



Species diversity of Amphibia, Reptilia and Lipotyphla (Mammalia) at Ambolokopatrika, a rainforest between the Anjanaharibe-Sud and Marojejy massifs, NE Madagascar

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Abstract. The Réserve Spéciale d'Anjanaharibe-Sud and the Parc National de Marojejy are two important areas of biodiversity and endemism in northeastern Madagascar. These reserves are separated by about 40 km, including the extensive Andapa Basin, and connected by a rather narrow mid-altitude montane ridge. Nothing was previously known about the biota of this corridor and its faunal relations with the two reserves. At this purpose, during 1997 the Ambolokopatrika rainforest (lying about midway between Anjanaharibe-Sud and Marojejy massifs) was surveyed for amphibians, reptiles, and for small mammals belonging to the order Lipotyphla. As a general rule these vertebrates may be important ecological indicators, while the herpetofauna (Amphibia, Reptilia) exhibits a high degree of habitat specialisation and endemism. Furthermore, the herpetofauna and lipotyphlans of Ambolokopatrika Forest were compared to those known from the forests of Anjanaharibe-Sud, Marojejy, and Tsararano massifs, the latter site being a southern extension of the Anjanaharibe-Sud chain. These animals were surveyed by use of opportunistic searching and pitfall trapping during two seasonal periods, May–June (winter), and November–December (summer). Forty-two species of amphibians, 23 of reptiles, and nine of lipotyphlans were recorded at Ambolokopatrika Forest. The biodiversity of Ambolokopatrika is comparable to those of other analysed sites, and this stresses the value of this forest in assuring biotic exchange between Anjanaharibe-Sud and Marojejy reserves. Considerations are also provided on the faunal similarities and differences in terms of exclusivity and endemisms. It is therefore suggested that a certain degree of protection should be given to Ambolokopatrika rainforest, to assure a biological connection and exchange between the protected areas of Anjanaharibe-Sud and Marojejy.

Key words: Amphibia, biodiversity, conservation, Lipotyphla, Madagascar, rainforest corridor, Reptilia

Introduction

As witnessed by recent studies (e.g., Raxworthy and Nussbaum 1995; Andreone 1996b; Goodman and Jenkins 1998; Nussbaum et al. 1998), northern Madagascar shows a rich species diversity of Amphibia, Reptilia, and Lipotyphla (Mammalia). This may be due to the heterogeneous geographic situation, with the presence of several massifs (such as Montagne d'Ambre, Tsaratanana, Marojejy, and Anjanaharibe-Sud) which act as biogeographic refugia and centers of endemism, as well as the occurrence of a rich variety of habitats.

Two protected areas in north-eastern Madagascar, the Parc National (PN) de Marojejy and Réserve Spéciale (RS) d'Anjanaharibe-Sud are about 40 km apart, separated by an area including the Andapa Basin. Between these two reserves a band of non-protected forest exists, and it should be argued if it still act as a corridor for biotic interchange. Indeed, Raxworthy et al. (1998) suggested that the study of the herpetofauna of corridor between Anjanaharibe-Sud and Marojejy would provide important information about the need for protection of the area. Although the Marojejy Massif has been recently the subject of a detailed study (Raselimanana et al. in press), no information was previously available on the fauna occurring in the corridor between Anjanaharibe-Sud and Marojejy and its biogeographic affinity. Since the two massifs are presumably centers of endemism the species presence in the corridor would give important indications of the colonization history and biogeography. Furthermore from a conservation perspective the species diversity in this area could help in the management of RS d'Anjanaharibe-Sud and PN de Marojejy in assuring a biological continuity between the two protected areas.

In this paper, we examine the geographic distribution and diversity of the amphibians, reptiles, and small mammals (Lipotyphla) inhabiting this corridor, gathered throughout two field surveys, conducted during May–June (winter) and November–December (summer) 1997. Furthermore, we discuss the importance of this forest in maintaining the connection with the adjacent protected areas, and the situation in terms of biogeographical relationships with the faunas of other rainforests in north-eastern Madagascar.

