**. Institut Royal des Sciences Naturelles de Belgique (ISNB), Bruxelles, Musée Royal de l'Afrique Centrale (MRAC), Tervuren, Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), Paris.
- . 1986b. Eleotridae, pp. 389–398. *In* Daget, J., J.-P. Gosse, and D. F. E. Thys van den Audenaerde, eds., *Check-list of the freshwater fishes of Africa*, **2**. Institut Royal des Sciences Naturelles de Belgique (ISNB), Bruxelles, Musée Royal de l'Afrique Centrale (MRAC), Tervuren, Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), Paris.
- . 1986c. Eleotridae, pp. 389–398. *In* Daget, J., J.-P. Gosse, and D. F. E. Thys van den Audenaerde, eds., *Check-list of the freshwater fishes of Africa*, **2**. Institut Royal des Sciences Naturelles de Belgique (ISNB), Bruxelles, Musée Royal de l'Afrique Centrale (MRAC), Tervuren, Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), Paris.
- McDOWALL, R. M. 1997. The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Reviews in Fish Biology and Fisheries*, **7**: 443–462.
- McKAY, S. I., AND P. J. MILLER. 1997. The affinities of European sand gobies (Teleostei: Gobiidae). *Journal of Natural History*, **31**: 1457–1482.
- MILLER, P. J. 1998. The West African species of *Eleotris* and their systematic affinities (Teleostei: Gobioidae). *Journal of Natural History*, **32**: 273–296.
- PARENTI, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). *Bulletin of the American Museum of Natural History*, **168**(4): 335–557.

- PATTERSON, C. 1993. Osteichthyes: Teleostei, pp. 622–656. In Benton, M. J., ed., *The fossil record*, 2. Chapman and Hall, London.
- PELLEGRIN, J. 1904. Contribution à l'étude anatomique, biologique et taxonomique des poissons des familles des Cichlidés. Mémoires de la Société zoologique de France, 16: 41–402.
- . 1935. Poissons de Madagascar recueillis par M. Catala. Description d'un *Sicydium* nouveau. Bulletin de la Société zoologique de France, 60: 69–73.
- PHILLIP, D. A. T. 1993. Reproduction and feeding of the mountain mullet, *Agonostomus monticola*, in Trinidad, West Indies. *Environmental Biology of Fishes*, 37: 47–55.
- RAND, A. L. 1936. The distribution and habits of Madagascar birds. Summary of the field notes of the Mission Zoologique Franco-Anglo-Américaine à Madagascar. Bulletin of the American Museum of Natural History, 72: 143–499.
- REINTHAL, P. N., AND M. L. J. STIASSNY. 1991. The freshwater fishes of Madagascar: A study of an endangered fauna with recommendations for a conservation strategy. *Conservation Biology*, 5(2): 231–243.
- . 1997. Revision of the Madagascan genus *Ptychochromoides* (Teleostei: Cichlidae), with a description of a new species. *Ichthyological Explorations of Freshwaters*, 7(3–4): 353–368.
- ROSEN, D. E. 1975. A vicariance model of Caribbean biogeography. *Systematic Zoology*, 24(4): 431–464.
- SAMPSON, S. D., L. M. WITMER, C. A. FORSTER, D. W. KRAUSE, P. M. O'CONNOR, P. DODSON, AND F. RAVOAVY. 1998. Predatory dinosaur remains from Madagascar: Implications for the Cretaceous biogeography of Gondwana. *Science*, 280: 1048–1051.
- SCHAEFER, S. A. 1997. The Neotropical cascudinhos: Systematics and biogeography of *Otocinclus* catfishes (Siluriformes: Loricariidae). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 148: 1–120.
- SCHMIDT, W., AND AQUA GEÖGRAPHIA EDITORS. 1996. La Grande île. *Aqua Geögraphia*, 13: 6–36.
- SKELTON, P. 1993. A Complete Guide to the Freshwater Fishes of Southern Africa. Southern Books, South Africa, 388 pp.
- SMITH, J. L. B. 1959. Gobioid fishes of the families Gobiidae, Periophthalmidae, Trypauchenidae, Taenioididae, and Kraemeridae of the Western Indian Ocean. *Ichthyological Bulletin of Rhodes University*, 13: 185–225.
- STIASSNY, M. L. J. 1990. Notes on the anatomy and relationships of the bedotiina fishes of Madagascar, with a taxonomic revision of the genus *Rheocles* (Atherinomorpha: Bedotiidae). *American Museum Novitates*, 2979: 1–33.
- . 1992. Phylogenetic analysis and the role of systematics in the biodiversity crisis, pp. 109–120. In Eldredge, N., ed., *Systematics, Ecology and the Biodiversity Crisis*. Columbia University Press, 220 pp.
- STIASSNY, M. L. J., AND P. N. REINTHAL. 1992. Description of a new species of *Rheocles* (Atherinomorpha: Bedotiidae) from the Nosivolo tributary of the Mangoro River, eastern Madagascar. *American Museum Novitates*, 3031: 1–8.
- STIASSNY, M. L. J., AND C. L. GERSTNER. 1992. The parental care behaviour of *Paratilapia polleni* (Perciformes, Labroidei), a phylogenetically primitive cichlid from Madagascar, with a discussion of the evolution of maternal care in the family Cichlidae. *Environmental Biology of Fishes*, 34: 219–233.
- STIASSNY, M. L. J., AND N. RAMINOSOA. 1994. The fishes of the inland waters of Madagascar. Biological diversity in african fresh- and brackish water fishes. Geographical overviews. *Annals Muséum Royal Afrique Centrale, Zoology*, 275: 133–149.
- TAGLIAVINI, J., G. GANDOLFI, A. M. DEIANA, S. SALVADORI. 1996. Phylogenetic relationships among two Atlantic and three Indo-Pacific *Anguilla* species (Osteichthyes, Anguillidae). *Italian Journal of Zoology*, 63: 271–276.
- TEUGELS, G. G., L. J. M. JANSSENS, J. BOGAERT, AND M. DUMALIN. 1985. Sur une collection de poissons de rivière des Comores. *Cybium*, 9(1): 41–56.
- THOMSON, J. M. 1978. Mugilidae [unpaginated]. In Fischer, W., ed., *FAO species identification sheets for fishery purposes*. Western Central Atlantic (Fishing Area 31), 3. FAO, Rome.
- . 1980. Mugilidae [unpaginated]. In Fischer, W., and G. Bianchi, eds., *FAO species identification sheets for fishery purposes*. Western Indian Ocean (Fishing Area 51), 3. FAO, Rome.
- . 1986. Mugilidae, pp. 344–349. In Daget, J., J.-P. Gosse, and D. F. E. Thys van den Audenaerde, eds., *Check-list of the freshwater fishes of Africa*, 2, Institut Royal des Sciences Naturelles de Belgique (ISNB), Bruxelles, Musée Royal de l'Afrique Centrale (MRAC), Tervuren, Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), Paris.
- . 1997. The Mugilidae of the world. *Memoirs of the Queensland Museum*, 41(3): 457–562.
- TREWAVAS, E. 1983. Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakilia*. *British Museum (Natural History)*, London, 583 p.
- TREWAVAS, E., AND G. G. TEUGELS. 1991. *Oreochromis*, pp. 307–346. In Daget, J., J.-P. Gosse, G. G. Teugels, and D. F. E. Thys van den Audenaerde, eds., *Check-list of the freshwater fishes of Africa*, 4, Institut Royal des Sciences Naturelles de Belgique (ISNB), Bruxelles, Musée Royal de l'Afrique Centrale (MRAC), Tervuren, Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), Paris.
- TSUKAMOTO, K., AND J. AOYAMA. 1998. Evolution of freshwater eels of the genus *Anguilla*: A probable scenario. *Environmental Biology of Fishes*, 52: 139–148.
- WATSON, R. E. 1995. Review of the freshwater goby genus *Cotylopus* (Teleostei: Gobiidae: Sicydiinae). *Ichthyological Exploration of Freshwaters*, 6(1): 61–70.
- . 1998. *Stiphodon martenstyni*, a new species of freshwater goby from Sri Lanka (Teleostei: Gobiidae: Sicydiini). *Journal of Asian Natural History*, 3(1): 69–78.
- WEBB, S. D. 1995. Biological implications of the Middle Miocene Amazon seaway. *Science*, 269: 361–362.
- WEITZMAN, S. H., AND M. WEITZMAN. 1982. Biogeography and evolutionary diversification in Neotropical

freshwater fishes, with comments on the refuge theory, pp. 403–422. *In* Prance, G. T., ed., *Biological Diversification in the Tropics*. Columbia University Press.

WHITE, B. N. 1986. The isthmian link, antitropicality and American biogeography: Distributional history of the Atherinopsinae (Pisces: Atherinidae). *Systematic Zoology*, **35**(2): 176–194.

Chapter 9

Herpetofaunal Species Diversity and Elevational Distribution Within the Parc National de Marojejy, Madagascar

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Abstract

Amphibians and reptiles were surveyed along the summit trail of the Parc National (PN) de Marojejy, between the village of Mandena, at 80 m elevation, and the Marojejy summit, at 2132 m elevation. A cumulative total of 75 days of surveying were completed during two visits made in the rainy seasons of 1992 and 1996.

A total of 51 species of amphibians and 62 species of reptiles were found within the park, and a further 3 amphibian and 7 reptile species were recorded within 5 km of the park boundary, thus representing a regional herpetofaunal diversity of 123 species. Despite previous studies made at Marojejy, 50% of the herpetofauna we recorded are new records for the park, and 10 species are undescribed. The actual herpetofaunal diversity of the PN de Marojejy is likely to exceed 113 species as an additional 26 species are recorded from the park or region, thus making this massif one of the most diverse areas of Madagascar. This exceptional species diversity is almost certainly due to both the large elevational range found within the park and the restricted elevational distribution of amphibians and reptiles in Madagascar. A weak mid-elevation "bulge" in species diversity (possibly produced as an artifact of greater survey effort at mid-elevation) was found at 700 m for both amphibians and reptiles, with minimum species diversity occurring at the highest elevations in both groups. Endemism is also evident for the Marojejy Massif, with 13 species currently known only from within the park.

The herpetofaunal species diversity and endemism of the PN de Marojejy demonstrate the value of this park within the protected areas network on Madagascar. Future conservation efforts must continue to maintain the integrity of the park, especially within its peripheral low-elevation areas, which are most vulnerable to habitat loss.

Résumé

Deux visites, d'une durée de 75 jours, le long du sommet du Parc National (PN) de Marojejy, pendant les saisons de pluie des années 1992 et 1996, ont permis de compléter l'inventaire des amphibiens et des reptiles entre le village de Mandena à 80 m jusque à la zone sommitale de Marojejy à 2132 m.

Cet inventaire a permis de trouver 51 espèces d'amphibiens et 62 espèces de reptiles au sein du parc, ainsi que 10 espèces supplémentaires aux alentours des limites du parc. Malgré les

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études effectuées à Marojejy auparavant, 50 pourcent de l'herpétofaune que nous avons enregistré sont nouveaux pour le parc et 10 espèces ne sont pas encore décrites. La diversité actuelle de l'herpétofaune du PN de Marojejy est sûrement supérieure à 113 espèces, car un supplément de 26 espèces est enregistré pour le parc et les régions avoisinantes, faisant de ce massif une des zones les plus riches en diversité de Madagascar. Cette diversité d'espèces exceptionnelle est sûrement due à la grande variation de l'altitude au sein du parc et à la stricte distribution altitudinale des amphibiens et reptiles de Madagascar. A 700 m d'altitude, il y a eu un de diversité à moyenne altitudinale pour les amphibiens et les reptiles, avec un minimum de diversité aux plus hautes altitudes pour les deux groupes. L'endémicité est aussi évidente pour le Massif de Marojejy avec 13 taxa connus pour le parc seulement.

La diversité et l'endémicité de l'herpétofaune du PN de Marojejy montre la valeur de cette réserve au sein du réseau des aires protégées de Madagascar. Les efforts de conservation doivent continuer afin de maintenir l'intégrité du parc, particulièrement les zones périphériques de basse altitude qui sont les plus vulnérables à la perte d'habitat.

Introduction

The Parc National (PN) de Marojejy (previously classified as the Réserve Naturelle Intégrale [RNI] no. 12 de Marojejy or Marojezy in older publications; see Chapter 1), with an area of 60,050 ha, includes the entire Marojejy Massif, ranging between 75 and 2132 m elevation. The massif is in northeastern Madagascar, with its summit at 14°24.03'S, 49°44.00'E. The primary vegetation of the park is rain forest, with ericoid heathland at elevations above 1800 m (Nicoll & Langrand, 1989; see Chapter 3). With the exception of the RNI de Tsaratanana, PN de Marojejy includes the largest elevational range within any protected area of Madagascar.

Although the Marojejy summit was first visited in 1937 by the Service Géographique, the herpetofauna of the massif remained unknown until collections were made in 1968 and 1972 by Charles P. Blanc and a multidisciplinary French research team (see Guillaumet et al., 1975). The 1968 collection resulted in the descriptions of *Brookesia karchei* and *Calumma gastrotaenia marojezensis*, the first reptiles described from the massif (Brygoo et al., 1970a,b). The second collection, 4 years later, led to the description of another three chameleon taxa (Brygoo et al., 1974a,b). Snakes collected during these surveys have been described more recently by Domergue (1984, 1988), and the Marojejy amphibians collected by Blanc were listed by Blommers-Schlösser and Blanc (1991).

In 1988, a British student expedition conducted a survey of birds of the PN de Marojejy that also included observations for 17 species of reptiles (Safford & Duckworth, 1990). However, because no

reptile vouchers were taken, tentative identifications were based on color photographs. The first amphibian and reptile inventory list for the park was published by Jenkins (1987), who used published literature taken from Blanc's collections. This list was further expanded by Nicoll and Langrand (1989) on the basis of additional literature sources and probably some personal observations (without vouchers) made by the authors during unspecified visits to the park prior to 1989. Nicoll and Langrand (1989) listed 17 amphibian and 22 reptile species.

The most recent herpetological inventory for Marojejy was published as localities within species accounts by Glaw and Vences (1994); it is based on a survey of the literature and at least one visit to the park made by one of the authors prior to the publication of their book. The dates of the survey are not given in this publication, but Vences et al. (1997) describe two visits made by Glaw to Marojejy, one in March 1994 and the second in February 1995. A total of 50 amphibian and 24 reptile species are listed from Marojejy by Glaw and Vences (1994).

In this chapter we report the results of our own surveys of the PN de Marojejy herpetofauna, completed during two surveys of the park. The first survey (University of Michigan) was made between 16 November and 5 December 1992, and the second survey (American Museum of Natural History/Université d'Antananarivo/World Wide Fund for Nature) was made between 4 October and 19 November 1996. The aim of these studies was to survey the complete elevational range within the park, to describe the distribution and diversity of amphibians and reptiles within the elevational gradient of the massif.

Study Sites

The following five sites (all positioned along the trail between the village of Mandena and the Marojejy summit) were surveyed during 1992 and 1996.

Site 1—Ampanasankolana (Bedinta), by the Ambinanitelo River, and Ampanasatongoira, 8 km NW of Manantenina Village, by the Manantenina River; 14°26.2'S, 49°46.5'E. Elevation 300–525 m. Dates: 16 November and 3–5 December 1992, 4–13 October 1996.

Site 2—Andampimbazaha Cascade, on the Ambavaomby River, a tributary of the Manantenina River; 14°26.0'S, 49°45.7'E. Elevation 550–850 m. Dates: 16 November–2 December 1992, 14–24 October 1996.

Site 3—Antranohofa, by the Ambavaomby Ridge; 14°26.2'S, 49°44.5'E. Elevation 1050–1350 m. Dates: 27–30 November 1992, 24 October–3 November 1996.

Site 4—Along the tributary Andranomifototra River; 14°26.4'S, 49°44.5'E. Elevation 1550–1700 m. Dates: 4–12 and 19 November 1996.

Site 5—Lohan Andranomifototra, Marojejy summit; 14°26.4'S, 49°44.1'E. Elevation 1800–2133 m. Dates: 30 November 1992, 13–19 November 1996.

Methods

The members of the herpetological field survey team during the 1992 survey were Ronald A. Nussbaum, Gabriella Raharimanana, Christopher J. Raxworthy, Angelin Razafimanantsoa, and Angeluc Razafimanantsoa; those during the 1996 survey were Achille P. Raselimanana and Bruno Zézé. The surveys were done during the early to middle period of the rainy season (October–December), when herpetofaunal activity is at its highest. Field techniques used to sample animals (by both day and night) included (1) pitfall trapping with drift fences; (2) visual and acoustic searching; and (3) refuge examination (under and in fallen logs and rotten tree stumps; under bark; under rocks; in leaf litter, root-mat, and soil; and in leaf axils of *Pandanus* screw palms and *Ravenala* traveller's palm).

The pitfall traps were buckets (275 mm deep, 290 mm top internal diameter, 220 mm bottom internal diameter) with the handles removed and

small holes (2 mm diameter) punched in the bottom to allow water drainage. Buckets were sunk into the ground below a drift fence made from plastic sheeting (0.5 m high) stapled in a vertical position to thin wooden stakes, with the fence bottom sealed 50 mm deep in the ground with soil and leaf litter. The traplines were checked each morning and late afternoon. After rain the buckets were sponge-dried. The drift fence (100 m in length) was positioned to run across the middle of each pitfall trap. Pitfall traps were positioned at both ends of the drift fence, with the other nine traps at 10 m intervals. Three lines were used, placed in the following forest types: ridge (along the crest of a ridge), slope (on a gradient, intermediate between ridgetop and valley bottom), and valley (within 20 m of a stream in a valley bottom). This is the procedure used in previous surveys (e.g., Raxworthy & Nussbaum, 1994, 1996a) and is recommended for use in future projects, to allow standardization of capture techniques and subsequent comparisons of results.

Visual searches and refuge examinations were made throughout the full elevation range of habitats available in the park. Night searches using headlights were made. The following information was recorded for each individual at the time of capture: date, time, longitude and latitude, elevation (measured by means of altimeters calibrated to 1:100,000 topographic maps), microhabitat, and circumstances of capture. Animals not retained as specimens were released at the site of original capture. Voucher specimens were selected on the basis of the following criteria: (1) documentation of species diversity and (2) collection of suitable material for future systematic research. Specimens were fixed in 10% buffered formalin and later transferred to alcohol. Color slides were taken of representative live individuals of many species. Frog calls were recorded during the 1992 survey. Collected material was deposited in three research collections: the 1992 material at the Museum of Zoology, University of Michigan (UMMZ), and Département de Biologie Animale, Université d'Antananarivo (UADBA); and the 1996 material at the American Museum of Natural History (AMNH) and UADBA.

Results

During our two surveys, a total of 51 amphibian and 62 reptile species were recorded in the PN de Marojejy, giving a total herpetofaunal di-

TABLE 9-1. Amphibians and reptiles identified during two surveys in five elevational zones within the PN de Marojejy or at indicated sites at the periphery of the park.

Species	Transect (m)					Elevation (m)	
	450	750	1225	1625	1875	Min.	Max.
Amphibia							
Microhylidae							
<i>Platypelis barbouri</i>	*	*				460	780
<i>Platypelis grandis</i>	*	*	*			350	1200
<i>Platypelis occultans</i>	*	*	*			350	1300
<i>Platypelis tsaratananaensis</i>				*		1560	1560
<i>Platypelis tuberifera</i>		*	*			700	1200
<i>Plethodontohyla bipunctata</i>	*					300	550
<i>Plethodontohyla coudreaui</i>		*	*			770	1225
<i>Plethodontohyla notosticta</i>		*	*			700	1300
<i>Plethodontohyla ocellata</i>	*					470	470
<i>Plethodontohyla serratopalpebrosa</i>					*	1120	1870
<i>Stumpffia grandis</i>			*			1150	1300
<i>Stumpffia roseifemoralis</i>		*	*			680	1250
<i>Stumpffia tridactyla</i>				*	*	1550	1875
<i>Stumpffia</i> sp.	*	*	*			350	1225
Hyperoliidae							
<i>Heterixalus madagascariensis</i>	Manantenina					80	80
Ranidae							
<i>Ptychadena mascareniensis</i>	Mandena					70	100
Mantellidae							
<i>Laurentomantis malagasias</i>	*	*				3560	790
<i>Mantella laevigata</i>	*	*				350	770
<i>Mantella nigricans</i>	*	*				450	850
<i>Mantella</i> sp.		*				750	850
<i>Mantidactylus aglavei</i>	*	*	*			350	1150
<i>Mantidactylus albofrenatus</i>	*	*	*			300	1100
<i>Mantidactylus asper</i>	*	*	*			430	1225
<i>Mantidactylus betsileanus</i>		*				720	800
<i>Mantidactylus bicalcaratus</i>		*	*		*	710	1850
<i>Mantidactylus biporus</i>	*	*	*	*		450	1550
<i>Mantidactylus cornutus</i>		*	*	*	*	680	1875
<i>Mantidactylus curtus</i>	*	*				350	700
<i>Mantidactylus femoralis</i>	*	*	*	*	*	350	1900
<i>Mantidactylus grandidieri</i>	*					100	500
<i>Mantidactylus klemmeri</i>	*	*	*			430	1300
<i>Mantidactylus leucomaculatus</i>	*	*				450	730
<i>Mantidactylus liber</i>	*	*	*	*		500	1550
<i>Mantidactylus lugubris</i>	*					450	460
<i>Mantidactylus luteus</i>	*	*				360	780
<i>Mantidactylus opiparis</i>	*					450	450
<i>Mantidactylus peraccae</i>			*	*		1150	1675
<i>Mantidactylus pulcher</i>		*	*			750	1220
<i>Mantidactylus redimitus</i>	*	*				350	780
<i>Mantidactylus rivicola</i>		*				700	850
<i>Mantidactylus ulcerosus</i>	*	*				375	760
<i>Mantidactylus</i> sp.					*	1875	1875
Rhacophoridae							
<i>Boophis albilabris</i>	*					760	760
<i>Boophis anjanaharibeensis</i>	*	*				350	700
<i>Boophis brachychir</i>	*	*	*	*		480	1550
<i>Boophis englaenderi</i>	*	*				450	650
<i>Boophis luteus</i>	*	*				450	780
<i>Boophis madagascariensis</i>	*	*				350	740
<i>Boophis marojezensis</i>	*	*	*	*		500	1560

TABLE 9-1. *Continued.*

Species	Transect (m)					Elevation (m)	
	450	750	1225	1625	1875	Min.	Max.
<i>Boophis reticulatus</i>	*					400	400
<i>Boophis rappiodes</i>	*	*	*	*		500	1560
<i>Boophis tephraeomystax</i>	Mandena					80	80
<i>Boophis</i> sp. 1	*					350	350
<i>Boophis</i> sp. 2	*					525	525
Reptilia							
Gekkonidae							
<i>Ebenavia inunguis</i>	*	*				350	730
<i>Geckolepis maculata</i>	*					350	375
<i>Blaesodactylus antongilensis</i>	*					350	520
<i>Lygodactylus miops</i>	*	*				470	750
<i>Microscalabotes bivittis</i>	*					480	480
<i>Paroedura gracilis</i>	*	*				350	800
<i>Phelsuma guttata</i>	*	*				250	850
<i>Phelsuma laticauda</i>	Mandena					100	100
<i>Phelsuma lineata</i>	*		*		*	1225	1850
<i>Phelsuma madagascariensis</i>	*					150	375
<i>Phelsuma pusilla</i>		*				100	600
<i>Phelsuma quadriocellata</i>		*				710	800
<i>Uroplatus ebenau</i>			*	*	*	1150	1950
<i>Uroplatus fimbriatus</i>	*	*				360	750
<i>Uroplatus lineatus</i>	*	*				350	720
<i>Uroplatus sikorae</i>		*	*			720	1200
<i>Uroplatus</i> sp.	*					380	550
Chamaeleonidae							
<i>Brookesia betschi</i>			*	*		1150	1650
<i>Brookesia griveaudi</i>	*	*				350	950
<i>Brookesia karchei</i>	*	*				380	850
<i>Brookesia minima</i>	*	*	*	*		450	1550
<i>Brookesia vadoni</i>		*	*			850	1150
<i>Calumma</i> cf. <i>brevicornis</i>					*	1800	2130
<i>Calumma boettgeri</i>			*			1100	1200
<i>Calumma cucullata</i>	*	*				440	720
<i>Calumma gastrotaenia</i>	*	*	*	*		450	1675
<i>Calumma</i> cf. <i>malthe</i>			*	*		1200	1570
<i>Calumma nasuta</i>	*	*	*			350	1350
<i>Calumma peyrierasi</i>				*	*	1675	1950
<i>Furcifer pardalis</i>	*	*				80	680
Scincidae							
<i>Amphiglossus astrolabi</i>	1 km S of Mandena					70	100
<i>Amphiglossus intermedius</i>	*	*				480	720
<i>Amphiglossus macrocercus</i>			*		*	1225	1900
<i>Amphiglossus mandokava</i>	*					300	350
<i>Amphiglossus melanopleura</i>		*	*			575	1220
<i>Amphiglossus melanurus</i>	*	*				470	700
<i>Amphiglossus minutus</i>	*	*	*			450	1250
<i>Amphiglossus mouroundavae</i>		*				720	770
<i>Amphiglossus ornaticeps</i>		*				700	700
<i>Amphiglossus punctatus</i>		*				700	750
<i>Mabuya gravenhorstii</i>	Mandena					100	100
<i>Paracontias holomelas</i>	*					380	380
<i>Paracontias milloti</i>	*					300	300
<i>Pseudoacantias angelorum</i>		*				650	650
Cordylidae							
<i>Zonosaurus madagascariensis</i>	*	*				380	750
<i>Zonosaurus rufipes</i>	*	*				360	750
<i>Zonosaurus subunicolor</i>	*	*				375	700

TABLE 9-1. *Continued.*

Species	Transect (m)					Elevation (m)	
	450	750	1225	1625	1875	Min.	Max.
Boidae							
<i>Boa manditra</i>	*	*				350	780
Typhlopidae							
<i>Typhlops</i> sp.	*	*				470	700
<i>Typhlops ocellaris</i>		*				640	700
Colubridae							
<i>Alluaudina bellyi</i>		*				150	380
<i>Dromicodryas quadrilineatus</i>	2 km NW of Mandena ¹					200	200
<i>Geodipsas laphystia</i>	*	*				350	790
<i>Geodipsas</i> sp.	*	*		*		470	1560
<i>Ithycyphus miniatius</i>	4 km E of Andapa					800	800
<i>Leioheterodon madagascariensis</i>	2 km NW of Mandena ¹					200	200
<i>Liophidium torquatus</i>	1 km S of Mandena					70	70
<i>Liophidium rhodogaster</i>		*				650	850
<i>Liopholidophis epistibes</i>	*	*		*		150	1600
<i>Liopholidophis stumpffi</i>	*	*				350	600
<i>Liopholidophis</i> sp.			*		*	1250	1875
<i>Pararhadinaea albignaci</i>	*					300	300
<i>Pseudoxyrhopus heterurus</i>	*					350	350
<i>Pseudoxyrhopus microps</i>		*				700	790
<i>Pseudoxyrhopus tritaeniatus</i>		*				750	750
<i>Lycodryas arcifasciatus</i>		*				740	740
<i>Lycodryas betsileanus</i>	*					350	350
<i>Lycodryas gaimardi</i>		*				700	740

¹ Observation only.

versity of 113 species (Table 9-1). In addition, a further three species of amphibians and seven species of reptiles were recorded from outside but within 5 km of the park boundary (Mandena, Manantenina, or Andapa). Five amphibians and five reptiles represented undescribed species. One of these, *Pseudoacantias angelorum*, has been described subsequently by Nussbaum and Raxworthy (1995). We recorded 64 species that were not previously known from the region, of which 57 species are new records for the park. This previously unknown component of the PN de Marojejy herpetofauna represents 50% of the entire species sampled by us and reflects both the high species diversity of the area and the relatively low-intensity surveying that has been conducted previously within the park.

Maximum herpetofaunal species diversity was recorded at mid-elevation, at the 750 m transect (76 species), and minimum diversity was recorded at the 1875 m transect (12 species; Fig. 9-1). A total of 1,155 pitfall trap days yielded 39 individual amphibians and reptiles, giving an overall daily pitfall capture success rate of 3.4%. All 13 species sampled by pitfalls were also captured by

other survey methods. The pitfall trap capture data are given in Table 9-2.

Discussion

Species Recorded by Previous Surveys

Table 9-3 is a summary of the species previously reported from the PN de Marojejy in inventory lists published by Nicoll and Langrand (1989), Safford and Duckworth (1990), Blommers-Schlösser and Blanc (1991), and Glaw and Vences (1994, 1997). We could not confirm the presence (inside the park) of 21 amphibian and 6 reptile species reported by these authors. Some of these species are likely to have been misidentified, such as *Zonosaurus aeneus*, or may reflect alternative taxonomic determinations within groups (especially amphibians) that are easily confused. Potential examples include *Heterixalus betsileo*, *Laurentomantis horrida*, *Mantidactylus majori*, *M. pseudoasper*, and *M. spiniferus*. Resolution of these taxonomic problems will require examina-

TABLE 9-2. Pitfall line characteristics and capture results from the 1996 survey of the PN de Marojej.

Line characteristic	Characteristics and results by line number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Habitat type*	R	V	S	R	V	S	S	V	R	S	R	V	V	R	S
Elevation (m)	470	450	480	770	720	750	1220	1170	1250	1560	1580	1550	1875	1950	1850
Trap-days	88	88	88	88	88	88	77	77	77	77	77	77	55	55	55
Capture results															
<i>Plethodontohyla bipunctata</i>		4			4										
<i>Plethodontohyla coudreaui</i>				1											
<i>Plethodontohyla serratopalpebrosa</i>									3		3	1			
<i>Stumpffia tridactyla</i>		1			2		1								
<i>Stumpffia</i> sp.															
<i>Amphiglossus punctatus</i>						1									
<i>Amphiglossus minutus</i>			2	3				1	1						
<i>Amphiglossus melanopleura</i>								1						2	
<i>Amphiglossus melanurus</i>															
<i>Amphiglossus mouroundavae</i>						3									
<i>Amphiglossus intermedium</i>		1	1												
<i>Zonosaurus rufipes</i>	1														
<i>Brookesia griveaudi</i>		1													
Line totals (39 total)	5	5	4	5	5	1	3	1	3	1	3	1	0	2	0

* R = ridge crest; S = slope; V = valley bottom.

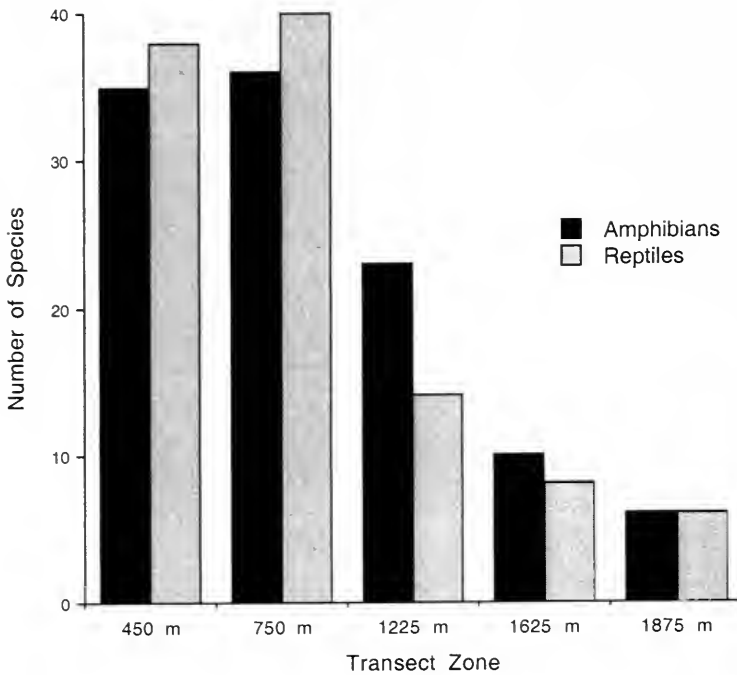


FIG. 9-1. Herpetofaunal diversity surveyed within each transect zone of the PN de Marojejy.

tion of the relevant collected material. In some instances, frog calls and live photographs are also required to confirm identifications, such as in the *Boophis goudoti* group frogs. For example, we suspect that some of our *B. reticulatus* material from Marojejy contain *B. rufioculis* and *B. burgeri* specimens, but diagnostic characters for these species include iris coloration and call characteristics (Glaw & Vences, 1997), which are no longer evident in the collected material.

Some of the Marojejy records reported by Blommers-Schlösser and Blanc (1991) and Glaw and Vences (1994) may include material collected outside the park. For example, we recorded eight species (8% of the total herpetofauna sampled by us in this area) at Mandena, Manantenina, or close to Andapa that were not sampled within the park itself. Finally, some Marojejy records may represent collecting efforts made on the eastern or northern sides of the massif. Brygoo (1978) recorded *Brookesia superciliaris* at Marojejy on the basis of a specimen from an unknown collector. This chameleon was not found on the summit trail during our surveys but was collected during a brief 1994 visit to the northern slopes of the Marojejy Massif at Antsirandrano (Ramanamanjato, pers. comm.). Because *Brookesia superciliaris* is easy to sample at other sites, we suspect this cha-

meleon may be absent from the eastern part of the PN de Marojejy, where we conducted our survey.

The herpetofaunal capture success rate of the pitfall traps (3.4%) is comparable with other eastern rain forest sites such as Andringitra (3.5%), Anjanaharibe-Sud (2.1%), and Andohahela (3.0%) (Raxworthy & Nussbaum, 1996; Raxworthy et al., 1998; Nussbaum et al., 1999). Trap success rates decreased with increasing elevation: 1.8% for lines above 1500 m, compared with 4.2% for lines between 450 and 1250 m elevation. No species was collected solely with pitfall traps, unlike prior studies that have used identical pitfall sampling methods (see references above). Probably the longer duration of transect surveying used in this study increased the sampling success of the other survey methods.

The species accumulation curves for each transect are plotted in Figure 9-2. For transects that were surveyed during both 1992 and 1996, the first part of the curve represents the 1992 sampling period. The longest period of sampling was 28 days, for the 750 m transect (however, for 6 days between 27 November and 2 December 1992, the majority of survey effort was made at other elevations), and the minimum period was 8 days for the 1875 m transect. The only transect that reached an obvious plateau with regard to

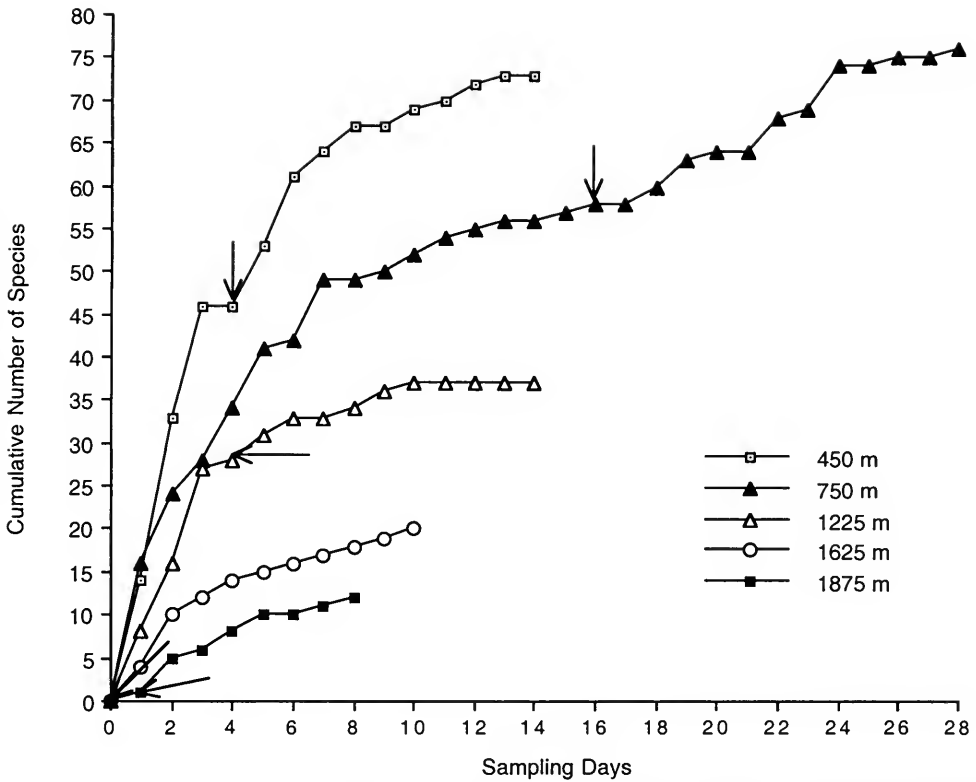


FIG. 9-2. Accumulation curves of herpetofaunal diversity (all sampling techniques) within each transect zone of the PN de Marojejy. Arrows indicate the end of the 1992 survey and the start of the 1996 survey, for each transect.

newly accumulated species was the 1225 m transect, during the final 4 days of sampling. However, for all transects, species were being accumulated at less than two species per day over the final 2 to 6 days. Although these results indicate that sampling cannot be considered complete for any transect (with the possible exception of 1225 m), visual extrapolation of these accumulation curves indicate that 80%–95% of the herpetofauna was sampled at each transect. The possibility that we did not find up to 27 previously recorded species within the park (but see comments above) also suggests that our 75 total days of survey effort was not sufficient time to achieve a complete herpetofaunal inventory of the PN de Marojejy.

Elevational Distribution

The large elevation range found within the park makes this one of the best areas in Madagascar to study elevational influences on patterns of species distribution. The elevational ef-

fect on distribution is well illustrated by the Chamaeleonidae. At elevations below 1000 m, the following species occur: *Brookesia griveaudi*, *B. karchei*, *Calumma cucullata*, and *Furcifer pardalis*. Middle elevation specialists (850–1650 m) are *Brookesia betschi*, *B. vadoni*, *Calumma boettgeri*, and *C. cf. malthe*. High-elevation specialists (1650–2132 m) are *Calumma cf. brevicornis* and *C. peyrierasi*. Three species have broader elevational distributions, occurring at both middle and lower elevations: *Brookesia minima*, *Calumma gastrotaenia*, and *C. nasuta*. Our surveys represent elevational range extensions for some species, such as *Calumma peyrierasi*, previously recorded at 1900–2000 m (Brygoo et al., 1974a) but found in this study at 1675 m. Two subspecies of *Calumma gastrotaenia* are known from within the park: *C. g. marojezensis* at 600 m (Brygoo et al., 1970a) and *C. g. guillaumeti* at 1300 m (Brygoo et al., 1974a). We found *Calumma gastrotaenia marojezensis* at the lower two transects, below 850 m, and *C. g. guillaumeti* at 1250–1675 m. The allopatric elevational distribution of these

TABLE 9-3. Published inventory lists for the herpetofauna of the PN de Marojejy and massif.

Species	Nicoll & Langrand (1989)	Safford & Duckworth (1990)	Blommers-Schlösser & Blanc (1991)	Glaw & Vences (1994 & 1997)	This study (1992 & 1996)
Amphibia					
Microhylidae					
<i>Anodontylia boulengeri</i>			*	*	
<i>Dyscophus insularis</i>	*		*	*	
<i>Platypelis barbouri</i>				*	*
<i>Platypelis grandis</i>			*	*	*
<i>Platypelis occultans</i>					*
<i>Platypelis pollicaris</i>			*	*	
<i>Platypelis isaratananensis</i>					*
<i>Platypelis tuberifera</i>			*	*	*
<i>Plethodontohyla bipunctata</i>					*
<i>Plethodontohyla coudreaui</i>					*
<i>Plethodontohyla minuta</i>	*		*	*	
<i>Plethodontohyla notosticta</i>	*		*	*	*
<i>Plethodontohyla ocellata</i>	*				*
<i>Plethodontohyla serratopalpebrosa</i>	*		*	*	*
<i>Rhombophryne testudo</i>	*		*	*	
<i>Stumpffia grandis</i>	*		*	*	*
<i>Stumpffia psologlossa</i>	*		*	?	
<i>Stumpffia roseifemorialis</i>	*			*	*
<i>Stumpffia tetradactyla</i>	*1			?	
<i>Stumpffia tridactyla</i>			*	*	*
<i>Stumpffia</i> sp.				*	*
Hyperoliidae					
<i>Heterixalus betsileo</i>			*	*	
<i>Heterixalus madagascariensis</i>					*
Ranidae					
<i>Ptychoadena mascareniensis</i>			*	*	*
Mantellidae					
<i>Laurentomantis horrida</i>	*		*	*	
<i>Laurentomantis malagasia</i>				*	*
<i>Mantella laevigata</i>				*	*
<i>Mantella madagascariensis</i>				*	*
<i>Mantella nigricans</i>					*
<i>Mantella</i> sp.				*	*
<i>Mantidactylus aglavei</i>					*
<i>Mantidactylus albofrenatus</i>			*	*	*
<i>Mantidactylus albolineatus</i>			*	*	
<i>Mantidactylus asper</i>	*		*	*	*
<i>Mantidactylus betsileanus</i>				*	*
<i>Mantidactylus bicalcaratus</i>	*		*	*	*
<i>Mantidactylus biporus</i>					*
<i>Mantidactylus cornutus</i>				*	*
<i>Mantidactylus curtus</i>			*	*	*
<i>Mantidactylus femoralis</i>			*	*	*
<i>Mantidactylus flavobrunneus</i>			*	*	
<i>Mantidactylus grandidieri</i>			*	*	*
<i>Mantidactylus grandisonae</i>				*	
<i>Mantidactylus granulatus</i>				*	
<i>Mantidactylus guttulatus</i>			*	*	
<i>Mantidactylus klenneri</i>	*		*	*	*
<i>Mantidactylus leucomaculatus</i>				*	*
<i>Mantidactylus liber</i>			*	*	*
<i>Mantidactylus lugubris</i>	*		*	*	*
<i>Mantidactylus luteus</i>			*	*	*
<i>Mantidactylus opiparis</i>					*

TABLE 9-3. *Continued.*

Species	Nicoll & Langrand (1989)	Safford & Duckworth (1990)	Blommers- Schlösser & Blanc (1991)	Glaw & Vences (1994 & 1997)	This study (1992 & 1996)
<i>Mantidactylus majori</i>			*	*	
<i>Mantidactylus peraccae</i>					*
<i>Mantidactylus pliciferus</i>			*	*	
<i>Mantidactylus pseudoasper</i>	*		*	*	
<i>Mantidactylus pulcher</i>			*	*	*
<i>Mantidactylus punctatus</i>			*	*	
<i>Mantidactylus rivicola</i>					*
<i>Mantidactylus redimitus</i>	*		*	*	*
<i>Mantidactylus spiniferus</i>			*	*	
<i>Mantidactylus ulcerosus</i>					*
<i>Mantidactylus</i> sp.					*
Rhacophoridae					
<i>Boophis albilabris</i>				*	*
<i>Boophis anjanaharibeensis</i>					*
<i>Boophis brachychir</i>					*
<i>Boophis</i> cf. <i>burgeri</i>				*	
<i>Boophis englaenderi</i>				*	*
<i>Boophis luteus</i>			*		*
<i>Boophis madagascariensis</i>			*	*	*
<i>Boophis majori</i>			*		
<i>Boophis marojezensis</i>				*	*
<i>Boophis rappiodes</i>					*
<i>Boophis reticulatus</i>					*
<i>Boophis tephraeomystax</i>					*
<i>Boophis</i> sp. 1					*
<i>Boophis</i> sp. 2					*
Reptilia					
Gekkonidae					
<i>Ebenavia inunguis</i>					*
<i>Geckolepis maculata</i>					*
<i>Blaesodactylus antongilensis</i>					*
<i>Lygodactylus miops</i>					*
<i>Microscalabotes bivittis</i>					*
<i>Paroedura gracilis</i>					*
<i>Phelsuma guttata</i>		*		*	*
<i>Phelsuma laticauda</i>					*
<i>Phelsuma madagascariensis</i>	*				*
<i>Phelsuma lineata</i>	*				*
<i>Phelsuma pusilla</i>					*
<i>Phelsuma quadriocellata</i>	*	*			*
<i>Uroplatus ebenau</i>					*
<i>Uroplatus fimbriatus</i>	*	*		*	*
<i>Uroplatus lineatus</i>					*
<i>Uroplatus sikorae</i>					*
<i>Uroplatus</i> sp.					*
Chamaeleonidae					
<i>Brookesia betschi</i>	*			*	*
<i>Brookesia griveaudi</i>	*	*		*	*
<i>Brookesia karchei</i>	*	*		*	*
<i>Brookesia minima</i>	*			*	*
<i>Brookesia superciliaris</i>	*			*	
<i>Brookesia vadoni</i>					*
<i>Calumma bifidus</i>	*			*	
<i>Calumma</i> cf. <i>brevicornis</i>	*			*	*
<i>Calumma boettgeri</i>					*
<i>Calumma cucullata</i>					*

TABLE 9-3. *Continued.*

Species	Nicoll & Langrand (1989)	Safford & Duckworth (1990)	Blommers- Schlösser & Blanc (1991)	Glaw & Vences (1994 & 1997)	This study (1992 & 1996)
<i>Calumma gastrotaenia</i>	*	*		*	*
<i>Calumma globifer</i>	*			*	
<i>Calumma</i> cf. <i>malthe</i>	*	*		*	*
<i>Calumma nasuta</i>	*	*		*	*
<i>Calumma peyrierasi</i>	*			*	*
<i>Furcifer pardalis</i>		*		*	*
Scincidae					
<i>Amphiglossus astrolabi</i>					*
<i>Amphiglossus intermedius</i>					*
<i>Amphiglossus macrocerus</i>					*
<i>Amphiglossus mandokava</i>					*
<i>Amphiglossus melanopleura</i>					*
<i>Amphiglossus melanurus</i>					*
<i>Amphiglossus minutus</i>					*
<i>Amphiglossus mouroundavae</i>					*
<i>Amphiglossus ornaticeps</i>					*
<i>Amphiglossus punctatus</i>					*
<i>Mabuya gravenhorstii</i>					*
<i>Paracontias holomelas</i>					*
<i>Paracontias milloti</i>					*
<i>Pseudoacantias angelorum</i>					*
Cordylidae					
<i>Zonosaurus aeneus</i>		*			
<i>Zonosaurus madagascariensis</i>		*			*
<i>Zonosaurus rufipes</i>	*	*		*	*
<i>Zonosaurus subunicolor</i>					*
Boidae					
<i>Boa manditra</i>	*	*		*	*
Typhlopidae					
<i>Typhlops</i> sp.					*
<i>Typhlops ocellaris</i>					*
Colubridae					
<i>Alluaudina bellyi</i>				*	*
<i>Dromicodryas quadrilineatus</i>					*2
<i>Geodipsas infralineata</i>				*	
<i>Geodipsas laphystia</i>					*
<i>Geodipsas</i> sp.					*
<i>Ithyocyphus blanci</i>				*	
<i>Ithyocyphus miniatus</i>					*
<i>Leioheterodon madagascariensis</i>	*	*		*	*2
<i>Liophidium torquatus</i>		*			*
<i>Liophidium rhodogaster</i>					*
<i>Liopholidophis epistibes</i>	*	*		*	*
<i>Liopholidophis stumpffi</i>					*
<i>Liopholidophis</i> sp.					*
<i>Pararhadinaea melanogaster</i>	*			*	*
<i>Pseudoxyrhopus heterurus</i>					*
<i>Pseudoxyrhopus microps</i>					*
<i>Pseudoxyrhopus tritaeniatus</i>				*	*
<i>Lycodryas arctifasciatus</i>					*
<i>Lycodryas betsileanus</i>		*			*
<i>Lycodryas gaimardi</i>				*	*

NOTE—The reported records in Nicoll and Langrand (1989) are based on published literature and personal observations. Those in Safford and Duckworth (1990) are based on personal observations. Those in Blommers-Schlösser

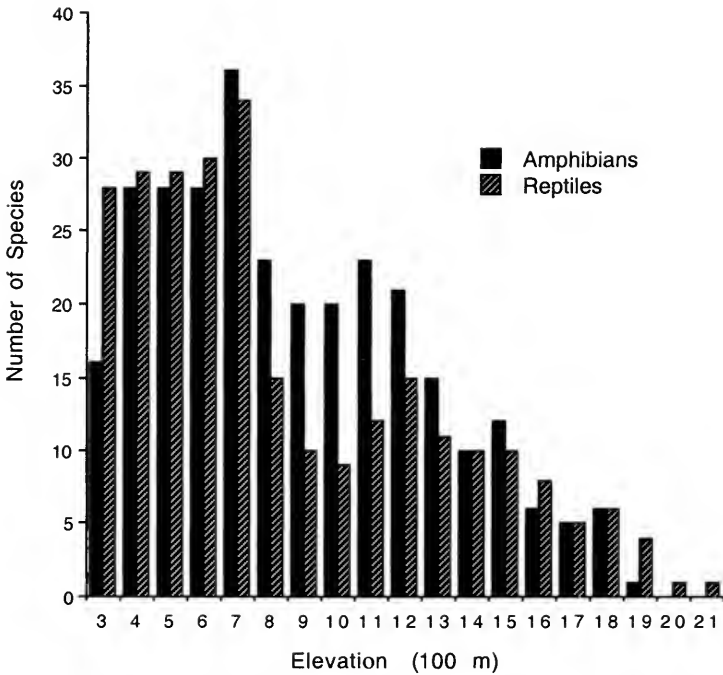


FIG. 9-3. Species diversity as a function of elevation, for amphibians and reptiles.

subspecies suggests that they are probably sibling species, but the taxonomic status of these forms awaits further study of the collected material. Böhme et al. (1997) have recently suggested that all *Calumma gastrotaenia* subspecies are independent species.

Fig. 9-3 shows the influence of elevation on species diversity. The species diversities of amphibians, reptiles, and both groups combined are shown for 100 m elevational increments, with the minimum and maximum elevations (recorded by us in the PN de Marojejy) used to calculate the elevational range of each species. This method makes the assumption that each species is distributed continuously between the minimum and maximum elevation recorded. The diversity of amphibians and reptiles increases from the lower elevation, peaking, for both groups, at the 700 m elevational band (700–799 m). Above the 700 m band, diversity drops off quickly until reduced to

just a single species (*Calumma cf. brevicornis*) above 2000 m.

The 700 m Marojejy mid-elevation bulge in species diversity is very similar to that described by Raxworthy and Nussbaum (1996a) for the PN d'Andringitra (maximum elevation 2658 m), where maximum species diversity was recorded at 800 m for amphibians and at 700 m for reptiles (but, in this study, transects below 700 m were not included, since they fell outside the park limit; thus, the increase phase of the bulge was weakly confirmed by only a single 100 m increment for amphibians).

However, we note that the Marojejy mid-elevation bulge in diversity might represent an artifact of the greater sampling time spent at the 750 m elevation transect (28 days) than at the 450 and 1225 m transects (14 days). Despite the 14 extra days of sampling at the 750 m transect, only three more species were recorded than at the 450 m

←

and Blanc (1991) are based on museum specimens. Those in Glaw and Vences (1994) are based on published literature, including Blommers-Schlösser and Blanc (1991), and additional collecting.

¹ Authors almost certainly meant *Stumpffia tridactyla* (*S. tetradactyla* had not yet been described at that time).

² Observations without vouchers, made by this survey.

TABLE 9-4. Distribution of Marojejy species (found in this study) at four other protected areas (see text for literature sources).

Species	Montagne d'Ambre	Anjanaharibe- Sud	Andringitra	Andohahela
Amphibia				
Microhylidae				
<i>Platypelis barbouri</i>		*		
<i>Platypelis grandis</i>	*	*		*
<i>Platypelis occultans</i>		*		
<i>Platypelis tsaratananaensis</i>		*		
<i>Platypelis tuberifera</i>		*	*	
<i>Plethodontohyla bipunctata</i>			*	*
<i>Plethodontohyla notosticta</i>		*	*	
<i>Plethodontohyla serratopalpebrosa</i>		*	*	
<i>Stumpffia grandis</i>	*	*		
<i>Stumpffia roseifemoralis</i>		*		
Mantellidae				
<i>Mantidactylus aglavei</i>		*	*	*
<i>Mantidactylus albofrenatus</i>		*		
<i>Mantidactylus asper</i>		*	*	*
<i>Mantidactylus betsileanus</i>		*	*	*
<i>Mantidactylus bicalcaratus</i>	*	*	*	*
<i>Mantidactylus biporus</i>		*	*	*
<i>Mantidactylus comutus</i>		*		
<i>Mantidactylus curtus</i>	*			
<i>Mantidactylus femoralis</i>	*	*	*	*
<i>Mantidactylus grandidieri</i>		*	*	
<i>Mantidactylus grandisonae</i>		*	*	
<i>Mantidactylus klemmeri</i>		*		
<i>Mantidactylus liber</i>	*		*	
<i>Mantidactylus lugubris</i>			*	*
<i>Mantidactylus luteus</i>		*	*	*
<i>Mantidactylus opiparis</i>		*	*	*
<i>Mantidactylus peraccae</i>		*	*	
<i>Mantidactylus pulcher</i>		*	*	
<i>Mantidactylus redimitus</i>		*	*	
<i>Mantidactylus rivicola</i>		*		
<i>Mantidactylus ulcerosus</i>		*	*	*
Rhacophoridae				
<i>Boophis albilabris</i>		*	*	*
<i>Boophis anjanaharibeensis</i>		*		
<i>Boophis brachyichir</i>		*		
<i>Boophis luteus</i>	*	*	*	*
<i>Boophis madagascariensis</i>	*	*	*	*
<i>Boophis marojezensis</i>		*		
<i>Boophis rappiodes</i>		*	*	
<i>Boophis reticulatus</i>		*	*	*
Reptilia				
Gekkonidae				
<i>Ebenavia inunguis</i>	*	*		
<i>Geckolepis maculata</i>	*			
<i>Lygodactylus miops</i>				
<i>Paroedura gracilis</i>		*		
<i>Phelsuma guttata</i>		*		
<i>Phelsuma lineata</i>	*	*	*	
<i>Phelsuma madagascariensis</i>	*			
<i>Phelsuma quadriocellata</i>		*	*	*
<i>Uroplatus ebenau</i>	*	*	*	
<i>Uroplatus fimbriatus</i>	*			
<i>Uroplatus sikorae</i>	*	*		*

TABLE 9-4. *Continued.*

Species	Montagne d'Ambre	Anjanaharibe-Sud	Andringitra	Andohahela
Chamaeleonidae				
<i>Brookesia betschi</i>		*		
<i>Brookesia vadoni</i>		*		
<i>Calumma boettgeri</i>	*			
<i>Calumma gastrotaenia</i>		*	*	*
<i>Calumma malthe</i>		*		
<i>Calumma nasuta</i>	*	*	*	*
<i>Furcifer pardalis</i>	*	*		
Scincidae				
<i>Amphiglossus macrocercus</i>			*	*
<i>Amphiglossus melanopleura</i>	*	*	*	*
<i>Amphiglossus melanurus</i>	*	*	*	
<i>Amphiglossus minutus</i>		*		
<i>Amphiglossus mouroldavae</i>	*	*		
<i>Amphiglossus ornaticeps</i>				*
<i>Amphiglossus punctatus</i>		*	*	*
<i>Mabuya gravenhorstii</i>		*	*	*
Cordylidae				
<i>Zonosaurus madagascariensis</i>		*		
Boidae				
<i>Boa manditra</i>	*	*		*
Colubridae				
<i>Alluaudina bellyi</i>	*			
<i>Liophidium rhodogaster</i>	*	*	*	
<i>Liopholidophis epistibes</i>		*	*	
<i>Lycodryas arctifasciatus</i>	*			*
<i>Lycodryas betsileanus</i>		*		
<i>Pseudoxyrhopus microps</i>	*	*		
<i>Pseudoxyrhopus tritaeniatus</i>		*		*
Total	26	61	37	28

transect (Fig. 9-1). For the first 14 days of sampling, the species accumulation curves show greatest species diversity at the 450 m transect (Fig. 9-2). These sampling curves suggest species diversity actually decreases with elevation for all five of our surveyed transects. More data are clearly needed to determine trends in herpetofaunal diversity below 800 m elevation, especially to confirm the increase phase. Further discussion of elevational patterns of species diversity is given by Raxworthy et al. (1998).