Methods

Study sites and periods

The Ambolokopatrika–Antsamihitsitso Forest (for simplicity hereafter referred to as the Ambolokopatrika Forest) is situated north-west of the Andapa Basin, and lies on the ridge which connects Anjanaharibe-Sud and Marojejy massifs (Figures 1 and 2). It comprises a north-south oriented crest (Ambatoharanana Chain), which continues northwards to the Anjanaharibe-Sud Chain. The highest peaks of this northern

chain extension are at 1730, 1542, and 1559 m. At the level of the Andasinizamahivoahangy Peak (1542 m of elevation; 14°34' S and 49°20' E) the chain turns eastwards. Here the crest elevation is at least 1000 m, with peaks of 1719 m

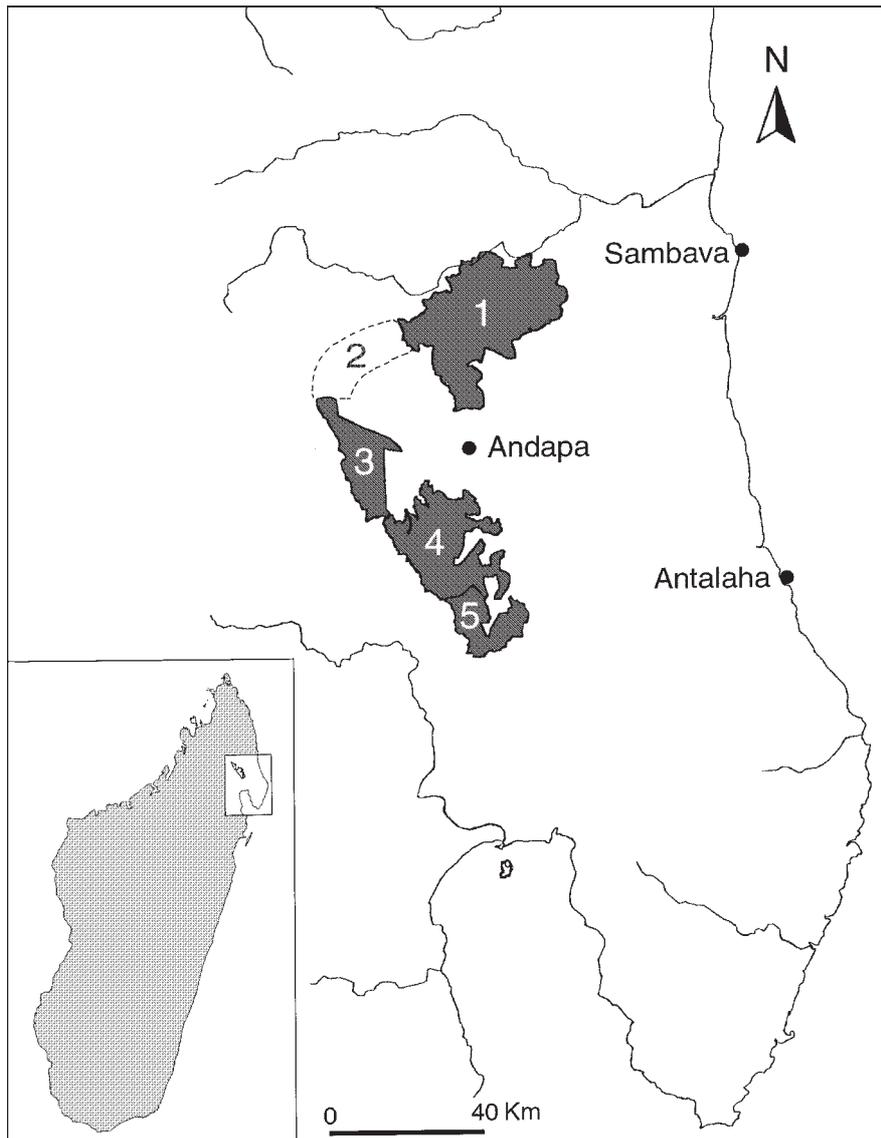


Figure 1. Location of Ambolokopatrika Forest and of other studied sites around the Andapa Basin, NE Madagascar: 1 = PN de Marojejy; 2 = Ambolokopatrika Forest; 3 = RS d'Anjanaharibe-Sud, 4 = Besariaka–Amponaomby Forest; 5 = Tsararano Forest. Administrative borders are given