Comparisons with Other Sites

On the basis of our field surveys during the last 6 years, we provide here a comparison of the shared herpetofaunal diversity between the PN de Marojejy and four other protected rain forest areas: PN de la Montagne d'Ambre (Raxworthy &

Nussbaum, 1994); PN d'Andringitra (Raxworthy & Nussbaum, 1996); Réserve Spécial (RS) d'Anjanaharibe-Sud (Raxworthy et al., 1998); and PN d'Andohahela (Nussbaum et al., 1999) (Table 9-4). The elevations surveyed at these sites varied from 400 to 2300 m. These reserves share many vegetation characteristics, such as moist rain forest at middle and low elevations and bamboo (and in some cases ericoid heathland) at higher elevations. The majority of species shared among these sites are low- and mid-elevation species. The PN de Marojejy and the RS d'Anjanaharibe-Sud have the highest number of shared species (61), and the PN de Marojejy and the RNI d'Andohahela have the lowest number (28). This corresponds to the geographic distance between these sites. However, the PN de Marojejy shares fewer species with the PN de la Montagne d'Ambre, just 200 km from Marojejy, than with PN d'Andringitra, which is 800 km from Marojejy. The herpetofauna of Mon-

tagne d'Ambre includes many species endemic to northwestern Madagascar (sometimes called the "Sambirano Domain"), whereas Andringitra and Marojejy share many eastern endemic species. A more detailed description of patterns of endemism for the rain forest regions of Madagascar is given by Raxworthy and Nussbaum (1996b, 1997).

The PN de Marojejy herpetofauna exhibit a significant number of taxa that are possibly endemic to the massif: *Stumpffia* sp., *Mantella* sp., *Mantidactylus* sp., *Boophis* sp. 1, *Boophis* sp. 2, *Uroplatus* sp., *Pseudocantias angelorum*, *Brookesia karchei*, *Calumma* cf. *brevicornis*, *C. gastrotaenia guillaumeti*, *C. peyrierasi*, *Geodipsas* sp., and *Liopholidophis* sp. These 13 taxa make up 12% of the park's herpetofauna, a degree of site endemism comparable with other sites, such as PN d'Andringitra (13%; Raxworthy & Nussbaum, 1996a). Of additional significance was the discovery of the rare and extremely poorly known gecko *Microscalabotes bivittis*, which represents the first record of this species in northern Madagascar (the only other known localities are Périnet and the Betsileo region; Pasteur, 1967).

Conservation Issues for the PN de Marojejy Region

PN de Marojejy protects at least 113 species of reptiles and amphibians. This is the highest diversity we have recorded so far within any of the protected areas of Madagascar. It is also likely that all 10 species that we found close to the park boundary occur within this protected area and that some of the 26 other species reported from Marojejy (that we failed to find) are also present. The only protected area that is likely to have more species than the PN de Marojejy is the RNI de Tsaratanana, which has an even greater elevational range (227 to 2876 m) and a comparable surface area (48,622 ha) (Nicoll & Langrand, 1989). These two "megadiversity" protected areas must play a key role within the future protected areas network of Madagascar.

The Andapa Basin, which is extremely favorable for paddy rice cultivation, has previously provided some protection for the preservation of forest on the western slopes of the park, by keeping local cultivation activities centered on the basin itself. However, continuing demographic growth, along with the migration of new settlers, constitutes an increased threat because of the need

for new agricultural areas. For the eastern slopes of the Marojejy Massif, slash and burn (*tavy*) is an important agricultural method, and much of the lowland forest in peripheral areas of the park has now been transformed into agricultural areas. We also noted many abandoned clearings produced by slash-and-burn activities within the park, especially at elevations below 600 m. According to one of our guides, this agricultural activity had continued until 1994.

Hunting is another threat to the park. According to our guides and some village elders, hunting groups of 5 to 10 men live in the forest for at least a week. These groups clear areas of forest to make camping sites where they can build shelters and dry bush meat. During our last visit, we found many cleared areas and trails that were made by hunters. The illicit exploitation of some resources, such as lemurs, might not be sustainable, and the frequent passages of these hunters into the park is also damaging the forest habitat itself. As an example, *Pandanus* palm fronds are used for the construction of temporary shelters, but *Pandanus* also provides the microhabitat or refugia for several species of amphibians and reptiles within the PN de Marojejy, such as *Mantidactylus pulcher*, *M. bicalcaratus*, *Platypelis tuberifera*, *Phelsuma lineata*, and *P. quadriocellata*.

The recent change in status of Marojejy to a Parc National will give local communities new opportunities to generate income from ecotourism, as tourists are allowed access to the park. However, studies to assess the environmental impact of ecotourism are urgently needed. The summit trail, currently the only access route to the summit, will inevitably be used heavily by tourists unless alternative routes are established. It is not difficult to imagine this trail quickly becoming damaged by tourists, making further research or long-term monitoring impossible at the sites of our transects. In view of the large investment of scientific research that has already been made along this trail over a period of 30 years, we strongly recommend that an alternative tourist access route be established within the newly created park.

The PN de Marojejy is the main source of water for many of the villages in the surrounding areas, and this water source also offers the possibility that irrigated paddy fields can be developed in the deforested valley bottoms. Increased cultivation of rice in paddy fields may help to reduce the degree of slash-and-burn hill rice cultivation, which continues to threaten the lowest-elevation

forests at the periphery of the park. Similar to the situation found in most of the rain forest protected areas of Madagascar, the low-elevation herpetofauna of the PN de Marojezy is the most vulnerable to habitat loss or degradation; therefore, this peripheral habitat of this park must be adequately protected.

Acknowledgments

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Literature Cited

- BÖHME, W. 1997. Eine neue Chamäleonart aus der *Calumma gastrotænia*—verwandschaft Ost Madagaskars. *Herpetofauna*, **19**: 5–10.
- BLOMMERS-SCHLÖSSER, R. M. A., AND C. P. BLANC. 1991. Amphibiens (première partie). Faune de Madagascar, **75**(1): 1–385.
- BRYGOO, E. R. 1978. Reptiles Sauriens Chamaelonidae. Genre *Brookesia* et complément pour le genre *Chamaeleo*. Faune de Madagascar, **47**: 1–174.
- BRYGOO, E. R., C. P. BLANC, AND C. A. DOMERGUE. 1970a. Notes sur les *Chamaeleo* de Madagascar. VI. *C. gastrotænia marojezensis* n. subsp. d'un massif montagneux du Nord-Est. *Annales de l'Université de Madagascar, Série Sciences de la Nature et Mathématiques*, **7**: 273–278.
- . 1970b. Notes sur les *Brookesia* de Madagascar. III. *B. karchei* n.sp. Du massif du Marojezy. *Annales de l'Université de Madagascar, Série Sciences de la Nature et Mathématiques*, **7**: 267–271.
- . 1974a. Notes sur les *Chamaeleo* de Madagascar
- XII. Caméléons du Marojezy. *C. peyrierasi* n.sp. et *C. gastrotænia guillaumeti* n.subsp. (Reptilia, Squamata, Chamaeleonidae). *Bulletin de l'Académie Malgache*, **51**(1): 150–164.
- . 1974b. Notes sur les *Brookesia* de Madagascar VIII. *Brookesia* du Marojezy. *B. betschi* et *B. griveaudi* n.sp. (Reptilia, Squamata, Chamaeleonidae). *Bulletin de l'Académie Malgache*, **51**(1): 151–166.
- DOMERGUE, C. A. 1984. Notes sur les serpents de la région malgache. IV. Le genre *Pararhadinaea* Boettger, 1898. Description d'une espèce et d'une sous-espèce nouvelles. *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 4th série, sect. A, **6**: 149–157.
- . 1988. Notes sur les serpents de la région malgache. VIII. Colubridés nouveaux. *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 4th série, sect. A, **10**: 135–146.
- GLAW, F., AND M. VENCES. 1994. A Fieldguide to the Amphibians and Reptiles of Madagascar, 2nd ed. Moss Druck, Leverkusen, Germany, 480 pp.
- . 1997. Neue ergebnisse zur *Boophis goudoti*-Gruppe aus Madagaskar: Bioakustik, fortpflanzungsstrategien und beschreibung von *Boophis ruftoculis* sp. nov. *Salamanandra*, **32**: 225–242.
- GUILLAUMET, J.-L., J.-M. BETSCH, C. BLANC, P. MORAT, AND A. PEYRIERAS. 1975. Etude des écosystèmes montagnards dans la région malgache. III. Le Marojezy. IV. L'Iremo et l'Ibity. Géomorphologie, climatologie, faune et flore (Campagne RCP 225, 1972–1973). *Bulletin de Muséum National d'Histoire Naturelle*, 3rd série, **309**(Écologie Générale 25): 29–67.
- JENKINS, M. 1987. Madagascar: An Environmental Profile. IUCN, Cambridge, 374 pp.
- NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la Conservation et des Aires Protégées. World Wide Fund for Nature, Gland, 374 pp.
- NUSSBAUM, R. A., AND C. J. RAXWORTHY. 1995. Review of the Scincine genus *Pseudoacantias* Barboza du Bodge (Reptilia: Sauria: Scincidae) of Madagascar. *Herpetologica*, **51**(1): 91–99.
- NUSSBAUM, R. A., C. J. RAXWORTHY, A. P. RASELIMANANA, AND J.-B. RAMANAMANJATO. 1999. Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, pp. 155–173. *In* Goodman, S. M., ed., A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With Reference to Elevational Variation. *Fieldiana: Zoology*, n.s., **94**: 1–297.
- PASTEUR, G. 1967. Redécouverte d'un genre de sauriens malgache: *Microscalabotes* (Gekkonidés). *Annales de l'Université de Madagascar, Série Sciences de la Nature et Mathématiques*, **5**: 75–78.
- RAXWORTHY, C. J., AND R. A. NUSSBAUM. 1994. A rain-forest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological Conservation*, **69**: 65–73.
- . 1996a. Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: A study of elevational distribution and local endemism, pp. 158–170. *In* Goodman, S. M., ed., A Floral and Faunal Inventory of the Eastern Slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With

- Reference to Elevational Variation. *Fieldiana: Zoology*, n.s., **85**: 1–319.
- . 1996b. Patterns of endemism for terrestrial vertebrates in eastern Madagascar, pp. 368–384. *In* Lourenço, W. R., ed., *Biogéographie de Madagascar*. ORSTOM, Paris.
- . 1997. Biogeographic patterns of reptiles in eastern Madagascar, pp. 124–141. *In* Goodman, S. M., and B. D. Patterson, eds, *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington, D.C.
- RAXWORTHY, C. J., F. ANDREONE, R. A. NUSSBAUM, N. RABISOA, AND H. RANDRIAMHAZO. 1998. Amphibians and reptiles of the Anjanaharibe Massif, Madagascar: Elevational distribution and regional endemism, pp. 79–92. *In* Goodman, S. M., ed., *A Floral and Faunal Inventory of the Eastern Slopes of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With Reference to Elevational Variation*. *Fieldiana: Zoology*, n.s., **90**: 1–246.
- SAFFORD, R., AND W. DUCKWORTH. 1990. Systematic list of reptiles recorded at Marojejy, pp. 136–138. *In* Safford, R., and W. Duckworth, eds., *A wildlife survey of Marojejy Nature Reserve, Madagascar*, International Council for Bird Preservation study report no. 40. International Council for Bird Preservation, Cambridge, U.K.
- VENCES, M., F. GLAW, AND F. ANDREONE. 1997. Descriptions of two new frogs of the genus *Mantidactylus* from Madagascar, with notes on *Mantidactylus klemmeri* (Guibé, 1974) and *Mantidactylus webbi* (Grandidson, 1953) (Amphibia, Ranidae, Mantellinae). *Alytes*, **14**: 130–146.

Chapter 10

Birds of the Parc National de Marojejy, Madagascar: With Reference to Elevational Distribution

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Abstract

Between 4 October and 20 November 1996, we evaluated bird species presence, relative abundance, and bird community variation with altitude and vegetation type on the southeastern slopes of the Parc National (PN) de Marojejy. This site, located in northeastern Madagascar, occurs in the eastern humid formation and encompasses a wide variety of vegetational formations. We collected data in elevational transect zones centered at 450, 775, 1250, 1625, and 1875 m, using mist-netting, point counts, call playback, and direct observation.

Eighty-four species, including 72 forest-limited birds, were recorded from the park. Species richness decreased with increasing elevation, as did canopy height, whereas shrub density increased. Of the 84 species recorded, 21 were detected only by direct observation and 1 only by mist-netting. Call-playback recording was ineffective. The only new species recorded during the survey for the reserve is *Bernieria tenebrosa*; *Newtonia fanovanae* was recorded subsequently. Mist-net capture rates in the PN de Marojejy were higher at the upper elevations than at other sites. Arboreal frugivores were most abundant at lower elevations. In degraded forest at 450 m, canopy and understory insectivores tended to be less frequent than in adjacent primary forest. Survey efficiency may have been reduced by poor weather.

Résumé

Entre le 4 octobre et le 20 novembre 1996, la présence des espèces d'oiseaux, l'abondance relative, et la variation de la communauté des oiseaux avec l'altitude et le type de végétation ont été évaluées sur les versants sud-est du Parc National de Marojejy. Ce site, situé au nord-est de Madagascar, fait partie des formations humides de l'est et contient une large variété de ces formations végétales. Les données sont collectées dans les zones de transects centrées à 450, 775, 1250, 1625, et 1875 m d'altitude, en utilisant les filets de capture, les comptages par point, l'appel par play-back, et l'observation directe.

Quatre-vingt-quatre (84) espèces dont 72 espèces limitées aux forêts ont été recensées dans le Parc. Sur ces 84 espèces inventoriées, 21 ont été découvertes seulement par observation directe et une espèce par filet de capture. L'appel par play-back a été inefficace. La seule nouvelle espèce recensée durant l'inventaire a été *Bernieria tenebrosa*; *Newtonia fanovanae*

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a été trouvé ultérieurement. Les seuils de captures par filet ont été plus élevés dans les hautes altitudes par rapport aux autres sites. Les frugivores arboricoles ont été plus abondantes dans les basses altitudes. Dans la forêt dégradée, à 450 m d'altitude, les insectivores des canopées et des sous-bois tendaient à être moins fréquentes que dans la forêt primaire voisine. L'efficacité de l'inventaire pourrait être réduite à cause du mauvais temps.

Introduction

In recent years there has been a rapid increase in studies and available information on the extant birds of Madagascar, including, for example, re-discoveries of species that were thought to be exceptionally rare and perhaps on the verge of extinction (e.g., Thorstrom et al., 1995), descriptions of two new species and a genus new to science (Goodman et al., 1995, 1997a), studies on behavior and breeding systems (Prum & Razafindratsita, 1997), and systematic studies (Schulenberg et al., 1993; Fjeldså et al., 1999; Goodman & Weight, in press). Perhaps the best indication of this rapid growth in information and general interest in the birds of the island is the production of no less than five field guides to Malagasy birds over the course of the past decade (Langrand, 1990, 1995; Yamagishi et al., 1997; Morris & Hawkins, 1998; Sinclair & Langrand, 1998). After primates, birds are the most frequently researched group of vertebrates in the protected areas system of Madagascar (ANGAP, 1998). On the basis of the efforts of national and foreign ornithologists working on the island, the avifauna of Madagascar has become much better understood over the past decade.

Since the early 1990s, there has been a resurgence in interest among biologists in documenting the fauna and flora of the island, particularly in forested regions that have never been properly surveyed or for groups that have not been adequately studied. A number of recent inventories have examined the distribution of biota along elevational gradients on various mountains in the eastern humid forests. All of these surveys were conducted in protected areas or in soon-to-become protected areas, both to document the plants and animals occurring locally and to provide baseline data for future biological monitoring. Ornithological surveys were conducted at the following sites (from north to south, Fig. 10-1): Parc National (PN) de la Montagne d'Ambre (Goodman et al., 1996a), the Réserve Spéciale (RS) d'Anjanaharibe-Sud (Hawkins et al., 1998), PN de Masoala (Thorstrom & Watson, 1997), RS

d'Ambatovaky (Thompson & Evans, 1992), Réserve Naturelle Intégrale (RNI) de Zahamena (Hawkins et al., in press), PN d'Andringitra (Goodman & Putnam, 1996; Goodman & Rasolonandrasana, in press), and the PN d'Andohahela (Goodman et al., 1997b; Hawkins & Goodman, 1999). As part of this series of inventories, we conducted a survey of the birds occurring in the PN de Marojejy, the results of which are presented here. Given that the sites listed above span the complete length of the eastern humid forests of the island, encompassing nearly 12° of latitude, and given that the complete elevational range of each mountain was surveyed, interesting questions can be addressed concerning the relationship between altitudinal and latitudinal gradients over a region that is relatively homogeneous with regard to the botanical community (Koechlin et al., 1974).

Review of Ornithological Research in the Marojejy Region

The Marojejy Massif, one of the ornithologically best-known mountains on Madagascar, harbors a large number of endemic Malagasy bird species. The current level of information on the avifauna of the site is based on the work of numerous researchers over the course of nearly 70 years. The following summary is a historical overview of the ornithological research conducted in the Marojejy region.

The earliest known avifaunistic work in the Marojejy area was conducted by members of the Franco-Anglo-Américaine (FAA) expedition, who visited many different localities across the island over the course of 26 months between 1929 and 1931. Between 19 August and 7 September 1930, they collected specimens at a site "one day west" of Andapa (Rand, 1932, 1936). This description has been interpreted as indicating a locality lying very close to the modern RS d'Anjanaharibe-Sud. Although the camp was reported to be at 1800 m and at the upper limit of rain forest, many of the

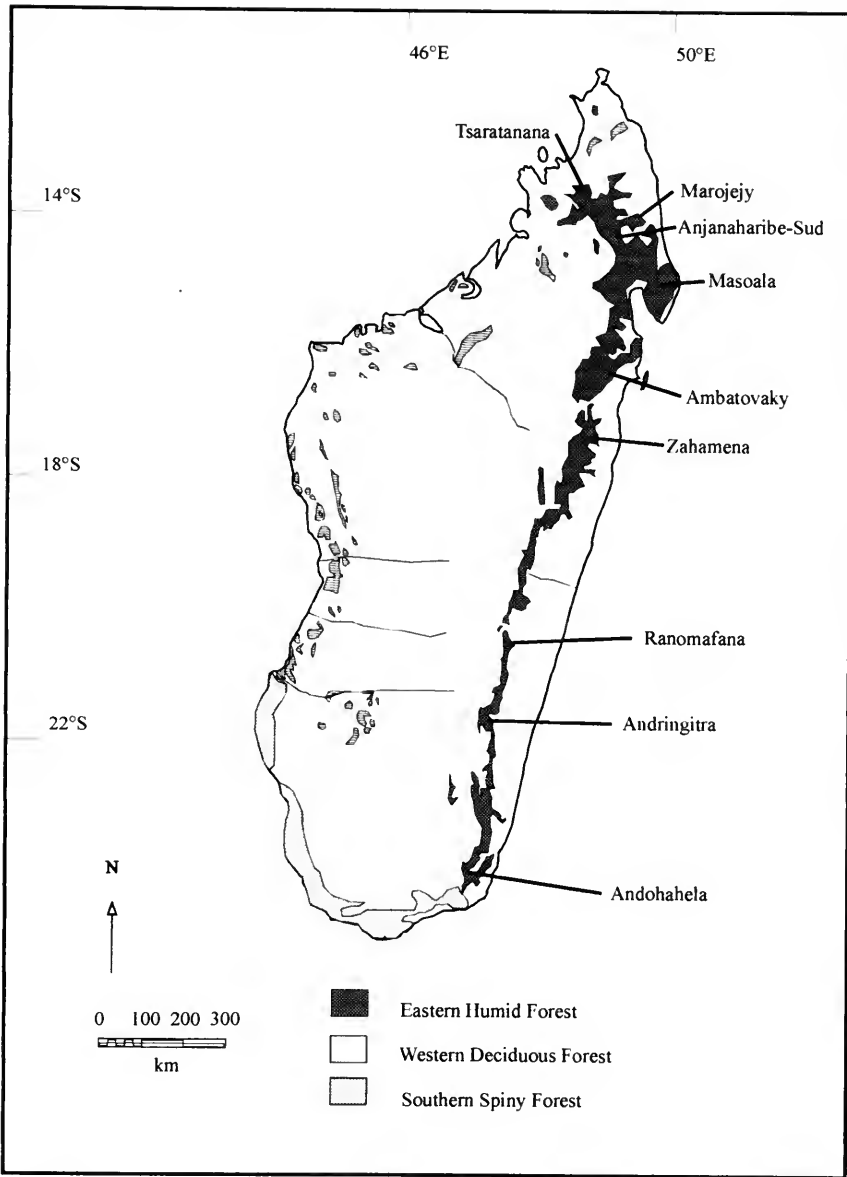


FIG. 10-1. Map showing the position of the Parc National de Marojejy and several other sites in the eastern humid forest in which the bird faunas have been studied along elevational transects.

species they reported from the site are characteristic, on the basis of specimen material, of lower elevations. It is probable that specimens were brought in from a wide range of altitudes (Hawkins et al., 1998). The bird specimens collected by the Mission FAA were divided between the American Museum of Natural History, New York; the British Museum (Natural History)—now known as the Natural History Museum, London;

and the Muséum National d'Histoire Naturelle, Paris.

In 1958, P. Griveaud visited the reserve for entomological studies, but also made some observations on the avifauna (Griveaud, 1960). He also made a small collection of birds. We have been unable to locate the Griveaud collection in a natural history museum. In September 1972, an ornithological team visited the southeastern portion

of the reserve and made several important observations, which are reported in Benson et al. (1976, 1977).

On the basis of a 1987 visit to the Marojejy Massif, made in the context of the World Wide Fund for Nature–Madagascar biodiversity and protected areas program, Nicoll and Langrand (1989) reported a list of 103 bird species. This list was partially reproduced by Jenkins (1990).

Between August and late October 1988, a student expedition from Cambridge University (United Kingdom), in collaboration with Malagasy researchers, conducted a biological inventory of several different sites within the reserve (Safford & Duckworth, 1990). They reported the presence of 104 bird species in and around the reserve. One of the many noteworthy findings of this group was the rediscovery of the Madagascar Serpent Eagle, *Eutriorchis astur*, which had not been reliably recorded since the 1930s (Sheldon & Duckworth, 1990).

Between mid-October and early December 1994, a multidisciplinary expedition conducted a biological inventory of the RS d'Anjanaharibe-Sud, about 40 km from the western slopes of the PN de Marojejy. This group visited four different sites on the eastern slopes of the Anjanaharibe-Sud Massif, between 875 m and the summital zone at 1950 m. The ornithological results of this survey have been published as two chapters in a monograph on the site: a general overview with natural history information and density estimates for selected species (Hawkins et al., 1998), and information on the birds of prey (Thiollay, 1998). The ornithological data from the RS d'Anjanaharibe-Sud provide an important opportunity for comparison with data obtained in the PN de Marojejy, and cross-references between these two sites are made throughout the current chapter.

Goals of the Study

In light of the intense rate of deforestation in Madagascar, it is critical to understand aspects of the island's bird fauna in relation to habitat requirements, geographical and elevational distribution, and relative densities. Our study had four main research objectives: (1) to add to previously available information on the birds occurring in the PN de Marojejy; (2) to determine the composition of bird communities across elevational gradients;

(3) to determine the relative abundance of forest species at different elevations; and (4) to compare various surveyed mountains on the eastern portion of the island with respect to the relationship between elevation and species richness along latitudinal gradients.

Study Site and Methods

Study Site

Our survey of the PN de Marojejy was conducted as part of the multidisciplinary study of the biota of the mountain, between 4 October and 20 November 1996. (For an overview of the survey and for more precise botanical details of the various study sites, see Chapters 1 and 3.) Ornithological data were collected within an altitudinal interval of ± 75 m elevation, centered around transect zones at 450, 775, 1250, 1625, and 1875 m. These transect zones were placed within 3 km horizontal walking distance from our camps 1 (450 m), 2 (775 m), 3 (1325 m), 4 (1550 m), and 5 (1875 m). Throughout this chapter, we refer to the elevational zones with respect to the placement of the camps.

Most of the camp sites were situated near rivers or streams in closed-canopy forest. The lowest camp (450 m) was between two small rivers that are tributaries of the Manantenina River. The vegetation type at this site was largely dominated by indigenous native lowland forest, although extensive areas of secondary forest were present. At the 775 m site, which was at a site called Andampimbazaha on an open rocky outcrop along the Ambavaomby River, the forest showed few signs of human disturbance and contained more floristic elements of montane forest than did the 450 m site (see Chapter 3). A marked change in the vegetational structure occurred between the 775 and 1250 m zones. Clear montane elements were present at this latter site: the canopy height was lower, epiphytic loads were heavier, and ground mosses were abundant. By 1625 m the forest was completely dominated by montane elements, including some sclerophyllous plants, and the forest was further reduced in stature. Tree root systems often formed hollow cavities under a superficial cover of mosses and lichens, especially along the ridges and slopes. The 1875 m site encompassed the ecotone between the upper limit of sclerophyllous forest and open grassland savanna. The

TABLE 10-1. Details of ornithological surveys in each elevational zone within the PN de Marojeje.

Elevational zone (m)	Duration of visit (days)	Point counts	Species recorded	Forest species recorded	Species restricted to zone
				No. (%)	
450 m	10	19	64	59 (92.2)	7
775 m	10	22	53	51 (96.2)	2
1250 m	10	22	57	55 (96.5)	1
1625 m	9	16	40	37 (92.5)	0
1875 m	7	11	32	22 (68.8)	6

camp site at 1875 m was on a ridge above the tree line and slightly above a small forest-lined stream (Andranomifototra). Within the open area, there were large exposed outcrops of rock, some covered by small geophytes. More detailed botanical descriptions of each transect zone are provided in Chapter 3.

Methods

Survey methods used to collect information about the birds of the PN de Marojeje included direct observation, point counts, static observations from areas with broken canopy cover, mist-netting, and call playback. To maximize information from each zone, particularly for the general observations, point counts, and mist-netting procedures, different microtopographical and microhabitat areas were surveyed (e.g., ridges, slopes, and valley bottoms).

J.-C. Razafimahaimodison was the principal field ornithologist on the mission. A. F. A. Hawkins was present for the 450 and 775 m samples and, together with Razafimahaimodison, conducted point counts and general observations. In higher altitude zones, Razafimahaimodison was solely responsible for the point counts. In all transect zones, S. M. Goodman, in collaboration with M. Ravokatra, was responsible for the bird netting and secondarily for bird observations. During inclement weather, such as strong wind and heavy rain, point counts were not conducted.

Survey Methods

POINT COUNTS—Point counts were used to estimate relative bird species frequency (Reynolds

TABLE 10-2. Accumulation of bird species previously unrecorded within each elevational zone in the PN de Marojeje.

Elevational zone	Cumulative no. of species recorded by working day									
	1	2	3	4	5	6	7	8	9	10
450 m	13	40	43	55	57	61	64	64	64	64
775 m	9	20	41	46	53	53	53	53	53	53
1250 m	4	13	33	44	45	57	57	57	57	57
1625 m	18	20	28	35	36	39	40	40	40	—
1875 m	14	28	32	32	32	32	32	32	—	—

et al., 1980; Bibby et al., 1992) occurring within each elevational zone surveyed. Sample points were located at 150 m intervals along preexisting or recently cut trails. We conducted a minimum of 15 point counts within each elevational zone except the 1875 m zone, in which only 11 point-count sites were installed, because of the limited area of forest.

Each point-count site was sampled twice on different days, once between 0500 and 0630 hr and once between 0630 and 0900 hr, for a period of 10 minutes. A 1-minute "rest period" was used for the equilibration of bird activity after arrival at a station (Reynolds et al., 1980). All bird contacts, visual and aural, were noted, and the horizontal distance to the observer was estimated in intervals of 0–5, 5–10, 10–20, 20–30, 30–50, and 50–100 m; distances greater than 100 m were not precisely estimated. In cases of unfamiliar bird-song, a tape recorder with a directional microphone was used to record the vocalization for later identification. If necessary, after a point-count session was finished, recorded calls and vocalizations of unfamiliar birds were played back, to attract the birds and thereby enable visual determination of the species involved.

DIRECT OBSERVATION—We made direct observations while walking along preestablished trails or bushwhacking in the forest. We noted bird species, nature of contact (auditory or visual), type of vocalization (song or call), the number of individuals seen or heard, behavior, foods consumed, and other information. In addition, mixed-species bird flocks were followed. Active searching was conducted after the daily point counts. At least 7 hours per day were spent in active searches for birds.

CANOPY OBSERVATIONS—Additional observations were made from spots with broken-canopy vistas to identify raptors and other bird species

TABLE 10-3. Elevational distribution of birds recorded in the elevational transects in the PN de Marojejy during the 1996 survey,¹ with information on their distributional status² and habitat use.³

Species	Presence in elevational zone					Outside reserve
	450 m	775 m	1250 m	1625 m	1875 m	
<i>Tachybaptus ruficollis</i> @	-	-	-	-	-	+
<i>Anhinga rufa</i> @	-	-	-	-	-	+
<i>Ardeola idae</i> *	-	-	-	-	-	+
<i>Ardeola ralloides</i> @	-	-	-	-	-	+
<i>Egretta alba</i> @	-	-	-	-	-	+
<i>Egretta dinorpha</i> @	-	-	-	-	-	+
<i>Ardea purpurea</i> @	-	-	-	-	-	+
% <i>Lophotibis cristata</i> *	+	+	-	-	-	
% <i>Aviceda madagascariensis</i> *	-	-	+	+	+	
% <i>Polyboroides radiatus</i> *	+	-	-	-	-	
% <i>Accipiter henstii</i> *	+	-	-	+	-	
% <i>Accipiter francesii</i> (*)	+	-	-	-	-	
% <i>Buteo brachypterus</i> *	+	+	+	+	+	
<i>Falco newtoni</i> (*)	-	-	-	-	-	+
<i>Falco peregrinus</i> @	+	-	-	-	-	
<i>Falco eleonorae</i> #	-	-	-	-	+	
<i>Margaroperdix madagascariensis</i> *	-	-	-	-	+	
<i>Coturnix coturnix</i> @	-	-	-	-	+	
% <i>Mesitornis unicolor</i> *	-	+	-	-	-	
% <i>Canirallus kiolooides</i> *	+	+	+	+	-	
% <i>Sarothrura insularis</i> *	-	-	-	-	+	
% <i>Alectroenas madagascariensis</i> *	+	+	+	-	-	
% <i>Streptopelia picturata</i> (*)	+	+	-	-	-	
% <i>Treron australis</i> (*)	+	-	-	-	-	
<i>Agapornis cana</i> *	-	-	-	-	-	+
% <i>Coracopsis</i> spp. ⁴ (*)	+	+	+	+	(+)	
% <i>Coua caerulea</i> *	+	+	+	+	(+)	
% <i>Coua reynaudii</i> *	+	+	+	-	(+)	
% <i>Coua serriana</i> *	+	+	+	-	-	
% <i>Coua cristata</i> *	-	-	-	-	-	+
% <i>Cuculus rochii</i> *	+	+	+	+	(+)	
% <i>Centropus toulou</i> (*)	+	+	+	-	-	
% <i>Otus rutilus</i> (*)	+	+	+	+	-	
% <i>Ninox superciliaris</i> *	+	-	+	-	-	
% <i>Asio madagascariensis</i> *	+	-	+	-	-	
<i>Caprimulgus madagascariensis</i> *	-	-	-	-	+	
% <i>Zoonavena grandidieri</i> (*)	-	+	-	-	+	
<i>Apus melba</i> @	+	+	+	+	+	
<i>Apus barbatus</i> @	+	-	+	+	+	
<i>Cypsiurus parvus</i> @	-	-	-	-	+	
<i>Merops superciliosus</i> @	-	-	-	-	-	+
<i>Alcedo vintsioides</i> (*)	+	-	-	-	-	
% <i>Ispidina madagascariensis</i> *	+	+	-	-	-	
% <i>Eurystomus glaucurus</i> *	-	-	+	-	-	
% <i>Leptosomus discolor</i> (*)	+	+	+	-	-	
% <i>Brachypteracias leptosomus</i> *	+	+	+	+	-	
% <i>Brachypteracias squamiger</i> *	+	+	-	-	-	
% <i>Atelornis pittoides</i> *	-	-	+	+	-	
% <i>Atelornis crossleyi</i> *	-	-	+	+	+	
% <i>Philepitta castanea</i> *	+	+	+	+	-	
% <i>Neodrepanis coruscans</i> *	+	+	+	-	-	
% <i>Neodrepanis hypoxantha</i> *	-	-	+	+	-	
<i>Mirafra hova</i> *	-	-	-	-	+	
<i>Phedina borbonica</i> (*)	+	+	-	-	+	
% <i>Motacilla flaviventris</i> *	+	+	-	+	-	
% <i>Coracina cinerea</i> *	+	+	+	+	-	
% <i>Hypsipetes madagascariensis</i> (*)	+	+	+	+	+	

TABLE 10-3. *Continued.*

Species	Presence at elevational zone					Outside reserve
	450 m	775 m	1250 m	1625 m	1875 m	
% <i>Bernieria cinereiceps</i> *	—	—	+	+	—	
% <i>Bernieria zosterops</i> *	+	+	+	—	—	
% <i>Bernieria tenebrosa</i> *	—	+	—	—	—	
% <i>Bernieria madagascariensis</i> *	+	+	+	—	—	
% <i>Bernieria xanthophrys</i> *	—	—	+	+	—	
% <i>Calicalicus madagascariensis</i> *	+	+	+	+	(+)	
% <i>Vanga curvirostris</i> *	+	+	+	—	—	
% <i>Leptopterus viridis</i> *	+	+	+	+	(+)	
% <i>Leptopterus chabert</i> *	+	+	—	—	—	
% <i>Cyanolanius madagascarinus</i> (*)	+	—	+	—	—	
% <i>Oriolia bernieri</i> *	+	—	—	—	—	
% <i>Euryceros prevostii</i> *	+	+	+	+	—	
% <i>Tylas eduardi</i> *	+	+	+	+	(+)	
<i>Saxicola torquata</i> @	—	—	—	+	+	
% <i>Copsychus albospectularis</i> *	+	+	+	—	—	
% <i>Monticola sharpei</i> *	—	—	+	+	(+)	
% <i>Neomixis striatigula</i> *	+	+	+	+	—	
% <i>Neomixis viridis</i> *	+	+	+	+	—	
% <i>Neomixis tenella</i> *	+	+	+	—	—	
<i>Cisticola cherina</i> (*)	—	—	—	—	—	+
% <i>Cryptosylvicola randrianasoloi</i> *	—	—	+	+	+	
% <i>Oxylabes madagascariensis</i> *	+	+	+	+	—	
% <i>Mystacornis crossleyi</i> *	+	+	+	+	—	
<i>Acrocephalus newtoni</i> *	—	—	—	—	—	+
% <i>Nesillas typica</i> (*)	+	+	+	+	+	
% <i>Dromaeocercus brunneus</i> *	—	—	+	+	+	
% <i>Randia pseudozosterops</i> *	+	+	+	+	—	
% <i>Newtonia brunneicauda</i> *	+	+	+	+	+	
% <i>Newtonia amphichroa</i> *	+	+	+	+	+	
% <i>Pseudobias wardi</i> *	+	+	—	+	—	
% <i>Terpsiphone mutata</i> (*)	+	+	+	+	—	
% <i>Nectarinia notata</i> (*)	+	+	+	—	—	
% <i>Nectarinia souimanga</i> (*)	+	+	+	+	+	
% <i>Zosterops maderaspatana</i> (*)	+	+	+	+	+	
<i>Lonchura nana</i> *	+	—	—	—	—	
% <i>Ploceus nelicourvi</i> *	+	+	+	—	—	
% <i>Foudia madagascariensis</i> *	+	+	+	—	+	
% <i>Foudia omissa</i> *	+	+	+	—	—	
% <i>Dicrurus forficatus</i> (*)	+	+	+	—	—	
% <i>Hartlaubius auratus</i> *	+	—	—	—	—	
Total no. of species	64	53	57	40	32	
Total no. of forest species	59	51	55	37	22	

NOTE.—Records are also presented for species observed in areas just outside the reserve limits.

¹ Key to presence/absence status: + = species recorded in zone; — = species not recorded in zone. Records from the 1875 m zone in parentheses are of species recorded only in the lower portion of the transect, below tree line.

² Key to distributional status: * = breeding species endemic to Madagascar; (*) = breeding species endemic to Madagascar and nearby islands; # = migrant to Madagascar; @ = breeding species also occurring outside of region.

³ Key to habitat use: % = forest-dependent species (species depends on forest for a portion of its life cycle).

⁴ Because of difficulties in distinguishing between *Coracopsis vasa* and *C. nigra* in the field, we have combined these species here. The vast majority of our records concern *C. nigra*.

that fly above the trees. Such sites were found along rivers, on top of rocky outcrops, on ridges, and in other open areas. We spent at least 10 hours within each elevational zone conducting this type of census.

MIST-NETTING—Mist-netting was used to provide information on the abundance of individual species, as expressed by the number of captures per net-day (Karr, 1981). Ten nets were set up at each of the five elevational zones and were run

continuously for 5 days. Sites were generally within 500–750 m trail distance from the camps. All nets were 36 mm mesh size, 2.6 m high, and 12 m long. In most cases they were left open during the night, to capture nocturnal bird species and bats. They were checked nearly every hour from sunrise to sunset and occasionally during the night.

Most captured birds were weighed, measured, and marked before being released near the original site of capture. A mark was made with indelible ink on the bird's primary feathers. Within each elevational zone, the first primary feather was marked for birds captured on the first day of netting, the second primary feather on the second day, and so on, until the fifth and final day of netting. This marking technique provided a means to recognize recaptured individuals and indicated the chronology of the recaptures. Some birds were collected and prepared as standard study skins, skeletons, or fluid-preserved specimens. Tissue samples of collected individuals were preserved in a solution of EDTA. The specimens are deposited in the Field Museum of Natural History, Chicago, and the Département de Biologie Animale, Université d'Antananarivo, Antananarivo.

Vegetation Structure Measurement

At each point-count site, the following vegetation structure measurements were made: (1) habitat type (ridge, slope, or valley) and condition of forest (primary, degraded, secondary, or grassland); (2) estimated canopy height and estimated percentage canopy cover; and (3) shrub layer density, estimated by taking the mean of four estimates of distance visible through the shrub layer at eye level.

Systematic Order, Nomenclature, and Common Names

We have generally followed the systematic order, scientific names, and vernacular names of Langrand (1995). The major exceptions include a generic revision of *Pseudocossyphus*, now placed in the genus *Monticola* (Goodman & Weight, in press), and that of *Phyllastrephus* and *Crossleyia*, now placed in the genus *Bernieria* (Fjeldså et al., 1999). For the latter two genera, to reflect this taxonomic change, we resurrect vernacular names proposed by earlier authors.

Results

For each of the five transect zones, information on the duration of each survey, the number of point-count sites, and number of species recorded at each site is presented in Table 10-1. At most of the sites, 5–6 days was sufficient to reach an apparent plateau in the species discovery curve (Table 10-2). The major exception was the 1625 m zone, where inclement weather reduced the rate of species accumulation. We often spent the first and second days in each elevational zone installing the camp, opening trails, and choosing sites for the point counts.

Overall, 84 species of birds were recorded during the 1996 inventory of the PN de Marojejy, 72 (86%) of which are forest-dwelling forms and 60 (71%) of which are endemic to Madagascar. An additional 18 (22%) species breed in the Malagasy region, 5 (6%) nest on the island but have much broader distributions, and 1 (1%) is a Holarctic migrant (Table 10-3). Thirteen species were recorded in the area just outside the reserve, which gives a total of 97 species recorded during the 1996 inventory.

Several species of birds previously reported from the PN de Marojejy were not recorded during the 1996 inventory. These comprise a variety of non-forest-dwelling species, including six open-country, four aquatic, and eight predominantly forest-dwelling species (Table 10-4). When this tally is added to the list produced during the 1996 survey, the known avifauna of the park and immediate surroundings includes 115 species.

The elevational distributions of bird species observed during this inventory are presented in Table 10-3. In total, 64 species were recorded in the 450 m zone, 53 in the 775 m zone, 57 in the 1250 m zone, 40 in the 1625 m zone, and 32 in the 1875 m zone. This pattern of decreasing bird species richness with increasing elevation is typical of eastern humid forests on the island (Hawkins, 1999).

The vast majority of species recorded during the inventory had broad elevational distributions across the Marojejy Massif. In a few cases, certain species were noted only in a single elevational zone (Table 10-3). Two species were restricted to the 450 m zone (*Treron australis* and *Oriolia bernieri*). Both species tend to be lowland forest species, and this result is concordant with their known altitudinal distribution (Hawkins, 1999). Further, *Lonchura nana* is not a forest species, and its occurrence in this zone is almost certainly

TABLE 10-4. Species not recorded during 1996 survey of the PN de Marojejy, but previously reported from area.

Species	Habitat	Previous record
<i>Tachybaptus pelzelinii</i>	Aquatic	1
<i>Bubulcus ibis</i>	Open areas	1
<i>Butorides striatus</i>	Aquatic	1
<i>Milvus migrans</i>	Open areas	1, 2
<i>Accipiter madagascariensis</i>	Forest	1
<i>Eutriorchis astur</i>	Forest	2
<i>Falco concolor</i>	Open areas	1
<i>Falco zoniventris</i>	Forest, open areas	1, 2
<i>Turnix nigricollis</i>	Open areas	1
<i>Rallus madagascariensis</i>	Aquatic	1, 3
<i>Dryolimnas cuvieri</i>	Aquatic	1, 2
<i>Caprimulgus enarratus</i>	Forest	1, 2
<i>Riparia paludicola</i>	Open areas	1
<i>Hartertula flavoviridis</i>	Forest	1, 2
<i>Schetba rufa</i>	Forest	1, 2
<i>Hypositta corallirostris</i>	Forest	1, 2
<i>Xenopirostris polleni</i>	Forest	4
<i>Corvus albus</i>	Open areas	1, 2

Source of previous records: 1 = Nicoll and Langrand (1989); 2 = Safford and Duckworth (1990); 3 = Griveaud (1960); 4 = Benson et al. (1977).

related to the open areas associated with forest degradation. Six other species (*Polyboroides radiatus*, *Accipiter francesii*, *Treron australis*, *Falco peregrinus*, *Alcedo vintsiodes*, and *Hartlaubius auratus*) generally have much broader altitudinal distributions on other surveyed mountains on Madagascar (Hawkins, 1999), and we assume the same holds for the Marojejy Massif. Two species that tend to be uncommon were restricted to the 775 m zone: *Mesitornis unicolor* is known to occur from lowland to middle elevations in other areas of the eastern humid forest, but it was recorded only at 860 m in the nearby RS d'Anjanaharibe-Sud (Hawkins et al., 1998), and *Bernieria tenebrosa* tends to be a lowland species (Langrand, 1995). The single species restricted to the 1250 m zone, *Eurystomus glaucurus*, normally occurs across a broad elevational zone (Langrand, 1995). Six species were recorded only in the 1875 m zone (*Falco eleonora*, *Margaroperdix madagascariensis*, *Coturnix coturnix*, *Sarothrura insularis*, *Caprimulgus madagascariensis*, and *Mirafra hova*), none of which are forest-restricted birds, and these species occurred on the Marojejy Massif in the zone near or above forest line. In the cases of the galliforms, nightjar, and lark, this is

TABLE 10-5. Vegetation structure measures at point-count sample sites in the PN de Marojejy.

Altitude and vegetation category	Mean canopy height (m)	Mean canopy cover (%)	Mean shrub density ¹ (m)
450 m			
Degraded forest			
Ridge (N = 3)	18.3	56	6.0
Valley (N = 5)	18.0	36	4.8
Slope (N = 3)	11.0	5	3.1
Nondegraded forest			
Ridge (N = 3)	31.5	80	7.6
Valley (N = 2)	27.5	80	5.8
Slope (N = 3)	30.0	90	8.0
775 m			
Ridge (N = 4)	23.0	90	5.5
Valley (N = 6)	25.0	80	6.9
Slope (N = 12)	20.0	80	5.1
1250 m			
Ridge (N = 9)	10.0	60	3.0
Valley (N = 5)	20.0	80	6.0
Slope (N = 8)	15.0	90	5.3
1625 m			
Ridge (N = 3)	5.0	25	1.9
Valley (N = 4)	15.0	75	5.3
Slope (N = 9)	10.6	60	3.7
1875 m			
(all) (N = 6)	4.0	40	3.1

¹ Estimated by taking the mean of four estimates of distance visible through the shrub layer at eye level (see p. 182).

almost certainly related to the available habitat, whereas the case of the falcon is probably due to the broad, open expanses, in which such birds are much easier to observe than in closed forest. Normally the rail has a broad elevational distribution on the island, from near sea level to 2300 m (Langrand, 1995), and we can offer no clear explanation as to why it should be limited to the upper portions of the massif. It was not recorded during the 1988 expedition to the site (Safford & Duckworth, 1990), but it appears on Griveaud's list of Marojejy species. Madagascar lacks species of birds restricted to the zone above tree line as found in other areas of the world with high mountains, such as the Andes, Himalayas, and sites on the African continent (Maclean, 1990; Inskipp & Inskipp, 1991; Stotz et al., 1996). This is largely because the highest peak on the island is slightly more than 2800 m, the surface area of habitat above tree line is rather restricted, and, in recent

TABLE 10-6. Netting results by elevational transect in the PN de Marojejy.

Species	No. of individuals netted by altitude					Total
	450 m	775 m	1250 m	1625 m	1875 m	
<i>Accipiter francesii</i>	1	0	0	0	0	1
<i>Otus rutilus</i>	0	2	1	0	0	3
<i>Alcedo vintsioides</i>	1	0	0	0	0	1
<i>Ispidina madagascariensis</i>	2	4	0	0	0	6
<i>Brachypteracias leptosomus</i>	0	0	1	0	0	1
<i>Philepitta castanea</i>	3	16	11	2	0	32
<i>Neodrepanis coruscans</i>	4	9	0	0	0	13
<i>Neodrepanis hypoxantha</i>	0	0	10	1	0	11
<i>Bernieria madagascariensis</i>	0	4	0	0	0	4
<i>Bernieria zosterops</i>	2	2	0	0	0	4
<i>Bernieria cinereiceps</i>	0	0	7	7	0	14
<i>Bernieria xanthophrys</i>	0	0	2	1	0	3
<i>Hypsipetes madagascariensis</i>	0	2	1	0	0	3
<i>Copsychus albospectularis</i>	1	10	0	0	0	11
<i>Monticola sharpei</i>	0	0	3	2	0	5
<i>Saxicola torquata</i>	0	0	0	0	5	5
<i>Nesillas typica</i>	0	0	9	4	8	21
<i>Newtonia amphichroa</i>	0	2	7	5	0	14
<i>Newtonia brunneicauda</i>	0	2	0	0	0	2
<i>Cryptosylvicola randrianasoloi</i>	0	0	0	0	2	2
<i>Terpsiphone mutata</i>	3	4	5	0	0	12
<i>Oxylabes madagascariensis</i>	0	0	7	0	0	7
<i>Nectarinia souimanga</i>	5	5	4	3	5	22
<i>Zosterops maderaspatana</i>	6	2	2	1	2	13
<i>Vanga curvirostris</i>	0	3	0	0	0	3
<i>Euryceros prevostii</i>	1	0	0	0	0	1
<i>Ploceus nelicourvi</i>	1	1	1	0	0	3
<i>Foudia madagascariensis</i>	0	0	0	0	7	7
<i>Foudia omissa</i>	4	3	1	0	0	8
Total no. of individuals	34	71	72	26	26	232
Total no. of species	13	16	16	9	6	28
Average no. of birds/net-day	0.7	1.4	1.4	0.5	0.6	0.9

NOTE.—Netting results are for 50 cumulative net-days at each zone, for a total of 250 net-days. Figures do not include recaptures.

geological periods, there have been considerable shifts in the elevation of montane habitats as a function of warm and cool periods (Straka, 1996).

Important vegetational differences were recorded in the different zones in which the transects were conducted (see Chapter 3 for more details). Mean canopy cover and height declined with increasing elevation, and, between 1250 m and 1625 m, the canopy height tended to be highest in valley bottoms, moderate on slopes, and lowest on ridges (Table 10-5). Shrub density increased with increasing elevation and was thickest on ridges in the 1250 and 1625 m samples. There was a dramatic difference between degraded and intact forest in the 450 m sample; the degraded forest had a lower and more open canopy and a much more dense shrub layer.

In each elevational zone, 50 net-days were ac-

rued (Table 10-6). We captured a total of 232 individual birds belonging to 28 species. The numbers of individuals and species captured were highest at the 775 and 1250 m sites, slightly lower at 450 m, and notably lower at 1625 and 1875 m. The weight data for captured birds are presented in Table 10-7.

Discussion

Methodological Considerations

We recorded 84 bird species in the survey area of the PN de Marojejy during the 1996 expedition, using three different methods: point counts (59 species [70%]), direct observation (about 75

TABLE 10-7. Mass (g) of birds netted during the survey of the PN de Marojejy.

Species	N	Mass (g), Range ¹	Mean ± SD ²
<i>Accipiter francesii</i>	1	166 (♀)	—
<i>Otus rutilus</i>	1	114.5	—
<i>Alcedo vintsioides</i>	1	16.5	—
<i>Ispidina madagascariensis</i>	5	16.0–19.5	18.1 ± 1.4
<i>Philepitta castanea</i>	31	24.5–43.5	35.3 ± 3.7
<i>Neodrepanis coruscans</i>	10	4.5–7.5	6.5 ± 1.0
<i>Neodrepanis hypoxantha</i>	11	6.5–9.0	7.0 ± 0.7
<i>Bernieria madagascariensis</i>	4	22.0–34.5	27.9 ± 6.5
<i>Bernieria zosterops</i>	3	19.5, 20.5, 21.0	—
<i>Bernieria cinereiceps</i>	13	13.5–20.0	18.3 ± 1.7
<i>Bernieria xanthophrys</i>	3	17.0, 18.5, 20.5	—
<i>Hypsipetes madagascariensis</i>	3	41.5, 41.5, 41.5	—
<i>Copsychus albospecularis</i>	11	20.0–28.5	24.7 ± 2.3
<i>Monticola sharpei</i>	5	23.0–27.0	24.9 ± 1.8
<i>Saxicola torquata</i>	5	12.0–14.5	13.4 ± 1.1
<i>Nesillas typica</i>	20	14.0–22.0	18.3 ± 2.4
<i>Newtonia amphichroa</i>	14	9.0–15.0	11.8 ± 1.7
<i>Newtonia brunneicauda</i>	2	9.5, 13.5	—
<i>Cryptosylvicola randrianasoloi</i>	2	7.1, 7.4	—
<i>Terpsiphone mutata</i>	12	10.0–15.5	13.8 ± 1.5
<i>Oxylabes madagascariensis</i>	7	21.0–26.5	23.1 ± 2.3
<i>Nectarinia souimanga</i>	22	6.5–10.5	7.6 ± 1.0
<i>Zosterops maderaspatana</i>	13	9.0–13.0	10.5 ± 1.0
<i>Vanga curvirostris</i>	3	58.5, 65.0, 70.0	—
<i>Euryceros prevostii</i>	1	87	—
<i>Ploceus nelicourvi</i>	3	22.5, 26.0, 30.0	—

¹ When three or fewer measurements were available, only the masses themselves are given.

² SD = standard deviation.

species [89%]), and mist-netting (28 species [33%]). Among these 84 species, 21 (25%) were recorded only from direct observation and 1 species (1%) only from mist-netting. The results from the three methods used during the field expedition (point count, direct observation, and mist-netting) are therefore complementary. Of the three techniques, mist-netting provided the least amount of total or unique information on the presence of birds within any elevational transect. For this technique to be more effective, a far greater number of nets must be run in each elevational zone. Further, several important biases are inherent in use of this technique to measure relative abundance of birds (Remsen & Good, 1996).

The use of playback recordings of bird vocalizations provided mixed results during this survey. For example, it was not possible to attract *Mesitornis unicolor* with this technique, although it was used numerous times in an area of forest where this species was known to occur. However, with some other species, such as *Bernieria tenebrosa*, the recordings attracted the birds, and we were able to confirm the identifications when they came closer. *Ispidina madagascariensis* was the

only bird recorded by mist-netting but not by the other techniques. This species is a secretive, understory animal that is easily overlooked.

The bird species recorded by general observations but not during point-count observations can be divided into four groups: generally rare or uncommon species that were observed on only a few occasions: *Lophotibis cristata*, *Mesitornis unicolor*, and *Bernieria tenebrosa*; high aerial foraging species that were difficult to see in the dense forest in which most point-count sites were located: *Phedina borbonica*, *Apus barbatus*, and *Cypsiurus parvus*; nocturnal species that were not active during the period in which point counts were conducted: *Asio madagascariensis*, *Ninox supercilialis*, and *Caprimulgus madagascariensis*; and forest raptors that are easily overlooked, particularly when they occur in relatively low densities and fly over the forest canopy: *Aviceda madagascariensis* and *Polyboroides radiatus*.

Calculation of Point-Count Frequencies

The method used for the point counts was intended to provide sufficient data for the calcula-

TABLE 10-8. Contact frequency and frequency per point-count sample of bird species detected on point counts in the PN de Marojeje.

Species	450 m degraded (9 samples)		450 m intact (10 samples)		775 m (22 samples)		1250 m (22 samples)		1625 m (16 samples)		1875 m (11 samples)	
	No. of contacts sample	Frequency per sample	No. of contacts sample	Frequency per sample	No. of contacts sample	Frequency per sample	No. of contacts sample	Frequency per sample	No. of contacts sample	Frequency per sample	No. of contacts sample	Frequency per sample
<i>Accipiter henstii</i>	1	0.11	1	0.10	1	0.05			1	0.06		
<i>Cathartus klotzoides</i>												
<i>Sarothra insularis</i>			1	0.10							7	0.64
<i>Streptopelia picturata</i>					1	0.05						
<i>Alectroenas madagascariensis</i>												
<i>Coracopsis uinga</i>	4	0.44	6	0.60	9	0.41	13	0.59	3	0.19	1	
<i>Cuculus rochii</i>	1	0.11	6	0.60	19	0.86	19	0.86				
<i>Cona serritana</i>	5	0.56	3	0.30	5	0.23	7	0.32				
<i>Cona reynaudii</i>	1	0.11	1	0.10	7	0.32	3	0.14	4	0.25	4	0.36
<i>Cona caerulea</i>	1	0.11	8	0.80	5	0.23	6	0.27	5	0.31	1	0.09
<i>Centropus toulou</i>	7	0.78	5	0.50	3	0.14	1	0.05				
<i>Otus rufus</i>					2	0.09						
<i>Eurystomus glaucurus</i>												
<i>Brachypteracias leptosomus</i>			3	0.30	2	0.09	1	0.05	1	0.06		
<i>Aelornis pittoides</i>							1	0.05	1	0.06		
<i>Aelornis crossleyi</i>							2	0.09	2	0.13	1	0.09
<i>Leptosomus discolor</i>					2	0.09						
<i>Philepitta castanea</i>			1	0.10	3	0.14	7	0.32				
<i>Neodrepanis coruscus</i>	3	0.33	2	0.20	7	0.32	6	0.27				
<i>Neodrepanis hypoxantha</i>							21	0.95	3	0.19		
<i>Coraciina ciurea</i>	4	0.44	3	0.30	1	0.05	2	0.09				
<i>Bernieria madagascariensis</i>	4	0.44	3	0.30	6	0.27	6	0.27				
<i>Bernieria zosterops</i>			7	0.70	5	0.23			6	0.38		
<i>Bernieria xanthophrys</i>							2	0.09				
<i>Hypsipetes madagascariensis</i>	8	0.89	11	1.10	14	0.64	23	1.05	21	1.31	6	0.55
<i>Copsychus albospectularis</i>	4	0.44	7	0.70	6	0.27	1	0.05				
<i>Saxicola torquata</i>							4	0.18			9	0.82
<i>Mouticola sharpei</i>							33	1.50	18	1.13	5	0.45
<i>Nesittia typica</i>											30	2.73
<i>Dromaeoecerus brunneus</i>											1	0.09
<i>Randia pseudozosterops</i>	6	0.67	2	0.20	6	0.27	2	0.09	7	0.44	8	0.73
<i>Newtonia amplichris</i>	1	0.11	1	0.10	2	0.09	12	0.55	10	0.63	2	0.18
<i>Newtonia brunneicauda</i>	1	0.11	9	0.90	16	0.73	14	0.64	17	1.06		
<i>Neoutxis tenella</i>	9	1.00	8	0.80	10	0.45	9	0.41				
<i>Neoutxis viridis</i>	5	0.56	8	0.80	8	0.36	6	0.27	2	0.13		

TABLE 10-8. Continued.

Species	450 m degraded (9 samples)		450 m intact (10 samples)		775 m (22 samples)		1250 m (22 samples)		1625 m (16 samples)		1875 m (11 samples)	
	No. of contacts	Frequency per sample	No. of contacts	Frequency per sample	No. of contacts	Frequency per sample	No. of contacts	Frequency per sample	No. of contacts	Frequency per sample	No. of contacts	Frequency per sample
<i>Neomixis striatigula</i>	7	0.78	6	0.60	11	0.50	3	0.14	14	0.88	14	1.27
<i>Cryptosylvicola randrianasoloi</i>							12	0.55	18	1.13	14	
<i>Terpsiphone mutata</i>	6	0.67	9	0.90	8	0.36	8	0.36	1	0.06		
<i>Oxylabes madagascariensis</i>			1	0.10	6	0.27	3	0.14	4	0.25		
<i>Mystacornis crossleyi</i>					3	0.14	9	0.41	3	0.19		
<i>Nectarinia souimanga</i>	19	2.11	21	2.10	33	1.50	60	2.73	38	2.38	29	2.64
<i>Nectarinia notata</i>	4	0.44	5	0.50	5	0.23	6	0.27				
<i>Zosterops maderaspatana</i>	9	1.00	11	1.10	18	0.82	12	0.55	12	0.75	3	0.27
<i>Calicalicus madagascariensis</i>	7	0.78	15	1.50	13	0.59	14	0.64	4	0.25	1	0.09
<i>Vanga curvirostris</i>					3	0.14	1	0.05	5	0.31	2	0.18
<i>Leptopterus viridis</i>	1	0.11	4	0.40	6	0.27	7	0.32	2	0.13	2	0.18
<i>Leptopterus chabert</i>	1	0.11										
<i>Cyanolanius madagascarinus</i>					2	0.09	6	0.27	2	0.13		
<i>Euryceros prevostii</i>			3	0.30	2	0.09	3	0.14	1	0.06		
<i>Tylas eduardi</i>	1	0.11	2	0.20	9	0.41	17	0.77	7	0.44	5	0.45
<i>Dicrurus forficatus</i>	4	0.44	4	0.40	2	0.09	1	0.05				
<i>Ploceus nelicourvi</i>			1	0.10	5	0.23	3	0.14				
<i>Foudia madagascariensis</i>							1	0.05	3	0.19	1	0.09
<i>Foudia omissa</i>	1	0.11	1	0.10	4	0.18						
<i>Lonchura nana</i>	1	0.11										
Total no. of species	29		34		39		41		31		20	

tion of densities. However, as can be seen from Table 10-8, contact frequencies with all but the most common species were low. Densities calculated on the basis of fewer than 20 contacts are subject to very large error estimates, making comparisons with other data (e.g., for ecological monitoring) unreliable. In this study, the only species for which density estimates would be usable for comparative purposes is *Nectarinia souimanga*, an abundant species in degraded and secondary habitats as well as in forest and, thus, of little use as an indicator. A possible reason for the low level of contacts may have been the unseasonably cold and wet weather we experienced at the first four camps.

To permit crude relative abundance comparisons between species and sites, we have calculated a contact frequency per sample for each species detected on point counts (Table 10-8). This figure is simply the overall number of contacts per elevational sample divided by the number of point-count sites within that sample.

Comparisons with Other Rain Forest Inventories

Eighty-four species were recorded during the 1996 expedition to the PN de Marojejy, whereas during the 1988 inventory, 104 species were observed in and around the reserve (Evans et al., 1992). The only forest species newly identified in the reserve during the 1996 survey was *Bernieria tenebrosa*. *Sarothrura insularis* was not recorded by the 1988 group, but it had been noted previously on the massif (Griveaud, 1960; Nicoll & Langrand, 1989). A number of species are noted in the literature from the reserve (Griveaud, 1960; Benson et al., 1976, 1977; Nicoll & Langrand, 1989; Evans et al., 1992) that were not recorded during the 1996 inventory. Approximately half of these birds are open-country or aquatic forms (Table 10-4). *Newtonia fanovanae* was recorded by Hawkins in 1997 in the western portion of the reserve. The only species recorded in and around the nearby RS d'Anjanaharibe-Sud that has not yet been reported from the PN de Marojejy is *Tyto soumagnei* (Hawkins et al., 1998).

For the most part, capture rates for the mist-netting operations in the RS d'Anjanaharibe-Sud and PN de Marojejy were comparable within similar elevational zones. At the former site, the number of accrued net-days was 45 per elevational zone, and at the latter site, 50 per elevational

zone. On the Anjanaharibe-Sud Massif, at 875 m, the average number of individuals captured per net-day was 1.0 (46 individuals of 13 species); on the Marojejy Massif, at 775 m, 1.4 individuals per net-day (71 individuals of 16 species). At 1260 m, 1.0 individuals were captured per net-day (46 individuals of 13 species) and, at 1250 m, 1.4 individuals per net-day (72 individuals of 16 species), respectively; at 1550 m, 1.9 individuals per net-day (85 individuals of 15 species) and, at 1625 m, 0.5 individuals (9 species) per net-day, respectively; at 1950 m, 0.6 individuals per net-day (27 individuals of 8 species) and, at 1875 m, 0.6 individuals per net-day (29 individuals of six species), respectively. Thus, the major differences between the massifs seem to be in the montane forest, where the capture rate in the RS d'Anjanaharibe-Sud (1550 m) was more than three times greater than in the PN de Marojejy (1625 m). Factors such as differences in season and associated variation in bird density or differences in canopy height between the two sites cannot be invoked to explain the variation between these two sites.

When all available information on the birds documented in and around the PN de Marojejy (Tables 10-3 and 10-4) is combined, the total number of recorded forest species is 79. To our knowledge, this is the most diverse forest bird species list for any single mountain site on Madagascar. In comparison with other massifs on which elevational transects have been conducted, 69 forest bird species were recorded between 720 and 2450 m in the PN d'Andringitra (Goodman & Rasolonandrasana, in press), 74 between 875 and 1950 m in the RS d'Anjanaharibe-Sud (Hawkins et al., 1998), 69 between 440 and 1875 m in parcel 1 of the PN d'Andohahela (Goodman et al., 1997b), and 73 between 450 and 1500 m in the RNI de Zahamena (Hawkins et al., in press).

Although the elevational range surveyed for birds on each of these mountains is not the same and the amount of effort at each of these sites is not really comparable, some generalizations can be offered. The three sites that are perhaps the most similar with regard to elevational range and work effort are (from north to south) the PN de Marojejy, the RNI d'Andringitra, and the PN d'Andohahela (parcel 1), in which 79, 69, and 69 species of birds have been recorded, respectively. On the basis of these results and other inferences, it is clear that the humid forest portions of northern Madagascar are ornithologically richer than the southern portion of the island.

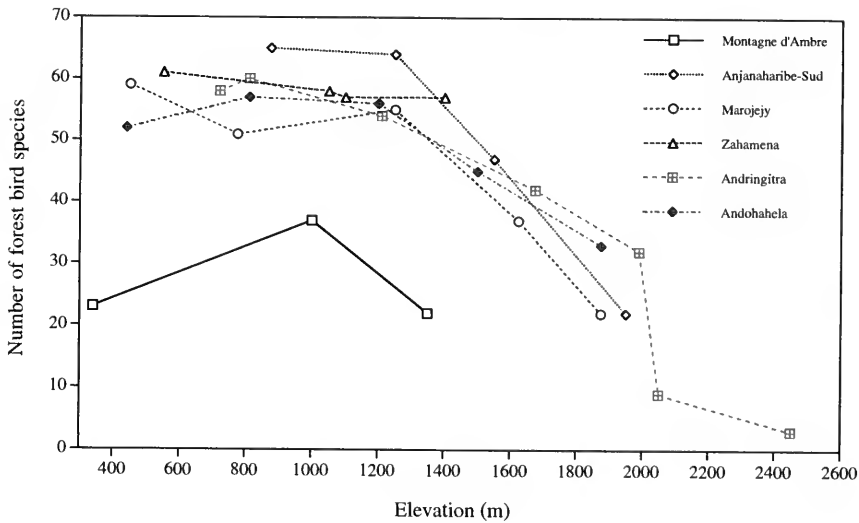


FIG. 10-2. Comparison of bird species richness as a function of elevation at several mountainous sites on Madagascar. Data are from Montagne d'Ambre (Goodman et al., 1996), Anjanaharibe-Sud (Hawkins et al., 1998), Marojejy (herein, Nicoll & Langrand, 1989; Evans et al., 1992), Zahamena (Hawkins et al., in press), Andringitra (Goodman & Rasolonandrasana, in press), and Andohahela (Goodman et al., 1997b).

A series of plots of each of these sites with regard to the number of bird species recorded per elevational zone indicates a consistent pattern of decreasing species richness with increasing elevation (Figure 10-2). Deviations from this pattern include the PN de la Montagne d'Ambre, in which there was a greater number of species at 1000 m than at 340 m. However, this shift largely reflects a change in forest type—the lowland forests of this mountain are distinctly drier than the montane zone (Goodman et al., 1996). Evidence of a slight mid-elevational bulge has been recorded in the PN d'Andohahela (parcel 1) at 810 m and in the PN de Marojejy at 1250 m.

The Frugivorous Bird Community

The greatest number of large frugivorous bird species was found in the lowland habitat at 450 m, where all three species of columbids known from the Marojejy Massif (*Alectroenas madagascariensis*, *Streptopelia picturata*, and *Treron australis*) were found, as well as both *Coracopsis* parrots. *Treron*, a species that appears to feed extensively on fruits, particularly those of *Ficus*, and perhaps the most obligate large frugivore in the eastern humid forest, did not occur above 450 m. The highest altitude at which *Streptopelia* and *Alectroenas* were recorded during the 1996 sur-

vey was 1250 m, although these species are known to occur at higher elevations elsewhere on Madagascar (Hawkins, 1999). The diet of the former species is composed of a high proportion of seeds (Langrand, 1995; Goodman & Parrillo, 1997), and, probably for this reason, it has a broader elevational distribution on the massif. Further, *Alectroenas* is known to make large-scale movements, and within forest habitat they are not sedentary. The *Coracopsis* parrots often consume seeds, flowers, and other food resources besides fruits. The other species of frugivore on the Marojejy Massif, *Philepitta castanea*, which feeds on small understory fruits (Goodman & Putnam, 1996; Razafindratsita, 1995), occurred across a broad elevational range, from 450 to 1625 m.

On the basis of line transects and general collections made by N. Messmer and P. J. Rakotomalaza (Chapter 3), the 450 m site had the largest number of *Ficus* trees in fruit of any of the zones during the period of the inventory. However, the highest density of these trees was in the 775 m zone, and this genus was not found at elevations above 1200 m. On the basis of this data and the importance of *Ficus* in the diet of *Treron*, we suspect that, as the season advanced and *Ficus* fruited at higher zones, this pigeon would become more common at higher elevations.

In summary, for large frugivores such as *Treron*—or for other species that often feed exten-

sively on fruits, such as *Alectroenas*, *Streptopelia*, and *Coracopsis* spp.—particular life-history traits need to be invoked to explain their elevational distribution on the Marojejy Massif as well as on other mountains in the eastern humid forest. The two reasons for this are closely linked: (1) few obligate frugivores occur in this forest type on Madagascar, compared with other areas of tropical forest, and (2) the phenology and distribution of fruiting trees does not provide a consistent pattern of fruit availability to allow the evolution of sedentary obligate frugivores (Goodman & Ganzhorn, 1997). Thus, more specifically, *Treron* consumes proportionately more fruit and is limited to lower altitudes, where this food source, particularly Moraceae, is more abundant, whereas the other large semifrugivorous species (*Alectroenas*, *Streptopelia*, and *Coracopsis* spp.) have a broader diet preference and accordingly occur across a wider elevational zone, perhaps with seasonal altitudinal migrations based on the availability of fruit resources.

Congeneric Overlap and Replacement

The altitudinal distribution of the two sunbird-asities, *Neodrepanis coruscans* and *N. hypoxantha*, appear to abut rather than overlap in the 1250 m zone. Parallel cases for the replacement of these two species have been found on several mountains where they occur along the same versant; irrespective of latitude, the zone is generally between 1200 and 1300 m (e.g., Goodman & Putnam, 1996; Goodman et al., 1997b). At some sites the transition zone occurs at higher elevations: at 1500–1600 m on the slopes of the RS d'Anjanaharibe-Sud (Hawkins et al., 1998) and at 1800 m in the RNI de Tsaratanana (Hawkins, unpubl. data). It would be interesting to study what factors are responsible for this consistent and abrupt shift. Perhaps this is the zone of transition of important food plants, such as *Bakerella* (Loranthaceae).

Three species of ground-rollers were recorded in the 1250 m zone; this is discussed below, in the species accounts, under *Brachypteracias leptosomus* (p. 192).

The most speciose genus of forest-dwelling birds in the PN de Marojejy is *Bernieria* (formerly consisting of the genera *Phyllastrephus* and *Crossleyia*), composed of five species. Two of these birds, *B. xanthophrys* and *B. tenebrosa*, were rare on the slopes of Marojejy, and we hesitate to infer

too much on the basis of limited information. The former species appears to be a bird of montane forests, occurring between approximately 1000 and 2000 m (Hawkins, 1999). During the 1996 survey, it was recorded in the 1250 and 1625 m zones. The latter species is a lowland species, noted only in the 775 m zone. The balance of the three members of this genus have been previously noted to show signs of both syntopy and elevational replacement on other mountains on Madagascar (e.g., Goodman & Putnam, 1996; Goodman et al., 1997b; Hawkins et al., 1998). The general pattern is for *B. madagascariensis* and *B. zosterops* to occur together in lowland habitats and to be largely or completely replaced by *B. cinereiceps* at elevations above 1200 or 1300 m. This pattern has been documented at sites in the north from the Marojejy and Anjanaharibe-Sud Massifs south to the PN d'Andohahela. Although this zone covers nearly 10° of latitude, the altitude of replacement is relatively consistent between these sites. In the PN d'Andohahela, the three species occurred sympatrically from 810 to 1200 m.

Another interesting case is that of the genus *Neomixis*. At all of the sites surveyed to date in the eastern humid forest, where *N. striatigula*, *N. viridis*, and *N. tenella* occur along the same slopes, a relatively consistent pattern emerges, once again irrespective of latitudinal gradients. *N. striatigula* and *N. viridis* are found across a broad elevational gradient, from lowland forest to at least montane forest and sometimes to forest line (Goodman et al., 1997b; Goodman & Rasolonandrasana, in press). *N. tenella* is a bird of lowland to middle elevation forest, to approximately 1200 m and, rarely, to 1500 m.

Bird Communities in Intact and Degraded Forest

In the 450 m zone, point-count sample sites were approximately equally divided between relatively intact forest and degraded forest, which were intimately interdigitated on a scale of hundreds of meters. The latter habitat was largely composed of a mixture of bamboo and *Aframomum* sp., with a few relict canopy trees. Evidently this area was burned for cultivation before the establishment of the reserve in 1952. The fact that degraded and intact forest were present so close together permitted a comparison of the bird communities of each without the usual problems of controlling for larger-scale variability in other

ecological parameters, such as soil type, original vegetation type, exposure, and altitude.

In Table 10-8 we show the frequency of contacts of species on point-count samples in degraded and intact forest. The number of species recorded in each habitat is not markedly different (29 in degraded and 34 in intact forest), but there is a marked difference in the distribution of certain species. Four species (*Streptopelia picturata*, *Ploceus nelicourvi*, *Oxylabes madagascariensis*, and *Philepitta castanea*) were not recorded on point counts in degraded forest but were recorded once each in intact forest. Meanwhile, *Lonchura nana* and *Leptopterus chabert* were recorded once each in the degraded sector and not in the intact sector. The significance of these records is difficult to judge, since contact frequencies in these samples are too low to allow much extrapolation from these data. It is certainly true that *Oxylabes* and *Philepitta* can be thought of as forest interior species and that *Lonchura* and *Leptopterus* are most common outside forest. Although differences in frequencies of other species between degraded and intact forest are sometimes large, they are insufficient for statistical testing. However, we can draw inferences from these disparities that merit further investigation.

Nine other species were recorded more than twice as often in one or the other habitat. *Cuculus rochii*, *Coua caerulea*, *Brachypteracias leptosomus*, *Bernieria zosterops*, *Newtonia brunneicauda*, *Calicalicus madagascariensis*, *Leptopterus viridis*, and *Euryceros prevostii* all were much less frequent or absent entirely from the degraded area. Several of these taxa are generally either canopy insectivores (*Cuculus*, *Newtonia*, *Calicalicus*, and *Leptopterus*), which may be unable to find sufficient food resources in degraded forest with an open canopy (Table 10-5), or understory insectivores (*Coua*, *Brachypteracias*, *Bernieria*, and *Euryceros*), which depend on finding prey in rather open primary forest understory and not in the dense vegetation found in the degraded areas (Table 10-5). It is striking that no understory insectivore was recorded in the degraded forest.

Only one species, *Randia pseudozosterops*, was recorded more than twice as frequently in degraded forest; all individuals detected in degraded forest were singing from the tops of isolated trees in areas of bamboo or *Aframomum*. The significance of this finding is difficult to evaluate. This species is absent from degraded areas far from primary forest (Morris & Hawkins, 1998), and it may only be the presence of primary forest less than 100 m

from the degraded forest in which these birds were singing that permitted them to use the degraded area.

Another point about the ability of certain birds to colonize open areas is demonstrated by some of the species occurring in the zone above tree line. *Mirafra hova* is common to abundant in herbaceous savanna habitats. It was not recorded in any of the degraded open areas in the 450 m transect or in any other forested area in the reserve, but it was relatively common from tree line to the summital zone of the Marojejy Massif. The case of *Foudia madagascariensis* is slightly different. This species is common in open habitats across most of the island and seems able to penetrate forest areas through either natural or human-related habitat disturbance. Within forest habitat, *F. madagascariensis* tends to occur along river margins and at the ecotone between open areas and forest. It was recorded in the three lowest zones, was absent in the 1625 m zone, and was abundant in the open area above forest line. In both cases, these two species of birds are able to colonize open habitats above forest line, although their elevational distribution is not continuous across the mountain. Thus, they are clearly dispersing across habitats in which they do not otherwise occur.

Species Accounts

In this section we provide details on particular bird species of interest. These include those classified as threatened or near threatened by Collar et al. (1994). One aspect of the growing amount of information on the birds of Madagascar is that many species previously designated as rare are now known to be relatively common but restricted to particular habitats or elevational zones. This point is discussed in more detail in the Conservation Considerations section at the end of this chapter.

Madagascar Crested Ibis, *Lophotibis cristata*

The Madagascar Crested Ibis was recorded on a few occasions in the 450 and 775 m zones. It was recorded at 1300 m in this same sector of the PN de Marojejy in 1988 (Safford & Duckworth, 1990). The density of this species in the reserve was low; it is unclear whether this reflects natural levels or is related to habitat disturbance and hunt-

ing pressure in the lower-lying areas of forest. Few observations of *L. cristata* were made during the inventory of the RS d'Anjanaharibe-Sud (Hawkins et al., 1998).

Madagascar Cuckoo-falcon, *Aviceda madagascariensis*

This species was observed on a few occasions in the 1250, 1625, and 1875 m zones and near the summit, at 1975 m. In the literature, the maximum elevation of this species was previously noted as 1800 m (Rand, 1936). This raptor usually frequents open areas and forest edge. In the RS d'Anjanaharibe-Sud, it was recorded between 875 and 1550 m (Hawkins et al., 1998).

Madagascar Serpent-eagle, *Eutriorchis astur*

Until recently, this species was thought to be very rare and was classified as threatened with extinction (Sheldon & Duckworth, 1990). More recently, after more than 50 years of not being documented in the wild, it has been found at several forested sites in the northern portion of the island, including the RS d'Ambatovaky (Raxworthy & Colston, 1992; Thompson & Evans, 1992), the Marojejy forest (Sheldon & Duckworth, 1990), the RS d'Anjanaharibe-Sud (Thiollay, 1998), the Masoala Peninsula (Thorstrom et al., 1995), and the RNI de Zahamena (Hawkins et al., in press).

During our 1996 expedition to the reserve, an exhaustive search in different parts of the forest was conducted, but no sign of this species was discovered. This effort included many hours of canopy searching from the Andampimbazaha outcrop (the site of the 775 m camp), a site with a panoramic view of birds flying over the canopy. The fact that this species was not recorded in the reserve during the 1996 expedition, although it has been previously recorded in the region, probably indicates that densities are extremely low or that this species is difficult to detect. Several recent records of this species are based on birds discovered vocalizing. The inclement weather experienced at the lowland camps during our survey of the Marojejy Massif may have reduced the calling frequency of this species and hence its detectability.

Henst's Goshawk, *Accipiter henstii*

Henst's Goshawk was recorded rarely during the survey. Records from our inventory include a single bird at 450 m and one individual heard vocalizing at 1625 m for approximately 15 minutes. In general, almost all contacts with this species involve calling birds, and it is possible that the inclement weather during the mission reduced vocalizations. Safford and Duckworth (1990) reported fairly regular contact with this species in the same sector of the reserve. In the nearby RS d'Anjanaharibe-Sud, it was observed on a few occasions at elevations between 875 and 1950 m (Hawkins et al., 1998).

Brown Mesite, *Mesitornis unicolor*

This forest-dependent species was recorded only in the 775 m zone, between the elevational range of 725 and 875 m. On 16 October, it was observed and heard calling in a forested valley with dense undergrowth. During the next few days, playback song of this species was broadcast with a tape recorder to attract the bird, but it did not respond. During the 1988 survey of Marojejy, this species seemed equally uncommon (Safford & Duckworth, 1990). In the RS d'Anjanaharibe-Sud, this species was recorded only in the 875 m zone (Hawkins et al., 1998).

Short-legged Ground-roller, *Brachypteracias leptosomus*

Records of this species from the Marojejy forest were obtained at the four lowest sites surveyed and encompassed an elevational range from 450 to 1625 m. In the 450 m zone, one individual was observed singing approximately 5 m from the camp site. Two individuals were heard calling each morning at approximately 0430 hr, not far from the camp site.

Playback song was also used to attract this species. In the 1250 m zone, one individual approached to within 2 m of the observer and remained perched 1 m above the ground for approximately 30 minutes. It stopped calling for a period and then resumed. At the same time this bird was vocalizing, another individual of this species was heard calling nearby. The Pitta-like Ground-roller (*Atelornis pittoides*) was also observed in this same area of forest. Finally, a third

species of ground-roller, Crossley's Ground-roller (*A. crossleyi*), was found in this same zone. Thus, three species of ground-roller occur sympatrically within this elevational stratum. At other sites in the eastern humid forest, the same three species have been recorded in sympatry, including the 1260 m zone of the RS d'Anjanaharibe-Sud (Hawkins et al., 1998) and the 1200 m zone of the PN d'Andohahela (Goodman et al., 1997b).

Scaly Ground-roller, *Brachypteracias squamiger*

This species was recorded in the Marojejy forest between 450 and 775 m. It is generally considered a bird of lowland forest, below 1000 m (Langrand, 1995). A nest site of the Scaly Ground-roller was found at approximately 450 m, in an area of slightly degraded forest with steep slopes and rolling hills. The nest was a hole, approximately 10 cm in diameter, approximately 1 m above ground level in a nearly vertical earth bank in a shallow valley. On 11 October, an adult was seen and heard calling as it approached this nest. This species is broadly distributed across intact zones of lowland forest, from the Marojejy and Anjanaharibe-Sud Massifs south to PN d'Andohahela (Goodman et al., 1997b; Hawkins et al., 1998).

Pitta-like Ground-roller, *Atelornis pittoides*

In general, this species is the most common of the four ground-rollers occurring in the humid forests of eastern Madagascar. In the PN de Marojejy, it was rarely noted during our 1996 survey. Records were obtained in the 1250 and 1625 m zones. During the 1988 inventory of the reserve, this species was regularly recorded in the southwestern and northwestern sectors but was not recorded in the southeastern sector (Safford & Duckworth, 1990), which includes the area of our 1996 survey. It was also recorded only once in the RS d'Anjanaharibe-Sud during 2 months of field work in 1994. Further south—for example, in the PN de Ranomafana and PN d'Andohahela—it is distinctly more common (J. C. Razafimahaimodison, pers. obs.; Goodman et al., 1997b; Hawkins & Goodman, 1999). This species is often more common than other species of ground-rollers in drier and more degraded forests.

Rufous-headed Ground-roller, *Atelornis crossleyi*

This ground-roller was recorded between 1250 and 1875 m. In the 1250 m zone, this species was observed in a variety of microhabitats, including ridges, valleys, and, less frequently, on slopes. This species was regularly heard calling in the early morning, often starting at 0400 hr. In the 1625 m transect, it appeared not to be uncommon and was observed almost daily.

Common Sunbird-asiy, *Neodrepanis coruscans*

This species was recorded from 450 to 1250 m and, on the basis of point-count data, appears to be more common toward the upper limit of this elevational range. (See next account for more details on this species' elevational range.)

Yellow-bellied Sunbird-asiy, *Neodrepanis hypoxantha*

The Yellow-bellied Sunbird-asiy was recorded within the elevational swath from 1125 to approximately 1775 m. The highest recorded observation occurred just below the ecotone between the sclerophyllous forest and the open savanna. Five individuals were caught in mist nets: four at 1250 m and one at 1625 m. The contact frequency of this species in the former zone was much higher than in the latter (Table 10-8). Although both species of *Neodrepanis* were observed within the 1250 m transect, they appear to have abutting elevational distributions. *N. coruscans* was found only in the lower end of the 1250 m zone, down to lowland forest, and *N. hypoxantha* was found only in the upper portion of the 1250 m zone, up to forest line. During the 1988 mission to this reserve, *N. hypoxantha* was observed on six occasions between 1500 and 1700 m (Safford & Duckworth, 1990). Further, in the RS d'Anjanaharibe-Sud, this species was recorded between 1500 and 1950 m (Hawkins et al., 1998). Thus, in the PN de Marojejy, the number of observations and netted individuals from the 1250 m zone seems slightly lower than previously noted for this species in northern Madagascar.

Brown Emu-tail, *Dromaeocercus brunneus*

The Brown Emu-tail was recorded in the higher elevational zones of the PN de Marojejy, from 1125 to 1800 m. Generally we had only fleeting glimpses of this terrestrial species as it scurried away in dense vegetation. One individual was captured in a live trap set for small mammals in the ecotone between sclerophyllous forest and the open grassland zone. The entrance of the trap was embedded in a tunnel passageway in the ground, and the only way for the bird to have entered the trap was as it was exiting the burrow. During the 1988 Cambridge survey of the Marojejy forest, this species was relatively common in the same zone of forest we worked, with up to 10 observations per day between 1300 and 2000 m (Safford & Duckworth, 1990). In the RS d'Anjanaharibe-Sud, *D. brunneus* is broadly distributed, from 875 to 1950 m, being distinctly more common at higher elevations (Hawkins et al., 1998).

Rand's Warbler, *Randia pseudozosterops*

In the Marojejy forest, Rand's Warbler was recorded within the altitudinal zone from 450 to 1625 m. This species always frequented the canopy zone of the forest.

Cryptic Warbler, *Cryptosylvicola randrianasoloi*

In the PN de Marojejy, from 1250 to 1875 m, the Cryptic Warbler was a common member of the local bird community. In the latter zone, this species occurred in the highest forested corridors hugging stream lines and surrounded by open grassland. It was noted numerous times completely out of the forest zone, perched on top of grass tufts and singing. The lower limit of this species is above the 775 m zone and below the 1250 m zone, which corroborates its elevational distribution on other mountains on the island (Goodman et al., 1995, 1997b; Hawkins et al., 1998).

Red-tailed Newtonia, *Newtonia fanovanae*

This species was recently known from only a single specimen captured in 1931 in the Sihanaka Forest (in the region between Didy and Fito). In 1989, it was rediscovered in the southeast, in the

forest of the Andohahela Massif (Goodman & Schulenberg, 1991), and in the northeast, in the RS d'Ambatovaky (Evans, 1991). Since then it has been found (from north to south) in the RS d'Anjanaharibe-Sud (Hawkins et al., 1998), in the RNI de Zahamena (Hawkins et al., in press), and in the region in and around the PN d'Andohahela (Goodman et al., 1997b).

Neither the 1988 nor the 1996 inventories of the PN de Marojejy detected this species. In July 1997, A. F. A. Hawkins saw an individual Red-tailed Newtonia in a mixed-species flock at approximately 500 m, in the far western portion of the reserve, on the trail from Ambalamanasy to Doany. This site is in the corridor linking the Marojejy Forest with the large forest block to the west, which includes the RS d'Anjanaharibe-Sud. Despite its loud and characteristic song, this species has not been located in numerous other apparently suitable eastern humid forest localities. From the above data, it appears to be most common at low elevations, with patchy distribution within this habitat.

Ward's Flycatcher, *Pseudobias wardi*

This species was recorded in the altitudinal swath between 325 and 1675 m. It was generally observed flying short distances between trees, in dense forests along the riverside or at forest edge.

Dusky Tetraka, *Bernieria tenebrosa*

This species is poorly known and recorded from only a few scattered localities on Madagascar. During our field survey in the PN de Marojejy, it was observed on one occasion—on 16 October, at 0900 hr, in the 775 m zone. A group of three individuals was seen not far from a stream, within an area of forest with few large trees and with areas of open understory vegetation. The ground was covered by a thick carpet of leaves. The group was seen foraging on the ground and, occasionally, climbing up to 0.5 m on low branches, when calling. The call was a single or repeated "tsit," like other small members of this genus. Their vocalizations were recorded, and subsequent play-backs brought the birds to approximately 1 m from the observer. This species was not previously reported for the Marojejy Massif and is apparently uncommon in the reserve. Its

northern limit was previously thought to be the Maroantsetra region (Langrand, 1995).

On the basis of the published literature, the Dusky Tetraka was known only from a small number of museum specimens and from sight observations from the region of Andasibe, the Sihanaka Forest, and Maroantsetra (Langrand, 1990). More-recent records of this species are from lowland forest around the Baie d'Antongil (Langrand, 1995), Zahamena (Randriamanindy, 1995), and Analamazaotra (Langrand, 1995). This species was not recorded on any of the previous World Wide Fund for Nature (WWF) elevational transects (PN d'Andringitra, RS d'Anjanaharibe-Sud, or PN d'Andohahela).

Gray-crowned Tetraka, *Bernieria cinereiceps*

In the Marojejy forest, this species was observed within an elevational band from 1125 to 1675 m. It was not detected frequently on point counts, perhaps largely because of its rather weak calls (Hawkins et al., 1998). Twelve individuals were captured in mist nets, evenly distributed between these two elevational zones (Table 10-6). In the 1250 m zone, this species was seen feeding in dense understory habitat; at 1625 m, it was observed on several occasions in mixed-species flocks. At numerous localities across the mountains of eastern Madagascar, this species is common in montane habitat, generally at elevations above 1000 m or so.

Madagascar Yellowbrow, *Bernieria xanthophrys*

This species was recorded in the 1250 m and 1625 m zones. A small group was found in dense primary forest vegetation, where they were observed calling along a shaded valley. Safford and Duckworth (1990) found this species to be common between 1200 and 1400 m in the same sector of the reserve.

As with several other species of small passerines found in the montane forest zone of eastern Madagascar, this species was previously thought to be fairly rare (e.g., Langrand, 1995). However, with recent exploration of the montane regions, it is now known to occur at many localities between the Anjanaharibe-Sud Massif (Hawkins et al., 1998) and the Andohahela Massif (Goodman et al., 1997b).

(Pollen's Vanga, *Xenopirostris polleni*

This species has been tentatively identified from the Marojejy region [Benson et al., 1977], but it was not recorded in the reserve either during the 1988 Cambridge mission [Safford & Duckworth, 1990] or during our 1996 field trip to the site. Further, this species was not recorded in the nearby RS d'Anjanaharibe-Sud [Hawkins et al., 1998]. It appears to be more widespread in the southern Malagasy eastern forest, particularly in the vicinity of the PN d'Andohahela [Goodman et al., 1997b], than in the northern portion of the island.)

Bernier's Vanga, *Oriolia bernieri*

During our field observations in the PN de Marojejy, Bernier's Vanga was recorded only in the lowland forest between 325 and 600 m. The latter elevation was on a ridge along the trail between the 450 and 775 transect zones. *O. bernieri* appears to be uncommon to rare in the area of the Marojejy forest we visited. However, it is fairly common in the southwestern portion of the reserve, at approximately 800 m (Safford & Duckworth, 1990). In the RS d'Anjanaharibe-Sud, it was observed once, at 900 m, during nearly 2 months of field work (Hawkins et al., 1998).

Helmet Vanga, *Euryceros prevostii*

The majority of records of the Helmet Vanga are from northeastern Madagascar, including the region of the Marojejy and Anjanaharibe-Sud Massifs (Griveaud, 1960; Hawkins et al., 1998). During the 1996 mission to this site, the Helmet Vanga was recorded between 400 and 1675 m. One individual was captured in a mist-net at 445 m (Table 10-6).

Close observations were made of the foraging habits of a Helmet Vanga. This bird captured insects while in flight and then perched 4–6 m above the ground to consume the prey. After this feeding bout, it flew to a nearby stream, wetted its feathers, and then flew to a branch to dry off. Not long after that, the bird was observed feeding on the ground, foraging just alongside an individual of *Bernieria madagascariensis*. *Euryceros* appears to be widely distributed within the Marojejy forest. In the RS d'Anjanaharibe-Sud, it was fairly common at 875 m and was recorded once at 1260 m (Hawkins et al., 1998).

Common Myna, *Acridotheres tristis*

This species, introduced to Madagascar, has not yet been recorded in the PN de Marojejy (Nicoll & Langrand, 1989; Safford & Duckworth, 1990; present study). However, it was noted in 1996, along the main road not far from Manantenina, and is common in the Andapa Basin.

Conservation Considerations

In recent years, with the expansion of the number of conservation projects in the world, great emphasis has been placed on the importance of reserves having high diversity and high levels of endemic species. Numerous systems have been devised to validate and quantify these variables or to measure levels of threat to organisms (e.g., Mace & Lande, 1991; Mace et al., 1992). In a world in which the remaining tropical forests are disappearing before us, such a system of prioritization is perhaps obligatory. We would like to point out that these systems are often based on insufficient data, and the outcome is often an emphasis on species rather than on habitat. In turn, these values often reflect a misrepresentation of the importance of certain areas or, in another sense, may diminish the conservation values of other, lesser known sites.

In 1994, Collar et al. published an important document that used new criteria established by the IUCN for assessment of the threat status of bird species. The categories, based on or modified from the system of Mace and Stuart (1994), were proposed for extant birds. The definitions of these categories are based on a complicated series of variables and are too detailed and beyond the scope of currently available population and demographic information for many species. To help put these definitions into context, we provide short summary statements of the categories, based on Collar et al. (1994, p. 15): (1) critical: "facing an extremely high risk of extinction in the wild in the near future"; (2) endangered: "facing a very high risk of extinction in the wild in the near future"; (3) vulnerable: "facing a high risk of extinction in the wild in the medium-term future"; and (4) near-threatened: not falling into any of the above categories but "close to qualifying for the [above] threatened categories." (This category does not directly follow the Mace et al. classification.)

Collar et al. (1994) thoroughly reviewed ornithological information available at that time and, for Madagascar, they classified 5 species as critical, 5 as endangered, 18 as vulnerable, and 16 as near-threatened, of which 1, 2, 8, and 10 species, respectively, are known from the PN de Marojejy (Table 10-9). On the basis of numerous biological inventories since the publication of this compilation and the ensuing rapid increase in ornithological knowledge on Malagasy birds, a re-evaluation of these categories is needed.

Eutriorchis astur was previously thought to be extremely rare and on the verge of extinction. With a series of recent observations of this species at several different sites on the island (see p. 192), it is now known to have a much broader distribution than previously thought. On the basis of new information, this species should probably be moved from the critical to the endangered category.

The case of *Neodrepanis hypoxantha* is an excellent example of how further research has greatly elucidated the status of this species (Hawkins et al., 1997). This bird, which once was known only from slightly more than a dozen museum specimens and a handful of observations, has recently been documented as occurring in montane and sclerophyllous forest from the Marojejy and Anjanaharibe-Sud Massifs in the north to the Andohahela Massif in the far south. It is a species with a limited altitudinal distribution but a broad geographic range. At some sites it is common; density estimates based on point counts yielded up to several thousand individuals per square kilometer, although in some cases these may be overestimates (Hawkins et al., 1998, p. 112). This species should probably be removed from the near-threatened list.

Several other species previously classified as either vulnerable (*Mesitornis unicolor*, *Brachypteryx leptosomus*, *B. squamiger*, *Atelornis crossleyi*, *Bernieria cinereiceps*, *B. xanthophrys*, *Xenopirostris polleni*, and *Oriolia bernieri*) or near-threatened (*Accipiter madagascariensis*, *A. henstii*, *Atelornis pittoides*, *Euryceros prevostii*, *Monticola sharpei*, *Dromaeocercus brunneus*, *Randia pseudozosterops*, and *Pseudobias wardi*) are all more common and broadly distributed than previously thought. Further, several of these species are known to live and nest in degraded habitats (Table 10-9) and occur in relatively high densities (Table 10-8). Examples from forests outside the PN de Marojejy include *Atelornis crossleyi*, with more than 65 individuals per square kilo-

TABLE 10-9. Forest birds recorded in the PN de Marojejy that were considered threatened by Collar et al. (1994), and their current status.

Species	Category	Threat codes ¹	Current status ²
<i>Eutriorchis astur</i>	Critical	1, 2, 3, 5	A, B
<i>Neodrepanis hypoxantha</i>	Endangered	1	B, C
<i>Bernieria tenebrosa</i>	Endangered	1	D
<i>Mesitornis unicolor</i>	Vulnerable	1	B
<i>Brachypteracias leptosomus</i>	Vulnerable	1	B, E
<i>Brachypteracias squamiger</i>	Vulnerable	1, 2, 4	B
<i>Atelornis crossleyi</i>	Vulnerable	1	B, C, E
<i>Bernieria cinereiceps</i>	Vulnerable	1	B, C, E
<i>Bernieria xanthophrys</i>	Vulnerable	1	B, C, E
<i>Newtonia fanovanae</i>	Vulnerable	1	A, D
<i>Xenopirostris polleni</i>	Vulnerable	1	B, E
<i>Oriolia bernieri</i>	Near-threatened	1	B
<i>Lophotibis cristata</i>	Near-threatened	—	F
<i>Accipiter madagascariensis</i>	Near-threatened	—	B
<i>Accipiter henstii</i>	Near-threatened	—	B, F
<i>Atelornis pittoides</i>	Near-threatened	—	B, E
<i>Euryceros prevostii</i>	Near-threatened	—	B
<i>Monticola sharpei</i>	Near-threatened	—	B, C, E, F
<i>Hartertula flavoviridis</i>	Near-threatened	—	B
<i>Dromaeocercus brunneus</i>	Near-threatened	—	B, C, E
<i>Randia pseudozosterops</i>	Near-threatened	—	B, E
<i>Pseudobias wardi</i>	Near-threatened	—	B, E

¹ Key to threat codes (Collar et al., 1994): 1 = loss or alteration of habitat; 2 = hunting, persecution (including accidental trapping), egg collecting (subsistence); 3 = disturbance (by humans, stock); 4 = introduced species (predators, competitors, herbivores, diseases); 5 = small range or population. Threat codes were not provided for near-threatened species.

² Key to current status: A = rediscovered after a long hiatus of information on this species in the wild; B = now known to have a much broader range than previously surmised; C = occurs in altitudinally limited but geographically widespread habitat; D = still poorly known, but apparently more widespread than previously thought; E = in some areas a common forest inhabitant; F = occurs in disturbed habitat with moderate to considerable human pressure.

meter, *Monticola sharpei*, with more than 140 individuals per square kilometer, and *Dromaeocercus brunneus*, with almost 50 individuals per square kilometer (Hawkins et al., 1998; Hawkins & Goodman, 1999). One enigmatic species, *Bernieria tenebrosa*, remains poorly known, and its “threatened” status should remain unchanged.

Recent biogeographic analyses of the distribution of forest-dependent species in the eastern humid forest has shown that most species are distributed widely and that the avifauna across this vast region is relatively homogeneous (Wilmé, 1996; Goodman et al., 1997b), although there is a decrease in bird species richness from north to south (see p. 188 for further discussion of this point). The high conservation status allocated to the PN de Marojejy by Collar and Stuart (1988) and Evans et al. (1992) is a direct result of the site’s rich avifauna; however, this is also one of the more intensively studied mountains in the ornithologically rich northern portion of the island.

Almost certainly, other sites in the north that include a broader elevational range of intact forests, from the lowlands to above tree line, hold rich avifaunas equal to that known from the PN de Marojejy. Several such sites, such as the RNI de Tsaratanana and adjoining forest blocks, include vast expanses of relatively intact forest and are of key biogeographic importance, since the vegetational structure on the east and west slopes are distinctly different. Thus, in light of these points and the fact that Marojejy is already part of an extensive conservation program, future conservation work should emphasize nearby forested areas, particularly those that are connected to one another. An excellent example is the forest of Betaolana, a forested corridor that connects the PN de Marojejy and the RS d’Anjanaharibe-Sud, and other forested corridors in the north that link various massifs and large forest blocks. These forested corridors are presumably critical for movements and genetic exchange between populations,

and the corridors should be given high priority for research and conservation status. The remaining lowland forest within and outside these reserves is the most threatened habitat type in the region, and conservation programs should pay particular attention to amelioration of the human pressures on this biotope.

Several other regions of the eastern humid forest that are not part of the current protected areas of the island have been identified as biologically poorly known and of probable high biotic importance (Ganzhorn et al., 1997). Further south, these sites include large areas of lowland forest. Examples of these forests include Rantabe, the "Sihanaka Forest" southeast of Lac Alaotra, and between Didy and Fito, the corridor between the PN de Ranomafana and the PN d'Andringitra, including the forests of Tolongoina and Ikongo. The Sihanaka Forest is an interesting case in point. Collar and Stuart (1988) gave this site the highest conservation status of any forest on the island, although this zone is largely unknown in modern times, and all current information is based largely on extensive collections made at the site more than 50 years ago. Until the recent wave of ornithological activity on Madagascar, such old collections represented a considerable proportion of the available data on the birds of the island. We now know that, although such information is extremely important, it does not represent the true distribution of the vast majority of forest-dwelling species.

Finally, the recent increase in inventory work in the eastern humid forest of Madagascar has been conducted largely in areas that are already protected. Given that baseline data exist for many such sites and that human pressure is higher outside rather than inside protected areas, now is the critical time to document the biota existing outside the reserves, to clearly set the priorities for future conservation on the island. In the northern portion of the island, certain reserves and surrounding forests are poorly known. An excellent example is the RNI de Tsaratanana, which contains the highest mountain on the island and extensive areas of forest. Little is known about the biota of this site, and only the drier western slope of the mountain is within the reserve. The regions on the eastern portion of the massif are almost certainly of critical biological importance but are in need of baseline data from biological inventories as well as assessments of human pressures.

These arguments are by no means meant to detract from the importance of the PN de Marojejy for safeguarding the high and remarkable biodi-

versity that the reserve holds. As clearly mentioned by Evans et al. (1992), the extensive lowland areas of the reserve have experienced severe deforestation, and these pressures continue. Many key species (*sensu* Evans et al. [1992]) are restricted to these habitats. On the other hand, another suite of their key bird species occurs in the upper montane and sclerophyllous forests, and they are under little threat associated with habitat loss. These forest types are still relatively extensive although not well represented in the protected areas system (Du Puy & Moat, 1996). The factors that have led to high human pressure on montane forest at sites such as the PN d'Andringitra—particularly easy access, local cultural traditions, and vast zones for cattle pasturage (Berner, 1997)—do not exist in the PN de Marojejy. Thus, these forest types are not under any serious threat in the PN de Marojejy.

One of the proposed reasons to change the status of the Marojejy Massif from Réserve Naturelle Intégrale (with highly restricted access) to Parc National was to allow tourist access to the site (see Chapter 1). Thus, in principle, an influx of revenue divided among people living around the reserve would result in improvement of their financial means and, at the same time, reduce their need to exploit forest products or to use slash-and-burn agricultural practices for subsistence. In the final assessment, the PN de Marojejy contains an important number of endemic bird species. Among the currently protected areas of Madagascar, it has tremendous possibilities for attracting ecotourism and continued scientific investigations, and the avifauna of the massif will be one of the main features to sustain this interest.

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Literature Cited

- ASSOCIATION NATIONALE POUR LA GESTION DES AIRES PROTÉGÉES. 1998. Synthèse de Recherches dans le Réseau d'Aires Protégées de Madagascar. Association Nationale pour la Gestion des Aires Protégées, Antananarivo, 219 pp.
- BENSON, C. W., J. F. R. COLEBROOK-ROBJENT, AND A. WILLIAMS. 1976. Contribution à l'ornithologie de Madagascar. *L'Oiseau et Revue Française d'Ornithologie*, **46**: 103–134, 209–242, 367–386.
- . 1977. Contribution à l'ornithologie de Madagascar. *L'Oiseau et Revue Française d'Ornithologie*, **47**: 41–61, 167–191.
- BERNER, P. O. 1997. Les forêts de transition de la région Nord-Est du massif de l'Andringitra, Madagascar: Monitoring d'impacts anthropiques et proposition d'aménagement. *Akon'ny Ala*, **21**: 9–26.
- BIBBY, C. J., N. D. BURGESS, AND D. A. HILL. 1992. *Bird Census Techniques*. Academic Press, London, 257 pp.
- COLLAR, N. J., M. J. CROSBY, AND A. J. STATTERSFIELD. 1994. *Birds to Watch, 2: The World List of Threatened Birds*. Bird Life International, Cambridge, 407 pp.
- COLLAR, N. J., AND S. N. STUART. 1985. *Threatened Birds of Africa and Related Islands: The ICBP/IUCN Red Data Book, part 1, 3rd ed.* International Council for Bird Preservation and International Union for the Conservation of Nature and Natural Resources, Cambridge, United Kingdom.
- . 1988. *Key Forests for Threatened Birds in Africa*. International Council for Bird Preservation, Monograph no. 3, Cambridge, United Kingdom.
- DU PUY, D. J., AND J. MOAT. 1996. A refined classification of the primary vegetation of Madagascar based on the underlying geology: Using GIS to map its distribution and to assess its conservation status, pp. 205–218. *In* Lourenço, W. R., ed., *Biogéographie de Madagascar*. ORSTOM Editions, Paris, 588 pp.
- EVANS, M. I. 1991. The Red-tailed *Newtonia Newtonia fanovanae* in the Ambatovaky Reserve, north-east Madagascar. *Bird Conservation International*, **1**: 47–52.
- EVANS, M. I., J. W. DUCKWORTH, A. F. A. HAWKINS, R. J. SAFFORD, B. C. SHELDON, AND R. J. WILKINSON. 1992. Key bird species of Marojejy Strict Nature Reserve, Madagascar. *Bird Conservation International*, **2**: 201–220.
- FJELDSÅ, J., S. M. GOODMAN, T. S. SCHULENBERG, AND B. SLIKAS. 1999. Molecular evidence for relationships of Malagasy birds, pp. 3084–3094. *In* Adams, N., and R. Slotow, eds., *Proceedings of the 22nd International Ornithological Congress*. University of Natal, Durban.
- GANZHORN, J. U., B. RAKOTOSAMIMANANA, L. HANNAH, J. HOUGH, L. IYER, S. OLIVIERI, S. RAJAABELINA, C. RODSTROM, AND G. TILKIN. 1997. Priorities for biodiversity conservation in Madagascar. *Primate Report, Special Issue*, **48-1**: 1–81.
- GOODMAN, S. M., A. ANDRIANARIMISA, L. E. OLSON, AND V. SOARIMALALA. 1996. Patterns of elevational distribution of birds and small mammals in the humid forests of Montagne d'Ambre, Madagascar. *Ecotropica*, **2**: 87–98.
- GOODMAN, S. M., AND J. U. GANZHORN. 1997. Rarity of figs (*Ficus*) on Madagascar and its relationship to a depauperate frugivore community. *Revue d'Ecologie*, **52**: 321–329.
- GOODMAN, S. M., A. F. A. HAWKINS, AND C. A. DOMERGUE. 1997a. A new species of vanga (Vangidae, *Calicalicus*) from southwestern Madagascar. *Bulletin of the British Ornithologists' Club*, **117**: 4–10.
- GOODMAN, S. M., O. LANGRAND, AND B. M. WHITNEY. 1995. A new genus and species of passerine from the eastern rainforest of Madagascar. *Ibis*, **138**: 153–159.
- GOODMAN, S. M., AND P. PARRILLO. 1997. A study of the diets of Malagasy birds based on stomach contents. *Ostrich*, **68**: 104–113.
- GOODMAN, S. M., M. PIDGEON, A. F. A. HAWKINS, AND T. S. SCHULENBERG. 1997b. The birds of southeastern Madagascar. *Fieldiana: Zoology*, n. s., **87**: 1–132.
- GOODMAN, S. M., AND M. S. PUTNAM. 1996. The birds of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 171–190. *In* Goodman, S. M., ed., *A Floral and Faunal Inventory of the Eastern Slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With Reference to Elevational Variation*. *Fieldiana: Zoology*, n. s., **85**: 1–319.
- GOODMAN, S. M., AND B. RASOLONANDRASANA. In press. Elevational zonation of birds, insectivores, rodents, and primates on the slopes of the Andringitra Massif, Madagascar. *Journal of Natural History*.
- GOODMAN, S. M., AND T. S. SCHULENBERG. 1991. The rediscovery of the Red-tailed *Newtonia Newtonia fanovanae* in south-eastern Madagascar with notes on the natural history of the genus *Newtonia*. *Bird Conservation International*, **1**: 33–45.
- GOODMAN, S. M., AND L. E. WEIGHT. In press. The generic and species relationships of the reputed endemic Malagasy genus *Pseudocossyphus* (family Turdidae). *Ostrich*.
- GRIVEAUD, P. 1960. Une mission entomologique au Marojejy. *Naturaliste Malgache*, **12**: 43–55.
- HAWKINS, A. F. A. 1999. Altitudinal and latitudinal distribution of east Malagasy forest bird communities. *Journal of Biogeography*, **26**: 447–458.
- HAWKINS, A. F. A., AND S. M. GOODMAN. 1999. Bird community variation with elevation and habitat in parcels 1 and 2 of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, pp. 175–186. *In* Goodman, S. M., ed., *A Floral and Faunal Inventory of Réserve Naturelle Intégrale d'Andohahela, Madagascar: With Reference to Elevational Variation*. *Fieldiana: Zoology*, n. s., **94**: 1–297.
- HAWKINS, A. F. A., R. J. SAFFORD, J. W. DUCKWORTH, AND M. I. EVANS. 1997. Field identification and status of the sunbird asities *Neodrepanis* of Madagascar. *Bulletin of the African Bird Club*, **4**: 36–41.
- HAWKINS, A. F. A., J.-M. THIOLLAY, AND S. M. GOODMAN. 1998. The birds of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, pp. 43–147. *In* Goodman, S. M., ed., *A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With Reference to Elevational Variation*. *Fieldiana: Zoology*, n. s., **90**: 1–246.
- HAWKINS, A. F. A., A. ANDRIANARIMISA, O. M. RAKOTONOMENJANAHARY, AND V. RAMINOARISOA. In press.

- Inventaire des oiseaux dans la Réserve Naturelle Intégrale de Zahamena. Ostrich.
- JENKINS, M. D., ED. 1990. Madagascar: Profil de l'Environnement. UICN/PNUE/WWF Gland et Cambridge, 439 pp.
- KARR, J. R. 1981. Surveying birds with mist nets. *Studies in Avian Biology*, **6**: 62–67.
- KOECHLIN, J., J.-L. GUILLAUMET, AND P. MORAT. 1974. Flore et Végétation de Madagascar. J. Cramer, Vaduz, 629 pp.
- INSKIPP, C., AND T. INSKIPP. 1991. Birds of Nepal, 2nd ed. Christopher Helm, London.
- LANGRAND, O. 1990. Guide to the Birds of Madagascar. Yale University Press, New Haven, 364 pp.
- . 1995. Guide des oiseaux de Madagascar. Delachaux et Niestlé, Lausanne, 415 pp.
- MACE, G., N. COLLAR, J. COOKE, K. GASTON, J. GINSBURG, N. LEADER-WILLIAMS, M. MAUNDER, AND E. J. MILNER-GULLAND. 1992. The development of new criteria for listing species on the IUCN Red List. *Species*, **19**: 16–22.
- MACE, G. M., AND R. LANDE. 1991. Assessing extinction threats: Toward a reevaluation of IUCN threatened species categories. *Conservation Biology*, **5**: 148–157.
- MACE, G. M., AND S. STUART. 1994. Draft IUCN Red List categories. *Species*, **21–22**: 13–24.
- MACLEAN, G. L. 1990. Ornithology for Africa. University of Natal Press, Pietermaritzburg.
- MORRIS, P. A. J., AND A. F. A. HAWKINS. 1998. The Birds of Madagascar: A Photographic Guide. Pica Press, East Sussex, United Kingdom, 316 pp.
- NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la Conservation et des Aires Protégées. World Wide Fund for Nature, Gland, 374 pp.
- PRUM, R. O., AND V. R. RAZAFINDRATSITA. 1997. Lek behavior and natural history of the Velvet Asity (*Philepitta castanea*: Eurylaimidae). *Wilson Bulletin*, **109**: 371–392.
- RAND, A. L. 1932. Mission Franco-Anglo-Américaine à Madagascar: Notes de Voyage. L'Oiseau et la Revue Française d'Ornithologie (nouvelle série), **2**: 227–282.
- . 1936. The distribution and habits of Madagascar birds: A summary of the field notes of the Mission Zoologique Franco-Anglo-Américaine à Madagascar. *Bulletin American Museum of Natural History*, **72**: 143–499.
- RANDRIAMANINDRY, J.-J. 1995. The Dusky Greenbul *Phyllastrephus tenebrosus* in Zahamena Strict Nature Reserve, Madagascar. Newsletter of the Working Group on Birds in the Madagascar Region, **5**(2): 5.
- RANWORTHY, C. J., AND P. R. COLSTON. 1992. Conclusive evidence for the continuing existence of the Madagascar Serpent-eagle *Eutriorchis astur*. *Bulletin of the British Ornithologists' Club*, **112**: 108–111.
- RAZAFINDRATSITA, V. R. 1995. Etude biologique et écologique de *Philepitta castanea* (Muller, 1776) son rôle dans la régénération du sois-bois forestier du Parc National de Ranomafana. Mémoire de Diplôme d'Etudes Approfondies. Université d'Antananarivo, Antananarivo.
- REMSEN, J. V., JR, AND D. A. GOOD. 1996. Misuse of data from mist-net captures used to assess relative abundance in bird populations. *Auk*, **113**: 381–398.
- REYNOLDS, R. T., J. M. SCOTT, AND R. A. NUSSBAUM. 1980. A variable circular-plot method for estimating bird numbers. *Condor*, **82**: 309–313.
- SAFFORD, R. J., AND J. W. DUCKWORTH, EDs. 1990. A wildlife survey of Marojejy Reserve, Madagascar. ICBP Study Report 40. International Council for Bird Preservation, Cambridge.
- SCHULENBERG, T. S., S. M. GOODMAN, AND J.-C. RAZAFIMAHAIMODISON. 1993. Genetic variation in two subspecies of *Nesillas typica* (Sylviinae) in south-east Madagascar. pp. 173–177. *In* Wilson, R. T., ed. Birds and the African Environment: Proceedings of the 8th Pan-African Ornithological Congress. Annales Musée Royale de l'Afrique Centrale (Zoologie), **268**.
- SHELDON, B. C., AND J. W. DUCKWORTH. 1990. Rediscovery of the Madagascar Serpent-eagle *Eutriorchis astur*. *Bulletin of the British Ornithologists' Club*, **110**: 126–130.
- SINCLAIR, I., AND O. LANGRAND. 1998. Birds of the Indian Ocean Islands. Struik Publishers, Ltd., Cape Town, 184 pp.
- STOTZ, D. F., J. W. FITZPATRICK, T. A. PARKER, III, AND D. K. MOSKOVITS. 1996. Neotropical Birds: Ecology and Conservation. The University of Chicago Press, Chicago, 478 pp.
- STRAKA, H. 1996. Histoire de la végétation de Madagascar oriental dans les derniers 100 millénaires. pp. 37–47. *In* Lourenço, W. R., ed., Biogéographie de Madagascar. Editions ORSTOM, Paris.
- THIOLLAY, J.-M. 1998. The diurnal raptors (Falconiformes) of the Réserve Spéciale d'Anjanaharibe-Sud: Abundance, distribution, and conservation, pp. 129–138. *In* Goodman, S. M., ed., A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With Reference to Elevational Variation. *Fieldiana: Zoology*, n.s., **90**: 1–246.
- THOMPSON, P. M., AND M. I. EVANS. 1992. The threatened birds of Ambatovaky Special Reserve, Madagascar. *Bird Conservation International*, **2**: 221–237.
- THORSTROM, R., AND R. T. WATSON. 1997. Avian inventory and key species of the Masoala Peninsula, Madagascar. *Bird Conservation International*, **7**: 99–115.
- THORSTROM, R., R. WATSON, B. DAMARY, F. TOTO, M. BAB, AND V. BABA. 1995. Repeated sightings and recent capture of a live Madagascar Serpent-eagle *Eutriorchis astur*. *Bulletin of the British Ornithologists' Club*, **115**: 40–45.
- WILMÉ, L. 1996. Composition and characteristics of bird communities in Madagascar. pp. 349–362. *In* Lourenço, W. R., ed., Biogéographie de Madagascar. ORSTOM Editions, Paris, 588 pp.
- YAMAGISHI, S., T. MASUDA, AND H. RAKOTOMANANA. 1997. [A Field Guide to the Birds of Madagascar.] [In Japanese and Malagasy.] Kaiyusha Publishers, Ltd., Tokyo, 160 pp.