for the considered protected areas (RS d'Anjanaharibe-Sud and PN de Marojejy), or classified forests (Ambolokopatrika, Besariaka–Amponaomby, and Tsararano). Map source: GIS Service of WWF-Antananarivo, based upon FTM (Foiben-Taosarintanin'i Madagascar/Institut Géographique et Hydrographique National) maps.

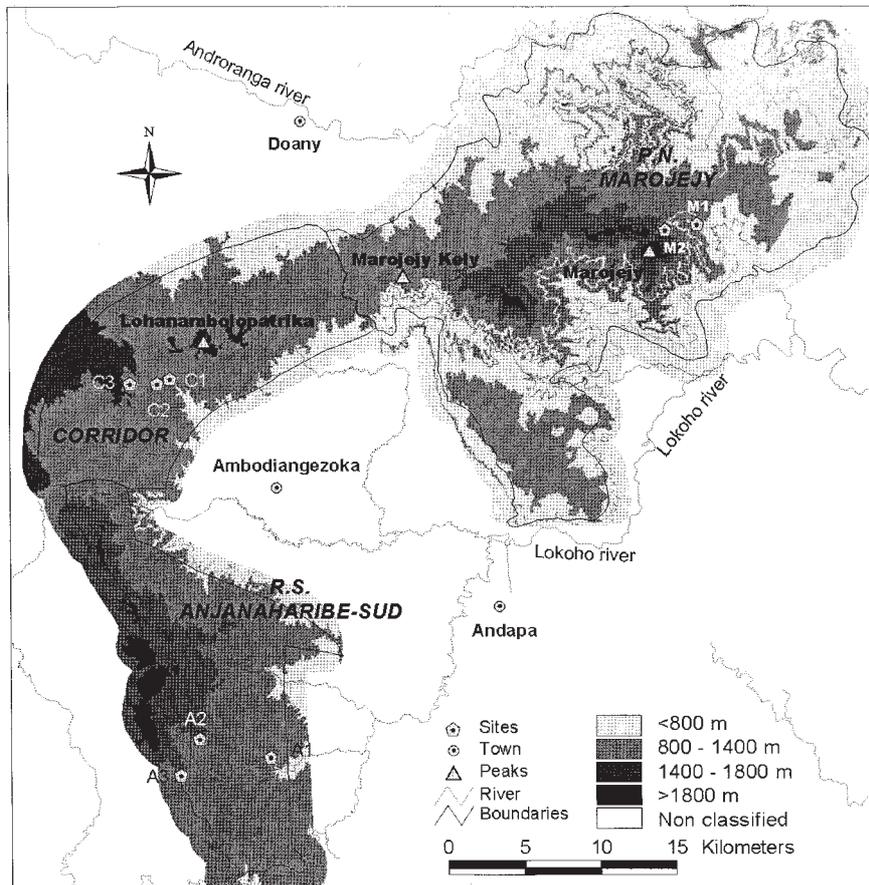


Figure 2. Map of the Andapa Basin and its montane system, including Anjanaharibe-Sud and Marojejy massifs (and homonymous protected areas), the corridor between them (where the Ambolokopatrika is sited), and the related campsites (A1-3 = study sites at Anjanaharibe-Sud; C1-3 = study sites at Ambolokopatrika; M1-2 = study sites at Marojejy). Borders of the studied areas as in Figure 1. Forest elevations are given for reliefs within the considered limits and for a limited exterior band. Graphic elevational representations for outer localities are still not available. Map source: GIS Service of WWF-Antananarivo, based upon FTM maps.