Chapter 11

Tenrecs (Lipotyphla: Tenrecidae) of the Parc National de Marojejy, Madagascar

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Abstract

Tenrecs (Lipotyphla: Tenrecidae) were studied in northeastern Madagascar in the Parc National (PN) de Marojejy in five zones across a forested elevational gradient from 450 to 1875 m. The transect went through a variety of habitats, including lowland (450–775 m), montane (1225–1625 m), and sclerophyllous/mossy (1875 m) forests. Trapping techniques involved pit-fall buckets and standard live small mammal traps. Fifteen species of lipotyphlans were recorded in the reserve, including 12 species of shrew tenrecs (*Microgale*). Among *Microgale*, there is no clear evidence of species replacement along the elevational gradient surveyed within the PN de Marojejy. New information is presented on morphology, reproduction, development, and ecology of the Tenrecidae captured in this reserve.

No species of Tenrecidae was recorded across the complete elevational gradient. The two most elevationally widespread species were *Microgale talazaci* and *M. parvula*, which were trapped between 450 and 1625 m. Five species occurred within the montane forest zone: *M. dobsoni*, *M. fotsifotsy*, *M. gymnorhyncha*, *M. longicaudata*, and *M. sorcoides*, and three species occurred across the montane and sclerophyllous/mossy forest habitats: *M. cowani*, *M. monticola*, and *M. principula*. Only two species were captured in traps at a single elevational zone: *M. brevicaudata* at 475 m and *M. gracilis* at 1875 m. The only species with an apparently disjunct altitudinal distribution was the mole tenrec *Oryzorictes hova*, which was collected in lowland forest at 450 m and in montane forest at 1625 m; this result is almost certainly an artifact of the difficulty in trapping members of this genus.

The greatest Tenrecidae species richness was at 1625 m, where nine species (including eight species of *Microgale*) were found. The 775 m and 1875 m zones had the lowest species richness, with only four species each. The highest densities of lipotyphlans in the reserve, as measured by pitfall trap success, were in the montane forest, which across the different pitfall lines averaged 19.5% in the 1225 m zone (range 14.3%–24.7%) and 15.6% in the 1625 m zone (range 11.7%–19.5%). The lowland forests at 450 and 775 m had the lowest Tenrecidae capture rates; 3.8% at 450 m and 1.9% at 775 m.

A comparison is made between the Tenrecidae found in the PN de Marojejy and those captured by means of identical trapping techniques along an elevational transect in the Réserve Spéciale (RS) d'Anjanaharibe-Sud, 40 km to the west. The vast majority of species were found in common between these two reserves (*Oryzorictes hova*, *Microgale cowani*, *M. dobsoni*, *M. fotsifotsy*, *M. gymnorhyncha*, *M. longicaudata*, *M. monticola*, *M. parvula*, *M. principula*, *M. sorcoides* and *M. talazaci*), but there are a few differences, with *M. brevicaudata* and *M. gracilis* obtained only in PN de Marojejy and *M. dryas* only in the RS d'Anjanaharibe-Sud. The altitudinal distributions of these species in the two reserves are broadly similar.

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Résumé

Les Tenrecs (Lipotyphla: Tenrecidae) ont été étudiés au nord-est de Madagascar dans le Parc National (PN) de Marojejy où les cinq zones d'études retenues traversaient un gradient altitudinal de 450 à 1875 m. Le transect parcourait une variété d'habitats incluant la forêt de basse altitude (450–775 m), de montagne (1225–1625 m), et sclérophylle/de mousses (1875 m). Les techniques de piégeage comprenaient les lignes de seaux enterrés et les pièges standard pour la capture de petits mammifères vivants. Quinze espèces des lipotyphlans ont été relevées dans la réserve, y compris 12 espèces de tenrec-musaraignes (*Microgale*) pour lesquels aucune évidence claire n'a permis de montrer un remplacement d'espèces le long du gradient altitudinal examiné dans le PN de Marojejy. Les nouvelles informations relatives à la morphologie, la reproduction, le développement, et l'écologie des Tenrecidae capturés dans cette réserve sont ici présentées.

Aucune espèce de Tenrecidae n'a été enregistrée sur l'ensemble du gradient altitudinal. Les deux espèces les plus largement distribuées sur le gradient étaient *Microgale talazaci* et *M. parvula*, capturées à tous les niveaux entre 450 et 1625 m d'altitude. Cinq espèces ont été rencontrées dans la zone de forêt de montagne: *M. dobsoni*, *M. fotsifotsy*, *M. gymnorhyncha*, *M. longicaudata* et *M. soricoides*, et trois espèces à travers les habitats de la forêt de montagne et la forêt sclérophylle/de mousse: *M. cowani*, *M. monticola*, et *M. principula*. Seules deux espèces étaient limitées à une seule zone altitudinale: *M. brevicaudata* à 475 m and *M. gracilis* à 1875 m.

La richesse spécifique la plus importante a été relevée à 1625 m d'altitude avec 9 espèces (y compris 8 espèces de *Microgale*). Dans les zones à 775 m et 1875 m, aura été relevée la plus basse richesse spécifique avec quatre espèces. Les densités de lipotyphlans les plus élevées de la réserve, mesurées par le succès de la ligne de piégeage employant les baquets, ont été mesurées dans la forêt de montagne avec une moyenne, calculée sur les différentes lignes, de 19,5% dans la zone à 1225 m (écart 14,3–24,7%) et 15,6% dans la zone à 1625 m (écart 11,7–19,5%). Le plus faible taux de capture de Tenrecidae a été relevé dans forêt de basse altitude à 450 et 775 m: 3,8% à 450 m et 1,9% à 775 m.

Une comparaison est faite entre les Tenrecidae relevés dans le PN de Marojejy et ceux capturés en utilisant des techniques de piégeage identiques le long d'un transect altitudinal d'élévation dans le Réserve Spéciale (RS) d'Anjanaharibe-Sud, située 40 kilomètres à l'ouest. La grande majorité des espèces sont communes aux deux réserves (*Oryzorictes hova*, *Microgale cowani*, *M. dobsoni*, *M. fotsifotsy*, *M. gymnorhyncha*, *M. longicaudata*, *M. monticola*, *M. parvula*, *M. principula*, *M. soricoides*, et *M. talazaci*), mais il y a quelques différences dont *M. brevicaudata* et *M. gracilis* qui n'ont été relevés que dans le PN de Marojejy et *M. dryas* que dans la RS d'Anjanaharibe-Sud. La distribution altitudinale de ces espèces est globalement semblable dans les deux réserves.

Introduction

In 1987 MacPhee published an important revision of *Microgale*, the most speciose genus of Tenrecidae, that provided the critical foundation for more recent studies on the species limits and biogeography of this group. One of the problems that plagued advancement of tenrecid systematics was the lack of comparative material, particularly specimens with intact skulls and indicators of external measurements, sex, and provenance. MacPhee (1987) amassed the *Microgale* material held in virtually all the major museums of the

world but was able to study only approximately 120 specimens. Faced with sorting out synonymies and species limits for 22 named taxa, he had an average of only 5.5 specimens per taxon. Clearly, such sample sizes are insufficient for understanding aspects of age, sexual, and geographic variation within a species.

Over the course of the past decade there has been a resurgence in field efforts on Madagascar, and a portion of this work has centered on biological inventories in poorly known areas of forest. A considerable amount of new small mammal material has been obtained. These new collections, combined with further research on existing

specimens in museums, have resulted in the description of numerous new species of Malagasy insectivores and rodents and have allowed mammalogists to completely revamp ideas about the diversity, species limits, and biogeography of these animals on Madagascar. For *Microgale* alone, the collections now available to help clarify the relationships of this group are many times greater than what was available for MacPhee's revision. Further, this new material, combined with preserved tissues for biochemical analyses, has provided the means to commence studies on aspects of the phylogeny and relationships of the Tenrecidae.

As part of these surveys of poorly known areas of Malagasy forest, a group of biologists conducted an inventory in late 1996 of the Parc National (PN) de Marojejy in the northeastern portion of the island (see Chapter 1). This survey, organized by World Wide Fund for Nature in the context of a conservation project in this reserve, was the fourth annual survey to examine the distribution of biota along elevational gradients in eastern humid forests, and, during all of these surveys, concerted efforts have been made to study Tenrecidae.

Thirteen species of oryzorictine tenrecs were collected during the 1996 survey of the PN de Marojejy: *Microgale brevicaudata*, *M. cowani*, *M. dobsoni*, *M. fotsifotsy*, *M. gracilis*, *M. gymnorhyncha*, *M. longicaudata*, *M. monticola*, *M. parvula*, *M. principula*, *M. soricoides*, *M. talazaci*, and *Oryzorictes hova*. In this chapter we present details of synonymy, measurements, key characters for identification, reproduction and population structure, and distribution for the various species captured in the reserve. We follow the basic format used in previous, similar surveys of Malagasy lipotyphlans (Jenkins et al., 1996; Goodman et al., 1996a, 1999a; Goodman & Jenkins, 1998). Furthermore, we provide a more comprehensive description for *Microgale brevicaudata*, a poorly known species for which only five specimens, including the holotype, were available for MacPhee's (1987) study.

One of the mountains surveyed during the past few years in a manner comparable to the work conducted in the PN de Marojejy is the Réserve Spéciale (RS) d'Anjanaharibe-Sud. These two mountains are 40 km from one another, on opposite sides of the Andapa Basin (Fig. 11-1). Throughout this chapter we compare the results of tenrecid distribution, density, and species richness between these two sites, which are at nearly

the same latitude. Information is now available on the shrew tenrecs occurring at five different mountains in the eastern part of the country, spanning the complete latitudinal gradient of the island (12°E–25°E S; Fig. 11-1). In this chapter we also examine trends in species richness, elevational zonation, and geographic distribution related to this gradient. Finally, we analyze variation in species distribution and provide details of altitudinal and ecological separation.

Materials and Methods

Traplins

The principal technique used to capture lipotyphlans consisted of pitfall traps with drift fences. In each of the elevational zones surveyed (450, 775, 1225, 1625, and 1875 m) separate pitfall lines were installed in three different topographic settings (valley bottom, slope, and ridge crest) to assess possible variation in microhabitat use by lipotyphlans. Each line was 100 m long and consisted of 11 buckets (275 mm deep, 290 mm top internal diameter, 220 mm bottom internal diameter), 10 m apart, in operation for a minimum of 7 nights. (The only exception was the lines at 1875 m, which were in place for 5 nights.) Small holes (2 mm diameter) were drilled in the bottom of each bucket to allow water drainage. Buckets were sunk to a depth at which the rim was even with ground level. A barrier (drift fence) made from plastic sheeting (0.5 m high and 100 m long) was stapled in a vertical position to thin wooden stakes. The drift fence bisected all of the buckets in the line (Voss & Emmons, 1996 [Fig. 7]). A flange of approximately 50 mm at the bottom of the standing plastic fence was covered with soil and leaf litter to prevent animals from moving under the barrier. Lipotyphlans were also captured with standard Sherman live traps. The trap types, placement, baits, and other details for these lines are described in Chapter 12.

Traps and pitfalls were visited at least twice per day, once at dawn and again in the late afternoon, and captured animals were removed. A "trap-day" and a "bucket-day" are defined as a 24-hour period of use of one of these devices (dawn to dawn). After heavy rain, water was removed from the traps by means of a sponge. The survey of the PN de Marojejy was conducted between 5 October and 19 November 1996, a season during

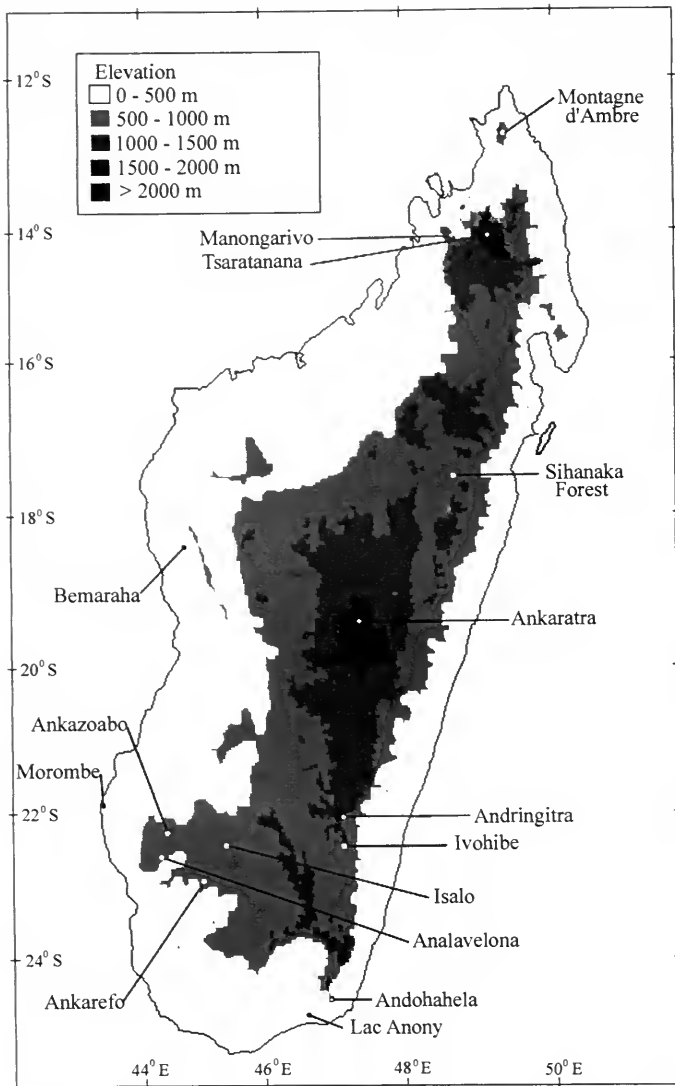


FIG. 11-1. Map of mountains for which detailed information is available for the distribution of Lipotyphla along elevational gradients, and various other sites mentioned in the text.

which all Tenrecidae, including those that are known to hibernate or aestivate, are expected to be active (Stephenson, 1994). However, the results of previous surveys conducted during this same calendar period seem to indicate that some of the large spiny tenrecs (*Tenrec ecaudatus*, *Hemicentetes* spp., and *Setifer setosus*) may not be very active, or at least that population cycles are at a low before reproduction, associated with the upcoming rainy season (Goodman et al., 1996a; Goodman & Jenkins, 1998).

The majority of captured animals were prepared as standard museum skins with associated

skulls and skeletons, as fluid-preserved carcasses, or as full skeletons. Voucher specimens will be divided equally between the Field Museum of Natural History (FMNH), Chicago, and the Département de Biologie Animale, Université d'Antananarivo (UA). Specimens deposited immediately after the survey in the latter institution have not yet been catalogued and are referenced individually by the collector's field numbers (UA-SMG). Animals not kept as voucher specimens were first marked by clipping a small area of fur on their backs and then released near the original trap site. This marking technique allowed first-

time and previously captured animals to be differentiated.

Measurements

Crania were measured by means of digital calipers and a microscope measuring stage. Dental nomenclature follows Mills (1966), Swindler (1976), Butler and Greenwood (1979), MacPhee (1987), and Jenkins et al. (1996, 1997). Dental notations are given in parentheses in the text; premaxillary and maxillary teeth are denoted by uppercase and mandibular teeth by lowercase letters, as follows: incisor (*I/i*), canine (*C/c*), premolar (*P/p*), and molar (*M/m*). A prefix "d" indicates deciduous teeth; thus, dI3 refers to the deciduous third upper incisor. The following measurements were made either from specimens in the flesh or from prepared crania. Abbreviations and definitions for these measurements (all in millimeters, with the exception of weight, in grams) are as follows:

- BB (breadth of braincase): the greatest distance measured across the squamosals.
- CIL (condyloincisive length): cranial length from the anterior surface of the first upper incisor to the articular surface of the occipital condyle.
- E (ear length): measured from the notch at the base of the ear to the distal-most edge of the pinna.
- HB (head and body length): measured from the tip of the nose to the distal-most point of the body (at base of tail).
- HF (hind foot length): measured from the back edge of the heel to the tip of the longest toe (not including claw).
- TL (tail length): measured from the base of the tail (at right angles to the body) to the end of the distal-most vertebra. Does not include terminal hair tufts.
- UTL (upper tooth-row length): measured from the anterior surface of the first upper incisor to the posterior surface of the third upper molar, parallel to the long axis of the skull.
- WT (weight): measured in grams by means of Pesola spring scales. Animals weighing less than 10 g were weighed within 0.2 g; those weighing 10–100 g were weighed within 0.5 g.

Reproductive condition was recorded for males as length \times width of the testes and degree of con-

volution of the epididymides. Females were noted as nonperforate or perforate and as nonparous or parous, and the number and location of any embryos and placental scars were recorded. The mammary formula is presented as the number of paired axial, abdominal, and inguinal nipples.

The following age classes are recognized:

- "Infant": Individuals in which the deciduous antemolar dentition and the molars are not fully erupted and premaxillary, parietal, and basioccipital sutures are unfused.
- "Juvenile": Individuals in which the molars are fully erupted, the deciduous antemolar dentition is erupted but still in the process of replacement by the permanent teeth, and cranial sutures are in the process of fusing. The eruption sequence of the permanent teeth has been subdivided into four stages by MacPhee (1987); these stages have been accepted in this text unless otherwise stated.
- "Adult": Individuals with a fully erupted permanent dentition; cranial sutures are generally fused, although their position is more or less clearly marked.

Other abbreviations used are as follows: PN, Parc National; RNI, Réserve Naturelle Intégrale; RS, Réserve Spéciale; BM (NH), The Natural History Museum, London (formerly British Museum [Natural History]); FMNH, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology (Harvard), Cambridge; MNHN, Muséum National d'Histoire Naturelle, Paris; SMG, Field catalog of S. M. Goodman; UA, Département de Biologie Animale, Université d'Antananarivo, Antananarivo; UMMZ, University of Michigan, Museum of Zoology, Ann Arbor; and USNM, United States National Museum, Washington, D.C.

Systematics

Family Tenrecidae

Subfamily Tenrecinae

Setifer setosus Schreber, 1778

HOLOTYPE—Unknown.

TYPE LOCALITY—Madagascar.

KEY FEATURES (see Key 1, p. 228)—Dorsum covered with spines; very short spinous tail present. Skull moderately robust, dorsal profile

curved in lateral view; rostrum deep and broad; interorbital region broad and elongated, frontals posterodorsally inflated; interorbital region deeper than braincase; braincase short, lambdoid crest present. Dental formula $2/2 \ 1/1 \ 3/3 \ 3/3 = 36$; I1 well developed, slightly shorter than C; short diastemata on either side of C and first lower premolar (p2).

REMARKS—This species was not captured during the 1996 survey of the PN de Marojejy. It was observed on two occasions in the 450 m zone and once at 775 m. It has been previously reported as occurring in the reserve (Nicoll & Langrand, 1989). *Setifer setosus* was also found at low elevation in the RS d'Anjanaharibe-Sud (Goodman & Jenkins, 1998). This species occurs across the complete length of the eastern humid forest, generally at lower-lying elevations, from the PN de la Montagne d'Ambre in the north to the PN d'Andohahela in the extreme south (Raxworthy & Nussbaum, 1994; Goodman et al., 1996b, 1999a). It is also known from a variety of sites in western deciduous forest (Ganzhorn et al., 1996) and spiny forest (Nicoll & Langrand, 1989).

Tenrec ecaudatus (Schreber, 1778)

HOLOTYPE—Unknown.

TYPE LOCALITY—Unknown.

KEY FEATURES (see Key 1, p. 228)—The largest of the Tenrecinae. Adult with dorsal pelage of coarse bristly hair intermixed with soft spines; short tail present. Skull elongated; rostrum with deep sockets in ventrolateral region of the premaxillae, which accommodate the lower canines when the jaw is closed; interorbital region narrow, elongated; braincase short, narrow, angular, pronounced sagittal and lambdoid crests form deep posterodorsal flanges. Dental formula $2/3 \ 1/1 \ 3/3 \ 3/3 = 38$; upper and lower canines very long, robust, and prominent; pronounced diastemata on either side of C and posterior to C; short diastemata posterior to first upper and lower premolars.

REMARKS—*Tenrec ecaudatus* was observed on three occasions in the 450 m zone and once in the 775 m zone. Generally this species was noted in the late afternoon or toward sunset, scuffling along on the forest floor and presumably foraging for food. It has been reported previously as occurring in the reserve (Griveaud, 1960; Nicoll & Langrand, 1989). In the RS d'Anjanaharibe-Sud, this species was observed in the elevational zone between 875 and 1260 m (Goodman & Jenkins,

1998). It is one of the most broadly distributed tenrecids on Madagascar and occurs in a wide variety of habitat types, including humid and deciduous forests as well as spiny bush.

Subfamily Oryzoricinae

Microgale breviceps G. Grandidier, 1899

Microgale breviceps Kaudern, 1918

Paramicrogale occidentalis Grandidier and Petit, 1931

LECTOTYPE—MNH 1986-387, adult male, skull and skeleton, no skin, collector unknown. Lectotype designation by MacPhee (1987, p. 6).

TYPE LOCALITY—Environs of Mahanara, 75 km S of Vohémar, NE coast of Madagascar. (MacPhee [1987] provides coordinates of $13^{\circ}58'S$, $49^{\circ}58'E$ for Antsirabe Avaratra, where the Mahanara River crosses Route Nationale 5A, Province d'Antsiranana.)

REFERRED MATERIAL—FMNH 159652, 159653, 159654, and UA-SMG 8267; tributary of the Manantenina River, 8 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 450 m, $14^{\circ}26.2'S$, $49^{\circ}46.5'E$.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—The following description is based on the lectotype and two adult specimens from PN de Marojejy. Body small to medium in size, tail short relative to body length (TL as a percentage of HB 51.1, 51.7 in adult specimens from PN de Marojejy [50% in the lectotype, based on measurements in the original description]; ratio of TL to CIL 1.76, 1.85 [1.52 in the lectotype]). Dorsal pelage moderately short and coarse in texture, brown with buffy brown speckling; ventral pelage pale grayish brown, demarcated from dorsal coloration; tail and feet brown; tail scale hairs moderately short, scales visible. Skull with short, broad, and deep rostrum and moderately broad interorbital region; braincase short, scarcely broader than zygomatic process of maxillae; superior articular facets angular and visible in dorsal view, lambdoid crest prominent; mandible moderately robust, corpus short and deep, coronoid process broad. Dentition with short diastemata separating I1 from I2 and I3 from C; I2 and I3 closely adpressed; I1 one-third to one-half as tall as I2; C prominent, accessory cusps poorly developed; talonid of m3 well developed, hypoconid, hypoconulid and entoconid ridge well marked, entoconid poorly defined.

TABLE 11-1. Selected measurements (mm) and weight (g) of *Microgale* ordered by size (small to large) collected during the survey of PN de Marojejy.

Species and Age	HB	TL	HF	E	Wt	CIL	UTL	BB
<i>M. parvula</i>								
Adults	55 ± 3.6 50-61 (6)	58 ± 3.9 54-66 (6)	9.5 ± 0.5 9-10 (6)	9.0 ± 0.4 8-9 (6)	3.4 ± 0.4 3.0-4.1 (7)	16.7 ± 0.2 16.4-17.0 (7)	7.5 ± 0.2 7.2-7.9 (7)	7.0 ± 0.1 6.6-7.0 (7)
Juveniles	58 ± 3.3 51-58 (3)	56 ± 2.1 53-58 (3)	10 ± 0.8 9-11 (3)	8 ± 0.5 7-8 (3)	2.1, 3.2 (2)	15.9, 16.8 (2)	7.7 ± 0.2 7.3-7.8 (3)	6.8 ± 0.2 6.5-6.9 (3)
<i>M. longicaudata</i>								
Adults	68 (2)	145, 146 (2)	12, 17 (2)	14 (2)	7.5, 8.2 (2)	20.3, 20.7 (2)	9.5, 9.8	8.4, 8.5
<i>M. fofsifotsy</i>								
Adult	71	90	16	14	7.5	20.7	9.9	9.2
<i>M. brevicaudata</i>								
Adults	72, 74 (2)	37, 39 (2)	11, 12 (2)	14 (2)	10.5, 12 (2)	21.2, 21.5 (2)	9.6 (2)	9.0, 9.1 (2)
Juvenile	71	39	12	14	8.5	20.7	9.4	8.8
<i>M. cowani</i>								
Adults	78.5 ± 3.8 72-85 (16)	67.5 ± 2.7 64-74 (14)	17 ± 0.9 15-18 (16)	14 ± 1.2 12-16 (16)	13.8 ± 2.0 10.5-16.5 (16)	22.9 ± 0.4 22.3-23.7 (16)	11.1 ± 0.3 10.8-11.5 (16)	10.2 ± 0.2 9.9-10.7 (16)
Infants	62, 72 (2)	54, 60 (2)	16 (2)	11, 17 (2)	7.5, 7.9 (2)	20.0, 20.5 (2)	10.0, 10.1 (2)	9.6, 10.1 (2)
<i>M. principula</i>								
Adults	72.5 ± 0.9 71-73 (6)	151 ± 4.8 146-161 (6)	18 ± 0.5 18-19 (6)	15.5 ± 0.8 14-16 (6)	10 ± 0.8 8.5-10.5 (6)	21.9 ± 0.3 21.5-22.3 (6)	10.6 ± 0.1 10.5-10.7 (6)	9.1 ± 0.2 9.0-9.4 (6)
<i>M. monticola</i>								
Adults	79.5 ± 3.0 72-85 (14)	105.5 ± 4.6 98-117 (14)	19 ± 0.5 19-20 (14)	15.5 ± 1.0 12-16 (14)	12.5 ± 1.2 12-16 (14)	24.8 ± 0.2 24.5-25.3 (14)	12.4 ± 0.1 12.1-12.6 (14)	10.4 ± 0.1 10.1-10.6 (14)
<i>M. soricoides</i>								
Adults	87 ± 3.8 85-96 (6)	96 ± 3.8 88-101 (7)	18 ± 0.5 17-18 (7)	16 ± 0.5 15-16 (7)	18.5 ± 1.8 17-21.5 (7)	25.7 ± 0.2 25.2-25.8 (7)	12.5 ± 0.1 12.3-12.6 (7)	11 ± 0.2 10.8-11.3
<i>M. gracilis</i>								
Adult	85 (1)	93 (1)	20 (1)	15 (1)	19.5 (1)	27.7 (1)	9.9 (1)	9.2 (1)
<i>M. gymnorhyncha</i>								
Adults	96 ± 5.9 84-96 (3)	75 ± 0 75 (3)	17 ± 0 17 (3)	14 ± 0.5 14-15 (3)	21 ± 2.8 19.5-26.0 (3)	28.0 ± 0.3 28.0-28.7 (3)	14.9 ± 0.7 14.6-15.0 (3)	11.0 ± 0.1 11.0-11.1 (3)

TABLE 11-1. *Continued.*

Species and Age	HB	TL	HF	E	Wt	CHL	UTL	BB
<i>M. dobsoni</i>								
Adults	102.5 ± 3.1 100-107 (4)	116 ± 4.6 110-120 (4)	22.8 ± 1.0 22-24 (5)	18 ± 1.0 17-20 (5)	24.5 ± 3.3 23.5-31.0 (5)	30.8 ± 0.5 30.7-31.4 (5)	15.1 ± 0.3 14.9-15.6 (5)	11.6 ± 0.2 11.2-11.8 (5)
<i>M. talazaci</i>								
Adults	117 ± 6.1 105-123 (7)	143.5 ± 8.0 132-158 (6)	24 ± 1.1 22-26 (7)	19 ± 0.8 18-20 (7)	38 ± 2.2 34-38.5 (7)	35.5 ± 0.8 34.5-37.3 (7)	17.9 ± 0.5 17.2-18.7 (7)	12.5 ± 0.3 12.0-12.9 (7)
Juvenile	100 (1)	134 (1)	24 (1)	18 (1)	28 (1)	34.2 (1)	17.1 (1)	12 (1)

NOTE.—Statistics are presented as mean ± standard deviation; ranges are followed by number of specimens, in parentheses.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

REPRODUCTION—The testes of the two adult males (FMNH 159654 and 159652) collected measured 8×5 and 9×8 mm, respectively, whereas those of the juvenile (FMNH 159653) measured 5×4 mm; nonetheless, the epididymides of all three specimens were convoluted. No females were collected during the survey.

REMARKS—*M. brevicaudata* was captured only during the inventory of the PN de Marojejy in the lowland forest at 450 m (Table 11-2). The modern distribution of this species along the western coast includes the deciduous forest of Kirindy and near Maintirano and the slightly more humid habitat of the RS de Manongarivo (MacPhee, 1987; Nicoll & Langrand, 1989; Nicoll & Rathbun, 1990; Ganzhorn et al., 1996; Fig. 11-2). The details of the Manongarivo record are not clear, but presumably this species was found in the lowland forest, which contains dry deciduous floristic elements (Humbert, 1951). *M. brevicaudata* has recently been collected in deciduous forest of the RNI d'Ankarafantsika, between 160 and 200 m (Randrianjafy Rasoloarisoa, 1993; Rakotondravony, Randrianjafy Rasoloarisoa, and Goodman, unpubl. data). In the extreme north, it is known from the PN de la Montagne d'Ambre, in the ecotone between dry and humid forest (Raxworthy & Nussbaum, 1994; Goodman et al., 1996b). As mentioned earlier, the lectotype of *M. brevicaudata* comes from the Mahanara River region, between Vohémar (Iharana) and Sambava, approximately 50 km NE of the site where this species was captured in the PN de Marojejy. There is no evidence that *M. brevicaudata* occurs in the Périnet region, and the damaged specimen cited by Eisenberg and Gould (1970, p. 30) as a record of it at this site (USNM 341694) is a misidentified *M. cowani*. In summary, this species occurs in a variety of habitat types, from lowland humid forest, including the lower slopes of several mountains, to dry deciduous forest. It seems to ring the coastal regions of the island, from the northeast near Sambava and Vohémar, north to the Antsiranana region, and south to at least near Morondava.

Further evidence of the broad habitat tolerance of *M. brevicaudata*—or at least of their apparent former larger geographical range—comes from bones recovered from various Holocene deposits on the island. Material of this species has been recovered in the cave Lakoton'i Akanga, north of Antsiranana, which may have been a former car-

TABLE 11-2. Elevational distribution of tenrecids on the slopes of the PN de Marojejy.

Species	Individuals captured at elevation (m)				
	450	775	1225	1625	1875
<i>Setifer setosus</i>	(+)	(+)			
<i>Tenrec ecaudatus</i>	(+)	(+)			
<i>Microgale brevicaudata</i>	+				
<i>Microgale cowani</i>			+	+	+
<i>Microgale dobsoni</i>			+	+	
<i>Microgale fotsifotsy</i>			+		
<i>Microgale gracilis</i>					+
<i>Microgale gymnorhyncha</i>			+	+	
<i>Microgale longicaudata</i>			+		
<i>Microgale monticola</i>				+	+
<i>Microgale parvula</i>	+	+	+	+	
<i>Microgale principula</i>				+	+
<i>Microgale soricoides</i>			+	+	
<i>Microgale talazaci</i>	+	+	+	+	
<i>Oryzorictes hova</i>	+			+	
Total number of Lipotyphla	6	4	8	9	4
Total number of <i>Microgale</i> spp.	3	2	8	8	4
<i>Microgale</i> spp. (N = 12) in each zone (%)	25	17	67	67	33

NOTE—Includes sight records (in parentheses) and information of species obtained in live traps and pitfall traps from the 1996 survey.

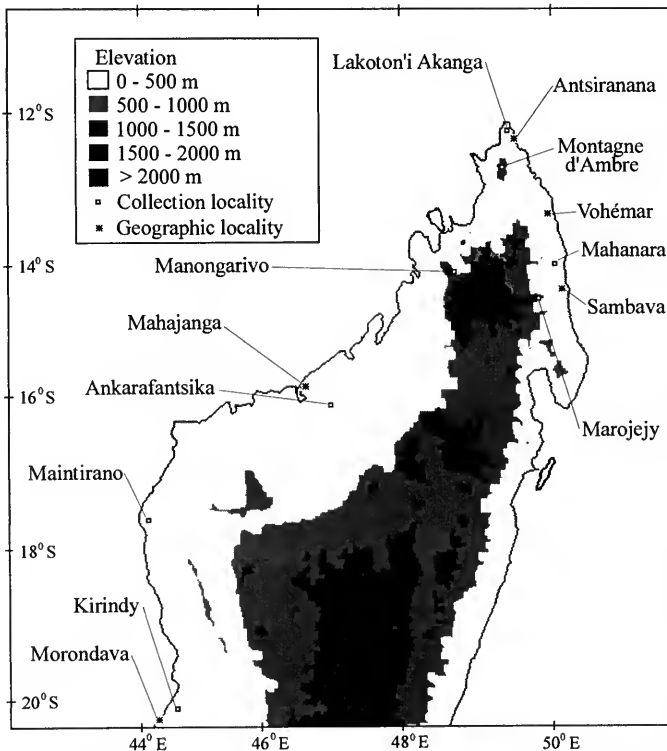


FIG. 11-2. Sites where *Microgale brevicaudata* has been collected or reported from.

nivore den (MacPhee, 1987; Dewar & Rakoto-
vololona, 1992). A toothless mandible found at a
site in the extreme southwest has been tentatively
assigned to *M. brevicaudata* (MacPhee, 1986).
Further, two mandibles recovered from a cave
near Mahajanga were described tentatively as a
new species, *M. breviceps* (Kaudern, 1918),
which was subsequently synonymized with *M.*
brevicaudata (MacPhee, 1987).

Microgale cowani Thomas, 1882

HOLOTYPE—BM (NH) 82.3.1.25, adult female,
body preserved in alcohol, skull extracted, col-
lected mid-February to mid-March 1880 by the
Reverend W. Deans Cowan.

TYPE LOCALITY—Ankafana Forest, eastern Bet-
sileo. (Ankafana = Ankafina, Fianarantsoa, Fian-
arantsoa Province, 21°12'S, 47°12'E; see Mac-
Phee [1987], Carleton & Schmidt [1990].)

REFERRED MATERIAL—FMNH 159516, 159518,
159519, 159520, 159521, 159522, 159523,
159524, 159525, and 159655, and UA-SMG 8365
and 8381: Antranohofa, 11 km NW of Mananten-
ina, Province d'Antsiranana, PN de Marojejy,
1225 m, 14°26.02'S, 49°44.5'E; FMNH 159526,
159527, 159528, 159529, 159530, 159531,
159532, 159533, 159534, 159535, 159536,
159656, 159657, 159658, and 159659: tributary
at head of Andranomifototra River, 10.5 km NW
of Manantenina, Province d'Antsiranana, PN de
Marojejy, 1625 m, 14°26.04'S, 49°44.5'E; FMNH
159651, 159660, and 159661: source of Andran-
omifototra River, 11 km NW of Manantenina,
Province d'Antsiranana, PN de Marojejy, 1875 m,
14°26.08'S, 49°44.1'E.

KEY FEATURES (see Table 11-1 and Key 2, p.
228)—Medium sized, tail moderately short, short-
er or subequal to HB. Pelage dark brown dorsally,
gray ventrally with a reddish brown wash; tail bi-
colored, dark brown dorsally, sharply demarcated
from paler reddish buff venter. Skull medium in
size, rostrum elongated. Dentition with pro-
nounced diastemata separating upper teeth from
I1 to P3, also lower teeth from i3 to p2. All ele-
ments of talonid of m3 present, including hypo-
conid, entoconid ridge, talonid basin, and ento-
conid.

MEASUREMENTS—External and cranial measure-
ments are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—
The ratio of males to females was 1 : 1.3 and that
of infants to adults was 1 : 8; no juveniles of this

species were collected during the survey. Two of
the adult females (FMNH 159660 and 159661)
were pregnant, each with three embryos (with one
embryo in the left and two in the right oviduct
[FMNH 159660] and with two embryos in the left
and one in the right oviduct [FMNH 159661]); the
embryos measured 21 mm and 13 mm, crown-to-
rump lengths, respectively. Two other females
(FMNH 159529 and 159651) were lactating, the
latter showing two placental scars in the left and
one in the right oviduct. Mammary formula: 1-0-
2 (N = 4), 0-1-2 (N = 5). The testes of three
adult males with convoluted epididymides
(FMNH 159655, 159657, and 159659) measured
10 × 7, 8 × 6, and 7 × 5 mm, respectively,
whereas those of the infant male (FMNH 159658)
with nonconvoluted epididymides measured 2 ×
2 mm.

REMARKS—One specimen (FMNH 159651), al-
though readily assigned to this species on the ba-
sis of skull characters, is aberrant in that its tail
is longer than its head and body length.

M. cowani was previously reported from the
PN de Marojejy (Nicoll & Langrand, 1989; Duck-
worth, 1990). During the 1996 survey, it was cap-
tured between 1225 and 1875 m, which is very
similar to its elevational range (1260–1950 m) in
the RS d'Anjanaharibe-Sud (Table 11-3; Good-
man & Jenkins, 1998). These two sites are the
northernmost localities on the island for this wide-
spread species, which occurs in humid forests
along the Central High Plateau and eastern es-
carpment south to the PN d'Andohahela (Good-
man et al., 1996c; Goodman et al., 1998a, 1999a).

In the 1875 m zone, one pitfall line was placed
on a ridge, above forest line, in a zone of open
savannah. The only lipotyphlan captured in this
pitfall line was a single individual of *M. cowani*
(Table 11-4), which supports evidence from other
localities that this species is not strictly forest-
dwelling (Langrand & Goodman, 1997).

Microgale dobsoni Thomas, 1884

Nesogale dobsoni Thomas, 1918

HOLOTYPE—BM (NH) 84.10.20.1, immature
male, preserved in alcohol, skull extracted. Col-
lected February or March 1884 by W. Waters.

TYPE LOCALITY—Nandésien forest, Central Bet-
sileo (Nandihizana, 10 miles S of Ambusitra—
manuscript note in Thomas' private copy of origi-
nal description, archived in BM [NH]. Nandihiz-
ana, approximately 20 miles (30 km) SSW of

TABLE 11-3. Elevational distribution of various Lipotyphla on mountains in eastern humid forests of Madagascar (all sites sampled with similar trapping techniques).

Species	PN de la Montagne d'Ambre ¹ (340–1350 m; 12°S)	PN de Marojejy ² (450–1875 m; 14°S)	RS d'Anjanaharibe-Sud ² (875–1950 m; 15°S)	PN d'Andringitra ³ (720–2450 m; 22°S)	PN d'Andohahela ⁵ (440–1875 m; 25°S)
Tenrecidae					
<i>Hemicentetes nigriceps</i>				1,350–2,050	
<i>Setifer setosus</i>	650–660	450–775	875	810	440
<i>Tenrec ecaudatus</i>	650–1,350	450–775	875–1,260	720–810	440–1,200
<i>Microgale brevicaudata</i>	300–670	450			
<i>Microgale cowani</i>		1,225–1,875	1,260–1,950	810–2,450	1,200–1,875
<i>Microgale dobsoni</i>		1,225–1,625	1,260	1,210–2,050	440–1,875
<i>Microgale drouhardi</i>	980–1,380			720–810	
<i>Microgale fotsifotsy</i>	650–1,250	1,225		1,210–1,990	440–1,500
<i>Microgale gracilis</i>		1,875		1,210	1,500–1,875
<i>Microgale gymnorhyncha</i>		1,225–1,625	1,260–1,550	1,210–1,990	1,500–1,875
<i>Microgale longicaudata</i>	650–1,380	1,225	1,260–1,950	720–1,990	440–1,875
<i>Microgale monticola</i>		1,625–1,875	1,550–1,950		
<i>Microgale parvula</i>	1,125–1,320	450–1,625	1,260–1,950	720–1,990	440–1,875
<i>Microgale principula</i>		1,625–1,875	875		
<i>Microgale soricoides</i>		1,225–1,625	1,260–1,550	1,210–1,990	440–1,200
<i>Microgale taiva</i>				720–1,990	810–1,875
<i>Microgale talazaci</i>	660–1,380	450–1,625	1,260–1,550	1,990	
<i>Microgale thomasi</i>					
<i>Oryzorictes hova</i>		450–1,625		1,200–1,875	440–1,200
<i>Oryzorictes tetradactylus</i>				2,450	
Soricidae					
<i>Suncus murinus</i> ⁶	1,000–1,320				
Total number of Tenrecidae	8	15	11 ⁷	16	12
Total number of <i>Microgale</i> spp.	6	12	9 ⁸	11	10

¹ Raxworthy and Nussbaum (1994); Goodman et al. (1996b); Jenkins et al. (1997).

² This study.

³ Goodman and Jenkins (1998).

⁴ Goodman et al. (1996a); Langrand and Goodman (1997); S. M. Goodman (unpubl. data).

⁵ Goodman et al. (1999a).

⁶ Introduced to Madagascar.

⁷ An unidentified species of *Hemicentetes*, *Oryzorictes talpoides* (= *hova*), *Microgale taiva*, *M. fotsifotsy*, and *M. dryas* were recorded on the slopes of the Anjanaharibe-Sud Massif during other surveys (Goodman & Jenkins, 1998). Thus, with these additions, the number of Tenrecidae on the mountain would increase to 16 species.

⁸ With the information presented in the above footnote, this figure would be increased to 12 species.

Ambositra [see MacPhee, 1987]. Estimated as 20°50'S, 47°10'E).

REFERRED MATERIAL—FMNH 159538, 159539, 159540, 159541, 159542, 159543, and 159662, and UA-SMG 8352: Antranohofa, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1225 m, 14°26.02'S, 49°44.5'E.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—Large, TL subequal to or longer than HB. Dorsal pelage brown, venter gray with buff wash. Skull large and robust, sutures fused and obscure; rostrum moderately broad, interorbital region long; braincase angular, superior articular facets very prominent, supraoccipital crests well devel-

oped; occipital region reduced. Diastemata between I1 and I2 and between I3 and C. The I1 larger than I2, and i2 considerably larger than canine. Talonid of m3 reduced, hypoconid low, hypoconulid prominent, entoconid ridge and talonid basin poorly defined, entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—Only adults were collected during the survey. Sex ratio 1 female : 4 males. The testes of one male (FMNH 159662) with convoluted epididymides measured 7 × 3 mm. The mammary formula of the single female (FMNH 159540) was 1-0-2.

TABLE 11-4. Pitfall line capture results of tenrecids in the PN de Marojejy, based on 1,155 bucket-days across five elevational zones.

Variable	Capture data for forest type (altitude)												Total cap- tured									
	Lowland (450 m)			Transitional lowland-montane (775 m)			Montane/mossy (1225 m)			Montane/mossy (1625 m)				Montane/ sclerophyllous (1875 m)								
	V	S	R	V	S	R	V	S	R	V	S	R	V	S	R	S	R	V	S	R	R [†]	
Line placement*	5/10	5/10	5/10	15/10	15/10	15/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10	26/10
First sample day (day/month)	12/10	12/10	12/10	22/10	22/10	22/10	1/11	1/11	1/11	1/11	1/11	1/11	1/11	1/11	1/11	1/11	1/11	1/11	1/11	1/11	1/11	1/11
Last sample day (day/month)	88	88	88	88	88	88	77	77	77	77	77	77	77	77	77	77	77	77	77	77	77	77
Total trap-days																						
Mammalia sampled:																						
<i>Oryzorictes hova</i>	2																					2
<i>Microgale breviceaudata</i>	3		1																			4
<i>Microgale parvula</i>	1	1	2	4		1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	14
<i>Microgale talazaci</i>																						7
<i>Microgale longicaudata</i>																						2
<i>Microgale dobsonii</i>																						8
<i>Microgale fotsifotsy</i>																						1
<i>Microgale soricooides</i>																						12
<i>Microgale gymnorhyncha</i>																						5
<i>Microgale cowani</i>																						27
<i>Microgale monticola</i>																						20
<i>Microgale principula</i>																						7
Total number of captures	1	6	3	4	0	2	11	19	15	12	9	15	12	9	15	5	6	1	6	1	109	
Specimen capture rate (%)	1.1	6.8	3.4	4.5	0	2.2	14.3	24.7	19.5	15.6	11.7	19.5	15.6	11.7	19.5	9.1	10.9	1.8	10.9	1.8	9.4	
Altitudinal capture rate (%)		3.8			1.9			19.5														
Total number of species	1	3	2	1	0	2	7	8	6	4	5	6	4	5	6	3	3	1	3	3	1	12
Species capture rate (%)	8.3	25.0	16.7	8.3	0	16.7	58.3	66.7	50.0	33.3	41.7	50.0	33.3	41.7	50.0	25.0	25.0	7.3	25.0	7.3	8.3	
Total number of species per altitude		3		2		2	9	8	8	8	8	8	8	8	8	3	3	3	3	3	3	
Altitudinal species capture rate (%)		25.0		16.7		16.7	75.0	66.7	66.7	66.7	66.7	66.7	66.7	66.7	66.7	25.0	25.0	25.0	25.0	25.0	25.0	

* R = ridge; S = slope; and V = valley.

† This line was placed above the tree line in a zone of open savanna.

REMARKS—In the PN de Marojejy, *M. dobsoni* was captured at 1225–1625 m (Table 11-2). In the RS d'Anjanaharibe-Sud, it was captured only at 1260 m (Table 11-3). This species is broadly distributed across much of the Central High Plateau and eastern humid forest, from the mountains skirting the Andapa Basin south to the PN d'Andohahela (Goodman et al., 1996a, 1996c, 1998a; Goodman & Jenkins, 1998). On the Andohahela Massif, *M. dobsoni* was collected in the elevational zone between 440 and 1875 m, and on the Andringitra Massif, from approximately 1210 m to above tree line, at 2050 m (Table 11-3).

***Microgale fotsifotsy* Jenkins, Raxworthy, and Nussbaum, 1997**

Microgale sp. A Jenkins, Goodman, and Raxworthy, 1996

Microgale nov. sp. Goodman, Andrianarimisa, Olson, and Soarimalala, 1996b

HOLOTYPE—UMMZ 168468, adult male, preserved in alcohol, skull extracted, collected 13 January 1992 by Christopher J. Raxworthy.

TYPE LOCALITY—Antomboka River Fitsahana, PN de la Montagne d'Ambre, Antsiranana Fivondronana, Antsiranana Province, 12°29'S, 49°10'E, altitude 650 m.

REFERRED MATERIAL—FMNH 159663: Antranofofa, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1225 m, 14°26.02'S, 49°44.5'E.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—Dorsal pelage pale grayish brown, soft in texture, venter with lighter buffy wash; digits of fore and hind feet and extreme tail tip contrastingly lighter colored; pinnae prominent and conspicuous; fifth digit of hind foot elongated, scarcely shorter than second. Skull with maxillary process of zygoma at right angles to long axis of cranium; braincase broad and short. I3 and i3 small, I3 slightly greater in crown height than distostyle of I2, i3 subequal in height to posterior accessory cusp of i2; i2 greater in breadth than i1; C and c greater in crown height than P3 and p3, respectively.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—The testes of the adult male measured 6 × 5 mm and epididymides were convoluted.

REMARKS—*Microgale fotsifotsy* is broadly dis-

tributed along the complete length of the eastern humid forests of Madagascar, from the PN de la Montagne d'Ambre in the north to the PN d'Andohahela in the extreme south (Jenkins et al., 1997; Goodman et al., 1999a). It is currently unknown from isolated forest fragments on the Central High Plateau.

At some of the various sites where *M. fotsifotsy* has been documented, it is captured infrequently. The basis of this apparent rarity or absence at some localities is unclear; it may simply be trap shyness or low population density, although there is some evidence of population cycling. In the PN de la Montagne d'Ambre, pitfall lines were established at identical sites during the same season over 3 consecutive years (Goodman et al., 1997). With standardized pitfall trapping efforts, two individuals were captured in 1994, eight in 1995, and five in 1996.

In the PN de Marojejy, the single individual captured during the 1996 survey was in the 1225 m zone. During the 1994 survey of the eastern slopes of the RS d'Anjanaharibe-Sud, *M. fotsifotsy* was not recorded. However, this species was captured with pitfall traps during a field trip conducted by F. Andreone in February 1996 on the western slopes of Anjanaharibe-Sud (Goodman & Jenkins, 1998).

***Microgale gracilis* Major, 1896**

Oryzoryctes [sic] *gracilis* Major, 1896

Leptogale gracilis Thomas, 1918

HOLOTYPE—BM (NH) 97.9.1.78, adult of undetermined sex, skin and skull. Collected November 1894 by C. I. Forsyth Major.

TYPE LOCALITY—Ambohitombo forest. (Ambohitombo town, 43 km [by road] SE of Ambositra, 10 km into eastern forest; Fianarantsoa, Fianarantsoa; 20°43'S, 47°26'E [see MacPhee, 1987]. MacPhee gives the altitude for this locality variously as 1300 m [p. 6] and 1200 m [his Table 5], but, as pointed out by Carleton and Schmidt [1990], the altitude recorded for this locality by Major [1897] is higher [1500–1600 m].)

REFERRED MATERIAL—FMNH 159664: source of Andranomifototra River, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1987 m, 14°26.08'S, 49°44.1'E.

KEY FEATURES (see Table 11-1 and Key 2, pp. 228)—Size large, TL shorter than HB. Pelage dark brown dorsally with buff speckling. Muzzle very long; large, naked rhinarium anteriorly retic-

ulated, striae on posterior region incomplete. Eyes very small; ears small, partially concealed by pelage. Forefeet broad, claws enlarged. Skull very elongated and gracile; rostrum slender, markedly attenuated; braincase rounded, moderately broad and long. Dentition reduced; upper incisors subequal in height, incisors and canine very slender; large diastemata between all anterior teeth, particularly P2 and P3; talons on molars very reduced, resembling cingula; talonid of m3 slightly reduced, entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—The single adult female had one placental scar in each oviduct; the mammary formula was 1-0-2.

REMARKS—This relatively poorly known and difficult to capture shrew tenrec was obtained on only one occasion in the PN de Marojejy. The single individual was taken at 1875 m, in a Sherman trap placed on the ground along a passageway, in moss-covered roots and branches in a transitional zone between mossy and sclerophyllous forest. This species was not recorded in the RS d'Anjanaharibe-Sud and is known only from scattered localities on the Central High Plateau and on the slopes of Andringitra and Andohahela (MacPhee, 1987; Goodman et al., 1996a, 1996c, 1999a; Goodman & Jenkins, 1998). The record reported for this species in the Fanovana area by MacPhee (1987) is referable to *M. gymnorhyncha* (Jenkins et al., 1996). On the basis of these combined records, *M. gracilis* is known to have an elevational distribution of 1210–2000 m.

Microgale gymnorhyncha Jenkins, Goodman, and Raxworthy, 1996

Microgale gracilis (Major): MacPhee, 1987, in part

HOLOTYPE—FMNH 151807, adult female, preserved in alcohol, skull extracted (field number SMG 6697), collected 13 December 1993 by Steven M. Goodman and Christopher J. Raxworthy.

TYPE LOCALITY—38 km S of Ambalavao, RNI d'Andringitra, on ridge E of Volotsangana River, Fianarantsoa Province, 22°11'39"S, 46°58'16"E, altitude 1625 m.

REFERRED MATERIAL—FMNH 159544, 159665, and 159666, and UA-SMG 8414: Antranohofa, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1225 m, 14°26.02'S, 49°44.5'E; FMNH 159545: tributary at head of Andranomi-

fototra River, 10.5 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1625 m, 14°26.04'S, 49°44.5'E.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—Large, TL shorter than HB. Dorsal pelage dark brown, dark gray brown ventrally. Muzzle very long, forming a proboscis; rhinarium very large, with transversely striated naked region. Eyes very small. Ears small, virtually concealed in pelage. Forefeet broad, claws enlarged. Skull long, moderately gracile; rostrum slender and elongated; braincase short and broad. Dentition moderately reduced, with long diastemata between all anterior teeth from I1 to P3 and i2 to p3; talonid of m3 slightly reduced; talonid basin, hypoconid, hypoconulid, and entoconid ridge present, entoconid indicated.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—Sex ratio 1 male : 2 females; age ratio 1 juvenile : 3 adults. The mammary formula in both females was 0-1-2.

REMARKS—The elevational zones where *M. gymnorhyncha* was captured in the PN de Marojejy and the RS d'Anjanaharibe-Sud are similar: 1225–1625 m in the former and 1260–1550 m in the latter (Goodman & Jenkins, 1998). This species is known to have a broad distribution from the mountains surrounding the Andapa Basin south to the PN d'Andohahela (Goodman et al., 1999a). It has been collected at sites on the Central High Plateau and along the eastern escarpment (Jenkins et al., 1996; Goodman et al., 1998a, 1998b).

The elongated rostrum and rhinarium, reduced dentition, small eyes and ears, digging claws, short forelimbs, and dense short pelage of *M. gymnorhyncha* are very reminiscent of *M. gracilis*, and these two species probably occupy a similar ecological niche. They are known to occur in sympatry in the PN d'Andohahela and PN d'Andringitra (Jenkins et al., 1996; Goodman et al., 1996a, 1999a), where they were captured in the same elevational zone and, in a few cases, in the same pitfall line. Whether there is overlap in the prey taken by these two species would be an interesting line of research.

Microgale longicaudata Thomas, 1882

Microgale majori Thomas, 1918: MacPhee, 1987

HOLOTYPE—BM(NH) 82.3.1.15, adult female, body preserved in alcohol, skull extracted, col-

lected mid-February to mid-March 1880 by the Reverend W. Deans Cowan.

TYPE LOCALITY—Ankafana Forest, eastern Bet-sileo. (Ankafana = Ankafina, Fianarantsoa, Fianarantsoa Province; 21°12'S, 47°12'E; see MacPhee, 1987; Carleton & Schmidt, 1990).

REFERRED MATERIAL—FMNH 159546, 159667: Antranohofa, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1225 m, 14°26.02'S, 49°44.5'E.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—Small in size; tail very long, more than twice as long as HB; distal portion of tail naked and transversely wrinkled on dorsal surface; fifth hind digit elongated, subequal in length to second digit. Dorsal pelage reddish brown, venter gray with bright reddish buff or buff wash. Skull small, rostrum moderately short; braincase moderately narrow and long. Diastemata present between I1 and I2 and either side of C and P2; well-developed anterior and posterior accessory cusps present on I2, C, and P2; C subequal to or taller than I1; P4 scarcely greater in crown height than P3. The p2 caniniform. Talonid of m3 with low hypoconid, hypoconulid well developed, narrow talonid basin, reduced entoconid ridge, and entocoid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—Sex ratio 1 : 1. Mammary formula 1-0-2 (N = 1).