(Tsiakarantalata), and 1640 m (Lohanambolokopatrika). The Tsimaintandrano crest separates the Betaolana Forest northwards (maximum altitude: 1051 m), and the Ambolokopatrika Forest southwards. The Ambolokopatrika Forest is delimited by the Beloha Forest to the north, the Betaolana Forest to the north-east, and the Anajavidy Forest to the west. The vegetation of the forest belongs to the domains of East and Center (Humbert 1955). The climax vegetation is of the evergreen type, which corresponds to the eastern ombrophile primary and secondary forest and to transitional low-mid altitude and montane wet forest (White 1986). Due to an intense anthropic activity, the Ambolokopatrika corridor is currently a mosaic of fairly intact forest,

'savoka' (a degraded formation mainly constituted of herbaceous species, such as *Harungana madagascariensis*, *Aframomum angustifolium*, *Hedychyum coronarium*, *Clidemia hirta*, and the traveller's palm *Ravenala madagascariensis*), and secondary forest. According to data for the town of Andapa (Randriamaherisoa et al. 1993; Goodman and Lewis 1998) the region is characterised by a humid and tropical climate. The mean temperature ranges from 18 °C in July to 25 °C in February. The relative humidity is generally about 87% but reaches 97% in March and April. The annual precipitation is slightly more than 2 m. On average it rains 271 days per year. The 'dry' season lasts about two months (September and October), with 41.1 and 52.6 mm of rain distributed throughout 14.7 and 15.1 days.

Fieldwork took place in two different periods: May–June (which is a comparatively 'dry' and 'cold' time), and November–December (which corresponds to the beginning of the warm rainy season, when most amphibian species are breeding, and reptiles and small mammals are at peak of their activity). These different periods were chosen to maximise information on the species diversity of the region, since some species – especially amphibians – show levels of seasonality (Andreone 1994, 1996a).

Three study sites were chosen, all occurring in the Commune Rurale d'Ambodiantgezoka, Fivondronana d'Andapa, Province (Faritany) d'Antsiranana (Diégo Suarez): 'Andemakatsara'¹ (Site 1), 14°31.8' S, 49°26.5' E, 810 m, 27 May–3 June 1997; this site was next to a tributary of the Bekona River; 'Andranomadio' (Site 2), 14°32.4' S, 49°26.3' E 860 m, 4–12 June 1997 and 29 November–8 December 1997; this site was next to the Ambolokopatrika River; 'Antsinjorano' (Site 3), 14°32.6' S et 49°25.8' E, 950–1250 m, 9–20 December 1997. The forest around Sites 1 and 2 is transitional between lowland and montane moist rainforest, while at Site 3 it is a mid-altitude rainforest; at all sites there are patchworks of pristine and altered rainforest. Members of the surveys: May–June 1997 – F. Andreone and J.E. Randrianirina; November–December – F. Andreone, G. Aprea, and J.E. Randrianirina.

The data collected for the Ambolokopatrika Forest were successively compared with those of three other massifs/chains (transitional low-mid altitude and mid-altitude only) for which information was gathered using the same methods: Anjanaharibe-Sud, Marojejy, and Tsararano. For the first two sites faunal inventories have already been published or are in press (Goodman and Jenkins 1998; Raxworthy et al. 1998; Goodman and Jenkins in press; Raselimanana et al. in press), while data for Tsararano were collected during a field survey carried out in 1996. For the small mammals the data here utilized are those obtained with the pitfall traps only, excluding information with live traps at Anjanaharibe-Sud and Marojejy (Goodman and Jenkins 1998, in press).

The Anjanaharibe-Sud Massif is situated to the south–west of Marojejy Massif on one side and to the west of Andapa Basin on the other. It forms a north–south oriented chain about 20 km long, with a surface area of about 32 100 ha, and ranging between 500 and 2064 m (Nicoll and Langrand 1989). Five elevational zones

were sampled during a mid-October to late November survey of this reserve (Goodman et al. 1998). Analysed sites (according to Raxworthy et al. 1998): E1 (eastern slope, Site 1), 14°45.3' S, 49°30.3' E, survey dates 18–30 October 1994, altitude 800–950 m; E2 (eastern slope, Site 2), 14°44.7' S, 49°27.7' E, survey dates 1–12 November 1994, altitude 1100–1350 m; W1 (western slope, Site 1), 14°46.7' S, 49°27.8' E, survey dates 25 January–3 February 1996, altitude 1000–1100 m. Members of the surveys: N. Rabibisoa (eastern slope); F. Andreone, J.E. Randrianirina, and H. Randriamahazo (western slope).

The Marojejy Massif, is 60 150 ha in area and 75 to 2132 m in altitude, with east–west and north–south crests, and is currently managed as a national park. The east–west oriented crest has peaks at 1384 m (Marojejy Kely), 1478, 1852, 1548, and 2132 m; the north–south oriented crest has a lower mean elevation, with peaks at 1102, 962, 766, 1804, and 1193 m. The primary vegetation of the reserve is rainforest, with *Philippia* [= *Erica*] ericoid heathland at elevations above 1800 (Nicoll and Langrand 1989). For standardizing purposes we only took into considerations the amphibians and reptiles found by Raselimanana et al. (in press) during their surveys, while we did not include in our comparison further taxa found at Marojejy by other teams, such as Glaw and Vences (1994). Analysed sites (Raselimanana et al. in press; Goodman and Jenkins in press): 'Andampimbazaha' waterfall (Site 2, 14°26.0' S, 49°45.7' E, altitude 550–850 m; dates: 16 November–2 December 1992, 14–24 October 1996), and 'Ambavanaomby' (Site 3, 14°26.2' S, 49°44.5' E altitude 1050–1350 m; dates: 27–30 November 1992, 24 October–3 November 1996). Members of the surveys: R.A. Nussbaum, G. Raharimanana, C.J. Raxworthy, A. Razafimanantsoa, and A. Razafimanantsoa (1992 survey); A.P. Raselimanana (1996 survey).

The Tsararano Chain lies south of the Andapa Basin, approximately midway between the Anjanaharibe-Sud Massif and the Masoala Peninsula. It is formed by several hills, ranging in altitude from 400 to 1269 m. It is separated towards the north from the Besariaka Massif, to the south from the Ambatomikililo and Bezavona massifs, to the west from the Andranofotsihely Massif, and to the east from the Behovitra Massif. Analysed sites: 'Antsarahana'ny Tsararano' (Site 1, 14°54.4' S and 49°41.2' E, altitude 700–850 m; dates: 28 November–7 December 1996), and 'Andatony Anivo' (Site 2, 14°54.8' S and 49°42.6' E, altitude 600–750 m; dates: 9–18 December 1996). Members of the survey: F. Andreone and J.E. Randrianirina.

Data collection

On a daily basis about five hours of search were spent, equally divided between daytime and nighttime periods; forest and riverine habitats were surveyed on alternate days. Secretive species were sought in their refuges (e.g., fallen logs, under bark, in leaf litter, soil, and leaf axils of *Pandanus* screw palms and *Ravenala madagascariensis*). Night searches were made with the aid of head-lamps and flashlights.