REMARKS—This species is one of the more widespread shrew tenrecs. It is known from the complete breadth of the eastern humid forest (Montagne d'Ambre to Andohahela) and from several sites on the Central High Plateau (MacPhee, 1987; Raxworthy & Nussbaum, 1994; Goodman et al., 1996c, 1998a, 1998b, 1999a). A single specimen collected in the Kirindy Forest, near Morondava, has been tentatively identified as part of the *M. longicaudata* cluster (Ade, 1996).

M. longicaudata was captured only twice during the inventory of the PN de Marojejy, and only in the 1225 m zone. In the RS d'Anjanaharibe-Sud, with nearly the same pitfall trapping effort, it was trapped twice in the 1260 m zone, was not recorded in the 1550 m zone, and was obtained twice in the 1950 m zone. Detailed information on the elevational range of *M. longicaudata* is difficult to glean from pitfall traps, since capture is infrequent. The elevational distribution of this species with regard to *M. principula*, a morphologically similar form, is discussed below, in the account of the latter species.

Microgale monticola Goodman and Jenkins, 1998

HOLOTYPE—FMNH 154012 (field number SMG 7020), adult female, skin and skull, collected 15 November 1994 by Steven M. Goodman.

TYPE LOCALITY—11 km WSW of Befingitra, RS d'Anjanaharibe-Sud, 14°44'S, 49°26'E, altitude 1550 m.

REFERRED MATERIAL—FMNH 159549, 159550, 159551, 159672, and 159673: Antranohofa, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1225 m, 14°26.02'S, 49°44.5'E; FMNH 159517, 159552, 159553, 159554, 159555, 159556, 159674, 159675, and 159676, and UA-SMG 8486: tributary at head of Andranomifototra River, 10.5 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1625 m, 14°26.04'S, 49°44.5'E; FMNH 159557, 159677, 159678, and 159679, and UA-SMG 8500: source of Andranomifototra River, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1875 m, 14°26.08'S, 49°44.1'E.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—Medium-sized *Microgale* with tail longer than head and body. Pelage dark dorsally and ventrally. Skull moderately robust, with broad interorbital region and broad, rounded braincase. Upper and lower canines robust, P2 and p2 large, P2 with well-developed anterior and posterior accessory cusps.

MEASUREMENTS—External and cranial measurements are given in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—Only adults were collected during the survey, and the sex ratio of females to males was 1 : 1.7. Of the females, one (FMNH 159676) was pregnant, another (FMNH 159553) lactating, and a third (FMNH 159554) pregnant and lactating. Both pregnant specimens contained single embryos in both left and right oviducts; in FMNH 159554, which appeared close to parturition, the well-developed embryo measured 30 mm (crown-to-rump length), whereas the small embryo in FMNH 159676 measured only 3 mm. Another female (FMNH 159675) had single placental scars in both oviducts. Mammary formula: 1-0-2 (N = 5), 0-1-2 (N = 1). Four of the adult males had convoluted epididymides and testes measuring 4 × 3 mm (FMNH 159673), 5 × 5 mm (FMNH 159674 and 159678), and 6 × 5 mm (FMNH 159672); in a fifth male with fully erupted, worn, permanent dentition (FMNH 159679) but with

nonconvoluted epididymides, the testes measured 4×3 mm.

REMARKS—This recently named species is currently known only from the mountains surrounding the Andapa Basin. In the PN de Marojejy, it was recorded in the elevational zone between 1625 and 1875 m, and in the RS d'Anjanaharibe-Sud, from 1550 to 1950 m (Tables 11-2, 11-3). At both of these sites, it was one of the most frequently captured shrew tenrecs. The morphologically similar *M. thomasi* is not known to occur in sympatry with *M. monticola*. *M. thomasi* has been documented at a variety of sites on the Central High Plateau and along the eastern escarpment, and its known range is from the Andranomay Forest south to the PN d'Andohahela (Goodman et al., 1996c, 1988a, 1999a).

Microgale parvula G. Grandidier, 1934

Microgale pulla Jenkins, 1988

HOLOTYPE—MCZ 45465, juvenile male, body preserved in alcohol, skull extracted, collected by M. Drouhard.

TYPE LOCALITY—environs of Diégo-Suarez (Antsiranana, approximately $12^{\circ}16'S$, $49^{\circ}18'E$; see MacPhee [1987]; probably Montagne d'Ambre; see Jenkins et al. [1997]).

REFERRED MATERIAL—FMNH 159558, 159559, 159680, and 159681: tributary of the Manantenina River, 8 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 450 m, $14^{\circ}26.2'S$, $49^{\circ}46.5'E$; FMNH 159560, 159682, 159683, and 159684, and UA-SMG 8292: tributary of Manantenina River, 10 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 775 m, $14^{\circ}26.0'S$, $49^{\circ}45.7'E$; FMNH 159561, 159562, 159563, and 159685: Antranohofa, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1225 m, $14^{\circ}26.02'S$, $49^{\circ}44.5'E$; FMNH 159686: tributary at head of Andranomifototra River, 10.5 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1625 m, $14^{\circ}26.04'S$, $49^{\circ}44.5'E$.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—Very small, TL slightly shorter than HB. Dorsal pelage dark brown, ventral pelage dark gray brown, tail uniform dark gray. Skull very small and delicate, rostrum slender, braincase shallow and long, occipital condyles posterodorsally oriented. Diastemata between I1 and I2 and on either side of C and P2; anterior and posterior accessory cusps present on I2, I3, and P2. Diaste-

ma between c and p2. Talonid of m3 with well-developed hypoconulid but with reduced hypoconid, entoconid, and entoconid ridge, and with narrow, shallow talonid basin.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—Sex ratio 1 : 1; juvenile to adult ratio 1 : 2.3. One female (FMNH 159682) had a single placental scar in the left and two in the right oviduct. Mammary formula: 0-1-2 (N = 1), 1-0-2 (N = 1). Two adult males (FMNH 159681 and 159683) with convoluted epididymides had testes measuring 5×3 mm and 3×3 mm, respectively; the testes of a juvenile male with nonconvoluted epididymides measured 2×1 mm.

REMARKS—Although never particularly common in any transect zone in the PN de Marojejy, as indicated by pitfall trap captures, *M. parvula* has a broad elevational range on the massif. It occurs from lowland forest at 450 m to montane forest at 1625 m (Table 11-2). In the RS d'Anjanaharibe-Sud, this species was recorded between 1260 and 1950 m (Table 11-3). Given the total number of animals of this species captured in pitfall traps at these two sites, it may be surmised that they have relatively similar elevational ranges on the two massifs.

When MacPhee (1987) conducted his revision of *Microgale*, only a single specimen of *M. parvula*, the holotype, was available for study. Since then, almost exclusively as a result of the use of pitfall trapping techniques, this very small species is now known from numerous sites along the complete length of the eastern humid forest, from the PN de la Montagne d'Ambre south to the PN d'Andohahela (Raxworthy & Nussbaum, 1994; Goodman et al., 1996a, 1996b, 1999a; Goodman & Jenkins, 1998) and at several sites on the Central High Plateau (Goodman et al., 1998a, 1998b). Throughout this zone, it has a broad elevational range, from 440 to 1990 m.

Microgale principula Thomas, 1926

Microgale sorella Thomas, 1926; MacPhee, 1987

HOLOTYPE—BM (NH) 25.8.3.15, adult female, body preserved in alcohol, skull extracted, collected by C. Lamberton.

TYPE LOCALITY—Midongy du Sud, SE Madagascar (Midongy Atsimo, $23^{\circ}35'S$, $47^{\circ}01'E$; see MacPhee [1987]).

REFERRED MATERIAL—FMNH 159547 and 159668, and UA-SMG 8489: tributary at head of Andranomifototra River, 10.5 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1625 m, 14°26.04'S, 49°44.5'E; FMNH 159548, 159669, 159670, and 159671: source of Andranomifototra River, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1875 m, 14°26.08', 49°44.1'E.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—Medium sized, tail very long, more than twice as long as HB; distal portion of tail naked and transversely wrinkled on dorsal surface; fifth hind digit elongated, subequal in length to second digit. Pelage distinctly bicolored, reddish brown dorsally, gray with buff wash ventrally. Skull medium in size, rostrum moderately short and broad, braincase moderately narrow. Short diastemata between I1 and I2 and on either side of C and P2; I2 and I3 more or less in contact; well-developed anterior and posterior accessory cusps present on I2, C, and P2; I1 greater in crown height than C; P4 distinctly greater in crown height than P3; lower p2 moderately caniniform, talonid of m3 with low hypoconid, well-developed hypoconulid, broad talonid basin, reduced entoconid ridge, and entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—Only adults were collected during the survey. Sex ratio 1 : 1. Mammary formula: 1-0-2 (N = 3). Two males (FMNH 159669 and 159671) with permanent dentition but nonconvoluted epididymides had testes measuring 4 × 3 mm and 6 × 4 mm, respectively.

REMARKS—It was previously proposed that the geographical range of *M. principula* was confined to the southern portion of the eastern humid forest (MacPhee, 1987). The results of recent surveys demonstrate that it has a much broader distribution and occurs from at least the mountains surrounding the Andapa Basin south to the PN d'Andohahela (Goodman et al., 1999a). Curiously, this species seems to have a patchy distribution. Intensive survey work in the PN d'Andringitra failed to find it (Goodman et al., 1996a), although it is known to occur not far to the south, near Midongy du Sud and Ranomena (MacPhee, 1987), and it is relatively common less than 80 km to the northeast, in the PN de Ranomafana (specimens in USNM).

Microgale soricoides Jenkins, 1993

HOLOTYPE—BM (NH) 91.565, adult male preserved in alcohol, skull extracted. Collected 13 April 1991 by Christopher J. Raxworthy.

TYPE LOCALITY—Mantady National Park (PN de Mantady), approximately 15 km north of Périnet (Andasibe), 18°51'S, 48°27'E, in primary rain forest, altitude 1100–1150 m.

REFERRED MATERIAL—FMNH 159564, 159565, 159566, 159568, 159687, 159688, and 159689, and UA-SMG 8395 and 8484: Antranohofa, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1225 m, 14°26.02'S, 49°44.5'E; FMNH 159567, 159568, 159569, 159570: tributary at head of Andranomifototra River, 10.5 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1625 m, 14°26.04', 49°44.5'E.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—Size large, TL subequal to or longer than HB. Pelage light buff brown dorsally, gray-brown ventrally with reddish buff wash. Skull moderately large and robust, rostrum and interorbital region broad, braincase short and broad; supraoccipital ridge present. I1 markedly robust and proodont. The i1 and i2 robust and procumbent, i2 smaller than i1 but larger than c. P2 and p2 very small, with a single root. Talonid of m3 reduced to very low hypoconid, an oblique crest, and a prominent hypoconulid.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—Only adults were collected during the survey. The ratio of males to females was 1 : 1.25. Two females (FMNH 159687 and 159688) were pregnant, the former with one embryo in the left and two in the right oviduct, the embryos measuring 23 mm crown-to-rump length; the latter with an embryo in each oviduct, 17 mm crown-to-rump length. Mammary formula: 1-0-2 (N = 5). One male (FMNH 159689) with convoluted epididymides had testes measuring 6 × 4 mm.

REMARKS—On the basis of the 1996 inventory of the PN de Marojejy, *M. soricoides* occurs in the 1225 m and 1625 m zones (Table 11-2), where it was relatively common; all individuals were captured in pitfall traps. At other sites it is not uncommon to capture this species in Sherman live traps (e.g., Goodman et al., 1999a). The elevational range of *M. soricoides* in the RS d'Anjanaharibe-Sud was 1260–1550 m (Goodman & Jenkins, 1998), very similar to that on the Marojejy Massif.

Just a few years after its description, we now know that *M. soricoides* is a widely distributed and relatively common species. Extensive surveys conducted in the PN de la Montagne d'Ambre have failed to find this species (Raxworthy & Nussbaum, 1994; Goodman et al., 1996b), and the known northern limit is along the slopes of Anjanaharibe-Sud and Marojejy. We strongly suspect that this species will be found in the Sambirano, particularly on the Manongarivo and Tsaratanana Massifs. To the south of the Andapa Basin it is broadly distributed in the eastern humid forest and on the Central High Plateau to the southern limit of this forest type in the PN d'Andohahela (Jenkins, 1993; Goodman & Jenkins, 1998; Goodman et al., 1998a, 1999a). Further, this species occurs across a wide elevational range: in the PN d'Andohahela, it was recorded between 810 and 1875 m (Goodman et al., 1999a).

M. soricoides, with its massive upper incisors, is clearly predatory. At numerous sites, this species, as well as *M. dobsoni* and *M. talazaci*, has been found trapped in the same pitfall bucket with smaller species of *Microgale*, and more often than not the *M. soricoides* has partially eaten the other individual. In some cases, the only evidence that remains of the consumed shrew tenrec is a portion of tail or rostrum.

Microgale talazaci Major, 1896

Nesogale talazaci Thomas, 1918

HOLOTYPE—BM (NH) 97.9.1.107, adult female; skin, skull, and skeleton. Collected 22 May 1896 by C. I. Forsyth Major.

TYPE LOCALITY—Forest of the Independant Tanala of Ikongo, in the neighborhood of Vinantelo, one day's journey south of Fianarantsoa (21°44'S, 47°16'E).

REFERRED MATERIAL—FMNH 159690: tributary of the Manantenina River, 8 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 450 m, 14°26.2'S, 49°46.5'E; FMNH 159537, 159571, 159691, 159692, and 159693: tributary of Manantenina River, 10 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 775 m, 14°26.0'S, 49°45.7'E; FMNH 159572, 159573, 159574, 159575, and 159576: Antranohofa, 11 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1225 m, 14°26.02'S, 49°44.5'E; FMNH 159694 and UA-

SMG 8450: tributary at head of Andranomifototra River, 10.5 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1625 m, 14°26.04'S, 49°44.5'E.

KEY FEATURES (see Table 11-1 and Key 2, p. 228)—Very large, TL longer than HB. Dorsal pelage brown, venter gray with reddish buff wash. Skull very large and robust, sutures fused and obscure; rostrum broad, interorbital region long, parallel-sided; braincase angular, short relative to cranial length, superior articular facets very prominent, supraoccipital crests well developed, occipital region very reduced, occipital condyles visible in dorsal view. Small diastemata between I1 and I2 and between I3 and C. I1 larger than I2; lower i2 considerably larger than canine. Talonid of m3 reduced, hypoconid low, hypoconulid well marked, entoconid ridge and talonid basin poorly defined, entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of males to females was 1 : 2, the juvenile to adult ratio 1 : 9. Mammary formula: 1-0-2 (N = 1), 1-1-2 (N = 1). The testes of one adult male (FMNH 159694), with convoluted epididymides, measured 8 × 6 mm.

REMARKS—*M. talazaci*, the largest species of shrew tenrec, has a broad distribution across much of the humid forest zones of the island, from the Antsiranana region, including the PN de la Montagne d'Ambre (MacPhee, 1987; Goodman et al., 1996b) south across the eastern escarpment and several sites on the Central High Plateau, to at least the Vondrozo region (MacPhee, 1987; Goodman & Jenkins, 1998; Goodman et al., 1998a). This species was not found in the PN d'Andohahela (Goodman et al., 1998a). Its presence in the PN de Marojejy was reported previously by Nicoll and Langrand (1989) and by Duckworth (1990), and it is also known to occur in the RNI de Tsaratanana (Albignac, 1970).

In the PN de Marojejy, it was found to have an elevational range of 450–1625 m (Table 11-2), which is slightly broader than its range in the RS d'Anjanaharibe-Sud, where it was documented at 1260–1550 m (Table 11-3). In the PN d'Andringitra, this species' known altitudinal distribution is more restricted—it was not found in the zone from 720 to 1650 m but was trapped near tree line, at 1990 m (Goodman et al., 1996a; Goodman, unpubl. data).

***Oryzorictes hova* A. Grandidier, 1870**

Oryzorictes talpoides G. Grandidier and Petit, 1930

HOLOTYPE—MNHN CG 1887-874, adult female, preserved in alcohol, skull extracted, collection date unknown.

TYPE LOCALITY—Ankaye et Antsianak (Ankaye = Ankay, along the Mangoro River near lac Alaotra; Antsianak = Antsianaka, to the east of lac Alaotra [Viette, 1991]).

REFERRED MATERIAL—FMNH 159577 and 159695: tributary of the Manantenina River, 8 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 450 m, 14°26.2'S, 49°46.5'E; FMNH 159578: tributary at head of Andranomifototra River, 10.5 km NW of Manantenina, Province d'Antsiranana, PN de Marojejy, 1625 m, 14°26.04'S, 49°44.5'E.

KEY FEATURES—(see Key 1, pp. 228) Pelage soft, slightly iridescent; TL approximately half HB (TL : HB mean 49.51 ± 2.70 , range 46.0–53.9; N = 5); forefeet with very enlarged claws; broad naked rhinarium; eyes very small; ears small, concealed in pelage. Skull moderately robust, premaxillae dorsolaterally flared, braincase short, broad, and deep, lambdoid crests well-marked; I3 very small, approximately as tall as distostyle of I2; diastema present between I3 and C, forming a sulcus to accommodate the distal tip of c; C and c markedly taller than all other teeth; distostyle of C very small.

MEASUREMENTS—External measurements are presented in Table 11-1.

POPULATION STRUCTURE AND REPRODUCTION—Only adults were collected during the survey. The single female (FMNH 159577) was perforate, and the mammary formula was 0-1-2. One of the males (FMNH 159695) with convoluted epididymides had testes measuring 9×8 mm.

REMARKS—This species is generally difficult to trap, probably because of its semifossorial habits. Captures of this animal in pitfall traps or standard live traps is sporadic and seems to be more common after heavy rain, when individuals may be more active on the ground surface. In the PN de Marojejy, this species was obtained in the 450 and 1625 m zones (Table 11-2); it probably occurs across this complete elevational range. Local guides that joined the 1996 Marojejy survey noted that this distinctive animal is common in the rice fields near Mandena and Manantenina.

Oryzorictes hova is probably more common and more broadly distributed than is currently

known. It has not been captured in the PN de la Montagne d'Ambre (Raxworthy & Nussbaum, 1994; Goodman et al., 1996b). No individual of this species was trapped on the 1994 mission to the eastern slopes of the RS d'Anjanaharibe-Sud, but in February 1996 it was collected by F. Andreone on the western slopes of this massif (Goodman & Jenkins, 1998). The northernmost known locality for this species in the eastern humid forests appears to be the mountains surrounding the Andapa Basin. It is known from a variety of forested and nonforested sites along the eastern escarpment and Central High Plateau south to the PN d'Andohahela (Goodman et al., 1998b, 1999a). It is also known from the Marovoay region, several sites on the Masoala Peninsula, and the Nosy Mangabe (specimens in BM(NH)).

Discussion

General

A total of 1,155 pitfall bucket-days were accrued during the inventory of the PN de Marojejy, which was conducted between 3 October and 20 November 1996. This effort was divided between five elevational zones: 264 bucket-days at 450 m, 264 days at 775 m, 231 days at 1225 m, 231 days at 1625 m, and 165 days at 1875 m (Table 11-4). The pitfall traps yielded 117 small mammals, including 107 *Microgale*, 2 *Oryzorictes*, 1 *Eliurus majori*, 2 *E. minor*, and 5 *Voalavo gymnocaudus* (for rodents, see Chapter 12). Furthermore, 3,390 trap-nights, during which small-mammal traps with a standard baiting regimen were used, were also accrued during the inventory (Chapter 12), and 10 (0.29%) lipotyphlans were captured. The following species were obtained in standard museum traps: *Microgale cowani*, *M. gracilis*, *M. talazaci*, and *Oryzorictes hova*. In three cases, shrew tenrecs were captured in an elevational transect by means of standard museum traps and were not obtained by means of the pitfall devices in the same zone: *Microgale talazaci* at 450 m, *M. gracilis* at 1875 m, and *Oryzorictes hova* at 1625 m. Further, the specimen of *M. gracilis* captured in the 1875 m zone is our only record of this species on the Marojejy Massif.

The combined trapping results, with pitfalls and standard live traps, found 13 species of Tenrecidae (12 species of *Microgale* plus *Oryzorictes hova*) in the PN de Marojejy. Further, individuals

of *Tenrec ecaudatus* and *Setifer setosus* were observed on the massif but were not trapped. Thus, in total, 15 species of Tenrecidae were found at this site during the 1996 survey. The only lipotyphlans previously reported from the reserve but not found during our inventory are *Hemicentetes semispinosus* and *Microgale pusilla* (Nicoll & Langrand, 1989; Duckworth, 1990). The absence of these two animals in the results of the 1996 faunal inventory is discussed below (p. 221). Before we proceed with the analysis of the trapping results, it is important to assess whether the sampling effort extended in the PN de Marojejy was sufficient to allow some confidence in our measure of lipotyphlan species richness within each elevational zone.

Species Accumulation Curves and Confidence in Measurement of Species Richness

The total number of species known from each elevational zone was plotted against sampling effort (33 pitfall bucket-days per 24-hour period) to determine whether the number of cumulative tenrec species at each site reached a plateau (Fig. 11-3a). An examination of these curves shows that, in the 450 and 1875 m zones and, to a slightly lesser extent, in the 775 m zone, the accumulation of previously unrecorded species was rapid. One or two nights were sufficient to reach an apparent plateau in the species of lipotyphlans readily captured by pitfalls (see below). Of the five sites sampled, these three elevational sites had the lowest species richness (Table 11-2). Thus, it is not surprising that plateaus were reached relatively quickly. At 1225 and 1625 m, the zones with the greatest number of lipotyphlans species on the slopes of Marojejy, clear plateaus were not reached. In the former zone, a new species (*M. fotsifotsy*) was added the fifth night of pitfall trapping, and in the latter zone, an additional species (*M. dobsoni*) was added on the sixth and final night.

Information on the accumulation of new species in each elevational zone, based on pitfall captures, can be summarized as follows: in the 450 m zone, no new species was added after 66 pitfall bucket-days (total, 3 species in 264 pitfall bucket-days); in the 775 m zone, after 198 pitfall bucket-days (total, 2 species in 264 pitfall bucket-days); in the 1225 m zone, after 198 pitfall bucket-days (total, 9 species in 231 pitfall bucket-days); in the 1625 m zone, after 198 pitfall bucket-days (total,

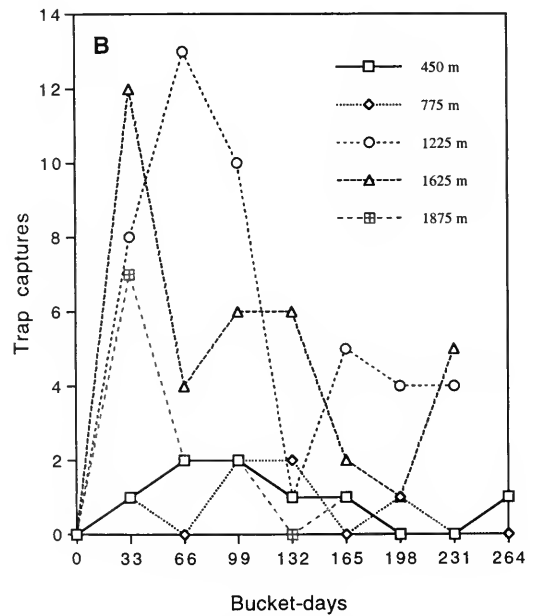
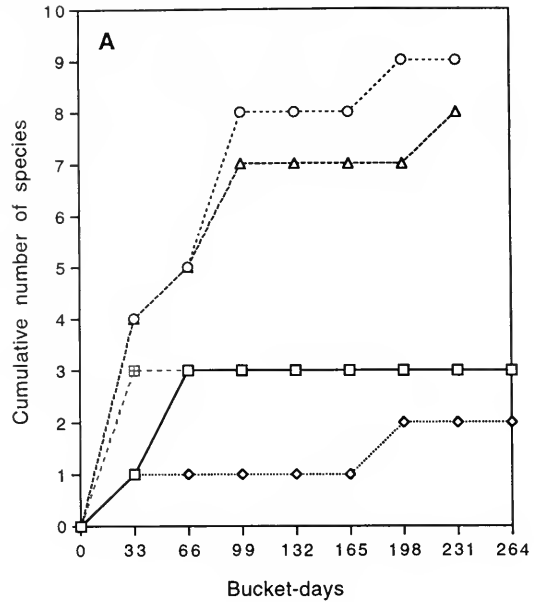


FIG. 11-3. Species accumulation curves (A) and pitfall trap success (B) plotted for each elevational zone in the PN de Marojejy against the total number of bucket-nights. The pitfall lines were placed in five different elevational zones (450, 775, 1225, 1625, and 1875 m). Information from the three lines in each zone is combined.

8 species in 231 pitfall bucket-days); and in the 1875 m zone, after 33 pitfall bucket-days (total, 3 species in 165 pitfall bucket-days). The leveling out of these curves within each elevational zone

through time did not generally coincide with a decline in pitfall trap success (Fig. 11-3b), although the number of animals captured in each elevational zone was generally higher at the beginning, rather than at the end, of each trapping season.

The *Microgale* species that are most difficult to capture in pitfall traps are the large-bodied animals, particularly *M. talazaci* and, to a lesser extent, *M. dobsoni*. *Oryzoricetes*, with its apparent subterranean mode of life, is also captured infrequently by this trapping system. In the 450 m zone, not a single *M. talazaci* was captured in the pitfall traps, but one was captured with a Sherman live trap on the second night of trapping (see Chapter 12). In the 775 m zone, this species was captured in Sherman live traps on the first, second, and fourth nights of trapping and was not obtained by pitfall traps until the sixth night. At 1625 m, an *Oryzoricetes hova* was trapped the seventh and final night of trapping, but it was not captured at this elevation in the pitfall traps. Finally, at the 1875 m site, the sole specimen of *M. gracilis* captured during the inventory of the PN de Marojejy was obtained with a Sherman trap.

In general, we feel that our combined trapping results (pitfall traps with standard traps) provide a good estimate of the actual species of lipotyphlans occurring within each elevational zone. (For further discussion of this point, see Goodman & Jenkins, 1998, p. 156.) Little previous information on the small mammals of this site is available (Griveaud, 1960; Nicoll & Langrand, 1989; Duckworth, 1990). Two species have been reported from the PN de Marojejy that were not encountered during the 1996 inventory: *Microgale pusilla* and *Hemicentetes semispinosus*. The former species was collected at 800 m in the northwestern portion of the reserve near the Antsahaberoakahely River (Duckworth, 1990). The specimen deposited in the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, could not be found in April 1998, and it is impossible to verify the determination. We suspect that the animal was misidentified and is probably referable to the very similarly small-sized *M. parvula*. *M. pusilla* was not recorded in the nearby RS d'Anjanaharibe-Sud (Goodman & Jenkins, 1998), and the nearest known locality for this species with respect to Marojejy is in the Didy region, approximately 400 km to the south. Duckworth (1990) reported observing *H. semispinosus* on 2 September in the southwestern portion of the reserve. An unidentified species of *Hemicentetes* was observed by F.

Andreone on the western slopes of RS d'Anjanaharibe-Sud (Goodman & Jenkins, 1998). *H. nigriceps* is known only from the central high plateau and higher altitudes of the eastern escarpment, and the animal observed in the RS d'Anjanaharibe-Sud is almost certainly *H. semispinosus*, as indicated by the geographical distribution. This species was not recorded during an inventory of this reserve between mid-October and late December 1994, and it seems distinctly less common in the warm season, before heavy rains (September through December) than during the heart of the rainy season (January through April). It has been reported from the Masoala Peninsula, near Rantabe, and the Mananara region (Nicoll & Langrand, 1990; Stephenson, 1995). There is little doubt that *H. semispinosus* occurs in the PN de Marojejy, and it was not recorded during the 1996 inventory of the reserve.

Virtually all of the species of tenrecs that might be expected to occur in the reserve were found during the 1996 survey. The only exceptions to this are *M. dryas* and *M. taiva*. The former species has been identified from owl pellets collected at the edge of the RS d'Anjanaharibe-Sud but not obtained during the inventory of that reserve in 1994, and the latter species was captured along the western slopes of the Anjanaharibe-Sud Massif (Goodman & Jenkins, 1998).

Several other studies have shown that pitfall buckets are an excellent method to document the diversity of Malagasy lipotyphlans living in humid forests. The use of this technique, combined with standard live traps, over the course of a rapid faunal inventory probably gives an excellent, although not 100% complete, estimate of the species living in an area.

The utility of pitfall traps in augmenting capture rates of *Microgale* and subsequently providing material for systematic studies can be nicely illustrated with *M. gymnorhyncha* and *M. fotsifotsy*, both of which have only recently been described. These two species are now known to be widely distributed throughout much of the humid forest on Madagascar. Both of these species had been represented in museum collections before their "discovery" during recent biological inventories. This newly collected material was necessary to clearly diagnose these new forms and to establish species limits.

Elevational Associations Among Lipotyphlans

ELEVATIONAL DISTRIBUTION—No oryzoricetine species was trapped in all of the five zones sam-

pled along the elevational transect of the PN de Marojejy (Table 11-2). *Microgale parvula* and *M. talazaci*, recorded at the four sites between 450 and 1625 m, appear to occupy the broadest altitudinal band among the *Microgale* found within the reserve. For the former species, this finding is in accordance with previous results from various surveys (Table 11-3), where it occurs from lowland to montane habitats. The case for *M. talazaci* is somewhat different. At other surveyed sites, this species apparently does not have as broad an elevational range as in the PN de Marojejy (Table 11-3). This may in part be an artifact of the number of individuals captured at these other sites. Only one species, *M. brevicaudata*, was restricted to the lowlands of the PN de Marojejy. Several species are apparently limited to the middle elevations of the reserve (*M. dobsoni*, *M. fotsifotsy*, *M. gymnorhyncha*, *M. longicaudata*, and *M. soricoides*), and a few others occur from this zone and up to the upper limit of forest cover on the mountain (*M. cowani*, *M. monticola*, and *M. principula*). *M. gracilis* is apparently restricted to the upper montane zone of the Marojejy Massif. However, this is based on a single capture of this species in the reserve. The only species with an apparently disjunct altitudinal distribution was *Oryzorictes hova*, which was collected in lowland forest at 450 m and in montane mossy forest at 1625 m. This latter result is almost certainly an artifact of the aforementioned difficulty in trapping *Oryzorictes*.

Among *Microgale*, there is no clear evidence of species replacement along the elevational gradient surveyed within the PN de Marojejy. At one site inventoried over the past few years, the two species of long-tailed shrew tenrecs, *M. principula* and the slightly smaller *M. longicaudata*, occur along the same slopes (Table 11-3). In the RS d'Anjanaharibe-Sud, there is some evidence that these two species might replace one another—*M. principula* was found only at 875 m and *M. longicaudata* at 1260–1950 m (Goodman & Jenkins, 1998). However, this pattern was not the case in the PN de Marojejy; here, *M. longicaudata* was recorded only at 1225 m, and *M. principula* occurred higher on the mountain, at 1625–1875 m. On the slopes of the PN d'Andohahela these two species were broadly sympatric, with *M. principula* occurring at 440–1200 m and *M. longicaudata* along the complete length of the transect, at 440–1875 m (Goodman et al., 1999a). Whether these differences in the elevational distribution of the two species are artifacts of the number of cap-

tures or reflect some aspect of habitat segregation requires further study.

COMPARISON BETWEEN THE PN DE MAROJEJY AND THE RS D'ANJANAHARIBE-SUD—Recent elevation transects of Lipotyphla in several reserves in the eastern humid forest biome, spanning the full latitudinal breadth of the island from 12.5° to 24.5°S, provide an excellent means to study the relationships between elevational and latitudinal gradients. If indeed there are latitudinal components involved in these patterns, then before testing for them it is important to look for consistency in species composition and elevational range between sites at the same latitude. The PN de Marojejy and the RS d'Anjanaharibe-Sud provide the opportunity for such a comparison. These two sites are separated by approximately 40 km, and the Andapa Basin lies between them. The summit of Anjanaharibe Anivo (2064 m) is at 14°44'S and that of Marojejy (2033 m) is at approximately 14°30'S. The botanical communities on these two mountains show many similarities (Goodman & Lewis, 1998; Chapter 3). A notable difference between them is that the summital zone of the Marojejy Massif contains a larger expanse of high-elevation grassland than that of Anjanaharibe-Sud. Furthermore, the Marojejy Massif lies closer to the coast, which certainly has an effect on annual rainfall (Donque, 1975); Marojejy is presumably wetter.

During the survey of the PN de Marojejy, 13 species of shrew tenrecs and a mole tenrec belonging to the subfamily Oryzorictinae were collected, and two species of spiny tenrecs belonging to the subfamily Tenrecinae were observed, giving a total of 15 species of Tenrecidae. This is in comparison with the RS d'Anjanaharibe-Sud, where 12 species of Oryzorictinae and three species of Tenrecinae (only one of which was collected) have been documented in this protected area (Goodman & Jenkins, 1998). Given that most of the Tenrecinae records for these two massifs are based on observations, we prefer to restrict our comparisons to oryzorictines. Of these animals, most species were found in both the PN de Marojejy and the RS d'Anjanaharibe-Sud (*O. hova*, *M. cowani*, *M. dobsoni*, *M. fotsifotsy*, *M. gymnorhyncha*, *M. longicaudata*, *M. monticola*, *M. parvula*, *M. principula*, *M. soricoides*, and *M. talazaci*), but there are a few anomalies, with *M. brevicaudata* and *M. gracilis* collected only in PN de Marojejy and *M. dryas* only in the RS d'Anjanaharibe-Sud. *Microgale brevicaudata* seems to be limited to the coastal plain and adjacent foothills (see pp. 208–209). For

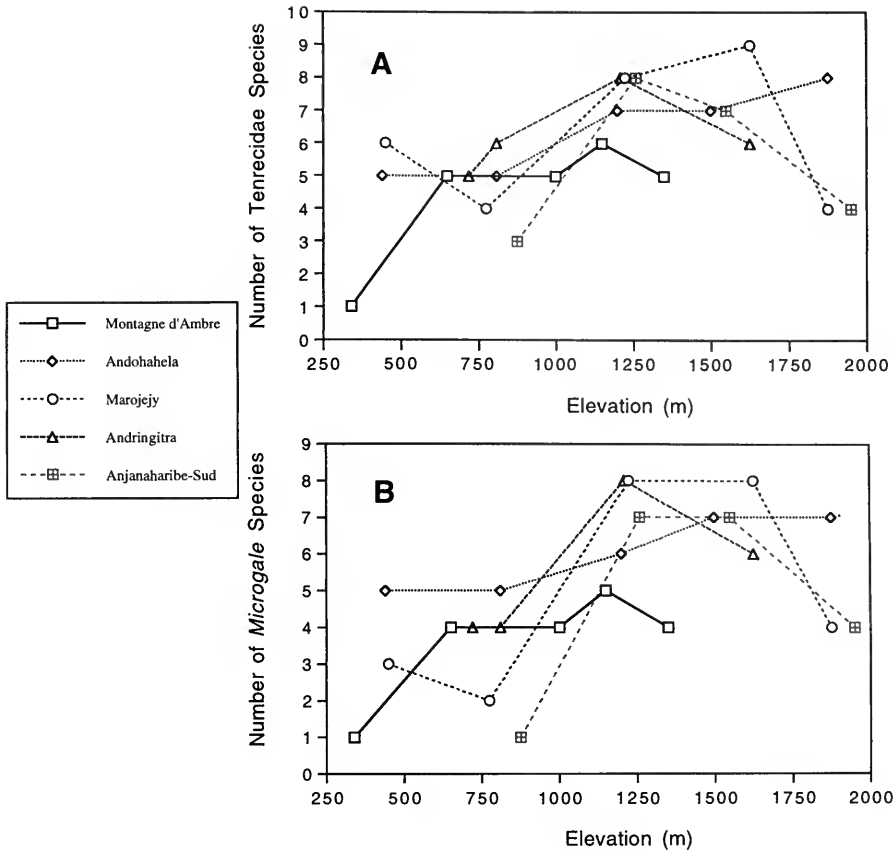


FIG. 11-4. Plots of Lipotyphla species richness in relation to elevational transects for five different mountains on Madagascar. Information is presented as all Tenrecidae species (A) and restricted to *Microgale* species (B). Data are derived from the same sources mentioned in the footnotes to Table 11-3.

M. gracilis and *M. dryas*, the differences between the sites is most likely an artifact of the difficulty in trapping these species.

As far as elevational separation is concerned, the altitudinal distribution of species is broadly similar in both reserves, with *M. parvula* and *M. talazaci* in lowland to montane zones and *M. longicaudata*, *M. dobsoni*, *M. soricoides*, *M. gymnorhyncha*, *M. cowani*, and *M. monticola* in montane zones. *M. principula* is a notable exception, since it was collected only in lowland areas in RS d'Anjanaharibe-Sud and only in montane habitats in PN de Marojejy. Thus, in general, the species compositions and elevational distributions of lipotyphlans, particularly Oryzorictinae, on these two mountains are very similar.

SPECIES RICHNESS—Over the past few years, there has been a flurry of articles and hypotheses to explain the distribution of plants and animals

along latitudinal and altitudinal gradients (e.g., Rahbek, 1997). Considerable attention has been given to the effects of forest productivity in molding these patterns (Ricklefs & Schluter, 1993; Rosenzweig & Abramsky, 1993). A repeated pattern of a species diversity gradient across a broad array of taxa involves the peaking of species numbers at middle elevations on mountains in tropical latitudes (e.g., Janzen et al., 1976; Terborgh, 1977; Heaney & Rickart, 1990; Olson, 1994; Raxworthy et al., 1998); such a mid-elevational bulge pattern may be related to measures of environmental complexity and ecological productivity (see review by Rosenzweig, 1992). In the PN d'Andringitra, an analysis of soil invertebrates showed that the elevational zone with the greatest invertebrate density and taxonomic diversity was in direct parallel with that portion of the mountain with the highest *Microgale* species richness and

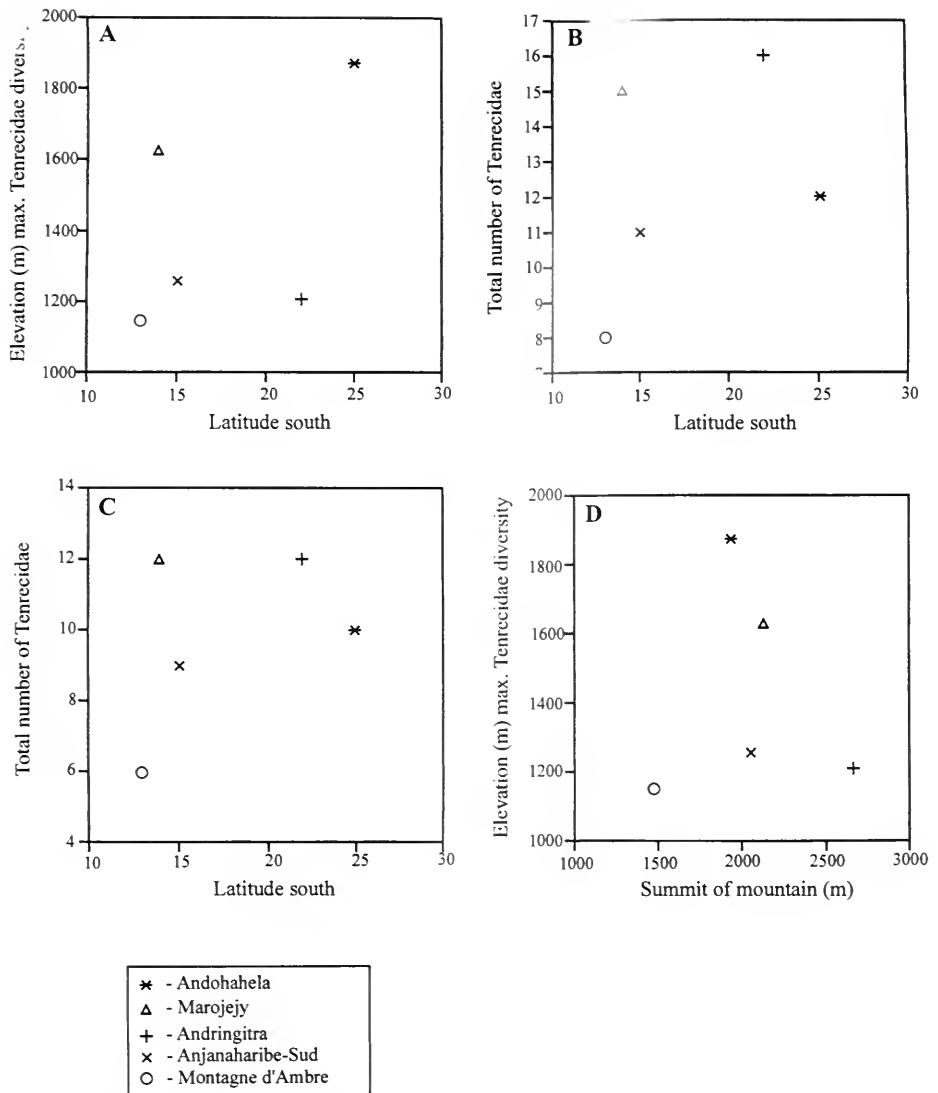


FIG. 11-5. Plots assessing the relationships between various latitudinal and topographic variables and species richness of Lipotyphla on Madagascar.

density (Goodman et al., 1996a). Thus, in this case there is a correlation between productivity, as measured by soil invertebrate density and diversity, and the distribution of Lipotyphla on these slopes. We interpret this result as support for the productivity hypothesis. Comparable data are not available for the PN de Marojejy, but we suspect the pattern found on the Andringitra Massif is applicable to Marojejy.

The distribution of Tenrecidae species in the PN de Marojejy conforms to a unimodal, hump-shaped pattern across the five altitudinal zones

surveyed (Fig. 11-4; Table 11-2). The highest species richness of this family on the massif is nine species, recorded at 1625 m, within the upper portion of montane forest. When this measure is confined to *Microgale*, both the 1225 and 1625 m sites, each with eight species, constitute the zone with the greatest diversity of shrew tenrecs. The fewest species of Tenrecidae found in any zone was four species at 775 m (transitional lowland-montane forest) and 1875 m (montane/sclerophyllous forest). When this comparison is restricted to the genus *Microgale*, the pattern changes

TABLE 11-5. Topographic settings in which Lipotyphla were captured by pitfall traps in the PN de Marojejy.

Species	No. of captures at altitude and placement*																		
	450 m			775 m			1225 m			1625 m			1875 m			Total			
	V	S	R	V	S	R	V	S	R	V	S	R	V	S	R	V	S	R	
<i>Microgale brevicaudata</i>			3	1														3	1
<i>Microgale cowani</i>							3	5	2	4	4	6	2	1	9	9	9		
<i>Microgale dobsoni</i>							1	1	5			1			1	1	6		
<i>Microgale fotsifotsy</i>							1								1				
<i>Microgale gymnorhyncha</i>							2	2				1			2	2	1		
<i>Microgale longicaudata</i>								1	1							1	1		
<i>Microgale monticola</i>								5		4	2	4	2	3	6	10	4		
<i>Microgale parvula</i>	1	1	2	4	1	1	2	1							6	4	4		
<i>Microgale principula</i>										2	1	1	1	3	3	3	1		
<i>Microgale soricoides</i>							1	2	4	2	1	2			3	3	6		
<i>Microgale talazaci</i>						1	2	1	2		1				2	2	3		
<i>Oryzomys hova</i>			2														2		
Total captures	1	6	3	4	2	11	19	15	12	9	15	5	6	1	33	40	36		

* V = valley; S = slope; and R = ridge.

somewhat: the lowest species richness, at two, remains the 775 m zone, followed by three species in the lowland forest at 425 m, and finally by four species at 1875 m. A parallel pattern of a mid-elevational bulge in Tenrecidae species richness has been found at several other mountains on the island: the PN d'Andringitra (Goodman et al., 1996a; Langrand & Goodman, 1997; Goodman, unpubl. data), the RS d'Anjanaharibe-Sud (Goodman & Jenkins, 1998), the PN d'Andohahela (Goodman et al., 1999a), and the PN de la Montagne d'Ambre (Goodman et al., 1996a). The sites, all inventoried by means of the same sampling protocol, span the full latitudinal breadth of the eastern humid forest biome in Madagascar, from 12.5° to 24.5°S. Further, the surveys of Andohahela, Andringitra, Anjanaharibe-Sud, and Marojejy were conducted during the same period (October to early December).

Although a mid-elevational bulge in species richness recurs among these five mountains, there is no consistent altitude at which diversity of Lipotyphla peaks, whether examined across all of the Tenrecidae (Fig. 11-4A) or restricted to *Microgale* spp. (Fig. 11-4B). Whether for the Tenrecidae as a whole or specifically for the genus *Microgale*, the zones that hold the largest number of species vary from 1150 m on Montagne d'Ambre to 1875 m on the Andohahela Massif.

There is no clear north-to-south trend suggestive of elevational shifts in vegetational communities along a latitudinal gradient in the elevation where maximum Tenrecidae species richness was recorded (Fig. 11-5A), in the total number of Ten-

recidae known from each mountain (Fig. 11-5B), or in the total number of *Microgale* spp. recorded on each mountain (Fig. 11-5C). The elevation of maximum diversity at Andohahela and Andringitra, the two southern mountains closest to one another in this sample, varies from 1210 m in Andringitra to 1875 m in Andohahela, and the intermediate value between these two sites is from Marojejy, toward the north end of the island. Further, the Anjanaharibe-Sud and Marojejy Massifs, within one degree of latitude of each other, show divergent patterns in the zone of maximum species richness.

Analyzing similar types of data to explain the elevational distribution of Nesomyine rodents on the slopes of the Montagne d'Ambre, Anjanaharibe-Sud, Andringitra, and Andohahela Massifs, Goodman et al. (1999b) found a very strong and positive correlation between a mountain's absolute height and the elevation with the most species. However, for Tenrecidae, this pattern does not hold (Fig. 11-5D). The strong correlation between these variables for Nesomyine rodents was explained in that, on each of these mountains, the zone showing the greatest species richness occurs within the belt of wet montane rain forest. This zone is wedged between the nearly perennial cloud shroud in the summital zone, with low levels of direct sunlight and with problems associated with waterlogging, and the lowland area, which has greater direct solar radiation, although, at least seasonally, it experiences higher evaporation rates and desiccation associated with water shortage. We strongly suspect that this same pattern holds

for the Tenrecidae, but we lack the statistical backing that was found for the rodents.

HABITAT PREFERENCES—Pitfall traps were placed in three different microhabitats at each elevation: in valley bottoms, on the slopes of hills, and on ridge crests. These three topographical zones generally have distinctly different botanical communities (see Chapter 3). The distribution of oryzoricines was roughly equal in all three habitats, with 33 individuals trapped in valley bottoms, 40 on slopes, and 36 on ridges (Table 11-5). This is in contrast to the other sites, where *Microgale* were captured more frequently in valleys than on slopes or ridges (Goodman et al., 1996a).

At the species level, there is little evidence of differential captures in any of these three microhabitats, but only one species, *M. monticola*, was captured in sufficient numbers to properly assess such preferences. Approximately 50% more individuals of this species were captured in the PN de Marojejy on slopes as compared with valleys and ridges. In the nearby RS d'Anjanaharibe-Sud, the same basic pattern exists: about half the number of this species were captured on ridges and in valleys as compared with slopes (Goodman & Jenkins, 1998).

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Literature Cited

ADE, M. 1996. Morphological observations on a *Microgale* specimen (Insectivora, Tenrecidae) from western Madagascar, pp. 251–255. In Ganzhorn, J. U., and J.-P. Sorg, eds., Ecology and Economy of a Tropical Dry

Forest in Madagascar. Primate Report, special issue, Deutsches Primatenzentrum, Göttingen.

ALBIGNAC, R. 1970. Mammifères et oiseaux du massif du Tsaratanana (Madagascar Nord). Mémoires ORSTOM, **37**: 223–229.

BUTLER, P. M., AND M. GREENWOOD. 1979. Soricidae (Mammalia) from the Olduvai Gorge, Tanzania. Zoological Journal of the Linnean Society, **67**: 329–379.

CARLETON, M. D., AND D. F. SCHMIDT. 1990. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. American Museum Novitates, **2987**: 1–36.

DEWAR, R., AND S. RAKOTOVOLOLONA. 1992. La chasse aux subfossiles: Les preuves du onzième siècle au treizième siècle. Taloha, **11**: 4–15.

DONQUE, G. 1975. Contribution géographique à l'étude du climat de Madagascar. Nouvelle Imprimerie des Arts Graphiques, Antananarivo, 478 pp.

DUCKWORTH, J. W. 1990. Systematic list of mammals recorded in Marojejy, pp. 114–129. In Safford, R., and W. Duckworth, eds., A Wildlife Survey of Marojejy Nature Reserve, Madagascar. Study Report no. 40. International Council for Bird Preservation, Cambridge, 171 pp.

EISENBERG, J. F., AND E. GOULD. 1970. The tenrecs: A study in mammalian behavior and evolution. Smithsonian Contributions to Zoology, **27**: 1–137.

GANZHORN, J. U., S. SOMMER, J.-P. ABRAHAM, M. ADE, B. M. RAHARIVOLOLONA, E. R. RAKOTOVAO, C. RAKOTONDRAISOA, AND R. RANDRIAMARISOA. 1996. Mammals of the Kirindy Forest with special emphasis on *Hypogeomys antimena* and the effects of logging on the small mammal fauna, pp. 215–232. In Ganzhorn, J. U., and J.-P. Sorg, eds., Ecology and Economy of a Tropical Dry Forest in Madagascar. Primate Report, special issue, Deutsches Primatenzentrum, Göttingen, **46-1**: 1–382.

GOODMAN, S. M., A. ANDRIANARIMISA, L. E. OLSON, AND V. SOARIMALALA. 1996b. Patterns of elevational distribution of birds and small mammals in the humid forests of Montagne d'Ambre, Madagascar. Ecotropica, **2**: 87–98.

GOODMAN, S. M., M. D. CARLETON, AND M. PIDGEON. 1999b. The rodents of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, pp. 217–249. In Goodman, S. M., ed., A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With Reference to Elevational Variation. Fieldiana: Zoology, n.s., **94**: 1–297.

GOODMAN, S. M., J.-M. DUPLANTIER, P. J. RAKOTOMALAZA, A. P. RASELIMANANA, R. RASOLOARISON, M. RAVOKATRA, V. SOARIMALALA, AND L. WILMÉ. 1998b. Inventaire biologique de la forêt d'Ankazomivady, Ambositra. Akon'ny Ala, **24**: 19–32.

GOODMAN, S. M., J. U. GANZHORN, L. E. OLSON, M. PIDGEON, AND V. SOARIMALALA. 1997. Annual variation in species diversity and relative density of rodents and insectivores in the Parc National de la Montagne d'Ambre, Madagascar. Ecotropica, **3**: 109–118.

GOODMAN, S. M., AND P. D. JENKINS. 1998. The insectivores of the Réserve Spéciale d'Anjanaharibe-Sud, pp. 139–161. In Goodman, S. M., ed., A Floral

- and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With Reference to Elevational Variation. *Fieldiana: Zoology*, n.s., **90**: 1–246.
- GOODMAN, S. M., P. D. JENKINS, AND M. PIDGEON. 1999a. The Lipotyphla (Tenrecidae and Soricidae) of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, pp. 187–216. In Goodman, S. M., ed., *A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With Reference to Elevational Variation*. *Fieldiana: Zoology*, n.s., **94**: 1–297.
- GOODMAN, S. M., AND B. A. LEWIS. 1998. Description of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, pp. 9–16. In Goodman, S. M., ed., *A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With Reference to Elevational Variation*. *Fieldiana: Zoology*, n.s., **90**: 1–246.
- GOODMAN, S. M., D. RAKOTONDRAVONY, L. E. OLSON, E. RAZAFIMAHATRATRA, AND V. SOARIMALALA. 1998a. Les insectivores et les rongeurs, pp. 80–93. In Rakoton-dravony, D., and S. M. Goodman, eds., *inventaire Biologique—Forêt d'Andranomay, Anjozorobe*. World Wide Fund for Nature—Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, Recherches pour le Développement. *Série Sciences Biologiques*, no. **13**: 1–110.
- GOODMAN, S. M., D. RAKOTONDRAVONY, G. SCHATZ, AND L. WILMÉ. 1996c. Species richness of forest-dwelling birds, rodents and insectivores in a planted forest of native trees: a test case from the Ankaratra, Madagascar. *Ecotropica*, **2**: 109–120.
- GOODMAN, S. M., C. J. RAXWORTHY, AND P. D. JENKINS. 1996a. Insectivore ecology in the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 218–230. In Goodman, S. M., ed., *A Floral and Faunal Inventory of the Eastern Slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With Reference to Elevational Variation*. *Fieldiana: Zoology*, n.s., **85**: 1–319.
- GRANDIDIER, A. 1870. Description de quelques animaux nouveaux, découverts à Madagascar, en novembre 1869. *Revue et Magasin de Zoologie*, série 2, **22**: 49–50.
- GRANDIDIER, G. 1899. Description d'une nouvelle espèce d'insectivore provenant de Madagascar. *Bulletin du Muséum d'Histoire Naturelle* **5**: 349.
- . 1934. Deux nouveaux mammifères insectivores de Madagascar, *Microgale drouhardi* et *M. parvula*. *Bulletin du Muséum National d'Histoire Naturelle*, série 2, **6**: 474–477.
- GRANDIDIER, G., AND G. PETIT. 1930. Description d'une espèce nouvelle d'Insectivore Malgache, suivie de remarques critiques sur le genre *Oryzoryctes*. *Bulletin du Muséum National d'Histoire Naturelle*, série 2, **2**: 498–505.
- . 1931. Un type nouveaux de centétidé malgache, *Paramicrogale occidentalis*. *Bulletin de la Société Zoologique de France*, **56**: 126–139.
- GRIVEAUD, P. 1960. Une mission entomologique au Marojejy. *Naturaliste Malgache*, **12**: 43–55.
- HEANEY, L. R., AND E. A. RICKART. 1990. Correlations of clades and clines: Geographic, elevational, and phylogenetic distribution patterns among Philippine mammals, pp. 321–332. In Peters, G., and R. Hutterer, eds., *Vertebrates in the Tropics*. Museum Alexander Koenig, Bonn.
- HUMBERT, H. 1951. Les territoires phytogéographiques du nord de Madagascar. *Compte Rendus des Séances de la Société de Biogéographie*, **246**: 176–184.
- JANZEN, D. H., D. M. ATAROFF, M. FARINAS, S. REVES, N. RINCON, A. SOLER, P. SORIANO, AND M. VERA. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica*, **8**: 193–203.
- JENKINS, P. D. 1988. A new species of *Microgale* (Insectivora: Tenrecidae) from northeastern Madagascar. *American Museum Novitates*, **2910**: 1–7.
- . 1993. A new species of *Microgale* (Insectivora: Tenrecidae) from eastern Madagascar with an unusual dentition. *American Museum Novitates*, **3067**: 1–11.
- JENKINS, P. D., S. M. GOODMAN, AND C. J. RAXWORTHY. 1996. The shrew tenrecs (*Microgale*) (Insectivora: Tenrecidae) of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 191–217. In S. M. Goodman, ed., *A Floral and Faunal Inventory of the Eastern Slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With Reference to Elevational Variation*. *Fieldiana: Zoology*, n.s., **85**: 1–319.
- JENKINS, P. D., C. J. RAXWORTHY, AND R. A. NUSSBAUM. 1997. A new species of *Microgale* (Insectivora, Tenrecidae), with comments on the status of four other taxa of shrew tenrecs. *Bulletin of the Natural History Museum London (Zoology)*, **63**: 1–12.
- KAUDERN, W. 1918. Quartäre Fossilien aus Madagascar. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere*, **41**: 519–533.
- LANGRAND, O., AND S. M. GOODMAN. 1997. Inventaire biologique des oiseaux et des micro-mammifères des zones sommitales de la Réserve Naturelle Intégrale d'Andringitra. *Akon'ny Ala* **20**: 39–54.
- MACPHEE, R. D. E. 1986. Environment, extinction, and Holocene vertebrate localities in southern Madagascar. *National Geographic Research*, **2**: 441–455.
- . 1987. The shrew tenrecs of Madagascar: Systematic revision and Holocene distribution of *Microgale* (Tenrecidae, Insectivora). *American Museum Novitates*, **2889**: 1–45.
- MAJOR, C. I. FORSYTH. 1896. Diagnoses of new mammals from Madagascar. *Annals and Magazine of Natural History*, series 6, **18**: 318–325.
- . 1897. On the general results of a zoological expedition to Madagascar in 1894–96. *Proceedings of the Zoological Society of London (for 1896)*: 971–981.
- MILLS, J. R. E. 1966. The functional occlusion of the teeth of Insectivora. *Journal of the Linnean Society (Zoology)*, **47**: 1–125.
- NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des aires protégées. *World Wide Fund for Nature, Gland, Switzerland*, 374 pp.
- NICOLL, M. E., AND G. B. RATHBUN. 1990. African Insectivora and Elephant-Shrews: An action plan for their conservation. *International Union for the Con-*

ervation of Nature and Natural Resources, Gland, Switzerland, 53 pp.