A second collecting method consisted in pitfall bucket traps. The pitfall traps were plastic buckets (about 280 mm deep, 290 mm top internal diameter, 220 mm bottom internal diameter), with the handles removed, sunk in the ground at intervals along a drift fence. Small holes were punched in the bottom to allow water to drain. The fence (0.5 m high and 100 m long) was made from plastic sheeting stapled to thin wooden stakes. The fence bottom was buried 50 mm deep into the ground using leaf litter and ground and positioned to run across or along each pitfall trap. A pitfall trap was positioned at both ends of the drift fence, while the other traps were at 10 m intervals. At each site three lines were placed along the crest of a ridge, on a gradient, intermediate between ridge top and valley bottom, and valley. The pitfalls were checked each morning and evening for captured animals. During the two surveys carried out in summer and winter at Site 2, the pitfalls were put in the same places (pitfall lines 4–6; see Tables 2 and 3). Information for the results of the pitfall trapping are reported separately for November–December and May–June periods. The following information was recorded at the time of capture or observation of each individual: date, time, longitude and latitude (obtained by GPS), altitude, microhabitat, and circumstances of capture. As a further aid to taxonomic identification, the acoustic repertoire of some amphibians was recorded with a SONY professional tape recorder, analysed with the program VOXYS 3.0 (Andreone et al. 1998), and compared to an existing database of frog vocalisations. Representative individuals were photographed to document their life coloration. Voucher specimens were captured and fixed in 10% buffered formalin or 90% ethanol, and later transferred in 65% (amphibians) or 75% (reptiles) ethanol. The small mammals were prepared as fluid preserved carcasses in 75% ethanol, with associated skulls. The amphibians and reptiles were identified by F. Andreone, G. Aprea, and J.E. Randrianirina, and small mammals by P.D. Jenkins and F. Andreone. Collected material has been deposited at the Museo Regionale di Scienze Naturali, Torino (Italy), and the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo (Madagascar). Based upon the data collected by all the observation and trapping methods we drew the specific accumulation curves; due to the differences in their natural history and discovery rate we took separated amphibian and reptile data, (Andreone and Randriamahazo 1997). Throughout the text we quote some museum acronyms: MRSN (Museo Regionale di Scienze Naturali, Torino), and FN (field catalogue numbers of F. Andreone, relative to specimens not yet definitely catalogued).

Nomenclature and taxonomy

The taxonomy of the herpetofauna follows Glaw and Vences (1994) and Andreone (1999). For chameleons we retain as correct family name Chameleonidae (according to Klaver and Böhme 1986). The frog genus *Aglyptodactylus*, formerly included within the Rhacophorinae (e.g., Glaw and Vences 1994), is now considered as belonging to Raninae (Glaw et al. 1998; Richards and Moore 1998). For the genera *Manti-*

dactylus and *Boophis* we follow the revisions of some species-groups (see Glaw and Vences 1997a,b; Vences et al. 1997; Andreone et al. 1998; Vallan et al. 1998). For this reason at Anjanaharibe-Sud we report the occurrence of *Mantidactylus phantasticus*, a species which was not yet described when the paper by Raxworthy et al. (1998) was written, and which was then included within *M. aglavei*. The green treefrogs found at Ambolokopatrika Forest belonging to the *Boophis luteus* group are here preliminarily attributed to two taxa: *B. anjanaharibeensis* and *B. cf. septentrionalis*. The two unnamed *Mantella* species quoted by Raxworthy et al. (1998) and by Raselimanana et al. (in press) are currently *M. nigricans* and *M. manery* (according to Vences et al. 1999a).

The Malagasy tree-boa, named *Boa manditra* by Kluge (1991) (classification as followed by some recent authors: e.g., Raxworthy et al. 1998) is here named after the former nomenclature (e.g., Glaw and Vences 1994), based upon recent, still unpublished genetic studies (M. Vences 1999 pers. comm.), and thus *Sanzinia madagascariensis*. For the colubrid genera *Liopholidophis* and *Geodipsas* we followed Cadle (1996a,b), while the *Pseudoxyrhopus* sp., as given by Raxworthy et al. (1998), is here *P. analabe*, according to Nussbaum et al. (1998).

Throughout our surveys at Anjanaharibe-Sud, Ambolokopatrika and Tsararano some taxa were not identified to the species level, some of which may therefore represent undescribed species. Among the amphibians (found by us, and thus excluding the specimens collected at Anjanaharibe-Sud, eastern slope, and Marojejy) they are *Platypelis* sp. 1 (MRSN A1980), *P.* sp. 2 (MRSN A1978, FN 6799, FN 7177, FN 7398, FN 7239), *P.* sp. 3 (MRSN A1848, FN 6812, FN 7190), *P.* sp. 4 (FN 7150), *Plethodontohyla* sp. 2 (MRSN A1845), *Stumpffia* sp. 1 (FN 7263, FN 7401), and *S.* sp. 2 (MRSN A1868-1870, MRSN A1979, FN 7262). One microhylid from Tsararano (FN 9467) was not yet attributed to any known genus and species, and is provisionally named 'Microhylid sp.' We also found two new chameleon species (F. Andreone et al., in preparation) belonging to the *Calumma furcifer*-group, which differ in morphology and hemipenial structure from the other known species of the group as recognized by Böhme (1997). They are here named as *Calumma* n.sp. 1 (MRSN R1690, MRSN R1703.1-2, MRSN R1681, MRSN R1682.1-2, MRSN R1683.1-2, MRSN R1684, MRSN R1685, MRSN R1686.1-2, MRSN R1687.1-2, MRSN R1688, MRSN R1689.1-3), and *C.* n.sp. 2 (MRSN R1628). Other unidentified reptile species were *Amphiglossus* sp. 1 (FN 6406), and *Typhlops* sp. 2 (FN 6296).

Raselimana et al. (in press) quote the occurrence of *Brookesia minima* at Marojejy, following in this sense the classification by Raxworthy and Nussbaum (1995). As it has been demonstrated by Glaw et al. (1999), and Böhme (1997) *B. minima* s.l. currently includes different species. We therefore named this species as *Brookesia* cf. *minima*, waiting for more detailed information on its taxonomic attribution. Likely, the same authors report for Marojejy the occurrence of *Calumma gastrotaenia*. According to F. Andreone et al. (in preparation) *C. gastrotaenia* is possibly absent from N. Madagascar, where it is replaced by *C. marojezensis*, *C. guillaumeti*, and

C. n.sp. 1. We tentatively attributed the specimens found by Raselimanana et al. (in press) to *C. marojezensis*, basing upon the known species altitudinal distribution.

Among the small mammals the Lipotyphla (this order being currently recognized as including the families Erinaceidae, Solenodontidae, Chrysochloridae, Tenrecidae, Soricidae, Talpidae, and their fossil relatives, all of which were formerly placed in the order Insectivora: see Butler 1988) is represented in Madagascar by Tenrecidae and Soricidae (Goodman et al. 1999). For the taxonomy and identification of Tenrecidae and Soricidae, particularly the genus *Microgale*, we followed Jenkins et al. (1996) and Goodman and Jenkins (1998, in press).

Statistical analysis

We calculated two community coefficients, which have been utilised for establishing relationships and similarities between the different analysed faunas, as well as differences between amphibians and reptiles. They are: (i) coefficient of similarity S (sensu Raxworthy and Nussbaum 1996), which is $S = C/N_{1+2}$, where C is the number of species in common and N_{1+2} is the total number of species found for both the transects or site localities; (ii) coefficient of exclusivity E , established as N_e/N_t , where N_e is the number of species apparently exclusive at each of the analysed site and altitude (and not found at other of the considered sites), and N_t the total number of species found at that site. Although some species exclusive to a site are presumably endemic too, the large majority of the species 'exclusive' to one of the analysed sites may be found elsewhere in Madagascar (usually within the eastern rainforest belt). Of both these coefficients the mean values \pm standard deviation were calculated. All data were analysed by a STATISTICA (version for Windows) personal computer package, with α set at 5%.

Results

A total of 42 species of amphibians, 23 reptiles, and 9 lipotyphlans was recorded during the survey within the Ambolokopatrika Forest (Table 1; Figure 3). Five species of amphibians (*Platypelis* sp. 4, *Plethodontohyla laevipes*, *Stumpffia* sp. 1, *Boophis* cf. *burgeri*, and *Mantidactylus* cf. *punctatus*), and three of reptiles (*Brookesia superciliaris*, *Furcifer willsii*, and *Liopholidophis rhadinaea*) found at Ambolokopatrika were not found at the analysed sites of Anjanaharibe-Sud, Marojejy, and Tsararano. The lipotyphlan fauna consisted mainly of oryzorictine tenrecs (Tenrecidae), including seven species of *Microgale*, and *Oryzorictes hova*. The only small mammal found at Ambolokopatrika, but not recorded at the neighbouring massifs, was the introduced *Suncus murinus* (Soricidae).