OLSON, D. M. 1994. The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. *Journal of Tropical Ecology*, **10**: 129–150.

RAHBEK, C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. *The American Naturalist*, **149**: 875–902.

RANDRIANJAFY RASOLOARISOA, V. N. R. 1993. Contribution à l'étude bio-écologique du peuplement de micromammifères dans la forêt de l'Ankarafantsika. Mémoire de Diplôme d'Études Approfondies, Sciences Biologiques Appliquées, Écologie Environnementale, Université d'Antananarivo, Antananarivo.

RAXWORTHY, C. J., AND R. A. NUSSBAUM. 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological Conservation*, **69**: 65–73.

RAXWORTHY, C. J., F. ANDREONE, R. A. NUSSBAUM, N. RABISOA, AND H. RANDRIAMAHAZO. 1998. Amphibians and reptiles of the Anjanaharibe-Sud Massif: Elevational distribution and regional endemism, pp. 79–92. *In* Goodman, S. M., ed., *A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With Reference to Elevational Variation*. Fieldiana: Zoology, n.s., **90**: 1–246.

RICKLEFS, R. E., AND D. SCHLUTER, EDs. 1993. *Species diversity in ecological communities*. University of Chicago Press, Chicago, 414 pp.

ROSENZWEIG, M. L. 1992. Species diversity gradients: We know more and less than we thought. *Journal of Mammalogy*, **73**: 715–730.

ROSENZWEIG, M. L., AND Z. ABRAMSKY. 1993. How are diversity and productivity related?, pp. 52–65. *In* Ricklefs, R. E., and D. Schluter, eds., *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago, 414 pp.

STEPHENSON, P. J. 1994. Seasonality effects on small mammal trap success in Madagascar. *Journal of Tropical Ecology*, **10**: 439–444.

———. 1995. Small mammal microhabitat use in lowland rain forest of northeast Madagascar. *Acta Theriologica*, **40**: 425–438.

SWINDLER, D. R. 1976. *Dentition of Living Primates*. Academic Press, London, 308 pp.

TERBORGH, J. 1977. Bird species diversity along an Andean elevational gradient. *Ecology*, **58**: 1007–1019.

THOMAS, (M. R.) OLDFIELD. 1882. Description of a new genus and two new species of Insectivora from Madagascar. *Journal of the Linnean Society (Zoology)*, **16**: 319–322.

———. 1884. Description of a new species of *Microgale*. *Annals and Magazine of Natural History*, series 5, **14**: 337–338.

———. 1918. On the arrangement of the small Tenrecidae hitherto referred to *Oryzorictes* and *Microgale*. *Annals and Magazine of Natural History*, series 9, **1**: 302–307.

———. 1926. On some small mammals from Madagascar. *Annals and Magazine of Natural History*, series 9, **17**: 250–252.

VIETTE, P. 1991. Principales localités où des Insectes ont été recueillis à Madagascar. Faune de Madagascar, supplément 2. Private Printing.

VOSS, R. S., AND L. H. EMMONS. 1996. Mammalian diversity in Neotropical lowland rainforests: A preliminary assessment. *Bulletin of the American Museum of Natural History*, **230**: 1–115.

Key 1. The genera of Tenrecidae occurring in PN de Marojejy.

1. Pelage spinous; tail very short 2
 Pelage soft, lacking spines; tail medium to long 4
2. Close-set, sharp spines cover dorsal surface *Setifer*
 Dorsal surface covered with a mixture of spines and long, coarse hair 3
3. Dorsal pelage dark with longitudinal pale stripes; head and body length < 200 mm ...
 *Hemicentetes**
 Dorsal pelage uniform brown; head and body length > 260 mm *Tenrec*
4. Body robust, forelimbs robust, forefeet broad with enlarged, stout claws; C longer than II *Oryzorictes*
 Body slender to moderately robust, forelimbs not enlarged, forefeet slender to moderately broad, claws short to moderately lengthened; II longer or subequal in length to C *Microgale*

* *Hemicentetes* was neither collected nor observed during the survey, but it has been recorded previously from this reserve. For further comments, see Discussion (p. 221).

Key 2. The species of *Microgale* occurring in PN de Marojejy.

1. Size very small, HB < 62, CIL < 17.1
 *M. parvula*
 Size larger, HB > 65, CIL > 20.0 2
2. Ratio of TL:HB > 2.0 3
 Ratio of TL:HB < 1.5 4
3. Size smaller, HB < 70, CIL < 21.0
 *M. longicaudata*
 Size larger, HB > 70, CIL > 21.0
 *M. principula*
4. Digits and tail tip contrastingly paler than body, tail, and feet *M. fotsifotsy*

- Tail tip and digits not obviously paler than rest of body 5
5. Proboscis long, large rhinarium extends posterodorsally onto muzzle; forefeet broad, foreclaws enlarged 6
 Small rhinarium confined to anterior of short proboscis; forefeet slender without lengthened foreclaws 7
6. Posterior region of rhinarium with transverse striae; ratio of I-P3 : UTL < 0.55
 *M. gymnorhyncha*
 Posterior region of rhinarium reticulated; ratio of I-P3 : UTL > 0.57 *M. gracilis*
7. Size smaller: CIL < 24; tail shorter < 75 8
 Size larger: CIL > 24; tail longer > 88 9
8. Tail shorter: ratio of TL : HB < 0.6
 *M. brevicaudata*
- Tail longer: ratio of TL : HB > 0.8
 *M. cowani*
9. Size smaller: HB < 100, CIL < 26.0 10
 Size larger: HB > 100, CIL > 30.0 11
10. Pelage dark brown dorsally, slightly lighter ventrally; TL longer than HB, ratio > 1.2
 *M. monticola*
 Pelage lightish buff brown dorsally, reddish buff ventrally; TL subequal to HB, ratio < 1.1 *M. soricoides*
11. Cranial size smaller, CIL < 32.0; body size averaging smaller, HB < 108, WT < 32
 *M. dobsoni*
 Cranial size larger, CIL > 34.0; body size averaging larger, HB > 104, WT > 33
 *M. talazaci*

Chapter 12

Rodents of the Parc National de Marojejy, Madagascar

Michael D. Carleton¹ and Steven M. Goodman²

Abstract

The small mammal inventory of the Parc National de Marojejy, conducted between 4 October and 20 November, 1996, in five elevational stations from 450 to 1875 m, produced vouchered evidence of seven species of native rodents (Muridae: Nesomyinae) that inhabit the park—*Eliurus grandidieri*, *E. majori*, *E. minor*, *E. tanala*, *E. webbi*, *Gymnuromys roberti*, and *Voalavo gymnocaudus*. Regular sightings of a large *Nesomys* (probably *N. rufus*) suggest the presence of this diurnal form, yet its numbers were low and none were live trapped. The introduced rodent *Rattus rattus* (Muridae: Murinae) was also collected, but unlike in field surveys of several other northern forest sites, it proved to be uncommon.

The variable incidence of white tail tips in the series of *E. majori* from Marojejy prompted taxonomic review of the status of *E. penicillatus*, a nominal species known only from its type locality in east-central Madagascar and uniformly possessing a white caudal tip. Morphometric evaluation, using craniodontal data, of *E. penicillatus* and six *E. majori* samples across much of its known range recommends that the two should be maintained as separate species. Comparable analyses of nine population samples of *E. webbi* from throughout its range uncovered only minor differences consistent with geographic variation within a single, widely distributed species.

The highest diversity of native species was documented at 1250 m, near the lower limit of montane forest (six species); fewer species occupied lowland rain forest, at 450 m (one), and sclerophyllous montane forest, at 1875 m (three). The sympatric coincidence, elevational limits, and ecological agreement of native species on the massifs of Marojejy and nearby Anjanaharibe-Sud are strongly concordant and reaffirm broad distributional themes of nesomyines within the eastern humid forest biome. Although certain nesomyine species do occur in sclerophyllous montane forest up to tree line, none has been recovered from the ericaceous grassland and bush near the summits of Marojejy and Anjanaharibe-Sud. The apparent absence of native rodents in comparable alpine habitat on these northern highlands and the presence of one genus (*Brachyuromys*) in similar settings on the Central High Plateau are discussed.

Résumé

L'inventaire des petits mammifères du Parc National de Marojejy, conduit entre le 4 octobre et le 20 novembre 1996, dans cinq stations réparties à des altitudes de 450 à 1875 mètres, permit d'obtenir des données de référence sur sept espèces des rongeurs indigènes (Muridae: Nesomyinae) distribuées dans le parc—*Eliurus grandidieri*, *E. majori*, *E. minor*, *E. tanala*, *E.*

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webbi, *Gymnuromys roberti* et *Voalavo gymnocaudus*. Des observations régulières d'un grand *Nesomys* (probablement *N. rufus*) confirment la présence de cette forme diurne bien que ses effectifs étaient bas et qu'aucun individu n'a été capturé vivant. Le rongeur introduit *Rattus rattus* (Muridae: Murinae) a également été capturé mais contrairement aux inventaires de terrain menés dans d'autres sites forestiers du nord, il s'est ici avéré rare.

L'incidence variable du blanc sur le bout de la queue de la série des *E. majori* obtenue du Marojejy incita à la révision taxinomique du statut de l'espèce nominative *E. penicillatus*, uniquement connue de la localité du type dans le centre est de Madagascar, et qui montre invariablement une queue terminée de blanc. L'évaluation morphométrique, en utilisant des données craniodentales de *E. penicillatus* et de six échantillons d'*E. majori* dont les provenances couvrent la plupart de son aire connue de distribution, montrent que les deux taxons devraient être considérés comme deux espèces distinctes. Des analyses comparables effectuées sur neuf échantillons d'*E. webbi* provenant de localités couvrant son aire de distribution ne montrèrent que des différences mineures en rapport avec une variation géographique au sein d'une espèce à large distribution.

La diversité d'espèces indigènes la plus importante a été relevée à 1250 m d'altitude près de la limite inférieure de la forêt de montagne (six espèces), peu d'espèces étant rencontrées dans la forêt humide de basse altitude à 450 m (une) ou dans la forêt sclérophylle de montagne à 1875 m (trois). La coïncidence dans la sympatrie, les limites altitudinales, et les associations écologiques des espèces indigènes des massifs du Marojejy et d'Anjanaharibe-Sud voisin concordent nettement et réaffirment les grands thèmes de la distribution des Nesomyinae dans le biome de la forêt humide de l'est. Si certaines espèces de Nesomyinae sont rencontrées dans la forêt sclérophylle de montagne jusqu'à la lisière supérieure, aucune espèce n'a été capturée dans les zones sommitales éricoïdes, couvertes d'herbes et de buissons, des massifs du Marojejy et d'Anjanaharibe-Sud. L'apparente absence de rongeurs indigènes dans l'habitat propice des sommets de ces hautes montagnes du nord et la présence d'un genre (*Brachyuromys*) dans des milieux similaires du Haut Plateau Central sont discutées.

Introduction

Between 1950 and 1985, approximately 35% of Madagascar's eastern humid forest was cleared (Green & Sussman, 1990), a trend that continues at an alarmingly high rate. The eastern humid forest (sensu Humbert, 1965) formerly covered much of Madagascar's eastern versant, forming a nearly unbroken swath of lowland and montane tropical vegetation that stretched nearly 1,500 km in length and extended inland from the coast, up the eastern escarpment, and onto the central highlands, a vertical step of at least 1,000 m. The majority of primary forest in eastern Madagascar now occurs only as disjunct parcels, often situated within the boundaries of protected areas. Information on the biota of these isolates is therefore important to approximate the original fauna of the eastern humid forest biome and to understand distributional patterns within it.

This report focuses on the endemic rodents (Muridae: Nesomyinae) of the Parc National (PN) de Marojejy (14.5° south latitude) in the northern highlands, as revealed by a field investigation un-

dertaken between 4 October and 20 November 1996 by Goodman. This contribution forms another part of the renewed inventory of small mammals occurring along the forested slopes of several mountains in eastern Madagascar: PN de la Montagne d'Ambre, 12.5° south latitude (Goodman et al., 1996, 1997), Réserve Spéciale (RS) d'Anjanaharibe-Sud, 14°S (Carleton & Goodman, 1998; Goodman & Carleton, 1998), the Réserve Naturelle Intégrale (RNI) d'Andringitra,* 22°S (Goodman & Carleton, 1996; Goodman & Rasolonandrasana, in press), and the RNI d'Andohahela, 25°S (Goodman, Carleton, & Pidgeon, 1999). The same kinds of traps and sampling regimen were employed at each of these sites, and the surveys were, for the most part, conducted during the same season. Collectively, the five sites span the complete latitudinal breadth of the island's eastern forests. Special attention is devoted to comparison of the rodent faunas of the PN de

* Since the publication of these faunal reports the status of the Andringitra and Andohahela reserves has been changed to Parc National.

Marojejy and the RS d'Anjanaharibe-Sud, which represent the reserves with the most complete faunal documentation in the northern highlands.

Previous Work in the Region

The Marojejy Massif has been the subject of numerous zoological inventories, most of them entomological (Griveaud, 1960; Guillaumet et al., 1975), but little information based on preserved and critically identified vouchers is available on the rodents occurring in the park.

Between 1929 and 1931, the Mission Zoologique Franco-Anglo-Américaine (MZFAA) conducted an extensive inventory of the birds of Madagascar and incidentally collected mammal specimens. Their closest approach to the Marojejy Massif was a highland site, 1800 m, about "one day west of Andapa" (Rand, 1936), which Jenkins (1987) reckoned as 14°39'S, 49°22'E. Although a single elevation was officially recorded, the birds collected appear to represent a mixture of highland and lowland forms. To judge from elevational ranges of the avifauna from other well-documented mountains, however, it appears that the MZFAA collectors gathered specimens from a broad range of habitats and altitudes (Hawkins et al., 1998). The few small mammals obtained near the Andapa site are *Rattus [rattus]*, *Eliurus minor*, and *Nesomys rufus* (Rand, 1932; Carleton & Schmidt, 1990), and these species are generally known to have broad elevational ranges in the region (Goodman & Carleton, 1998), including highland areas. Thus, the elevational occurrence of mammals reported from the site suggests no distributional irregularities such as are suspected for the bird data. The possibility that MZFAA material may have been collected over a wide elevational range is pertinent to interpretation of altitudinal records based on specimens obtained by their expedition.

In November 1958, an entomological mission to the Marojejy Massif was organized by the Institut de Recherche Scientifique de Madagascar (IRSM), under the direction of R. Paulian and with field supervision by P. Griveaud. The general results of the mission presented a list of small mammals observed but did not mention any rodent species (Griveaud, 1960).

In 1988, a student research group from Cambridge University, working with Malagasy counterparts, conducted small mammal trapping with

Sherman traps in several areas on the Marojejy Massif (Duckworth & Rakotondraparany, 1990). In the southeastern portion of the PN de Marojejy (then still classified as an RNI), the same area where Goodman worked in 1996, the team captured two *Eliurus cf. myoxinus* at 300 m (170 trap-nights) and six more individuals at 1300 m (165 trap-nights). Unfortunately, no voucher specimens were preserved, and the species taxonomy of the genus has changed dramatically in the past few years (Carleton, 1994). No specific determinations can be reliably made on the basis of the external measurements provided (Duckworth & Rakotondraparany, 1990, p. 128). This group also reported sight observations for *Brachytarsomys albicauda* in the southeastern portion of the reserve (700 m) and for *Nesomys* in both the southwestern (800 m) and northwestern sectors (between 1000 and 1400 m). In their summary of mammals known from the reserve, Nicoll and Langrand (1989) listed the rodent species as reported by the Cambridge University expedition.

In 1994, a multidisciplinary biological inventory was conducted in the RS d'Anjanaharibe-Sud, just to the west of the Marojejy Massif and Andapa Basin. The rodent fauna was documented in a monograph that included the description of a new genus and species, *Voalavo gymnocaudus*, as well as a new species of *Eliurus*, *E. grandidieri* (Carleton & Goodman, 1998), and a general review of the reserve's nine species of native rodents (Goodman & Carleton, 1998). Since the field techniques used during the 1996 inventory of the PN de Marojejy were identical to those employed in the nearby RS d'Anjanaharibe-Sud, we make regular comparisons between these two reserves throughout the chapter.

Materials and Methods

This study is based on fieldwork conducted between 4 October and 20 November 1996 by Goodman. Carleton verified taxonomic determinations and undertook systematic comparisons.

Field Methods and Trapping Protocol

The general field protocols followed those previously outlined in parallel reports on the rodents of the RNI d'Andringitra (Goodman & Carleton, 1996), the RS d'Anjanaharibe-Sud (Goodman &

Carleton, 1998), and the RNI d'Andohahela (Goodman, Carleton, & Pidgeon, 1999). In the PN de Marojejy, five altitudinal zones were sampled (450, 775, 1250, 1625, and 1875 m), representing the gamut of principal vegetational formations known in the region, from lowland forest through sclerophyllous forest to open savanna above tree line (see Chapters 1 and 3). The area surveyed at 450 m clearly showed signs of recent human disturbance, those at 775 and 1250 m much less so, while the two uppermost sites seemed pristine.

At each of the five elevations, trap lines were maintained for a minimum of six nights (Table 12-1). Each trap line, numbered sequentially starting with the 450 m zone, consisted of Sherman live traps ($9 \times 3.5 \times 3$ inch) and National live traps ($16 \times 5 \times 5$ in.) in a ratio of 4:1. Traps were baited daily, generally between 1500 and 1700 hours, with finely ground peanut butter. They were inspected at least twice per day, once at dawn and again in late afternoon. At each site, sampling was also conducted with pitfall traps, but this technique yielded few rodents (see Chapter 11), and these incidental captures were not included in calculations of trapping success and biomass.

A trap-night is defined as one live trap in use for a 24-hour period (dawn to dawn). The total number of trap-nights accrued in each elevation varied slightly; consequently, the first 500 trap-nights in an elevational zone are considered the "standardized" trapping regimen in order to facilitate comparisons among the sites sampled. Standing biomass of a species is based on the total catch of individuals during a standardized trapping regimen multiplied by average body weight of the species (see Table 12-5). We depended exclusively on live trap techniques during this inventory for reasons explained previously by Goodman and Carleton (1998, p. 201).

To quantify differences in spatial distribution of small mammal captures, several trapping variables were systematically recorded for each trap installed: (1) type of trap, (2) total length of trap line, (3) distance between traps, and (4) specific placement of trap, including its substrate, surrounding forest structure, and position on or height above the ground. A system for the categorization of microhabitat used during this survey is identical to that presented by Goodman and Carleton (1998), as follows:

ON GROUND—(1) in leaf litter, generally in area of open understory; (2) under decomposed downed trees or woody vegetation; (3) by tree

root or trunk, with or without cavity or hole; (4) miscellaneous, including placement under exposed rocks or boulders, at base of rock face, at entrance of hole in ground, in thick herbaceous vegetation or dense shrubbery, or on moss-covered rocks.

ABOVE GROUND—(1') on liana, limb, or trunk ≤ 10 cm diameter in horizontal to vertical position; (2') on liana, limb or trunk > 10 cm diameter in horizontal to vertical position; (3') on limbs or trunks suspended by lianas; (4') miscellaneous, including placement on bamboo stalks, in small cavities at junctions of tree limbs, or on large moss-covered rocks.

Specimens and Measurements

Captured animals were prepared either as standard museum skins with associated skulls and partial skeletons, or as fluid-preserved carcasses (some with skulls removed), or as full skeletons. Specimens prepared as whole carcasses were wrapped in fine cheesecloth before immersion in formalin to prevent loss or mixing of ectoparasites between their specific hosts (see Chapter 7). Nearly all rodents captured during our work in the PN de Marojejy were prepared as vouchers. This material is housed in the Field Museum of Natural History (FMNH) and Département de Biologie Animale, Université d'Antananarivo (UADBA). Specimens deposited immediately after the survey in the latter institution have not yet been catalogued and are individually referenced by the collector's field numbers (UA-SMG). To confirm taxonomic identifications, nesomyine holdings in other museums (see Appendix in Goodman & Carleton, 1996) were also consulted.

Six measurements, in millimeters (mm) or grams (g), were taken by Goodman for each specimen in the flesh. Measurement abbreviations and definitions are given below.

- TOTL (total length of body and tail): from the tip of the nose to the end of the last caudal vertebra (not including terminal hair tuft)
- HBL (head and body length): from the tip of the nose to the distalmost point of the body (at base of tail)
- TL (tail length): from the base of the tail (held at right angle to the body) to the end of the last caudal vertebra (not including terminal hair tuft)

TABLE 12-1. Summary of five trap lines (each with 100 live traps) in the PN de Marojejy.*

Elevation	Length (m) of line	Mean distance (m) between traps	No. of traps aboveground	Mean height (m) aboveground
450 m (5-12 Oct) Line 1	795	7.9 ± 4.96 (1-21)	31	1.3 ± 0.58 (0.2-2.5)
775 m (15-23 Oct) Line 2	575	5.8 ± 3.20 (2-16)	29	1.6 ± 0.28 (0.2-2.5)
1250 m (26 Oct-1 Nov) Line 3	575	5.9 ± 4.26 (1-26)	33	1.7 ± 0.71 (0.5-3)
1625 m (6-12 Nov) Line 4	385	3.9 ± 2.34 (1-9)	28	1.7 ± 0.65 (0.2-3)
1875 m (13-19 Nov) Line 5	540	5.6 ± 3.50 (1-20)	8	1.3 ± 0.62 (0.2-2)

* Each line consisted of National and Sherman live traps in a ratio of 4:1 (see p. 234). Descriptive statistics are presented as mean ± SD (and range).

HFL (hind foot length): from the heel to the tip of the longest toe (not including claw)
 EL (ear length): from the basal notch to the distal tip of the pinna
 WT (weight): measured with Pesola spring scales, to ±0.5 g for animals <100 g and to ±1.0 g for those between 101 and 300 g.

Sixteen cranial and two dental dimensions were measured by Carleton to the nearest 0.1 mm using handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations, follow the anatomical landmarks defined and illustrated in Carleton (1994).

BBC, breadth of the braincase
 BIF, breadth of incisive foramina
 BM1s, breadth of the bony palate across the first upper molars
 BOC, breadth across the occipital condyles
 BR, breadth of rostrum
 BZP, breadth of the zygomatic plate
 DAB, depth of the auditory bulla
 IOB, interorbital breadth
 LBP, length of bony palate
 LD, length of diastema
 LIF, length of the incisive foramina
 LM1-3, coronal length of maxillary toothrow
 LR, length of rostrum
 ONL, occipitonasal length
 PPB, posterior breadth of the bony palate
 PPL, postpalatal length
 WM1, width of the first upper molar
 ZB, zygomatic breadth

Standard descriptive statistics (mean, range,

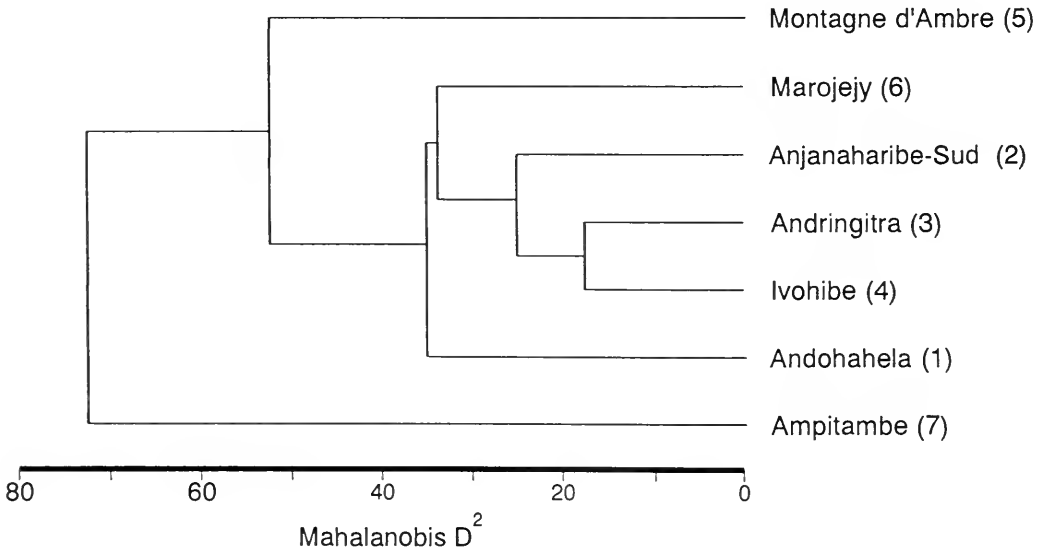
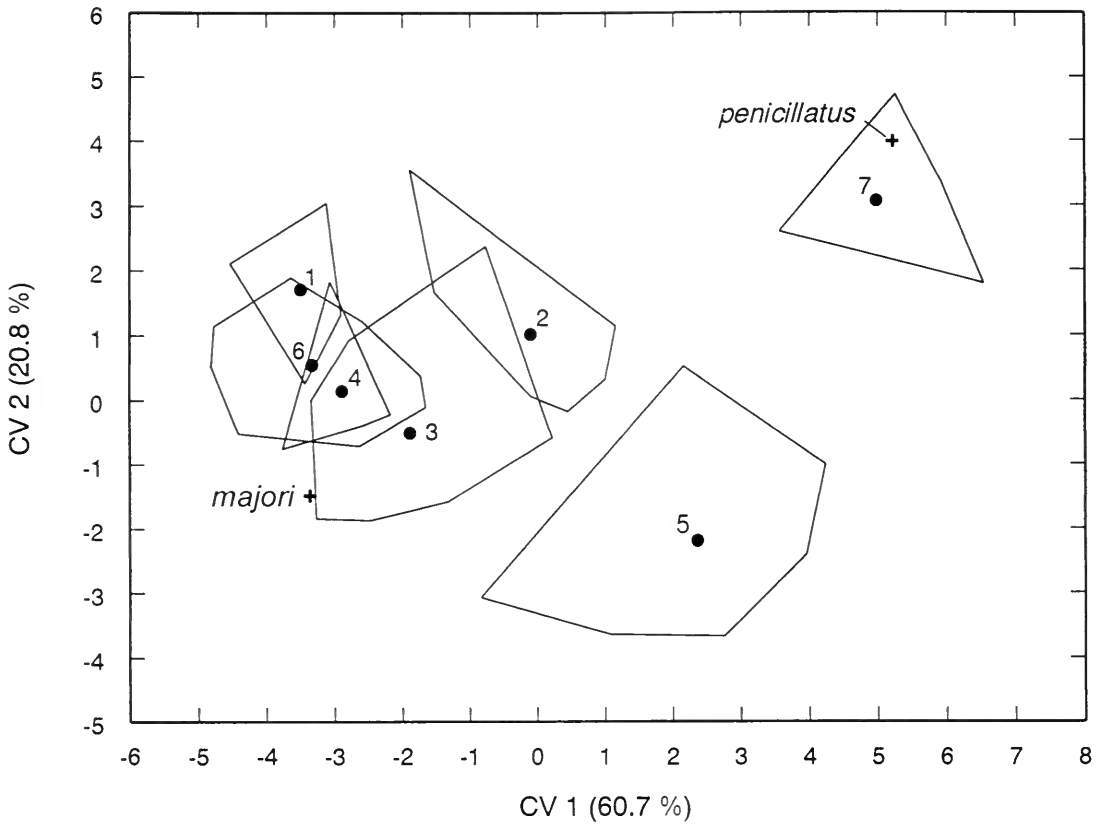
and standard deviation) were derived for adult specimens in each species sample. We define "adult" as the age cohort consisting of animals that lack the finer juvenile pelage and that possess fully erupted, though sometimes little worn, third molars. The mammae formula is presented as the number of paired postaxial, abdominal, or inguinal teats (sensu Voss & Carleton, 1993).

Where sample sizes permitted, two-sample *t*-tests and one-way analyses of variance were applied to the mensural variables with sex as the categorical variable. Principal components (PCs) and canonical variates (CVs) were extracted from the variance-covariance matrix and computed using natural logarithmic transformations of the 18 craniodental variables. Loadings are expressed as Pearson product-moment correlation coefficients between the PCs or CVs and the original skeletal and dental variables. Mahalanobis distances between group centroids were clustered based on the unweighted pair-group method using arithmetic averages (UPGMA). All univariate and multivariate computations were generated using Systat (version 8.0, 1998), a series of statistical routines programmed for microcomputers.

Taxonomic Comments

Variation Within *Eliurus majori* and the Status of *E. penicillatus*

Within the Marojejy series that we report here as *Eliurus majori* are several specimens that pos-



sess a white-tipped tail. Where specifically noted in Goodman's field catalogue or verifiable in preserved specimens, the terminal section in almost half of the series (9 of 20) is invested with white hairs, the white portion ranging from 9 to 54 mm long and averaging 29 mm. The remainder of the Marojejy series, and all *E. majori* from nearby RS d'Anjanaharibe-Sud, have a tail that is uniformly dark to the tip, conforming to the diagnosis of *E. majori* (Thomas, 1895). In other aspects of their cranium, dentition, pelage, and size, these nine individuals resemble typical *E. majori* as now known by populations reported elsewhere in the eastern forest (Goodman & Carleton, 1996, 1998; Goodman et al., 1997; Goodman, Carleton, & Pidgeon, 1999).

Possession of a white caudal tip is central to the diagnosis of the species *E. penicillatus*, a form that otherwise recalls a somewhat smallish version of *E. majori* (Thomas, 1908; Carleton, 1994). Of the eight species of *Eliurus* he recognized, Carleton (1994) regarded the specific separation of *E. penicillatus* Thomas (1908) from *E. majori* Thomas (1895) as the most weakly defended, but retained them as distinct based on the constancy of the contrast in tail color and the inadequacy of sample sizes to convincingly address the problem (5 specimens of *E. majori* and 17 of *E. penicillatus*). The variable presence of white tail tips in the Marojejy series of *E. majori* invites reevaluation of the status of *E. penicillatus*, a form so far recorded only from its type locality, Ampitambe, in east-central Madagascar.

The vastly improved population samples of *E. majori*, now well represented from Montagne d'Ambre in the north (Goodman et al., 1997) to Andohahela in the south (Goodman, Carleton, & Pidgeon, 1999), enhance the geographic scope of our reappraisal. For multivariate comparisons, we measured 95 specimens with intact skulls that represent six general population samples (operational taxonomic units, OTUs) of *E. majori* and one of *E. penicillatus*, as follows (specific locality data and museum numbers listed in Appendix 12-1): (1) RNI d'Andohahela (N = 4); (2) RS d'Anjanaharibe-Sud (N = 10); (3) RNI

d'Andringitra (N = 17); (4) RS d'Ivohibe (N = 4); (5) PN de la Montagne d'Ambre (N = 25); (6) PN de Marojejy (N = 17); (7) Ampitambe (N = 16; type locality of *E. penicillatus*). The type specimens of *E. majori* (BMNH 97.9.1.147, Ambohimombo) and *E. penicillatus* (BMNH 97.9.1.149, Ampitambe) were entered as unknowns for a posteriori classification by the multipliers generated from seven-group discriminant function analysis.

Three nonoverlapping clusters are evident in projections of specimen scores onto the first two CVs derived (cumulative variance explained = 81.5%). The largest includes those samples of *E. majori* from throughout the northern, central, and southern highlands (OTUs 1-4, 6; Fig. 12-1). Marginal to these is the series from the isolated peak in the north, Montagne d'Ambre (OTU 5). The series from Ampitambe (OTU 7), the type locality of *E. penicillatus*, exhibits the strongest differentiation among the geographic samples, which on average are separated from the other centroids by a generalized distance of 73.5 (Fig. 12-1). Except for the extreme separation of the Ampitambe series, Mahalanobis distances between centroids loosely approximate geographic distances between localities—namely, the pair-group association between Andringitra and Ivohibe on the Central High Plateau, and the linkage of samples from the northern highlands (Anjanaharibe-Sud and Marojejy), southern highlands (Andohahela), and Montagne d'Ambre at successively greater values. The central geographic location of Ampitambe, if correctly interpreted by Carleton and Schmidt (1990), and the peripheral phenetic divergence of *E. penicillatus* depart from this pattern. Ampitambe, an important Forsyth Major collecting site and the source of numerous holotypes of Malagasy mammals, is believed to be situated along the east-central flank (ca. 900 m) of the Central High Plateau, nearest Andringitra and Ivohibe in the southern Central High Plateau among the samples considered here.

Size, as a general factor, is negatively associated with the first CV, most of the variable correlations being moderately large (about $-.60$ to

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FIG. 12-1. Results of discriminant function analysis performed on 18 log-transformed craniodental variables, as measured on 95 specimens representing seven OTUs of the *Eliurus majori* complex. **Top**, Projection of individual scores onto the first two canonical variates extracted; polygons enclose the maximal dispersion of specimen scores around a group centroid, and crosses signify the type specimens of *E. majori* and *E. penicillatus*. **Bottom**, Phenogram produced from clustering (UPGMA) of Mahalanobis' distances among centroids of the seven OTUs. See Table 12-2.

TABLE 12-2. Discriminant function results and one-way ANOVAs derived from analysis of 18 log-transformed craniodental dimensions as measured on 95 adult specimens representing seven samples of the *Eliurus majori* complex.

Variable	Correlations		F (OTU)
	CV 1	CV 2	
ONL	-0.67	0.12	10.8**
ZB	-0.75	0.01	12.6**
BBC	-0.70	-0.13	18.3**
IOB	-0.32	0.39	4.2**
LR	-0.62	0.09	8.7**
BR	-0.53	0.09	7.5**
PPL	-0.59	0.16	7.5**
LBP	-0.64	-0.18	10.3**
LIF	-0.70	0.11	14.0**
BIF	-0.24	0.61	11.5**
LD	-0.61	-0.17	8.5**
BM1s	-0.77	0.06	15.3**
PPB	-0.82	0.04	18.7**
DAB	-0.35	0.62	10.6**
BZP	-0.75	-0.23	17.2**
BOC	-0.41	-0.24	4.0*
LM1-3	-0.86	0.21	35.6**
WM1	-0.80	0.15	16.6**
Canonical correlation	0.95	0.87	
Eigenvalue	9.34	3.21	
% Variance	60.7	20.8	

* $P \leq 0.01$; ** $P \leq 0.001$.

Abbreviations are explained in the Materials and Methods section. See also Figure 12-1.

-.80) and nearly all loading highly significantly on this factor (Table 12-2). Dispersion of OTUs along CV1 sensibly mirrors one's visual impression of size differences when reviewing samples, from the smaller animals of Ampitambe (OTU 7) and Montagne d'Ambre (OTU 5) to the larger specimens representing *E. majori* sensu stricto (OTUs 1-4, 6). Although nearly as diminutive as the Ampitambe series in many craniodental measurements, notably size of molars and occipitonasal length (Table 12-3), the sample from Montagne d'Ambre conforms more closely to the *E. majori* cluster in certain features of shape. Size of bullae and breadth of the incisive foramina, which correlate moderately strongly and positively with CV2, largely account for this association and the greater isolation of the topotypic sample of *E. penicillatus* (Table 12-2, Fig. 12-1). The first two PCs extracted from ordination of only the 41 specimens representing the Montagne d'Ambre and Ampitambe OTUs (not illustrated) disclose no overlap of the two series and emphasize the same shape contrasts on PCII (% variance ex-

plained = 43.5% and 23.7% on PCI and PCII, respectively), in addition to others whose significance is masked in the full data set (the shorter bony palate and narrower zygomatic plate of *E. penicillatus*—see Table 12-3).

The pattern of divergence in canonical space logically corresponds to jackknifed classification iterations, which commonly produced specimen misassociations among the large cluster of five OTUs (% correct = 25-76), uncommonly for that from Montagne d'Ambre (% correct = 92), and never for that from Ampitambe (% correct = 100). The holotype of *E. penicillatus* was assigned ($P = 1.00$) to OTU 7 from Ampitambe, its topotypic complement; that of *E. majori* was classified ($P = 0.82$) with OTU 3 from Andringitra, the locality geographically nearest to Ambohimombo, its type locality.

In summary, we regard these multivariate patterns of craniodental differentiation as insufficient to justify the synonymy of *E. penicillatus* Thomas (1908) under *E. majori* Thomas (1895). Other information sources must be brought to bear on the issue, as well as the collection of new material from or near Ampitambe, the type locality of Major's *penicillatus*. The substantial divergence revealed for the sample from Montagne d'Ambre also merits further evaluation, but in craniodental proportions, the affinity of this isolated population lies with *E. majori* proper. Relationships inferred from cytochrome *b* data actually affiliate the Montagne d'Ambre sample more closely with other *E. majori* from the northern highlands (Anjanaharibe-Sud) than with those from central and southern Madagascar (Jansa, 1998).

Variation Within *Eliurus webbi* Apropos the *E. majori* Complex

Evaluation of craniodental variation among populations of *Eliurus webbi* is instructive in light of the patterns revealed for the *E. majori* complex (that is, including *E. penicillatus*). The distributions of both forms span the full extent of eastern humid forest, as reported from the PN de la Montagne d'Ambre in the far north to parcel 1 of the RNI d'Andohahela in the far south (Goodman & Carleton, 1996, 1998; Goodman et al., 1996; Goodman, Carleton, & Pidgeon, 1999). Although geographic boundaries are broadly congruent, their elevational ranges are superpositioned, suggesting contiguous allopatry within the eastern humid forest biome. *Eliurus webbi* occurs in low-

TABLE 12-3. Comparison of craniodental measurements of adult *Eliurus majori* and *E. penicillatus* from localities in eastern Madagascar.

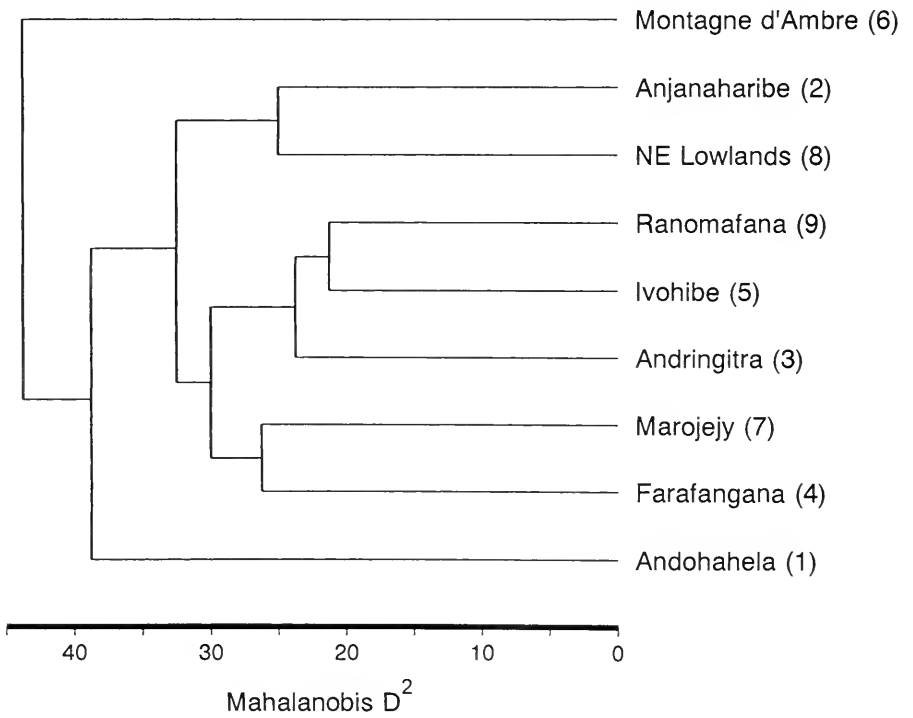
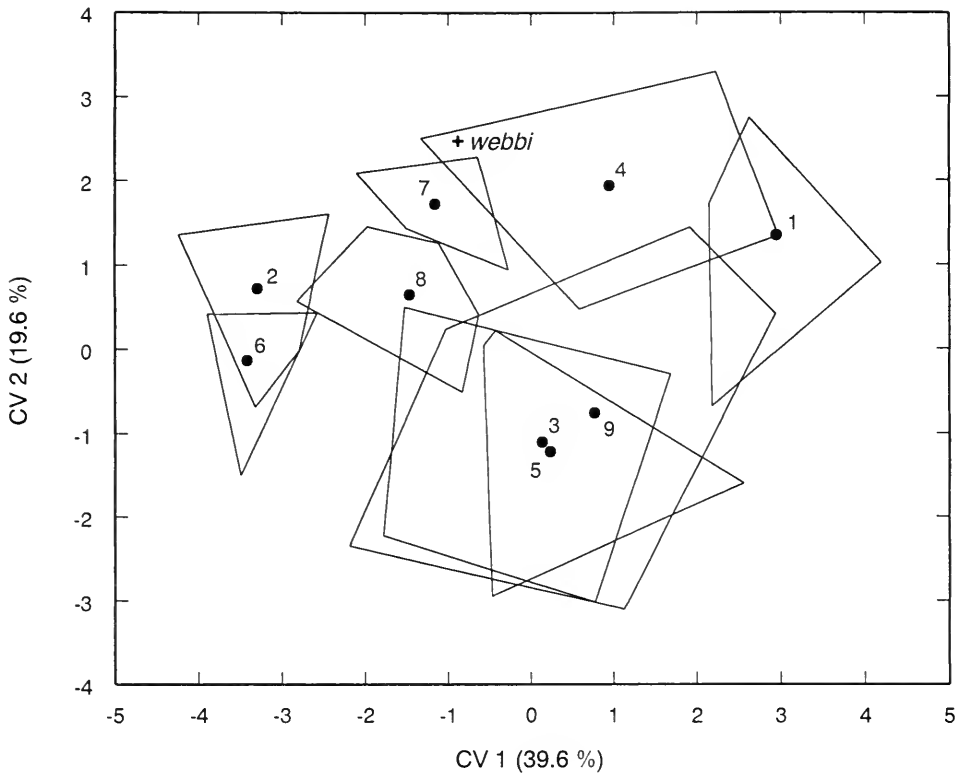
Variable	<i>E. majori</i>			<i>E. penicillatus</i>
	Mt. d'Ambre (n = 27)	Marojejy (n = 17)	Andringitra (n = 17)	Ampitambe (n = 16)
ONL	36.5 ± 1.2 33.5–38.1	39.1 ± 1.6 35.9–41.3	37.6 ± 1.0 35.5–39.4	36.1 ± 1.3 32.9–37.4
ZB	18.5 ± 0.7 16.9–19.5	19.9 ± 0.7 18.9–20.8	19.1 ± 0.5 18.1–19.8	17.9 ± 0.9 15.9–19.2
BBC	14.1 ± 0.4 13.2–14.8	15.1 ± 0.5 14.4–15.9	14.3 ± 0.4 13.4–14.8	13.6 ± 0.4 12.7–14.1
IOB	5.2 ± 0.2 4.8–5.6	5.5 ± 0.3 5.1–6.1	5.3 ± 0.2 4.9–5.7	5.3 ± 0.1 5.1–5.6
LR	12.6 ± 0.6 11.3–13.5	13.5 ± 0.6 12.2–14.3	13.1 ± 0.5 11.6–14.0	12.4 ± 0.6 10.8–13.2
BR	7.0 ± 0.3 6.3–7.6	7.5 ± 0.4 6.6–8.1	7.1 ± 0.2 6.8–7.6	6.9 ± 0.4 6.1–7.4
PPL	12.9 ± 0.6 11.4–13.8	13.8 ± 0.5 12.8–14.3	13.4 ± 0.5 12.4–14.6	12.9 ± 0.6 11.5–13.8
LBP	7.4 ± 0.4 6.6–8.5	7.9 ± 0.6 6.7–8.7	7.5 ± 0.4 6.9–8.6	6.8 ± 0.3 6.3–7.4
LIF	5.5 ± 0.4 4.7–6.3	6.1 ± 0.4 5.5–7.0	6.3 ± 0.3 5.6–6.7	5.5 ± 0.3 5.0–5.9
BIF	2.3 ± 0.2 2.0–2.6	2.6 ± 0.1 2.3–2.8	2.7 ± 0.2 2.4–3.1	2.7 ± 0.2 2.4–2.9
LD	10.5 ± 0.5 9.2–11.3	11.0 ± 0.6 9.9–12.2	10.8 ± 0.4 10.0–11.8	9.8 ± 0.6 8.5–10.7
BM1S	7.5 ± 0.3 7.1–8.3	8.2 ± 0.3 7.6–8.5	8.1 ± 0.3 7.1–8.6	7.3 ± 0.3 6.8–7.9
DAB	5.0 ± 0.2 4.7–5.4	5.5 ± 0.2 5.3–5.9	5.2 ± 0.1 5.1–5.5	5.4 ± 0.2 5.0–5.6
BZP	3.3 ± 0.2 2.9–3.6	3.8 ± 0.3 3.3–4.2	3.5 ± 0.2 2.9–3.9	2.9 ± 0.3 2.5–3.4
BOC	8.3 ± 0.3 7.7–8.7	8.4 ± 0.3 8.0–8.9	8.5 ± 0.3 8.0–9.0	8.0 ± 0.3 7.4–8.4
LM1-3	6.07 ± 0.21 5.69–6.43	6.69 ± 0.23 6.21–7.10	6.65 ± 0.24 6.13–7.15	6.03 ± 0.15 5.74–6.27
WM1	1.61 ± 0.09 1.43–1.79	1.78 ± 0.07 1.65–1.91	1.76 ± 0.07 1.66–1.88	1.58 ± 0.05 1.49–1.68

Abbreviations are explained in the Materials and Methods section. Sample parameters are given as mean ± standard deviation, and range.

land rain forest, usually below 875 m, whereas *E. majori* inhabits montane and sclerophyllous montane forest, usually above 1200 m (see Discussion, below). To date, the two species have been documented syntopically only on Montagne d'Ambre at 1000 m (Goodman et al., 1997).

As in the case of *E. majori*, availability of material has much improved the study of *E. webbi*. Ninety specimens representing nine general localities were measured for morphometric compar-

isons (see Appendix 12-1): (1) RNI d'Andohahela (N = 7); (2) RS d'Anjanaharibe-Sud (N = 6); (3) RNI d'Andringitra (N = 19); (4) 20 mi S Farafangana (N = 12; type locality of *E. webbi*); (5) RS d'Ivohibe (N = 7); (6) PN de la Montagne d'Ambre (N = 6); (7) PN de Marojejy (N = 5); (8) NE lowlands in the vicinity of Antongil Bay (N = 8); and (9) PN de Ranomafana (N = 20). As before, the type specimen of *E. webbi* (BMNH 47.1576) was entered as an unknown for a pos-



teriori classification by the multipliers generated from nine-group discriminant function analysis.

No clearly discrete, nonoverlapping clusters of OTUs were evident in projections of specimen scores onto the first two CVs derived (compare Fig. 12-2 with 12-1, and Table 12-4 with 12-2). The cumulative variance explained is smaller than in the example of *E. majori* (59.2% vs 81.5%), as are other multivariate statistics (canonical correlations, eigenvalues) that convey the success of distilling covariation among the original variables into fewer dimensions. Except for the unexpected pair-group association of Farafangana (southeastern) and Marojejy (northeastern), UPGMA clusters coarsely reflect geographic regions and relative isolation—namely, the union of Ranomafana, Ivohibe, and Andringitra along the Central High Plateau, the junction of Anjanaharibe-Sud and the lowlands OTU in the northeast, and the incrementally greater distances linking Andohahela from the southern Anosyenne Mountains and the sample on Montagne d'Ambre. On average, however, an OTU recovered only one-third of its preassigned specimens in post hoc jackknifed classifications by the discriminant coefficients generated (% correct = 0–57). Although the holotype of *E. webbi* falls within the maximal spread of Farafangana scores (OTU 4), the shorter distance between it and the centroid of OTU 7 (Marojejy) instead resulted in its classification with that sample, at a low probability level ($P = 0.45$).

We view these multivariate patterns of craniodental variation as indicative of a single, widely distributed species, *E. webbi* Ellerman (1949). These numerical results recall the amount of differentiation that Carleton and Goodman (1998) encountered among geographic samples of *E. tanala*, a form that occurs over nearly the same geographic extent as *E. webbi* but more broadly overlaps the latter's altitudinal range (sympatric from 450 to 875 m, as so far known). Although Carleton and Goodman construed the intraspecific variation of *E. tanala* as a weak north–south size cline, the variable correlation coefficients and sample statistics derived for *E. webbi* obscure any simple clinal explanation. As for *E. majori* proper,

TABLE 12-4. Discriminant function results and one-way ANOVAs derived from analysis of 18 log-transformed craniodental dimensions as measured in 90 adult specimens representing nine samples of *Eliurus webbi*.

Variable	Correlations		F (OTU)
	CV 1	CV 2	
ONL	0.25	0.31	3.3**
ZB	0.23	0.17	2.8**
BBC	0.43	0.35	4.8***
IOB	0.33	0.04	2.3*
LR	0.16	0.10	1.7
BR	0.16	0.22	2.1*
PPL	0.14	0.45	3.5**
LBP	0.29	0.07	3.7**
LIF	-0.18	0.47	2.6*
BIF	0.61	-0.09	7.9***
LD	0.18	0.21	1.8
BM1s	0.18	0.14	1.5
PPB	0.14	0.24	2.4*
DAB	0.47	0.41	7.4***
BZP	0.55	0.37	7.8***
BOC	0.14	0.08	1.9
LM1-3	0.21	-0.03	2.6*
WM1	-0.20	0.30	2.8**
Canonical correlation	0.87	0.78	
Eigenvalue	3.07	1.52	
% Variance	39.6	19.6	

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Abbreviations are explained in the Materials and Methods section. See also Figure 12-2.

the sample of *E. webbi* from Montagne d'Ambre exhibits the strongest craniodental differentiation, although of lesser magnitude (Fig. 12-2). In addition to smaller size, ventral pelage color of the Montagne d'Ambre series is exceptional for the expansive patches of creamy-white hairs, in contrast to the uniformly dingy gray underparts typical of *E. webbi* (Carleton, 1994).

Compared to the results obtained for the lowland species *E. webbi*, the greater structure apparent in the data matrix of the *E. majori* complex plausibly follows from the increased likelihood of populational fragmentation of a montane-dwelling organism and subsequent differentiation among the geographic isolates. Palynological data and distri-

FIG. 12-2. Results of discriminant function analysis performed on 18 log-transformed craniodental variables, as measured on 90 specimens representing nine OTUs of *Eliurus webbi*. **Top**, Projection of individual scores onto the first two canonical variates extracted; polygons enclose the maximal dispersion of specimen scores around a group centroid, and the cross signifies the type specimen of *E. webbi*. **Bottom**, Phenogram produced from clustering (UPGMA) of Mahalanobis' distances among centroids of the nine OTUs. See Table 12-4 and compare with Figure 12-1.

TABLE 12-5. External measurements and sample statistics for adult rodents collected in the PN de Marojejy.

Species	TOTL	HBL	TL	HFL	EL	WT
<i>Rattus rattus</i>	392, 430	160, 180	224, 224	33, 33	25, 27	83.5, 145
<i>Eliurus grandidieri</i>	291.3 10.0 275–309 (n = 42)	124.8 6.6 111–164 (n = 59)	161.5 8.7 144–176 (n = 42)	28.3 1.0 26–31 (n = 59)	20.1 0.9 19–23 (n = 60)	50.6 4.0 42.0–62.0 (n = 59)
<i>Eliurus majori</i>	363.9 21.7 321–394 (n = 20)	161.9 8.2 146–175 (n = 23)	189.5 15.1 164–213 (n = 20)	29.7 0.9 28–31 (n = 23)	18.6 1.0 17–20 (n = 23)	111.8 16.1 89.0–151 (n = 22)
<i>Eliurus minor</i>	239, 245	107, 113	126, 129	21, 23	16, 18	37.5, 50.5
<i>Eliurus tanala</i>	359	158, 162	140	30, 34	22, 24	102, 105
<i>Eliurus webbi</i>	324.8 14.3 303–344 (n = 6)	142.5 5.5 135–152 (n = 11)	176.5 8.8 161–186 (n = 6)	29.5 1.5 27–31 (n = 10)	22.4 1.1 21–24 (n = 10)	74.5 9.7 60.5–90.5 (n = 11)
<i>Gymnuromys roberti</i>	395	175	206	38	23	162
<i>Voalavo gymnocaudus</i>	211.2 8.3 200–219 (n = 5)	84.6 4.2 80–90 (n = 5)	120.6 5.3 113–126 (n = 5)	18.8 1.1 17–20 (n = 5)	15.0 0.0 15–15 (n = 5)	22.2 3.3 17.0–25.5 (n = 5)

Abbreviations are explained in the Materials and Methods section. Sample parameters are given as mean \pm standard deviation, range, and number.

butional information gathered on other Malagasy vertebrates certainly establish the profound vertical changes experienced by montane communities throughout the Late Pleistocene and into the Holocene (Burney, 1987, 1997; Gasse et al., 1994; Raxworthy & Nussbaum, 1996). The challenge is to interpret this data structure in light of current taxonomy and defensible criteria for species recognition, which in the case at hand persuades us to continue to regard *E. penicillatus* as distinct from *E. majori*.

Accounts of Species

General observations, information on the natural history, and the elevational range of each rodent species captured during the inventory of the PN de Marojejy are presented under the subheadings DISTRIBUTION, ECOLOGY AND REPRODUCTION, COMMENTS (if appropriate), and SPECIMENS EXAMINED. The exact position and coordinates of the sites presented under this last subheading can be found in Chapter 1. More detailed criteria for species identification and discussion of alpha-level taxonomic problems are presented in Carleton

(1994), Carleton and Goodman (1996, 1998), Goodman and Carleton (1996, 1998), and Goodman, Carleton, & Pidgeon (1999). External measurements and masses are given herein for the rodent species captured during the 1996 survey to aid researchers in identifying the rodents of northern Madagascar and to provide baseline data used in some analyses presented in the Discussion (Table 12-5).

Family Muridae: Subfamily Murinae

Rattus rattus (Linnaeus, 1758)

DISTRIBUTION—This introduced rodent has a broad distribution on the island. It is found as a commensal near human habitations and agricultural areas, in disturbed forest habitats, and in primary forest. A few *Rattus rattus* were trapped at 1250 and 1625 m, totaling only 4 (4.8%) of the 83 rodents captured at those middle elevations (Table 12-6) and suggesting that the species is uncommon within the PN de Marojejy.

ECOLOGY AND REPRODUCTION—On the basis of a limited number of captures of this species in the

TABLE 12-6. Number of individuals captured in live traps for each species of small mammal at all five elevations surveyed in the PN de Marojejy.

Species or parameter measured	450 m (690)	775 m (800)	1250 m (700)	1625 m (600)	1875 m (600)
Tenrecinae					
<i>Microgale cowani</i>			2		
<i>Microgale gracilis</i>					1
<i>Microgale talazaci</i>	1	4		1	
<i>Oryzorictes hova*</i>				1	
Murinae					
<i>Rattus rattus</i>			3	1	
Nesomyinae					
<i>Eliurus grandidieri</i>			44	11	8
<i>Eliurus majori</i>			2	19	1
<i>Eliurus minor</i>		2	1		
<i>Eliurus tanala</i>		2			
<i>Eliurus webbi</i>	9	4			
<i>Gymnuromys roberti</i>			1		
<i>Voalavo gymnocaudus</i>				1	
Total no. of individuals	10	12	53	34	10
Trap success, %	1.4	1.5	7.6	5.7	1.6
Total no. of rodents trapped	9	8	51	32	9
Total no. of rodent species	1	3	5	4	2
Rodent trap success, %	1.3	1.0	7.3	5.3	1.5
Total no. of nesomyines trapped	9	8	48	31	9
Total no. of nesomyine species	1	3	3	2	2
Nesomyine trap success, %	1.3	1.0	6.9	5.2	1.5

* We follow Goodman, Jenkins, and Pidgeon (1999) in considering *O. talpoides* a synonym of *O. hova*. Total number of trap-days accrued is given in parentheses. Pitfall results are excluded.

1250 to 1625 m zones of the PN de Marojejy, trap sets that yielded this animal were equally divided between ground and arboreal trap placements (Table 12-7). One of the successful sets off the ground was on a large, horizontal, moist, and presumably slippery branch of a tree that was covered with a dense epiphytic growth.

Both male *Rattus rattus* obtained in the reserve had scrotal testes. Of the females obtained, one had large mammae and a perforated vagina and the second was a subadult with small mammae and an imperforate vagina. The mammae formula of the adult female was 1-1-2.

COMMENTS—Remarkably few *Rattus rattus* were captured on the Marojejy Massif as compared to the Anjanaharibe-Sud Massif. In the 1250 m zone of the former locality, three individuals were trapped in 700 trap-nights, and in the 1625 m zone one individual was trapped in 600 trap-nights. In the RS d'Anjanaharibe-Sud, this species was found across the complete transect, from 875 to 1950 m, and was most common in the 1550 m zone, where 13 individuals were cap-

tured in 500 trap-nights (Goodman & Carleton, 1998). On the basis of short-term field studies at these two sites (which are only a few tens of kilometers distant) conducted two years apart during the same season, no clear explanation can be offered for the differences in elevational distribution and relative densities of this species.

In spite of the now substantial elevational data for *Rattus rattus* on various forested mountains in eastern Madagascar, a general pattern that explains the species' distribution cannot be gleaned. The highest density recorded to date is in the forest of the PN de la Montagne d'Ambre, in the extreme north, where 103 *R. rattus* were captured at 1350 m in 750 trap-nights (Goodman et al., 1996). In a broad swath of other elevational zones, such as Marojejy and Andohahela (Goodman, Carleton, & Pidgeon, 1999), few individuals of this species were captured in a nearly comparable number of trap-nights. Regression analyses were conducted to assess geographic location and variation in *Rattus* population density found at PN de la Montagne d'Ambre (12.5°S, Goodman et al.,

TABLE 12-7. Microhabitat occurrences of rodent species by elevation in the PN de Marojej.

Elevation and species	No. taken	Trap position			Ground location*					Aboveground location				
		On ground	Above-ground	Leaf litter	Under rotten wood	By roots, trunks	Misc.	Vine, limb, or trunk <10 cm	Limbs, trunks >10 cm	Suspended trunks	Misc.			
450 m														
Trap distribution		69	31	5	13	29	22	21	4	1	5			
<i>Eliurus webbi</i>	9	5	4			1	4	4						
775 m														
Trap distribution		71	29	11	13	33	14	15	11	2	1			
<i>Eliurus minor</i>	2	0	2					2						
<i>Eliurus tanala</i>	2	0	2					1	1					
<i>Eliurus webbi</i>	4	2	2		2			2						
1250 m														
Trap distribution		67	33	3	10	48	6	17	13	3	0			
<i>Rattus rattus</i>	3	1	2			1		1	1					
<i>Eliurus grandidateri</i>	44	41	3	1	8	28	3	0	3					
<i>Eliurus majori</i>	2	1	1		1				1					
<i>Eliurus minor</i>	1	1	0			1								
<i>Gymnuronys roberti</i>	1	1	0		1									
1625 m														
Trap distribution		72	28	4	6	50	12	12	12	4	0			
<i>Rattus rattus</i>	1	1	0			1								
<i>Eliurus grandidateri</i>	11	8	3	1	2	3	2		3					
<i>Eliurus majori</i>	19	6	13			5	1	2	10	1				
<i>Voalavo gymnocaudus</i>	1	0	1					1						
1875 m														
Trap distribution		92	8	18	0	53	21	6	0	0	2			
<i>Eliurus grandidateri</i>	8	8	0			7	1							
<i>Eliurus majori</i>	1	0	1					1						
Totals: 450-1875 m														
Trap distribution		371	129	41	42	213	75	71	40	10	8			
<i>Rattus rattus</i>	4	2	2			2		1	1					
<i>Eliurus grandidateri</i>	63	57	6	2	11	38	6	0	6					
<i>Eliurus majori</i>	22	7	15	1	1	5	1	3	11	1				
<i>Eliurus minor</i>	3	1	2			1		2						
<i>Eliurus tanala</i>	2	0	2					1	1					
<i>Eliurus webbi</i>	13	7	6	2	2	1	4	6						

TABLE 12-7. Continued.

Elevation and species	No. taken	Trap position		Ground location*				Aboveground location			
		On ground	Above-ground	Under rotten wood	Leaf litter	By roots, trunks	Misc.	Vine, limb, or trunk <10 cm	Limbs, trunks >10 cm	Suspended trunks	Misc.
<i>Gymnururomys roberti</i>	1	1	0	1							
<i>Voalavo gymnocaudus</i>	1	0	1								
Total captured	109	75	34	15	2	47	11	14	19	1	0

* See p. 234 for trap placement and habitat definitions.

1996), RS d'Anjanaharibe-Sud (14°S, Goodman & Carleton, 1998), Marojejy (14.5°S, this chapter), RNI d'Andringitra (22°S, Goodman & Carleton, 1996), and RNI d'Andohahela (24.5°S, Goodman, Carleton, & Pidgeon, 1999). No significant relationship was demonstrable between the latitude of these mountains and that elevational zone with the highest density of *Rattus* ($R^2 = 0.32$, $df = 4$, $F = 1.42$, $P = 0.32$), or between latitude and number of captures in the zone of highest density as measured by trap success ($R^2 = 0.12$, $df = 4$, $F = 0.41$, $P = 0.57$).

SPECIMENS EXAMINED—11 km NW Manantenina, Antranohofa, 1250 m (FMNH 159649; UASMG 8362, 8399); 10.5 km NW Manantenina, 1625 m (FMNH 159650).

Family Muridae: Subfamily Nesomyinae

Eliurus grandidieri Carleton and Goodman, 1998

DISTRIBUTION—The geographic range of *E. grandidieri*, as so far understood, includes the mountains surrounding the Andapa Basin in the north, specifically the Anjanaharibe-Sud and Marojejy massifs, and the highlands at least as far south as the Andranomay Forest of the Anjozorobe district (Carleton & Goodman, 1998; Goodman et al., 1998). A straight-line distance of about 340 km separates Andranomay and the mountains surrounding the Andapa Basin. The species is known over an elevational range of 1250–1875 m in the mountains surrounding Andapa and from about 1300 m in the Andranomay Forest. Little field survey of small mammals has been conducted in the area between these two locales, particularly on rodents of upland forests, but *E. grandidieri* may be anticipated in appropriate habitat across the region.

ECOLOGY AND REPRODUCTION—In general, this species is terrestrial, although a small percentage of individuals were trapped in sets placed off the ground (Table 12-7). Documented at 1250, 1625, and 1875 m, at least half of the *E. grandidieri* obtained on the ground were captured among roots of standing trees, by fallen tree trunks, or under rocks. Such sets were frequently placed in front of hollows and tunnels, suggesting that the species occupies subterranean burrows. It was

TABLE 12-8. Individual reproductive condition of rodents captured in the PN de Marojej using both live traps and pitfall traps.

Species	450 m		775 m		1250 m		1625 m		1875 m		450-1875 m		% actively reproductive
	A/S	M/F	A/S	M/F	A/S	M/F	A/S	M/F	A/S	M/F	A/S	M/F	
<i>Rattus rattus</i>					3/0	2/1	0/1	0/1			3/1	2/2	75
<i>Eliurus grandidieri</i>					26/15	21/20	8/3	7/4	3/5	4/4	37/23	32/28	62
<i>Eliurus majori</i>					2/0	2/0	17/3	12/8	1/0	1/0	20/3	15/8	87
<i>Eliurus minor</i>			2/1	1/2			1/0	1/0			3/1	2/2	75
<i>Eliurus tanala</i>			2/0	0/2							2/0	0/2	100
<i>Eliurus webbi</i>	3/6	4/5	2/3	2/3							5/9	6/8	36
<i>Gymnatomys roberti</i>					1/0	0/1					1/0	0/1	100
<i>Voalavo gymnocaudus</i>					4/0	4/0	1/0	0/1	0/1	0/1	5/1	4/2	84
Totals	3/6	4/5	6/4	3/7	36/15	29/22	27/7	20/14	4/6	5/5	76/38	61/53	67
% actively reproductive	33%		60%		71%		79%		40%		67%		

Abbreviations: A = adults; S = subadults; M = males with scrotal testes; F = females with large mammae, carrying embryos, or lactating. Not every specimen was examined for reproductive activity, so the tallies of individuals may be less than those presented for general trapping in Table 12-3.

rarely captured in areas of dense leaf litter or open understory within the forest.

Arboreal sets that produced samples of *E. grandidieri* were exclusively positioned on limbs and trunks >10 cm in diameter (Table 12-7). The species apparently prefers larger limb and trunk substrates when climbing since, within each elevational zone, at least as many traps were placed on smaller vines, limbs, and trunks (i.e., <10 cm in diameter).

Some differences in reproductive activity were found between the age and sex classes of *E. grandidieri* in the three elevational zones where it was captured (Table 12-8). In the 1250 m zone, about two-thirds of the individuals captured were adults. Of 21 males, 14 had scrotal or nearly scrotal testes and the balance had abdominal testes; of 20 females, 12 had large mammae and perforated vaginas and eight possessed small mammae and imperforate vaginas. At 1625 m, all seven males obtained had scrotal testes; one of four females had enlarged mammae and a perforated vagina; the other three females were subadults with imperforate vaginas. Finally, in the 1875 m zone, one of four males trapped had scrotal testes and the other three possessed abdominal testes; the four females were evenly split between individuals with large mammae and perforated vaginas and those with small mammae and imperforate vaginas.

All female *E. grandidieri* captured possessed three pairs of mammae (1-1-1, $n = 26$), a number and pattern identical to that found for this species in the RS d'Anjanaharibe-Sud (Goodman & Carleton, 1998). Although many females possessed enlarged mammae, only one of 28 appeared to be actively lactating. Furthermore, of seven females examined, not one contained embryos, and only one had placental scars, in this instance three. Reproduction in this species may be seasonal; the October–November 1996 survey of the PN de Marojejy was conducted after the most recent breeding period. A pattern of seasonal reproduction appears to hold for this species in the RS d'Anjanaharibe-Sud, where the survey was conducted between late October and November 1994 (Goodman & Carleton, 1998).

COMMENTS—*Eliurus grandidieri* was abundant in the 1250 m zone, where 44 individuals were captured in a trap line with 100 different trap stations (Table 12-6). Along a 120 m stretch of linear trap line, 18 *E. grandidieri* were captured, yielding a density of one individual per 6.6 m. In spite of this spatial clumping, the occurrence of multi-

ple captures in a single trap does not significantly deviate from a Poisson distribution. Of the traps that yielded this species, 21 captured single individuals, seven captured two individuals, and three trapped three individuals.

The fine sample of *E. grandidieri* from the PN de Marojejy conforms closely to the morphological description of the type series from the RS d'Anjanaharibe-Sud (Carleton & Goodman, 1998), as might be expected from their geographic proximity. Tail length, as noted for the species, is relatively long on the Marojejy specimens (TL 129% of HB, Table 12-6), and where recorded or observable on preserved material, the caudal tip consistently possesses white hairs, the white terminal section 3–33 mm in length and averaging 21.3 mm ($N = 9$). An alisphenoid strut is characteristically present and well developed on Marojejy crania (present on both sides in 22 skulls, present on one side in three, and absent in none), whereas the strut's occurrence is more variable in the type series (absent on both sides in four of 14 skulls).

SPECIMENS EXAMINED—11 km NW Manantenina, Antranohofa, 1250 m (FMNH 159579–159609, 159698–159703; UA-SMG 8342, 8347, 8361, 8386); 10.5 km NW Manantenina, 1625 m (FMNH 159610–159618, 159704, 159705); 11 km NW Manantenina, at source of Andranomifotra River, 1875 m (FMNH 159619–159623, 159706–159708).

Eliurus majori Thomas, 1895

DISTRIBUTION—The anticipated presence of *E. majori* in montane and sclerophyllous montane vegetation (1250–1875 m) of the PN de Marojejy conforms to our broad understanding of its distribution, documented in similar settings from Montange d'Ambre in the north to the Anosyenne Mountains in the south.

ECOLOGY AND REPRODUCTION—Approximately two-thirds of all *E. majori* captured had entered live traps placed aboveground (Table 12-7). Of the 15 individuals trapped in arboreal sets, 11 were obtained on limbs and trees >10 cm in diameter. These trapping results suggest that the species in the PN de Marojejy is largely scansorial, preferring thicker arboreal substrates, a generalization that seems to hold across its range (e.g., Goodman & Carleton, 1996, 1998).

Most examples of *E. majori* (20) were recorded in the 1625 m zone, 19 of these obtained in a

linear trap line extending 385 m. Eight (42%) of 19 were captured along a 23 m section of the line, consisting of six consecutive traps, two of which yielded two individuals each and one three individuals. Other *E. majori* trapped within this elevational zone did not show such a clumped distribution.

Signs of breeding are evident within each elevational zone. At 1625 m, 11 of 12 males obtained were either fully or partially scrotal. Of seven females obtained with data on reproductive condition, five had enlarged mammae but none showed signs of active lactation, and only one showed any sign of estrus—her uterine walls were highly vascularized. The mammae formula is consistently 1-1-1 ($n = 7$). Only two individuals were trapped at 1250 m and a single individual at 1875 m (Table 12-6), all of them adult males with scrotal testes.

SPECIMENS EXAMINED—11 km NW Manantenina, Antranohofa, 1250 m (FMNH 159624, 159709); 10.5 km NW Manantenina, 1625 m (FMNH 159625–159637, 159710–159715; UASMG 8463); 11 km NW Manantenina, at source of Andranomifototra River, 1875 m (FMNH 159638).

Eliurus minor Major, 1896

DISTRIBUTION—*Eliurus minor*, one of the most widely distributed nesomyine rodents, occurs throughout the eastern humid forest, from Montagne d'Ambre in the north to the Tolagnaro region in the south (Goodman et al., 1996; Goodman, Carleton, & Pidgeon, 1999). In the PN de Marojejy, the species was documented over middle elevations, 775–1625 m; elsewhere the species has been recorded from near sea level (vicinity of Antongil Bay) to about 1800 m (west of Andapa) (Carleton, 1994).

ECOLOGY AND REPRODUCTION—Using live traps, two *E. minor* were captured at the 775 m site and a single animal at 1250 m. Single individuals were taken in pitfall buckets in the 775 m and 1625 m zones (see Chapter 11); both were found during dawn checks after heavy rain the previous night.

Of the three specimens obtained in live traps, two were taken off the ground and one on the ground (Table 12-7). Both arboreal sets were at a height of 1.5–2 m on horizontal saplings or branches <4 cm in diameter. At other sites, the species has been taken on a greater range of substrate diameters, including on branches and trunks

>10 cm in width (Goodman & Carleton, 1998; Goodman, Carleton, & Pidgeon, 1999).

No external sign of breeding was noted in the two females captured, although both males collected had scrotal testes (Table 12-8).

SPECIMENS EXAMINED—10 km NW Manantenina, along tributary of Manantenina River, 775 m (FMNH 159716, 159717); 11 km NW Manantenina, Antranohofa, 1250 m (FMNH 159639; UASMG 8343); 10.5 km NW Manantenina, 1625 m (FMNH 159640).

Eliurus tanala Major, 1896

DISTRIBUTION—This species also ranges broadly across much of the eastern humid forest, so that its presence in the PN de Marojejy—two individuals obtained in the 775 m zone—was anticipated. On massifs such as Anjanaharibe-Sud, Andringitra, and Andohahela, *E. tanala* has been trapped over a broader swath of elevations, typically into middle montane forest formations as high as 1625 m (Goodman & Carleton, 1996, 1998; Goodman, Carleton, & Pidgeon, 1999).

ECOLOGY AND REPRODUCTION—Both individuals were trapped at arboreal stations, one positioned at 1 m on a 2-cm-diameter downed tree trunk and the other at 1.5 m on a 20-cm-diameter fallen tree trunk that spanned a small stream (Fig. 12-3). In nearby RS d'Anjanaharibe-Sud, five of the six *E. tanala* captured were taken in terrestrial sets (Goodman & Carleton, 1998). At other sites, capture of this species seems to be almost evenly divided between ground and arboreal sets (Goodman & Carleton, 1996; Goodman, Carleton, & Pidgeon, 1999).

The two *E. tanala* obtained, both females, were reproductively active. One had large mammae and two placental scars (one per each uterine horn), and the second was lactating and had three placental scars (two in the right horn, one in the left). The mammae formula in these individuals is 1-1-1.

SPECIMENS EXAMINED—10 km NW Manantenina, along tributary of Manantenina River, 775 m (FMNH 159696, 159697).

Eliurus webbi Ellerman, 1949

DISTRIBUTION—First described as a localized subspecies of *E. myoxinus* (Ellerman, 1949), the emerging distributional picture of this species reveals that it is the most broadly distributed neso-



FIG. 12-3. View of transitional lowland-montane forest at 775 m. An example of *Eliurus tanala* was captured alive in a trap placed on a 20-cm-diameter tree that had fallen across the small stream pictured here (trap placement category = above ground, on limb or trunk greater than 10 cm in diameter). Other *Eliurus* found in this kind of forest include *E. minor* and *E. webbi*. *Nesomys* cf. *rufus* was observed at this elevation but not captured.

myine of the eastern humid forest. It is now known to inhabit littoral forests of Tampolo (Rakoton-dravony et al., 1998) and near Tolagnaro (Goodman, Carleton, & Pidgeon, 1999), as well as low-

land formations across the full latitudinal expanse of the humid forest biome (Carleton, 1994; Goodman & Carleton, 1996, 1998; Goodman et al., 1998). Consistent with this lower elevational set-

ting, *E. webbi* was captured only in the 450 and 775 m zones of the PN de Marojejy.

ECOLOGY AND REPRODUCTION—Of 13 *E. webbi* trapped, seven were captured on the ground and six in arboreal sets (Table 12-7). All individuals captured on the ground were taken next to rotten wood, roots, trunks, or rock outcrops. All traps placed aboveground were on substrates <10 cm in diameter, as in the RNI d'Andringitra, where most *E. webbi* were captured on branches and vines <10 cm in diameter (Goodman & Carleton, 1996). In the RS d'Anjanaharibe-Sud and RNI d'Andohahela, on the other hand, a greater percentage of individuals was trapped on thicker substrates (Goodman & Carleton, 1998; Goodman, Carleton, & Pidgeon, 1999).

The condition of the reproductive organs suggested that few individuals had reached sexual maturity, the elevational samples composed of many subadults. In the 450 m zone, one of four males had scrotal testes and two of five females had large mammae and perforated vaginas. In the 775 m zone, the testes of one male had slightly descended and in the other were fully abdominal; of the three females, one had large mammae, a perforated vagina, and two placental scars and two had inconspicuous mammae and imperforate vaginas. The mammae formula in the three females examined was 1-1-1.

The timing of reproduction among populations of *E. webbi* seems to vary without a discernible pattern based on the field results so far obtained. For example, during the survey of the RS d'Anjanaharibe-Sud, conducted between mid-October and late November 1994, the majority of the *E. webbi* captured (875 m) showed signs of ongoing reproductive activity (Goodman & Carleton, 1998). Since the Anjanaharibe-Sud and Marojejy massifs are at nearly the same latitude, simple explanations of clinal variation in reproductive level are plainly insufficient. In like manner, surveys conducted during the same calendar period in the southern protected areas of Andringitra and Andohahela (Goodman & Carleton, 1996; Goodman, Carleton, & Pidgeon, 1999) revealed contrasting levels of breeding activity in this species.

SPECIMENS EXAMINED—8 km NW Manantenina, along tributary of Manantenina River, 450 m (FMNH 159718–159720, 159641–159645; UA-SMG 8275); 10 km NW Manantenina, along tributary of Manantenina River, 775 m (FMNH 159646, 159721–159723; UA-SMG 8294).

Gymnuromys roberti Major, 1896

DISTRIBUTION—Although infrequently recorded, this rodent is known to have a broad latitudinal distribution across the eastern humid forest. With the exception of Montagne d'Ambre in the extreme north, *G. roberti* has been captured at every eastern humid forest site surveyed by Goodman, but it appears to be absent at several seemingly appropriate sites on the Central High Plateau, for example in the RS d'Ambositantely (Stephenson et al., 1994; Goodman & Rakoton-dravony, 2000). *Gymnuromys roberti* is an elusive terrestrial species of middle elevations, although at some places, such as Andringitra, it has been trapped at lower elevations (720 m). Only one individual was captured (1250 m) in the PN de Marojejy.

ECOLOGY AND REPRODUCTION—The single specimen, an adult female, was collected in a Sherman trap placed at a hole opening into a fallen log that was rotting and covered with epiphytes and moss (Table 12-7). The individual possessed large mammae, without embryos but with two placental scars, one per each horn of the uterus. An *Eliurus grandidieri* was obtained in this same trap on the following night.

SPECIMENS EXAMINED—11 km NW Manantenina, Antranohofa, 1250 m (FMNH 159724).

Nesomys cf. rufus Peters, 1870

DISTRIBUTION—Although *N. rufus* is another ubiquitous inhabitant of the eastern humid forest, none was captured during the 1996 small mammal inventory of the PN de Marojejy. This richly colored, large diurnal rodent was one of the most abundant, commonly observed, and frequently trapped nesomyines in the nearby RS d'Anjanaharibe-Sud (Goodman & Carleton, 1998). However, individuals of *Nesomys*, presumably referable to *N. rufus*, were occasionally observed in the 775 and 1250 m zones of the PN de Marojejy. Other visual records of the species have been previously reported from the southwestern portion of the massif at 800 m and in the north-west portion between 1000 and 1400 m (Duckworth & Rakotondraparany, 1990). The failure to trap *Nesomys* during the 1996 survey may relate to an atypically low population density during the Marojejy inventory.

ECOLOGY—All *Nesomys* were observed during the day, mostly in areas of open understory forest

with relatively dense leaf litter, typical habitat for this species.

***Voalavo gymnocaudus* Carleton and Goodman, 1998**

DISTRIBUTION—This recently described form was previously known from the RS d'Anjanaharibe-Sud, at 1300 and 1950 m (Carleton & Goodman, 1998). Accordingly, its presence in the PN de Marojejy was expected, and individuals of *V. gymnocaudus* were captured between 1260 and 1875 m. These occurrences extend the range of the species slightly farther to the east, a distribution so far localized to mountains ringing the Andapa Basin.

ECOLOGY AND REPRODUCTION—*Voalavo gymnocaudus* has been captured on the slopes of the Marojejy and Anjanaharibe-Sud massifs, between 1260 and 1950 m and in vegetational formations ranging from montane forest to dwarf upper montane/sclerophyllous forest. Of the six individuals obtained in the PN de Marojejy, five were caught in pitfall buckets (see Chapter 11) and one in a Sherman trap. The live-trapped individual (1625 m) was collected in a set placed on a 5-cm-diameter limb, 1.5 m above the ground and slanting 10 degrees from a middle canopy tree. On the Anjanaharibe-Sud Massif, this diminutive species was also obtained in both pitfall buckets and elevated traps placed at low heights. *Voalavo gymnocaudus* appears to be largely terrestrial but with scansorial capabilities.

The four individuals taken at 1250 m are adult males with scrotal testes. The female captured in the 1625 m zone had large mammae, although not lactating; three placental scars but no embryos were noted. A subadult female obtained at 1875 m possessed small mammae and an imperforate vagina. The mammary formula of Marojejy *Voalavo* is 1-1-1 ($n = 2$), as reported for those specimens in the RS d'Anjanaharibe-Sud and members of *Eliurus*.

COMMENTS—The Marojejy specimens of *Voalavo gymnocaudus* possess most of the cardinal traits advanced for the new genus and species (Carleton & Goodman, 1998), especially as observed in the absence of a prominent tail tuft, the small third molars and the unlaminated configuration of M3, the relatively long incisive foramina, the reduction of the tegmen tympani, and lack of an entepicondylar foramen. However, each of the three cleaned skulls has very thin alisphenoid

struts, a feature not found on the four crania of the Anjanaharibe-Sud specimens. The molars of *Voalavo* are lower crowned than those of *Eliurus* species, as suggested by the usual lingual contact of the posterior lamina on M1-2, with only little to moderate wear.

Specimens Examined—11 km NW Manantenina, Antranohofa, 1250 m (FMNH 159725; UASMG 8393); 10.5 km NW Manantenina, 1625 m (FMNH 159647, 159648); 10.5 km NW Manantenina, 1625 m (FMNH 159726); 11 km NW Manantenina, at source of Andranomifototra River, 1875 m (FMNH 159727).

Discussion

The field survey of small mammals in the PN de Marojejy, conducted over seven weeks in 1996 at five elevations between 450 and 1875 m, has generated the first vouchered evidence of native rodents that inhabit this national park. Seven species of endemic Nesomyinae are represented among the 109 rodent specimens preserved (Table 12-6), including two forms recently described as new to science from the nearby RS d'Anjanaharibe-Sud (*Voalavo gymnocaudus* and *Eliurus grandidieri*; Carleton & Goodman, 1998). Previous faunal reports for the Marojejy Massif listed only three native species—*E. cf. myoxinus*, *Brachytarsomys albicauda*, and *Nesomys cf. rufus* (Nicoll & Langrand, 1989; Duckworth & Rakotondrapary, 1990). In view of the recent taxonomic changes within Nesomyinae, particularly the genus *Eliurus*, it is impossible to confirm observational field determinations for most members of the subfamily as reported under the antiquated nomenclature.

No rodent species new to science was encountered in the PN de Marojejy. This nondiscovery repeats that earlier obtained in the RNI d'Andohahela, where humid forest reaches its southern limits and where only known forms were documented using similar trapping equipment and sampling procedures in 1995 (Goodman, Carleton, & Pidgeon, 1999). In view of the new nesomyine genera (two) and species (five) described during the past few years from the eastern forest (Carleton, 1994; Carleton & Goodman, 1996, 1998), the lack of additional nesomyine variety from the Andohahela and Marojejy massifs, nearly at the polar ends of the island, suggests that present documentation of rodents occurring in this

biome approximates its actual species diversity. However, other habitats on the island have yet to be rigorously surveyed, notably in the west, and almost certainly other rodent species await discovery.

Trapping Effort and Sampling Confidence

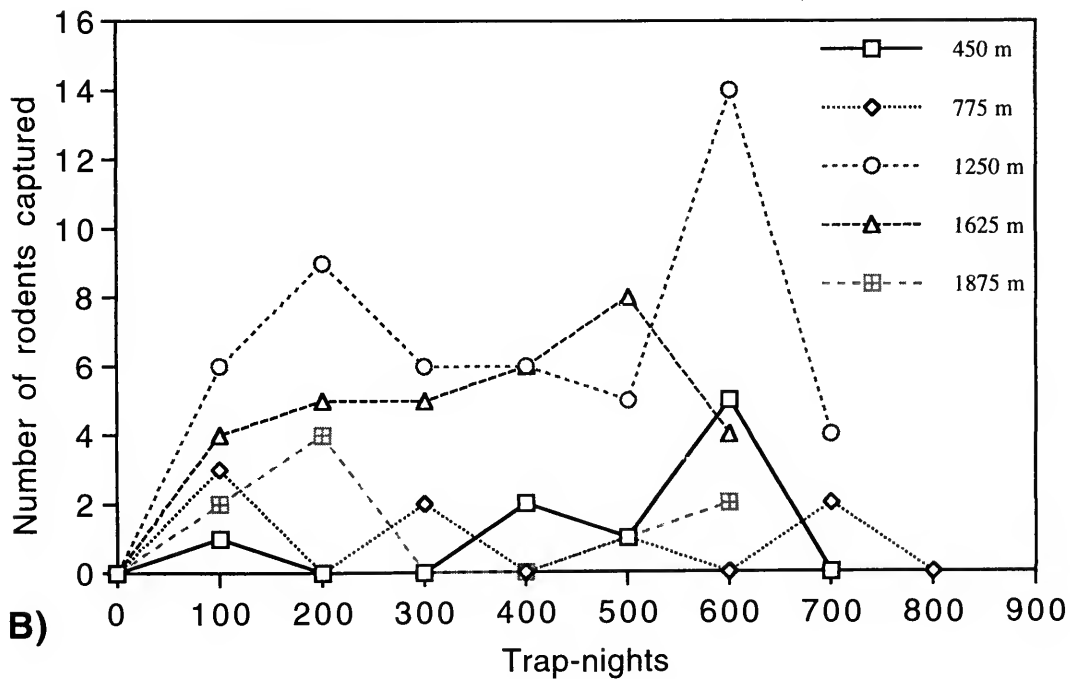
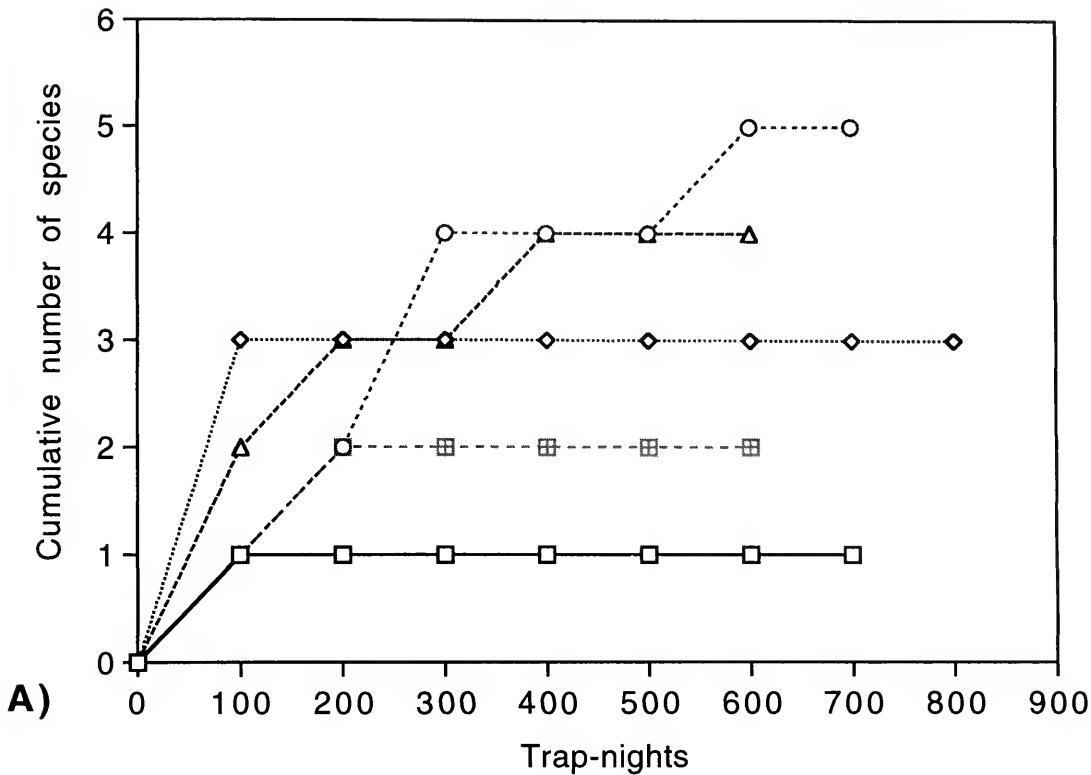
A total of 3,390 trap-nights of sampling effort were amassed during the Marojejy survey, ranging from 600 to 800 trap-nights per individual elevational zone (Table 12-6). Of the eight species of rodents captured, all except *Rattus rattus* are members of the endemic murid subfamily Nesomyinae. These animals were found across a broad cross-section of habitats encompassing over 1400 m of elevation, from lowland forest (450 m), a zone transitional between lowland and montane forest (775 m and 1250 m), montane forest (1625 m), and sclerophyllous forest (1875 m). A few rodents were obtained in pitfall traps installed mainly to capture lipotyphlans (see Chapter 11), which were also obtained regularly in live traps (Table 12-6).

Overall trap success for small mammals (rodents, native and introduced, and insectivores) varied appreciably among the five elevational zones. Relatively poor rates (1.4–1.6%) were realized at the lower and highest elevations (450, 775, and 1875 m) and better returns (5.7–7.6%) at the intermediate sites (1250 and 1625 m) (Table 12-6). Consideration of only Rodentia or only the first 500 trap-nights per zone discloses the same elevational profile of trapping success, although absolute values differ slightly (Tables 12-1 and 12-6). An increase in capture rates for rodents at middle elevations is proving typical of mountains surveyed in the eastern humid forests of Madagascar (for example, Goodman & Carleton, 1996, 1998). An exception to this pattern was found on forested slopes within parcel 1 of RNI d'Andohahela, where uniformly low levels of trap success (based on the standardized trapping period) were obtained for rodents (0.8–3.6% for five elevations between 440 and 1875 m; Goodman, Carleton, & Pidgeon, 1999).

The cumulative number of rodent species captured within each elevational zone generally reached an asymptote before termination of a trapping session, usually by the end of the third trap-night (Fig. 12-4A). At 1250 m, however, the first example of *Eliurus majori* was not caught until the sixth night of trapping, of seven total. Trap success varied unpredictably from night to night within each elevational zone. There is neither evidence of regularly diminishing trap success over time at an elevation, at least for the length of time trapped, nor clear indication that asymptotes in species accumulation curves are correlated with declines in capture rates (Fig. 12-4B).

Notwithstanding the level of effort summarized above, there is ample reason to question whether the 1996 survey of the PN de Marojejy was sufficiently comprehensive to document all rodent species that live there. Individuals of *Nesomys*, a comparatively large rodent conspicuous by its diurnal activity and reddish fur, were observed during the 1996 fieldwork but somehow avoided attempts at capture. *Nesomys*, as well as *Brachytaromys*, has been previously reported to occur on the Marojejy Massif (Duckworth & Rakotondrapary, 1990). Persuasive evidence for their presence issues from the RS d'Anjanaharibe-Sud, a reserve just to the southwest of Marojejy and part of the same northern highland complex (Fig. 12-5), where samples of both genera, identified as the species *N. rufus* and *B. albicauda*, were collected in 1994 (Goodman & Carleton, 1998). Except for these two, the RS d'Anjanaharibe-Sud otherwise contains the same species reported here for the PN de Marojejy, at comparable elevations and in comparable habitats (see below). Based on this ecological complementarity and geographic proximity, the aforementioned species of *Brachytaromys* and *Nesomys* should be expected as inhabitants of the PN de Marojejy. The possibility remains that some *Nesomys* spotted in the reserve represent the species *N. audeberti*, a form known from lowland areas of the eastern humid forest (see Goodman & Carleton, 1998, p. 214, for discussion).

→
FIG. 12-4. Plots of trap-nights against the cumulative number of rodent species (including *Rattus rattus*) obtained (A) and against the number of individuals trapped (B) for each of five elevational zones surveyed within the PN de Marojejy.



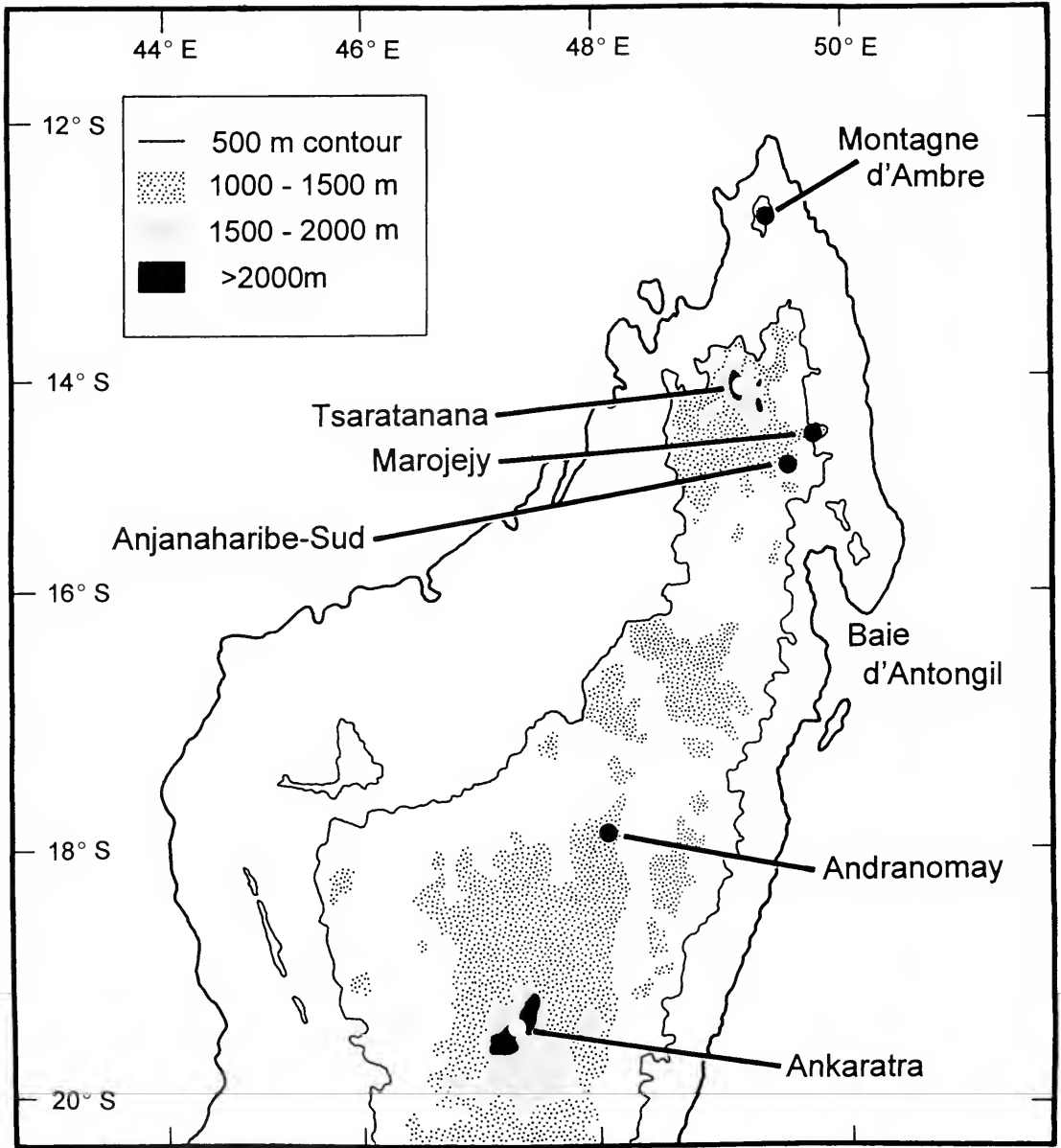


FIG. 12-5. Northern and central Madagascar, illustrating the close proximity of the PN de Marojejy and RS d'Anjanaharibe-Sud in the island's northern highlands and other places mentioned in the text.

Elevation and Rodent Associations

ELEVATIONAL DISTRIBUTION—None of the eight rodent species found in the PN de Marojejy was trapped in all five altitudinal zones surveyed (Table 12-9). *Eliurus grandidieri*, *E. majori*, and *Voalavo gymnocaudus* were recorded in the upper three zones, between 1250 and 1875 m, and these three species appear to occur across the widest

elevational belt of the native species living on the eastern slopes of the massif. The few examples of *Voalavo* were obtained in live traps only at 1625 m and in pitfall traps at 1250 and 1875 m. Whether the species occurs in low densities or behaves so as to avoid live traps is uncertain.

Three nesomyines and the one murine were found in two contiguous elevational zones: *Eliurus webbi* at 450 and 775 m, *E. minor* and *Ne-*

TABLE 12-9. Elevational occurrence of rodents in the PN de Marojejy during the 1996 survey based on live traps, pitfall traps, and sight observations.

Species	450 m	775 m	1250 m	1625 m	1875 m
Murinae					
<i>Rattus rattus</i>			+	+	
Nesomyiinae					
<i>Eliurus grandidieri</i>			+	+	+
<i>Eliurus majori</i>			+	+	+
<i>Eliurus minor</i>		+	+	+	
<i>Eliurus tanala</i>		+			
<i>Eliurus webbi</i>	+	+			
<i>Gymnuromys roberti</i>			+		
<i>Nesomys cf. rufus</i>		s	s		
<i>Voalavo gymnocaudus</i>			+	+	+
Total species	1	4	7	5	3
Total native species	1	4	6	4	3

S = sight record with no associated voucher specimen.

somys cf. rufus at 775 and 1250 m, and *Rattus rattus* at 1250 and 1625 m. *Eliurus minor* is known to have a wider altitudinal distribution elsewhere in Madagascar. In the northeastern region, the species has been recorded near sea level in the vicinity of Antongil Bay (Carleton, 1994); near the southern extent of the eastern humid forest, in the RNI d'Andohahela, it was captured between 810 and 1875 m (Goodman, Carleton, & Pidgeon, 1999). Introduced *R. rattus* proved to be exceptionally rare in traps as compared to other sites recently censused in the eastern humid forest. In the nearby site of Anjanaharibe-Sud, for instance, it was captured in all four elevations studied between 875 and 1950 m and in both secondary and pristine forest.

The other two nesomyine species captured in the PN de Marojejy originated from single zones. One, *Gymnuromys roberti*, taken at 1250 m, is notably difficult to trap and wherever found has never been recorded in large numbers. At other sites it has been documented to occur across a broader elevational range, from the upper reaches of lowland rain forest into upper montane forest (e.g., Goodman & Carleton, 1996). The second species, the usually common *Eliurus tanala*, was inexplicably captured only twice and only at 775 m, but it is well known to broadly inhabit lowland-montane transition and montane communities at other places in the eastern humid forest (Goodman & Carleton, 1996, 1998; Goodman, Carleton, & Pidgeon, 1999). Illuminated by the now substantial information base on nesomyine distributions, these examples underscore the need to temper conclusions on limited elevational oc-

currence, given the stochastic interplay of seasonally changing population densities, trapping likelihood, and the brevity of the field survey (6–8 days at any one elevational level).

No rodent species was recovered in traps placed in the open grassland above tree line of the 1875 m zone. Of the 100-trap, 540-m-long transect at this altitude, 49 stations extended through sclerophyllous forest, 10 across the ecotone between sclerophyllous forest and grassland, and 41 into the nonwooded grassland proper. *Voalavo gymnocaudus*, *Eliurus grandidieri*, and *E. majori* were obtained (the first in a pitfall trap) in sclerophyllous forest and only *E. grandidieri* in the ecotone traps. The cap of alpine habitat occurs on the Marojejy Massif between about 1850 m and the summit at 2132 m, and the absence of rodents wholly restricted to this highland zone conforms to findings for other tall mountains so far studied on Madagascar (see Goodman, Carleton, & Pidgeon, 1999, and below).

SPECIES RICHNESS—The elevational distribution of rodent species richness in the PN de Marojejy shows a hump-shaped profile, with fewer species ($N = 1-3$) co-occurring at the lowest and highest zones surveyed and more ($N = 4-7$) at middle heights (Table 12-9). The greatest number of native nesomyines, six species, was recorded at 1250 m, a number and elevation comparable to biodiversity maxima documented for other mountains surveyed in the eastern humid forest—seven species at 1625 m in the RNI d'Andringitra (Goodman & Carleton, 1996; Goodman & Rasolonandrasana, in press), six species at 1260 m in the RS d'Anjanaharibe-Sud (Goodman & Carle-

TABLE 12-10. Estimated biomass (g) of rodents trapped along an elevational transect in the PN de Marojejy.*

Species	450 m	775 m	1250 m	1625 m	1875 m
<i>Rattus rattus</i>			114	114	
<i>Eliurus grandidieri</i>			1,479	612	306
<i>Eliurus majori</i>				1,540	110
<i>Eliurus minor</i>		44	44		
<i>Eliurus tanala</i>		206			
<i>Eliurus webbi</i>	300	225			
<i>Gymnuromys roberti</i>			162		
<i>Voalavo gymnocaudus</i>				22	
Total biomass (g)	300	475	1,799	2,288	416
Total biomass (g) excluding <i>Rattus</i>	300	475	1,685	2,174	416
Total no. of species	1	3	4	4	2

* Summations from average weight of adults captured over the first 500 trap-nights within each zone.

ton, 1998), and five species at 1200 m in the RNI d'Andohahela (Goodman, Carleton, & Pidgeon, 1999). The mid-elevational bulge in species richness within the PN de Marojejy thus mirrors an elevational pattern common to a variety of organisms on mountains in tropical latitudes (see Goodman, Carleton, & Pidgeon, 1999, for discussion, with emphasis on Madagascar and the eastern humid forest biome).

Not surprisingly, biomass calculations, as based on animals captured during the first 500 trap-nights, exhibit the greatest values over the middle elevations (1250 and 1625 m) and decline markedly toward the lowest and highest elevations sampled (Table 12-10). At both middle sites, a single species of *Eliurus* (*E. grandidieri* at 1250 m and *E. majori* at 1625 m) accounted for more than half of the biomass of captured rodents. The mid-elevational bulge in standing biomass of rodent populations logically corresponds to both the number of species and number of individuals trapped, figures which were greatest at these middle heights (Tables 12-6 and 12-9). Certain species were necessarily excluded from the biomass comparisons among all elevations where known, due either to pitfall recovery (*Voalavo gymnocaudus*), visual record (*Nesomys rufus*), or capture after the standard trapping period (*Eliurus majori* at 1250 m). Their absences bias any closer examination of the relationship between biomass, species richness, and population size on Marojejy.

INTRA- AND INTERSPECIFIC DIFFERENCES IN REPRODUCTION—The adult sex ratio of most rodent species obtained on Marojejy, as inferred from trap returns, does not appear to differ substantially

from 1:1 (Table 12-8). For most taxa, however, sample size is too small to meaningfully test for significance. A notable exception is *E. majori*, nearly two-thirds of the individuals captured being male. In the RS d'Anjanaharibe-Sud, only *E. grandidieri* showed a slightly skewed population sex ratio, in this instance biased toward females, based on trap captures. The rodent faunas on the two massifs are nearly alike in specific composition, and no pattern in departure from even sex ratios is detectable for any species common to both sites. Whatever differences emerged can be plausibly attributed to the vagaries of trapping success.

Since a maximum lag of only 10 days separated the trapping sessions in the five elevational zones, initiated consecutively from the lowest to highest, and since age-class recognition does not address "subadult" physiological fertility, we cannot assess the incidence of breeding with respect to broader seasonal patterns and elevational trends. At the time of the survey (October and November), external signs of reproduction were apparent for all rodent species and across most elevational zones where sample size is appreciable (Table 12-8). Moreover, the proportion of subadults was relatively high in the total catch of *Eliurus grandidieri* and *E. webbi*, about 38% and 64%, respectively. The relative abundance of immature animals and the number of actively breeding adults within each elevational zone where these two species were captured suggest that reproduction for them was ongoing during the period of this survey. Among examples of *E. majori*, on the other hand, few subadults were present, but a majority

of adults (87%) exhibited some condition implying active reproduction. In other species, samples sizes are plainly insufficient to sustain insights on breeding status of their populations. Although conducted two years earlier, the survey of the RS d'Anjanaharibe-Sud (October–November 1994) occurred during the same calendar period as that in the PN de Marojejy (October–November 1996). There, most nesomyine species, in particular *E. grandidieri* and *E. majori*, showed high percentages of subadults relative to adults.

Information on the general natural history of Madagascar's native rodents has improved markedly in recent years, mainly through coordinated field surveys in faunistically poorly understood regions of the eastern humid forest (Goodman & Carleton, 1996, 1998; Goodman et al., 1997; Goodman, Carleton, & Pidgeon, 1999). In spite of this resurgent attention, detailed knowledge about the reproductive biology of any one species at the population level has advanced little. The annual timing and relative brevity of the surveys, most conducted in the last quarter of the year (October–December) and over the course of 5–10 days at a given elevation, prejudice inferences about the onset of reproduction, its cyclical regularity (or not), and relationship to environmental rhythms (rainfall patterns, fruiting cycles, insect fluctuations, etc.). By the criteria adopted (males with scrotal testes, females with embryos or lactating, prevalence of subadults), we can say that moderate to high levels of rodent reproduction were occurring in all of these protected areas for the quarter-year period of the surveys. Better understanding of annual nesomyine reproductive patterns and breeding systems, as well as appreciation of elevational or altitudinal variation within and among species, can only be addressed through site-specific field investigations, undertaken over a longer period and employing methodologies such as a grid-based, mark-and-release protocol.

The Rodent Faunas of the PN de Marojejy and RS d'Anjanaharibe-Sud

ELEVATIONAL CONCORDANCE—An initial goal for surveying small mammals on different mountains throughout Madagascar's eastern humid forest, which covers a latitudinal swath of 12 degrees, was to assess the relationship between species diversity and geophysical gradients like elevation and latitude. Such gradients, and the many abiotic environmental factors that covary with

them (e.g., rainfall, temperature, insolation, evaporation), potentially mold the composition and productivity of biological communities dwelling along mountain slopes (see, for example, Rahbek, 1997; Rosenzweig, 1992; Rosenzweig & Abramsky, 1993). The validity of these comparisons critically hinges on appropriate controls that will allow biological patterns to be distinguished from stochastic variation. If the pattern of rodent distributions on mountains in eastern Madagascar corresponds in part to gradients associated with latitude, then elevational affinities of these organisms on nearby mountains at the same latitude should be expected to closely conform.

The Marojejy and Anjanaharibe-Sud massifs, separated by a few tens of kilometers and one-half degree of latitude in the northern highlands (Fig. 12-5), offer a natural circumstance to explore this expectation. The rodent surveys of these two mountains were basically conducted during the same period: Anjanaharibe-Sud from 15 October to 30 November, 1994, and Marojejy from 4 October to 20 November, 1996. The same line-transect sampling, trapping methods (live traps and pitfalls), and baits were used at each reserve. On both massifs, the surveys were performed along their eastern-southeastern slopes, across about 1200 to 1400 m of vertical relief (875–1950 m in Anjanaharibe-Sud; 450–1875 m in Marojejy). The summits of the two mountain systems rise to nearly equivalent heights, that of Anjanaharibe-Anivo to 2064 m and Marojejy to 2132 m. The similar vertical relief of the two mountains lends further credence to the comparison, since Goodman, Carleton, & Pidgeon (1999) have disclosed a strong correlation between elevation at the summit and that elevation where most rodent species co-occur; they attributed the relationship to a combination of orographic variables and their multifaceted effects.

An exception to their similarity involves the southeastern side of the RS d'Anjanaharibe-Sud, whose lowest boundary ends at 875 m, above lowland rain forest proper like that sampled in the PN de Marojejy (at 450 m where only *Eliurus webbi* was caught). Pairwise comparisons between the two massifs are therefore restricted to the four more or less coordinate elevational samples, as follows (Marojejy and Anjanaharibe-Sud listed respectively): 775 and 875 m, 1250 and 1260 m, 1625 and 1550 m, and 1875 and 1950 m.

The elevational limits and sympatric coincidence of nesomyine species are strongly concordant on the two mountains (Table 12-11). For all

TABLE 12-11. Comparison of rodent species documented at four elevations in the PN de Marojejy and the RS d' Anjanaharibe-Sud.*

Species	Anjanaharibe-Sud		Anjanaharibe-Sud		Anjanaharibe-Sud		Anjanaharibe-Sud	
	Marojejy 775 m	875 m	Marojejy 1250 m	1260 m	Marojejy 1625 m	1550 m	Marojejy 1875 m	1950 m
Murinae								
<i>Rattus rattus</i>		+	+	+	+	+		+
Nesomyinae								
<i>Brachytarsomys albicauda</i>	(+)†	+	+	+	+	+	+	+
<i>Eliurus grandidieri</i>								
<i>Eliurus majori</i>								
<i>Eliurus minor</i>	+	+	+	+	+	+		
<i>Eliurus tanala</i>	+	+						
<i>Eliurus webbi</i>	+	+						
<i>Gymnuromys roberti</i>			+	+				
<i>Nesomys rufus</i>	(+)		(+)	+			+	+
<i>Vodlavo gymnocaudus</i>			+	+				
Total no. of species	5	4	7	8	4	4	3	4
Total no. of native species	5	3	6	7	3	3	3	3

Note: + = presence confirmed by vouchered specimens; (+) = presence based on observation.

* Data for the RS d' Anjanaharibe-Sud are derived from Goodman and Carleton (1998).

† As reported at 700 m by Duckworth and Rakotondrapary (1990).

‡ Specimens actually from western slope at 1300 m (see Goodman & Carleton, 1998).

TABLE 12-12. Comparison of rodent species and elevational ranges (in meters) documented to date for comparably censused regions in eastern humid forests.

Species	Montagne d'Ambre ¹ 340–1350 m	Marojejy ² 450–1875 m	Anjanaharibe- Sud ³ 875–1950 m	Andringitra ⁴ 720–2450 m	Andohahela ⁵ 440–1875 m
<i>Mus musculus</i>				2050	
<i>Rattus rattus</i>	340–1350	1250–1625	875–1950	810–2450	810–1875
<i>Brachytarsomys albicauda</i>	—	—	875	—	—
<i>Brachyuromys betsileoensis</i>	—	—	—	1990–2450	—
<i>Brachyuromys ramirohitra</i>	—	—	—	1210–1990	—
<i>Eliurus grandidieri</i>		1250–1875	1260–1550	—	—
<i>Eliurus majori</i>	1000–1350	1250–1875	1260–1950	1210–1990	1200–1500
<i>Eliurus minor</i>	1000	775–1250	875–1260	720–1625	810–1875
<i>Eliurus tanala</i>	—	775	1260	810–1625	810–1500
<i>Eliurus webbi</i>	650–1000	450–775	875	720–810	440–810
<i>Gymnuromys roberti</i>	—	1250	1260	720–1625	1200
<i>Monticolomys koopmani</i>	—	—	—	1625–1990	1875
<i>Nesomys rufus</i>	—	775–1250	1260–1950	810–1990	810–1200
<i>Voalavo gymnocaudus</i>	—	1250–1875	1950	—	—
Number of species of Nesomyinae	3	8	9	9	7

¹ Raxworthy and Nussbaum (1994), Goodman et al. (1996).

² This study. The listing of *Nesomys* cf. *rufus* is based on sight records.

³ Goodman and Carleton (1998). This tabulation does not include collections made by Franco Andreone on the western slopes of the Anjanaharibe-Sud Massif.

⁴ Goodman and Carleton (1996); Langrand and Goodman (1997); Goodman and Rasolonandrasana (in press).

⁵ Goodman, Carleton, and Pidgeon (1999).

36 possible pairwise comparisons (nine species by four elevational zones), no significant contrast in pattern of specific occurrence can be demonstrated between the neighboring massifs (Wilcoxon signed-ranks test, $z = -0.38$, two-sided $P = 0.71$). Or, stated in a complementary way, the correlation between a species presence and its highest elevation of occurrence on the two mountains is highly significant (Spearman's $\rho = 0.82$, $P = 0.011$). Further, that elevational belt with greatest species diversity is the same on Marojejy and Anjanaharibe-Sud (1250–1260 m), a zone corresponding to lower montane forest. Indeed, the co-presence, or joint absence, of a species within an elevational zone on the two massifs is so commonplace that the lack of complementarity is reasonably suspect as sampling error. The latter instances involve the infrequently captured species at each reserve, whose numbers seemed to be unusually low (*Eliurus tanala*) or whose habits may diminish conventional live-trapping success (*Voalavo gymnocaudus*). The other notable exception, and the only diurnal species at these two localities, *Nesomys rufus*, was commonly trapped from 1260 to 1950 m at Anjanaharibe-Sud, but was observed only at 775 and 1250 m in Marojejy. The contrast between Anjanaharibe-Sud and Marojejy

in abundance (and catchableness) of *Nesomys rufus* exposes the weakness of drawing conclusions from single-point field surveys conducted in different years. Level of reproduction in *Nesomys*, and other Nesomyinae, may be sensitive to a host of other environmental cues, which may vary in timing and degree between years and which may not simply track calendrical divisions.

The agreement between the rodent faunas on Marojejy and Anjanaharibe-Sud in elevational ranges and botanical associations reinforces the emerging picture of nesomyine distributions within the eastern humid forest biome (Table 12-12). *Eliurus webbi* is a species of lowland forest. At the upper limits of lowland forest or in transitional settings, it may occur in sympatry with *E. tanala*. Although *E. tanala* was found only at the upper limit of lowland forest in the PN de Marojejy (775 m), elsewhere it is known to extend from this belt into lower to middle montane forest proper. Elevational records of *E. minor* and *Nesomys rufus* typically bridge lowland and montane forest habitats, a distribution that may also characterize *Gymnuromys roberti* and *Brachytarsomys albicauda* across the eastern forest block insofar as intimated by their very limited trapping records. Prime montane forest and contiguous areas of

sclerophyllous montane forest harbor *E. majori*, *E. grandidieri*, and *Voalavo gymnocaudus*, at least in the northern highlands.

Nesomyine species broadly distributed within eastern humid forest, like *Eliurus majori* and *E. webbi*, demonstrate remarkable elevational fidelity throughout their ranges, from Anjanaharibe-Sud and Marojejy in the north to Andringitra and Andohahela in the south (Table 12-12). The apparent lack of notable shifts in elevational occurrence of these rodent species, across a north-south difference of nearly 10 degrees, suggests an absence of latitudinal dampening of vegetational zones on these mountain slopes. Nevertheless, understanding of variation of Malagasy plant communities with latitude and altitude still requires much detailed study (see Lewis et al., 1996; Messmer et al., this volume). Montagne d'Ambre (Fig. 12-5), with its unique geological history and remote location at the extreme northern tip of Madagascar (Goodman et al., 1996), seems to be an exception in that the lowland species *E. webbi* and the montane species *E. majori* do co-occur in montane forest (1000 m) below its low summit (1350 m).

THE ALPINE ZONE—Broad expanses of natural open habitat above tree line exist on Madagascar's highest mountains, and such alpine vegetation occurs on the uppermost slopes of the Marojejy Massif and to a much lesser extent on the Anjanaharibe-Sud Massif. At about 1800 m, dense mossy forest on the Marojejy Massif diminishes in stature and the woody vegetation is dominated by species with sclerophyllous leaves. Farther upslope, about 1850 m, continuous sclerophyllous forest grades into a patchwork of forest and ericoid grassland; the latter habitat is characterized by species of Gramineaceae and low-growing woody plants, predominantly Ericaceae. Dense bamboo stands are interdigitated across these ecotones. Around 1875 m and above, ericoid grassland is common and relatively extensive, except near the summit (2132 m), where grassland intermingles with areas of exposed rock sparsely covered with geophytic plants. On the upper slopes of Anjanaharibe-Anivo, the tree line occurs around 1980 m, below which is dense mossy forest of distinctly sclerophyllous character. Ericaceous habitat above tree line is altitudinally less extensive than on Marojejy but is visibly more dense and bushy in growth form, with large areas dominated by Gramineaceae and patches of bare rock near the summit. Botanists believe that the ericoid grassland on Marojejy is natural and lacks extensive anthropogenic modifications that char-

acterize some parts of the summital zones of the Tsaratanana and Andringitra massifs (e.g., Guillaumet et al., 1975; Nicoll & Langrand, 1989).

No native rodent was trapped on either of these northern mountains in open habitats above tree line. On the upper slopes of Marojejy, *Eliurus grandidieri*, *E. majori*, and *Voalavo gymnocaudus* were all captured below or just up to tree line, but not into the ericoid grassland. The native rodent fauna below the mossy forest-ericoid bush ecotone on Anjanaharibe-Anivo is similar to that of Marojejy, except that *E. grandidieri* was not trapped above 1550 m and *Nesomys rufus* was obtained in sclerophyllous forest just below tree line at 1950 m. Although native rodents are not known to occupy alpine vegetation on these northern mountains, birds (see Chapter 10) and tenrecs (see Chapter 11) do occur in this nonforested zone.

The apparent absence of native rodents in the ericoid zones of Marojejy and Anjanaharibe-Sud contrasts with the Andringitra Massif, near the southern end of the Central High Plateau, where the vole-like genus *Brachyuromys* is abundant in similar habitat at high elevations (Goodman & Rasolonandrasana, in press). This genus is relatively widespread across upland locales on the Central High Plateau: one species, *B. ramirohitra*, appears to be restricted to the southern portion of the central highlands (900–1625 m), and the second, *B. betsileoensis*, is more widely distributed, from Andringitra in the south to the vicinity of Lac Alaotra in the north (900–2450 m). This latter species is known to occur in human-modified habitats. The Andringitra Massif today bears ericoid grassland that is closest to those mountains surrounding the Andapa Basin, some 800 km to the north, although the Ankaratra Massif (Fig. 12-5) plausibly supported such vegetation prior to human disturbance in the form of forest clearance and fires. *Brachyuromys betsileoensis* has also been obtained in grassy wet meadows on Mount Ankaratra at elevations between 1705 and 1980 m (Carleton & Schmidt, 1990), a zone that probably bridged the upper limit of montane forest and open alpine vegetation before massive destruction of the natural habitats on this mountain. To date, *Brachyuromys* has not been found in the northern (Goodman & Carleton, 1998; this study) or southern highland blocks (Goodman, Carleton, & Pidgeon, 1999) that stand apart from the Central High Plateau. However, its possible occurrence in the broad expanse of ericoid grassland covering the

summital area of the Tsaratanana Massif in the north invites exploration.

Literature Cited

- BURNEY, D. A. 1987. Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. *Palaeoecology of Africa*, **18**: 357–381.
- . 1997. Theories and facts regarding Holocene environmental change on Madagascar before and after human colonization, pp. 75–89. *In* Goodman, S. M., and B. D. Patterson, eds., *Natural change and human impact in Madagascar*. Smithsonian Institution Press, Washington, D.C.
- CARLETON, M. D. 1994. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): Revision of the genus *Eliurus*. *American Museum Novitates*, **3087**: 1–55.
- CARLETON, M. D., AND S. M. GOODMAN. 1996. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): A new genus and species from the Central Highlands. *In* Goodman, S. M., ed., *A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation*. *Fieldiana: Zoology*, n.s., **85**: 231–256.
- . 1998. New taxa of nesomyine rodents (Muroidea: Muridae) from Madagascar's northern highlands, with taxonomic comments on previously described forms. *In* Goodman, S. M., ed., *A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation*. *Fieldiana: Zoology*, n.s., **90**: 163–200.
- CARLETON, M. D., AND D. F. SCHMIDT. 1990. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. *American Museum Novitates*, **2987**: 1–36.
- DUCKWORTH, J. W., AND F. RAKOTONDRAPARANY. 1990. The mammals of Marojejy, pp. 54–60. *In* Safford, R., and Duckworth, J. W., eds., *A wildlife survey of the Marojejy Nature Reserve, Madagascar*. International Council for Bird Preservation, Cambridge.
- ELLERMAN, J. R. 1949. The families and genera of living rodents, vol. 3, appendix II [Notes on the rodents from Madagascar in the British Museum, and on a collection from the island obtained by Mr. C. S. Webb]. *British Museum (Natural History)*, London, v + 210 pp.
- GASSE, F., E. CORTIJO, J.-R. DISNAR, L. FERRY, E. GILBERT, C. KISSEL, F. LAGGOUN-DEFARGE, E. LALLIER-VERGES, J.-C. MISKOVSKY, B. RATSIMBAZAFY, F. RANAVO, L. ROBISON, P. TUCHOLKA, J.-L. SAOS, A. SIFFEDINE, M. TAIEB, E. VAN CAMPO, AND D. WILLIAMSON. 1994. A 36 ka environmental record in the southern tropics: Lake Tritrivakely (Madagascar). *Comptes Rendus de l'Académie des Sciences, série II*, **318**: 1513–1519.
- GOODMAN, S. M., AND M. D. CARLETON. 1996. The rodents of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *In* Goodman, S. M., ed., *A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation*. *Fieldiana: Zoology*, n.s., **85**: 257–283.
- . 1998. The rodents of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. *In* Goodman, S. M., ed., *A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation*. *Fieldiana: Zoology*, n.s., **90**: 201–221.
- GOODMAN, S. M., AND D. RAKOTONDRAVONY. 2000. The effects of forest fragmentation and isolation on insectivorous small mammals (Lipotyphla) on the Central High Plateau of Madagascar. *Journal of Zoology*, London, **250**: 193–200.
- GOODMAN, S. M., AND B. P. N. RASOLONANDRASANA. In press. Elevational zonation of birds, insectivores, rodents, and primates on the slopes of the Andringitra Massif, Madagascar. *Journal of Natural History*.
- GOODMAN, S. M., M. D. CARLETON, AND M. PIDGEON. 1999. The rodents of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. *In* Goodman, S. M., ed., *A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation*. *Fieldiana: Zoology*, n.s., **94**: 217–249.
- GOODMAN, S. M., P. D. JENKINS, AND M. PIDGEON. 1999. The Lipotyphla (Tenrecidae and Soricidae) of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. *In* Goodman, S. M., ed., *A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation*. *Fieldiana: Zoology*, n.s., **94**: 187–216.
- GOODMAN, S. M., A. ANDRIANARIMISA, L. E. OLSON, AND V. SOARIMALALA. 1996. Patterns of elevational distribution of birds and small mammals in the humid forest of Montagne d'Ambre Madagascar. *Ecotropica*, **2**: 87–98.
- GOODMAN, S. M., J. GANZHORN, L. E. OLSON, M. PIDGEON, AND V. SOARIMALALA. 1997. Annual variation in species diversity and relative density of rodents and insectivores in the Parc National de la Montagne d'Ambre, Madagascar. *Ecotropica*, **3**: 109–118.
- GOODMAN, S. M., D. RAKOTONDRAVONY, L. E. OLSON, E. RAZAFIMAHATRATRA, AND V. SOARIMALALA. 1998. Les insectivores et les rongeurs, pp. 80–93. *In* Rakotondravony, D., and S. M. Goodman, eds., *Inventaire biologique, Forêt d'Andranomay, Anjozorobe*. World Wide Fund for Nature—Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, *Recherches pour le Développement, Série Sciences Biologiques*, no. **13**.
- GREEN, G. M., AND R. W. SUSSMAN. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science*, **248**: 213–215.
- GRIVEAUD, P. 1960. Une mission entomologique au Marojejy. *Naturaliste Malgache*, **12**: 43–55.
- GUILLAUMET, J.-L., J.-M. BETSCH, C. BLANC, P. MORAT, AND A. PEYRIERAS. 1975. Étude des écosystèmes montagnards dans la région malgache. III. Le Marojejy. IV. L'Itremo, et l'Ibity. *Géomorphologie, climatologie, fauna et flore (Campagne RCP 225, 1972–1973)*. *Bulletin du Muséum National d'Histoire Naturelle*, 3rd series, no. 309, *Écologie Générale*, **24**: 29–67.

- HAWKINS, A. F. A., J.-M. THIOLLAY, & S. M. GOODMAN. 1998. The birds of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. *In* Goodman, S. M., ed., A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **90**: 93–127.
- HUMBERT, H., AND G. COURTS DARNE. 1965. Carte internationale du tapis végétal et des conditions écologiques. Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry (hors série).
- JANSA, S. A. 1998. Molecular phylogeny and biogeography of Madagascar's native rodents (Muridae: Nesomyinae). Ph. D. thesis, University of Michigan, 200 pp.
- JENKINS, P. D. 1987. Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles. Part IV. Suborder Strepsirrhini, including the subfossil Madagascan lemurs and family Tarsiidae. British Museum (Natural History), London, x + 189 pp.
- LANGRAND, O., AND S. M. GOODMAN. 1997. Inventaire des oiseaux et des micro-mammifères des zones sommitales de la Réserve Naturelle Intégrale d'Andringitra. *Akon'ny Ala*, **20**: 39–54.
- LEWIS, B. A., P. B. PHILLIPSON, M. ANDRIANARISATA, G. RAHAJASOA, P. J. RAKOTOMALAZA, M. RANDRIAMBOLONA, AND J. F. McDONAGH. 1994. A study of the botanical structure, composition, and diversity of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **85**: 24–75.
- NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des Aires Protégées. World Wide Fund for Nature, Gland, Switzerland, xvii + 374 pp.
- RAHBEK, C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. *The American Naturalist*, **149**: 875–902.
- RAKOTONDRAVONY, D., S. M. GOODMAN, J.-M. DUPLANTIER, AND V. SOARIMALALA. 1998. Les petits mammifères, pp. 197–212. *In*: Ratsirarson, J., and S. M. Goodman, eds., Inventaire biologique de la Forêt Littorale de Tampolo. Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, Recherches pour le Développement, Série Sciences Biologiques, no. **14**.
- RAND, A. L. 1932. Mission Franco-Anglo-Américaine à Madagascar: Notes de voyage. Oiseau et Revue Française d'Ornithologie, **2**: 227–282.
- . 1936. The distribution and the habits of Madagascar birds: A summary of the field notes of the Mission Zoologique Franco-Anglo-Américaine à Madagascar. *Bulletin of the American Museum of Natural History*, **72**: 143–499.
- RAXWORTHY, C. J., AND R. A. NUSSBAUM. 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological Conservation*, **69**: 65–73.
- . 1996. Montane amphibian and reptile communities in Madagascar. *Conservation Biology*, **10**: 750–756.
- ROSENZWEIG, M. L. 1992. Species diversity gradients: We know more or less what we thought. *Journal of Mammalogy*, **73**: 715–730.
- ROSENZWEIG, M. L., AND Z. ABRAMSKY. 1993. How are diversity and productivity related? pp. 52–65. *In* Ricklefs, R. E., and D. Schluter, eds., *Species diversity in ecological communities*. University of Chicago Press, Chicago, 414 pp.
- STEPHENSON, P. J., H. RANDRIAMAHAZO, N. RAKOTOARISON, AND P. A. RACEY. 1994. Conservation of mammalian species diversity in Ambohitantely Special Reserve, Madagascar. *Biological Conservation*, **69**: 213–218.
- THOMAS, O. 1895. On a new species of *Eliurus*. *Annals and Magazine of Natural History*, series 6, **16**: 164–165.
- . 1908. A new species of the Mascarene genus *Eliurus*. *Annals and Magazine of Natural History*, series 8, **2**: 453–454.
- VOSS, R. S., AND M. D. CARLETON. 1993. A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an analysis of its phylogenetic relationships. *American Museum Novitates*, **3085**: 1–39.

Appendix 12-1

Listed below are vouchered specimens of *Eliurus* collected outside of PN de Marojejy that were used in the taxonomic comparisons and morphometric analyses. They are contained in the following museums: British Museum (Natural History), London (BMNH); Field Museum of Natural History, Chicago (FMNH); Merseyside County Museums, Liverpool (LMCM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Universitets Zoologisk Museum, Copenhagen (UZMC); and Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK).

Eliurus majori—Antsiranana Province: PN de la Montagne d'Ambre, 1000–1350 m (AMNH 100687, 100854; FMNH 154535–154539, 154603–154616, 156341–156345); RS d'Anjanaharibe-Sud, 1260–1950 m (FMNH 154052–154054, 154241–154245, 154266, 154289). Fianarantsoa Province: Ambohitombo (BMNH 97.9.1.147; MCZ 45929); RNI d'Andringitra, 1210–1625 m (FMNH 151661–151667, 151730–151732, 151752, 151847,

151848, 151852, 151853, 151855); Anjavidilava (MNHN 1972.602); RS d'Ivohibe, 1575 m (FMNH 161891, 162073–162075). Toliara Province: RNI d'Andohahela, 1200–1500 m (FMNH 156615–156617, 156658).

Eliurus penicillatus—Fianarantsoa Province: Ampitambe (BMNH 97.9.1.148–97.9.1.150, 97.9.1.152, 1939.1892; FMNH 18822; LCMC A19.4.98.26; MCZ 45932; MNHN 1897.536, 1909.191; USNM 49672; UZMC 1219, 1224, 7941; ZFMK 82.217, 83.56).

Eliurus webbi—Antsiranana Province: PN de la Montagne d'Ambre, 650–1000 m (MNHN 1957.781, 1970.248, 1970.249, 1973.517, 1973.518; UA-SMG 6755); RS d'Anjanaharibe-Sud, 875 m (FMNH 154035–154038, 154251, 154252). Toamasina Province: 3 mi E Andranofotsy, 12 km NE Maroantsetra, near sea level (BMNH 47.1585, 47.1586, 47.1588); Antalaha (MNHN 1961.179); Antalavia, E side Antongil Bay, near sea level (BMNH 47.1590); 40 km SW

Maroantsetra, 10 km WSW Maintimbato, 450–625 m (BMNH 1987.108); 40 km NE Maroantsetra, Ankovana, 900 ft (BMNH 47.1589); 8 mi W Rantabe, Antongil Bay, 500 ft (BMNH 47.1593). Fianarantsoa Province: 2 km NE Andrambovato, 575–625 m (USNM 449266–449268); 1 km NW Andrambovato, 875 m (USNM 449269); 12 km E Ifanadiana (MNHN 1961.216–1961.219); 0.5 km N Kianjavato, 300 m (USNM 448991–448995); 9 km ESE Kianjavato, 250–500 m (USNM 449257–449265); RNI d'Andringitra, 720–810 m (FMNH 151680–151686, 151739–151742, 151884, 151885, 151888, 151891–151895, 156513, 156523–156526, 156529, 156644); RS d'Ivohibe, 900 m (BMNH 47.1594–47.1599; FMNH 162091); 20 km W Vondrozo (MNHN 1932.3517, 1957.782); 20 mi S Farafangana, 4 mi from sea (AMNH 119707; BMNH 47.1574–47.1579, 47.1582–47.1584). Toliara Province: RNI d'Andohahela, 440–810 m (FMNH 156513, 156523–156526, 156529, 156644).

Chapter 13

Rapid Census of Lemur Populations in the Parc National de Marojejy, Madagascar

Eleanor Sterling¹ and Karen McFadden²

Abstract

This chapter discusses the results of a primate survey conducted between 4 October and 20 November 1996 in the Parc National de Marojejy, northeastern Madagascar. Research sites were established at five elevations—450, 775, 1250, 1625, and 1875 m; surveys were confined to areas 75 m higher or lower in altitude at each elevation. Species richness and an index of density were calculated for lemur species, at all sites, by means of both the line transect method and an experimental density estimation method. Ten lemur species were recorded in the reserve. Species richness did not differ greatly between the four lower elevational zones but dropped sharply at the highest elevation. Key taxa found within the reserve include *Daubentonia madagascariensis*, *Propithecus diadema candidus* and possibly *Phaner furcifer*. Other taxa observed in the reserve include *Eulemur fulvus albifrons*, *E. rubriventer*, *Hapalemur griseus griseus*, *Avahi laniger*, *Cheirogaleus major*, *Microcebus rufus*, and *Lepilemur mustelinus*.

Résumé

Cet article commente les résultats de l'inventaire des primates, conduit entre le 4 octobre et le 20 novembre 1996, dans le Parc National de Marojejy, dans le Nord-Est de Madagascar. Les sites de recherche ont été repartis sur cinq niveaux d'altitude: 450, 775, 1250, 1625, et 1875 m, l'inventaire étant limité à l'intérieur d'une bande de 75 m en dessus et au-dessous de chaque niveau d'altitude. La richesse spécifique et l'indice de la densité des lémuriens ont été mesurés dans tous les sites par l'utilisation simultanée de la méthode des transects et d'une méthode expérimentale pour estimer la densité. Dix espèces de lémuriens ont été enregistrées dans le parc. La richesse spécifique ne diffère pas beaucoup entre les quatre plus basses zones d'altitudes, mais elle baisse considérablement au niveau de l'altitude la plus élevée. Les groupes taxinomiques clés trouvés dans le parc comprennent *Daubentonia madagascariensis*, *Propithecus diadema candidus* et peut être *Phaner furcifer*. Les autres espèces observées dans le parc incluent *Eulemur fulvus albifrons*, *Eulemur rubriventer*, *Hapalemur griseus griseus*, *Avahi laniger*, *Cheirogaleus major*, *Microcebus rufus*, et *Lepilemur mustelinus*.

Introduction

Madagascar's northeastern forests, representing a majority of the country's remaining intact rain-forest tracts, harbor high levels of floral and faunal diversity and endemism. Although the lemur

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populations are a prominent feature of these rain-forest areas, comprehensive survey work in these communities remains to be done. Meanwhile, conversion of forest tracts for agricultural use continues to fragment the habitats of many species, and hunting pressures directly affect the primate populations.

The Parc National (PN) de Marojejy is composed primarily of moist montane and sclerophyllus montane forest. This area serves as a watershed for numerous outlying areas. Accurate baseline inventory data are critical for establishing an effective management plan for this reserve's biota. Ideally, such information would come from intensive, long-term surveys. However, hunting and resource extraction pressure on the reserve, coupled with inadequate protection measures and limited resources, necessitate that more-rapid and efficient methods of assessment be used.

As part of an extensive program to assess biodiversity in forested areas, a multitaxa survey and inventory expedition was undertaken in the PN de Marojejy from early October to mid-November 1996. Data on primate species richness and abundance were collected in the southeastern sector of the reserve. Earlier surveys identified a total of nine species of primates in the PN de Marojejy (Humbert, 1955; Guillaumet et al., 1975; Benson et al., 1976, 1977; Tattersall, 1982; Nicoll & Langrand, 1989; Safford & Duckworth, 1990), including endangered species such as the Sifaka (*Propithecus diadema*) and the Aye-aye (*Daubentonia madagascariensis*). Sightings from the Réserve Spéciale (RS) d'Anjanaharibe-Sud, 20 km to Marojejy's southwest (Schmid & Smolker, 1998), and the PN de Masoala, approximately 100 km to the southeast (Sterling & Rakotoarison, 1998), suggest that the PN de Marojejy could possibly include other endangered primate species, such as the Hairy-eared Dwarf Lemur (*Allocebus trichotis*). Information about the distribution and density of primate species in the PN de Marojejy and the degree of threat to these populations represents important data for the Association National pour la Gestion des Aires Protégées, which manages the reserve in the context of an integrated conservation and development project, under the direction of the World Wide Fund for Nature.

Methods

Study Area

The PN de Marojejy undergoes two extensive wet seasons—the intense November to April sea-

son, peaking in January, when cyclones occur, and the lesser June to August season, which is the time of year with the lowest temperatures in other northeastern rainforests (Sterling, 1993). In the present study, survey zones were established at five sites along an elevational gradient. Each elevational zone (450, 775, 1250, 1625, and 1875 m) encompassed an area ± 75 m in altitude, to create nonoverlapping 150 m bands.

Census Methods

Surveys were conducted between 4 October and 20 November 1996. During the 10 days we spent at each elevational zone, two survey methods were used, including the line transect method and an experimental technique that used both transect and nontransect observations. Previous expeditions of similar length had indicated that the line transect method may not yield enough data in 10 days to allow for the calculation of density estimates (Sterling & Rakotoarison, 1998); consequently, a second method was tested in this study.

The line transect method was used along four to six different trails at each elevational zone. Some of the trails were pre-existing; others were opened and marked for this study. Sightings were made by one observer while walking these trails for distances varying from 125 to 1475 m. Diurnal surveys were conducted between 500 and 1100 and between 1400 and 1700 hr, for an average of 6 hours per day. Nocturnal surveys occurred between 1830 hr and dawn, for an average of 4 hours on any one night. Transects were walked at a steady speed of 1 km per hour during the day and 0.75 km per hour at night. Low-power headlamps were used on night census walks to detect nocturnal species, whose eyeshine reflects the light. Brighter lights were then used to illuminate the animal for identification. Weather permitting, each trail was censused at least three times (ranging from two to six times per day/night) during the 10 days, for both diurnal and nocturnal censuses, but never consecutively during the same day or night session. When groups were detected along the transect trail, the perpendicular distance from the animal to the transect was estimated for the first individual in each sighted group. The distance and the angle from the observer to the animal were also recorded, to test the accuracy of our perpendicular distance estimates.

TABLE 13-1. Species richness by elevational zone for transect and nontransect data, October–November 1996, PN de Marojejy.

Species	Presence at elevational zone (m)				
	450	775	1250	1625	1875
<i>Eulemur fulvus albifrons</i>	X	X	X	X	
<i>Eulemur rubriventer</i>	X*	X	X	X	
<i>Hapalemur griseus griseus</i>	X	X	X	X	
<i>Propithecus diadema candidus</i>			X	X	X
<i>Avahi laniger</i>	X	X	X		
<i>Cheirogaleus major</i>	X	X	X	X	
<i>Microcebus rufus</i>	X	X	X	X	X
<i>Lepilemur mustelinus</i>	X?*	X	X	X	
<i>Phaner furcifer</i>	X?*				
<i>Daubentonia madagascariensis</i>	X	X	X	X	X
Total no. of species	8	8	9	8	3

* Species heard but not seen at this elevation.

When animals were sighted, pelage color, body size, height in tree, type of habitat, location along the transect, and behavioral and feeding information were noted, for each individual, as often as possible. For lemurs detected in groups (mainly diurnal species) the total number and demographic composition of the group was recorded.

The second census method (a modification of Merenlender et al., 1998) incorporated both transect and nontransect sightings of animals, to arrive at a density estimate. All sightings of lemurs by primatologists and other experienced primate observers on the expedition, whether on- or off-trail, were recorded, and morphological and behavioral information similar to that collected on the transects was noted. Distance and angle were taken from the nearest topographic feature if there was no nearby trail. Taxa seen more than three times were plotted on a map of the transect area. The outermost of these points were plotted by means of a global positioning system (GPS) and were corrected via topographical, hydrological, and altimeter data. Area calculations for density estimates were created by calculation of the minimum convex polygon linking up the outer points.

Groups were identified by means of one of two methods. First, several groups contained individuals with distinctive pelage characters. This information was combined with information on number of individuals and sex ratio to identify groups. Second, data on home range area for populations of the same species in other eastern rainforest reserves (Mittermeier et al., 1994) were used to estimate which of the sightings were within the species' average home range and which were outside the range. Sightings farther apart

than the average home range size for the species were presumed to be distinct animals or groups and were used to calculate a maximum population size. Sightings within home range size were treated as the same group or animal and were used to calculate a minimum population size.

During all observation periods, we looked for secondary signs of lemur presence, including nests, fallen fruit with tooth comb or incisor marks, and Aye-aye feeding holes in dead trees, in bamboo, or in *Canarium* (Bursaceae) seeds.

Results and Species Accounts

Ten species were recorded within the reserve, across all elevations (Table 13-1). Nine of those species were observed directly, whereas one (possibly *Phaner furcifer*) was only heard. None of the five elevational zones contained all ten species. At 450, 775, and 1250 m, the total number of species remained relatively similar (range, 8–9), but species composition varied. At the lowest elevational zone, we did not encounter *Lepilemur*, but we heard calls that were either *Phaner furcifer* or *Lepilemur*. At the second camp, we did see *Lepilemur*. At the highest elevational zone, only three lemur species were recorded.

Since the number of sightings at all elevational zones was insufficient to calculate transect width, no estimates of lemur densities were made for the line transect data. Data from line transects are instead presented as number of sightings of lemurs per kilometer transect (Tables 13-2 and 13-3). Data for the experimental method are presented

TABLE 13-2. No. of individuals seen per kilometer transect for diurnal primate species. PN de Marojejy, October–November 1996.

Altitude and site	Total distance walked (m)	No. of individuals of species				No. of species
		<i>Efa</i>	<i>Er</i>	<i>Hgg</i>	<i>Pdc</i>	
450 m						
1a	2975	1	0	1	0	2
1b	2400	5	0	1	0	2
1c	3050	0.3	0	1	0	2
1d	3200	0	0	3	0	1
Detection distance		6.0 ± 4.6	—	7.5 ± 1.2	—	
775 m						
2a	1000	0	0	0	0	0
2b	1600	0	3	0	0	1
2c	5000	1	0	2	0	2
2d	2550	0	0	2	0	1
2e	1800	3	1	0	0	2
Detection distance		14.5 ± 7.6	5.8 ± 6.0	12.9 ± 7.9	—	
1250 m						
3a	825	0	4	0	4	2
3b	1200	0	0	0	4	1
3c	5375	1	1	0	0	2
3d	3800	0	1	1	1	3
Detection distance		5*	14.2 ± 4.0	15*	19.0 ± 6.6	
1625 m						
4a	2000	0	1	0	0	1
4b	2325	0	2	0	2	2
4c	8325	0	0	2	0	1
4d	125	0	0	0	8	1
4e	500	0	0	0	0	0
Detection distance		—	13.3 ± 10.1	10*	13.5 ± 2.1	
1875 m						
		0	0	0	6	
5a	875	0	0	0	4	1
5b	1150	0	0	0	0	1
5c	500	0	0	0	0	0
5d	1300	0	0	0	0	0
5e	250	—	—	—	6.0 ± 5.7	0
Detection distance		9	10	11	7	
N						
Mean group size		3.1 ± 1.9	2.3 ± 0.8	3.2 ± 1.7	3.9 ± 1.7	

NOTE—*Efa* = *Eulemur fulvus albifrons*, *Er* = *E. rubriventer*, *Hgg* = *Hapalemur griseus griseus*, and *Pdc* = *Propithecus diadema candidus*. Detection distance is the mean distance (± standard deviation), perpendicular to the trail, at which lemurs were seen.

* Single sighting at this elevation.

as maximum and minimum density estimates (Table 13-4).

Five lemur traps, consisting of forest clearings of 20 m in width, with a branch traversing the open area covered with a spiral trap, were found at the first elevational zone. In one of these traps, we recovered the skull of an individual belonging to *Eulemur fulvus*. Many species, notably *Hapalemur griseus*, *Propithecus diadema candidus*, *E. fulvus albifrons*, and *E. rubriventer*, reacted

strongly to the presence of humans, generally fleeing or hiding and alarm calling.

Avahi laniger

Avahi laniger was found at the first three elevational zones and was not observed at 1625 or 1875 m. These lemurs were seen in a pair once.

TABLE 13-3. No. of individuals seen per kilometer transect for nocturnal primate species, PN de Marojejy, October–November 1996.

Altitude and site	Total distance walked (m)	No. of individuals of species				No. of species
		<i>Al</i>	<i>Lm</i>	<i>Mr</i>	<i>Cm</i>	
450 m						
1a	2425	0	0	0	0.4	1
1b	1200	0	0	1	0	1
1c	2050	0	0	0.5	0	1
1d	2100	0	0	1	0	1
Detection distance		—	—	3.9 ± 1.4	2.5*	
Total observations		—	—	4	1	
775 m						
2a	350	0	0	3	3	2
2b	800	0	0	0	0	0
2c	1475	0	0	0	0	0
2d	1600	0	1	0	0	1
2e	900	1	2	2	1	4
2f	150	0	0	7	7	2
Detection distance		20*	4.2 ± 4.7	8.8 ± 1.5	6.3 ± 5.5	
Total observations		1	3	3	3	
1250 m						
3a	500	0	0	0	0	0
3b	1200	1	0	0	2	2
3c	5900	0.2	1	0.2	0	3
3d	2550	0.4	0	1	0	2
Detection distance		11.0 ± 3.6	18*	—	10.5 ± 3.5	
Total observations		3	1	4	2	
1625 m						
4a	150	0	0	0	7	1
4b	2600	0	0	1	0	0
4c	375	0	0	3	0	1
4d	375	0	0	0	0	0
Detection distance		—	—	15.3 ± 8.7	25*	
Total observations		—	—	3	1	
1875 m						
5a	825	0	0	1	0	1
5b	275	0	0	0	0	0
Detection distance		—	—	10*	—	
Total observation		—	—	1	—	

NOTE—*Al* = *Avahi laniger*, *Lm* = *Lepilemur mustelinus*, *Mr* = *Microcebus rufus*, and *Cm* = *Cheirogaleus major*. Detection distance is the mean distance (\pm standard deviation), perpendicular to the trail, at which lemurs were seen.

* Single sighting at this elevation.

but otherwise singly. No young were observed during this study.

Cheirogaleus major

Cheirogaleus major was found at the four lowest elevational zones but was never particularly common. All individuals were observed singly. No significant size difference was noted between

different individuals in the reserve, and no young were observed during this study.

Daubentonia madagascariensis

Proximate evidence of *Daubentonia madagascariensis* was found in all elevational zones. This species was observed directly only once, during a nocturnal transect in the 450 m zone. It was seen

TABLE 13-4. Absolute density estimates in individuals per square kilometer for minimum convex polygon areas, October–November 1996, PN de Marojejy.

Species	Individuals per square kilometer, at altitude (m)									
	450		775		1250		1625		1875	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
<i>Eulemur fulvus albifrons</i>		*	37	57	10	20	5	—		
<i>Eulemur rubriventer</i>		*	37	—	33	47	*			
<i>Hapalemur griseus griseus</i>		24	57	82	*		*			
<i>Propithecus diadema candidus</i>					40	—	90	—		*
<i>Avahi laniger</i>		*		*	10	—				
<i>Lepilemur mustelinus</i>			16	20	16	20	*			
<i>Microcebus rufus</i>	18	24	20	—	7	13	10	15		*
<i>Cheirogaleus major</i>		*	12	—		*	*			
<i>Daubentonia madagascariensis</i>		*		†		†	†			†

NOTE. Min. = minimum; Max. = maximum.

* Taxa observed fewer than three times.

† For this species, presence was inferred at these elevations, on the basis of distinctive signs.

for only an instant as it crossed the path in front of the observers, at ground level, and then disappeared into a bamboo thicket. In the lowest elevational zone, we noted an old Aye-aye nest, and we saw several stands of bamboo with characteristic signs of Aye-aye feeding (Duckworth, 1993). In the 775 and 1250 m zones, we noted remains of *Canarium* spp. nuts with clear Aye-aye feeding marks (Iwano & Iwakawa, 1988; Goodman & Sterling, 1996). In the two uppermost elevational zones, observers located remains of deadwood and also of bamboo where Aye-ayes had fed.

Lepilemur mustelinus

Lepilemur mustelinus was found in the three middle elevational zones (Table 13-1). Animals were generally seen singly, although one observation included two animals, a female and a young animal, together. Observed pelage characteristics: upper parts mainly chestnut brown, tail black, and whitish whiskers on some individuals.

Microcebus rufus

Microcebus rufus occurs at all elevational zones. We often heard but had few direct observations of this species. Researchers located a nest just outside the 775 m zone in October 1996. The nest contained one young mouse lemur with newly opened eyes. At 1250 m, we recorded *Microcebus* feeding on fruit from a *Dypsis* sp. An owl

(*Asio madagascariensis*) pellet collected at the 1625 m site contained the remains of an *M. rufus* (S. Goodman, pers. comm.). Given the small home range size of this owl, the mouse lemur was mostly likely taken near where the pellet was deposited (S. Goodman, pers. comm.). Observed pelage characteristics: upper parts and dorsum reddish-brown, thin dorsal black stripe, and dark brown tail.

Diurnal Censuses

Hapalemur griseus griseus

Hapalemur griseus griseus groups were found in all but the highest elevational zone. Average group size in the reserve was 3.2 ± 1.7 individuals. Researchers observed them feeding on a fungus (undetermined) and on wild bananas (Musaceae) in the 450 m zone. *Cryptoprocta* scat collected in the 1250 m zone and subsequently analyzed by Steve Goodman contained bones of *H. griseus*. Notable pelage characteristics: dark rufous ventrum, and a pronounced white triangle around nose.

Eulemur fulvus albifrons

Groups of this species were observed in the first four elevational zones. Average group size in the reserve was estimated at 3.1 ± 1.9 individuals. This is low compared with populations in other

areas, and it may be a sampling artifact due to lemurs fleeing from humans in the area. At 450 m, researchers observed individuals feeding on *Meleastrum* sp., whereas in the 1250 m zone they were observed eating *Cryptocarya* sp.—the major fruiting species in this zone other than *Canarium*, during the transect study. Young individuals were seen in 30% of the observed groups. Observed pelage characteristics: upper and dorsal pelage color in males varied from dark brown to light gray.

Eulemur rubriventer

No group of this species was found in the highest elevational zone, although groups were observed in all others. One group was recorded on audiotape in the 450 m zone, but none were actually seen in this zone. Groups were seen every day in the 1250 m elevational zone. Average group size in the reserve was 2.3 ± 0.8 individuals. Researchers observed individuals in the 1250 m zone eating *Cryptocarya* sp.—the major fruiting species in this zone other than *Canarium*. We noted young individuals in 75% of these groups.

Propithecus diadema candidus

Propithecus diadema candidus groups were observed in the three highest elevational zones. Average group size in the reserve was 3.9 ± 1.7 individuals. Young animals were observed in all three zones, and 50% of the groups observed contained young individuals. *P. d. candidus* groups at the highest elevational zone came quite close to the observers, enabling us to observe their pelage color well. Individuals in the same group had coat colors that ranged from all white (the expected morph for the subspecies) to mostly white with a black or yellow pygal patch to animals with faint colors in a pattern that resembled *P. d. diadema* pelage. Notable pelage characteristics: some individuals were pure white; some had a dark brown or yellow pygal patch; face black or pink; thick white fur at underarm/triceps; two individuals had black heads; one individual had a thick black stripe from the top of the head down the back and across the shoulders that lightened posteriorly; one individual had light amber color on upper portions of shoulder and thigh; and one individual had a thin black stripe down the back.

Species Accumulation Curves

Diurnal and nocturnal primate species were observed along transects within 2 and 16 person-hours of observation (Figure 13-1) across elevations. One species (*Eulemur rubriventer*) was observed in the 450 m zone but was not observed along the transects. Total effort for both nocturnal and diurnal species was less than in previous studies because only one primatologist worked this survey, both day and night. In addition, at the highest elevational zone, the existing trails were surveyed at least once a day, but there was very little forest and the trails were quite short (Tables 13-3 and 13-4), so it was difficult to get quantitative results in a short time.

Discussion

The total number of lemur species found in the PN de Marojejy (10) is about average for eastern rainforest primate communities. The closest rainforests for which recent survey information is available are the RS d'Anjanaharibe-Sud, where 11 species were observed (Schmid & Smolker, 1998), and the PN de Masoala, where 10 species were seen (Table 13-5). Species composition varied among these sites, with some species observed in only one of the three sites (e.g., *Indri indri* in the RS d'Anjanaharibe-Sud and *Varecia variegata rubra* in the PN de Masoala). The PN de Masoala has a comparatively impoverished diurnal primate fauna of only four taxa. It is still unclear why *Indri indri* is found 20 km to the southwest in Anjanaharibe-Sud (Schmid & Smolker, 1998) and not in Marojejy.

At the lowest elevational zone of the PN de Marojejy, we heard two species that we did not expect to find. Outside Marojejy, *Eulemur rubriventer* has mainly been found at middle elevations and above. This is the first published record of *E. rubriventer* at low altitudes. They are probably present at low densities at this altitude. *Phaner* had not been observed previously in the PN de Marojejy, but eastern populations of this species are usually found in low density, and individuals seem to vocalize less often than those in western populations. If the individuals heard were indeed *Phaner*, it would not be too surprising, as their distribution includes areas to the north (Daraina) and south (Masoala Peninsula) of PN de Marojejy (Mittermeier et al., 1994). No *Allocebus trichotis*

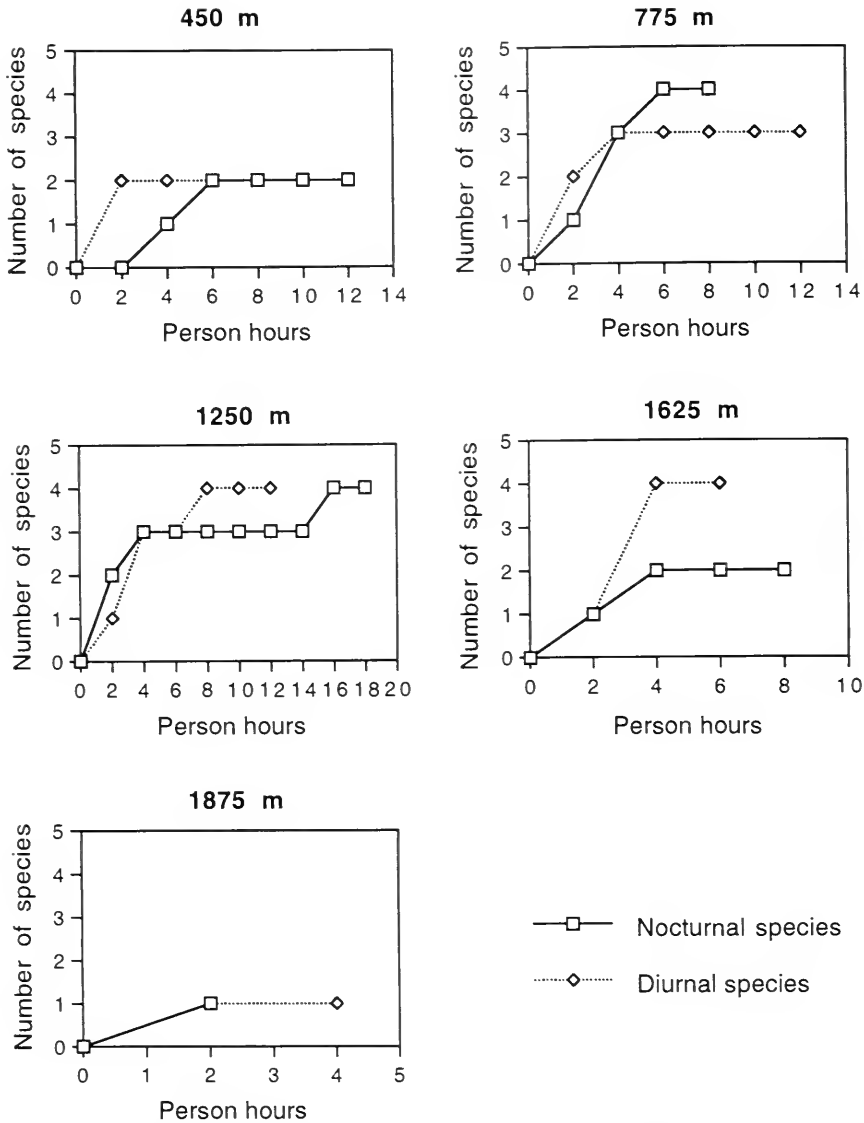


FIG. 13-1. Species accumulation curves for primate populations, October–November 1996, at five sites in the PN de Marojejy.

was observed during the course of this study, despite their having been found in RS d'Anjanaharibe-Sud, to the southwest (Schmid & Smolker, 1998).

The fact that a *Microcebus rufus* infant was found with its eyes open in mid-October is unusual, given that *M. rufus* populations in the PN de Ranomafana mate in mid-September, with births in November (Atsalis, 1998). Gestation in this species is thought to last 60 days, and infants open their eyes within 2–4 days of birth (Glatston,

1979), which puts conception at mid-August. Reproduction in mouse lemurs could be affected by a variety of factors, including temperature, which itself might vary at any one time between altitudes.

Experience from previous multitaxa expeditions has suggested that the line transect method may not always be the optimal method for estimation of primate density in short surveys because low numbers of sightings do not allow for the determination of the area surveyed (Sterling

TABLE 13-5. Species observed in the PN de Marojejy and neighboring protected areas.

Species	PN de Marojejy	RS d'Anjanaharibe-Sud*	PN de Masoala†
<i>Eulemur fulvus albifrons</i>	X	X	X
<i>Eulemur rubriventer</i>	X	X	
<i>Haplemur griseus griseus</i>	X	X	X
<i>Indri indri</i>		X	
<i>Propithecus diadema candidus</i>	X	X	
<i>Varecia variegata rubra</i>			X
<i>Avahi laniger</i>	X	X	X
<i>Lepilemur mustelinus</i>	X	X	X
<i>Allocebus trichotis</i>		X	X
<i>Microcebus rufus</i>	X	X	X
<i>Cheirogaleus major</i>	X	X	X
<i>Phaner furcifer</i>	X		X
<i>Daubentonia madagascariensis</i>	X	X	X
Total species	10	11	10

* Schmid and Smolker, 1998.

† Sterling and Rakotoarison, 1998.

& Ramarason, 1996; Duckworth, 1998; Sterling & Rakotoarison, 1998). This was the case in this particular study, as the total number of observations of lemur groups or individuals, diurnal or nocturnal, was low. The fact that *Eulemur rubriventer* was recorded on audiotape, but not observed, underscores the inadequacy of 10 days or less of surveys for estimation of primate richness and density by one experienced researchers in an area. Thus, it is difficult to analyze or compare the density data. Although density estimates are given for both methods (for the line transect method, we only calculated relative density estimates), we consider these data preliminary and subject to further research. The experimental method seems to be feasible from a logistical standpoint for collecting data on diurnal primates during short surveys, but it must be tested in an area of known density, to assess its accuracy. This method would be susceptible to differences in observer reliability, the quality of home range size data from other studies, and number of person-hours spent in the survey zone. The low number of total observations per species at each elevation limited the efficacy of this method during the current survey. These low numbers were probably related to climate, as the weather was unseasonably cold and wet during the survey.

Hunting pressure on lemurs on the lower slopes of the southeastern portion of the reserve appears to be relatively high, given both the reaction of diurnal groups to the presence of humans and the presence of lemur traps. Adequate conservation of this reserve is critical to the survival of *Propithecus diadema candidus*, as it is only one of two

existing protected areas (along with RS d'Anjanaharibe-Sud) that harbor this endangered subspecies.

Acknowledgments

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Literature Cited

- ATSALIS, S. 1998. Feeding ecology and aspects of life-history in *Microcebus rufus* (family Cheirogaleidae, order Primates). Ph.D. diss., City University of New York, New York, NY.
- BENSON, C. W., J. F. R. COLEBROOK-ROBJENT, AND A. WILLIAMS. 1976. Contribution à l'ornithologie de Madagascar. Oiseaux et R.F.O., **46**: 103-134, 209-242, 367-386.
- . 1977. Contribution à l'ornithologie de Madagascar. Oiseaux et R.F.O., **47**: 41-64, 167-191.
- DUCKWORTH, J. W. 1993. Feeding damage left in bamboos, probably by aye-ayes (*Daubentonia madagascariensis*). Folia Primatologica, **14**: 927-931.
- . 1998. The difficulty of estimating population densities of nocturnal forest mammals from transect counts of animals. Journal of Zoology, **264**: 466-468.
- GLATSON, A. R. H. 1979. Reproduction and behavior of

- the lesser mouse lemur (*Microcebus murinus*, Miller 1777) in captivity. Ph.D. diss. University of London, University College, London, United Kingdom.
- GOODMAN, S. M., AND E. J. STERLING. 1996. The utilization of *Canarium* (Burseraceae) seeds by vertebrates in the RNI d'Andringitra, Madagascar, pp. 83–89. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **85**: 83–89.
- GUILLAUMET, J. L., J. M. BETSCH, C. BLANC, P. MORAT, A. PEYRIERAS, SOUS LA DIRECTION DE R. PAULIAN. 1975. Etude des écosystèmes montagnards dans la région malgache. III. Le Marojezy. IV. L'tremo et l'Ibity. Géomorphologie, climatologie, faune et flore (Campagne RCP 225, 1972–73). *Bulletin du Muséum National d'Histoire Naturelle* (Paris), série 3, 309 (*Ecologie Générale*), **25**: 27–67.
- HUMBERT, H. 1955. Une merveille de la nature à Madagascar. Première exploration botanique du massif du Marojezy, et de ses satellites. *Mémoires de l'Institut Scientifique de Madagascar*, série B, **6**: 1–210.
- IWANO, T., AND C. IWAKAWA. 1988. Feeding behavior of the aye-aye (*Daubentonia madagascariensis*) on the nuts of rany (*Canarium madagascariensis*). *Folia Primatologica*, **50**: 136–142.
- MERENLENDER, A., C. KREMEN, M. RAKOTONDRATSIMA, AND A. WEISS. 1998. Monitoring impacts of natural resource extraction on lemurs on the Masoala Peninsula, Madagascar. *Conservation Ecology*, **2**: article 5. Available: www.consecol.org/Journal.vol2/iss2/art5/
- MITTERMEIER, R., I. TATTERSALL, W. R. KONSTANT, D. M. MEYERS, AND R. B. MAST. 1994. Lemurs of Madagascar. Conservation International, Washington, D.C.
- NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des aires protégées. World Wide Fund for Nature, Gland, Switzerland, 374 pp.
- SAFFORD, R., AND W. DUCKWORTH. 1990. A wildlife survey of Marojezy Nature Reserve, Madagascar. ICBP, Cambridge.
- SCHMID, J., AND R. SMOLKER. 1998. Lemurs of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, pp. 227–238. *In* Goodman, S. M., ed., A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **90**: 227–238.
- STERLING, E. J. 1993. The behavioral ecology of the Aye-aye on Nosy Mangabe, Madagascar. Ph.D. Diss., Yale University, New Haven, Conn.
- STERLING, E. J., AND M. G. RAMAROSON. 1996. Rapid assessment of the primate fauna of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 293–305. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **85**: 293–305.
- STERLING, E. J., AND N. RAKOTOARISON. 1998. Rapid assessment of the primate species richness and density on the Masoala Peninsula, eastern Madagascar. *Folia Primatologica*, **69**: (suppl. 1): 109–116.
- TATTERSALL, I. 1982. The primates of Madagascar. Columbia University Press, New York.

Gazetteer of Localities Mentioned in the Text*

Locality	Longitude South		Latitude East		Elevation (m)
	(°)	(')	(°)	(')	
Alaotra, Lac	48	30	17	30	
Ambalamanasy	49	36	14	32	
Ambanizana	49	58	15	37	
Ambatoharanana	48	45	14	26	
Ambatosoratra, Mt.	49	42	14	33	1583
Ambatovaky, RS	~49	15	~16	42	
Ambavaomby River	49	46	14	26	
Ambinanitelo River	49	47	14	26	
Ambodisovoka	48	17	20	05	
Ambohimitambo (see Ambohimitombo)					
Ambohimitombo	47	23	20	43	
Ambohitantely, RS	~47	16	~18	09	1450-1660
Ampahana	50	13	14	45	
Ampanasankolana	49	46.5	14	26.2	300-525
Ampanihy	44	45	24	42	
Ampitambe†	47	46	20	22	
Ampombilava	48	15	13	24	
Analamazaotra, RS	48	25	18	56	930-1040
Andampimbazaha River	49	45.7	14	26.0	775
Andapa	49	39	14	40	
Andasibe (see Analamazaotra)					
Andohahela, PN (parcel 1)	~46	11	~24	42	
Andranofotra River	49	46	14	28	
Andranomay Forest	47	57	18	29	1300
Andringitra, PN	~46	54	~22	14	700-2658
Androranga River	49	46	14	18	
Anjanaharibe-Anivo	49	27	14	44	2064
Anjanaharibe-Sud, RS	~49	26	~14	42	500-2064
Anjenabe, Mt.	49	44	14	18	
Ankafana (see Ankafina)					
Ankafina	47	12	21	12	
Ankarafantsika, RNI	~46	57	~16	09	80-330
Ankaratra Massif	47	12	19	25	2642
Anjozorobe	47	52	18	24	
Antalaha	50	16	14	53	
Antanana	47	31	18	55	
Antongil, Baie d'	49	50	15	45	
Antranofofa	49	44.5	14	26.0	
Antsahebe River	49	54	14	30	
Antsaheberoakahely River	49	39	14	23	
Antsiranana	49	17	12	16	
Bedinta (see Ampanasankolana)					
Behondroko, Mt.	49	46	14	24	
Belaoko	49	44	14	34	
Beondroka, Mt. (see Behondroko)					
Berenty, RP	46	17	24	59	
Betaolana	49	27	14	31	
Betsomanga River	49	45	14	17	
Camp 1 (1996)	49	46.5	14	26.2	450
Camp 2 (1995)	49	45.7	14	26.0	775
Camp 3 (1995)	49	44.5	14	26.2	1225
Camp 4 (1995)	49	44.5	14	26.4	1625
Camp 5 (1995)	49	44.1	14	26.8	1875
Daraina	49	40	13	12	
Didy	48	32	18	07	
Diégo-Suarez (see Antsiranana)					
Djabal River (see Djabala River)					
Djabala River	48	13	13	23	
Doany	49	31	14	22	

Locality	Longitude South		Latitude East		Elevation (m)
	(°)	(')	(°)	(')	
Fanovana	48	34	18	55	
Farafangana	47	50	22	49	
Farahalana	50	10	14	26	
Fito	48	54	18	05	
Fort-Dauphin (see Tolagnaro)					
Iharana (see Vohémar)					
Ikongo Forest	43	33	21	47	
Ivohibe, RS	~46	59	~22	32	775–2060
Kirindi Forest	44	43	20	03	
Lakato	48	22	19	03	1050
Lohan Andranomifototra	49	44.1	14	26.4	2133
Lokoho River	49	44	14	37	
Mahajanga	46	19	15	43	
Mahanara River	49	58	13	58	
Maimborondro (see Mainborondro)					
Mainborondro, Mt.	49	47	14	25	1119
Maintirano	44	01	18	03	
Majunga (see Mahajanga)					
Mananano River	48	03	22	02	
Mananara, RB	~49	42	~16	22	0–570
Mananara River	46	33	24	50	
Mananjary	48	20	21	14	
Manantenina (village)	49	49	14	30	
Manantenina River	49	49	14	29	
Mandena	49	49	14	29	
Manjakatombo	47	26	19	22	
Manombo, RS	47	44	23	02	0–137
Manongarivo, RS	~48	23	~13	59	150–1876
Mantadia (see Mantady)					
Mantady, PN	~49	27	~18	51	
Maroambihy	49	30	14	30	
Maroantsetra	49	44	15	26	
Marojejy, PN	~49	15	~14	26	75–2133
Marojejy (see Marojejy)					
Marolambo	48	07	20	02	
Marosse, Isle (see Nosy Mangabe)					
Marovoay	46	39	16	06	
Masoala, PN	~50	10	~15	38	
Midongy du Sud	~47	01	~23	35	850–1357
Montagne d'Ambre, PN	~49	10	~12	37	
Morondava	44	17	20	17	
Namorona River	48	13	21	39	
Nandihizana	~47	10	~20	50	
Nosivolo River	48	30	19	56	
Nossi-Bé (see Nosy Be)					
Nosy Be	48	15	13	20	
Nosy Mangabe	49	46	15	30	
Périnet (see Analamazaotra)					
Ranomafana, PN	~47	28	~21	16	
Ranomafana (Ifanadiana)	47	28	21	14	
Ranomena	47	17	23	25	
Rantabe	49	39	15	42	
Sahasinaka	47	49	21	49	
Sambava	50	10	14	16	
Sihanaka Forest	~48	32	~18	07	
Tamatave (see Toamasina)					
Tampolo	49	25	17	17	
Toamasina	49	23	18	10	
Tolagnaro	46	59	25	01	0–40
Tolongoina	47	31	21	33	
Tsaratana, RNI	~48	51	~13	59	227–2876

Locality	Longitude South		Latitude East		Elevation (m)
	(°)	(')	(°)	(')	
Vinanitelo	47	16	21	43	
Vohémar	50	01	13	21	
Vondrozo	47	20	22	49	
Zahamena, RNI	~48	50	~17	40	750-1512
Zombitse, PN	~44	40	~22	47	485-825

* For geographical localities such as rivers, large reserves, and mountain ranges, we have given an intersection of coordinates that allows for easy location on maps. Information presented in the Gazetteer is based partially on coordinates given by the U.S. Board on Geographic Names (1955) and Viette (1991). PN = Parc National, RNI = Réserve Naturelle Intégrale, RB = Réserve Biosphère, RS = Réserve Spéciale.

† Based on Carleton and Schmidt (1990).

Literature Cited

- CARLETON, M. D., AND D. F. SCHMIDT. 1990. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. *American Museum Novitates*, 2987: 1-36.
- U.S. BOARD ON GEOGRAPHIC NAMES. 1955. Madagascar, Réunion and the Comoro Islands. Gazetteer 2. U.S. Government Printing Office, Washington, D.C.
- VIETTE, P. 1991. Principales localités où des Insectes ont été recueillis à Madagascar. Faune de Madagascar, supplément 2. Private printing.



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