Table 1. Amphibia, Reptilia, and Lipotyphla found at Amboelokopatrika Forest (subfamilies are given for amphibians only).

Taxa	Sites			Altitude (m)	Dates
	Andemakatsara (Site 1)	Andranomadio (Site 2)	Antsinjorano (Site 3)		
	810	860	950–1250		
	27 May–3 June 1997	4–12 June 1997	29 November–8 December 1997		9–20 December 1997
Amphibia					
Microhylidae – Cophylinae					
<i>Platypelis barbouri</i>	+				
<i>Platypelis grandis</i>		+			
<i>Platypelis occultans</i>					
<i>Platypelis tuberifera</i>					
<i>Platypelis</i> sp. 2					
<i>Platypelis</i> sp. 3					
<i>Platypelis</i> sp. 4					
<i>Plethodontohyla alluaudi</i>					
<i>Plethodontohyla laevipes</i>					
<i>Plethodontohyla notosticta</i>					
<i>Plethodontohyla serratopalpebrosa</i>					
<i>Stumpffia roseifemoralis</i>					
<i>Stumpffia</i> sp. 1					
<i>Stumpffia</i> sp. 2					
Ranidae – Rhacophorinae ^a					
<i>Boophis albilabris</i>					
<i>Boophis anjanaharibeensis</i>					
<i>Boophis brachycheir</i>					
<i>Boophis</i> cf. <i>burgeri</i>					
<i>Boophis madagascariensis</i>					
<i>Boophis</i> cf. <i>mandraka</i>					
<i>Boophis marojezensis</i>					

Table 1. Continued.

Taxa	Sites			
	Andemakatsara (Site 1) Altitude (m)	Andranomadio (Site 2)	Andranomadio (Site 2)	Antsinjorano (Site 3)
	810	860	860	950–1250
	Dates			
	27 May–3 June 1997	4–12 June 1997	29 November–8 December 1997	9–20 December 1997
Gekkonidae				
<i>Ebenavia inunguis</i>	+			
<i>Lygodactylus cf. miops</i>	+	+		+
<i>Paroedura gracilis</i>	+	+		+
<i>Phelsuma lineata</i>	+	+		
<i>Phelsuma quadriocellata</i>		+		
<i>Uroplatus ebenau</i>	+			+
<i>Uroplatus sikorae</i>	+			+
Gerrhosauridae				
<i>Zonosaurus madagascariensis</i>			+	
Scincidae				
<i>Amphiglossus melanopleura</i>	+		+	+
<i>Amphiglossus mouroundavae</i>			+	+
<i>Androngo cremi</i>			+	
Typhlopidae				
<i>Typhlops mucronatus</i>				+
Colubridae				
<i>Geodipsas boulengeri</i>			+	+
<i>Geodipsas laphystia</i>			+	+
<i>Liopholidophis epistibes</i>			+	+
<i>Liopholidophis rhadinaea</i>			+	
Total number of species (Reptiles)	9	12	18	15

Mammalia				
Tenrecidae				
<i>Microgale cowani</i>				+
<i>Microgale fotsifotsy</i>		+		
<i>Microgale longicaudata</i>				+
<i>Microgale parvula</i>		+		+
<i>Microgale soricooides</i>				+
<i>Microgale taiva</i>				+
<i>Microgale talazaci</i>	+			
<i>Oryzorictes hova</i>	+			
Soricidae				
<i>Suncus murinus</i> ^b		+		
Total number of species (Mammals)	2	3	4	6
Overall total	33	35	53	48

^a The taxonomic status of mantellines and rhacophorines is sometimes matter of controversy. Some authors have considered them as either families (Blommers-Schlösser and Blanc 1991; Raxworthy et al. 1998), or subfamilies of Ranidae (Blommers-Schlösser 1993; Glaw and Vences 1994). Here we give them the status of subfamilies.

^b Species introduced to Madagascar.

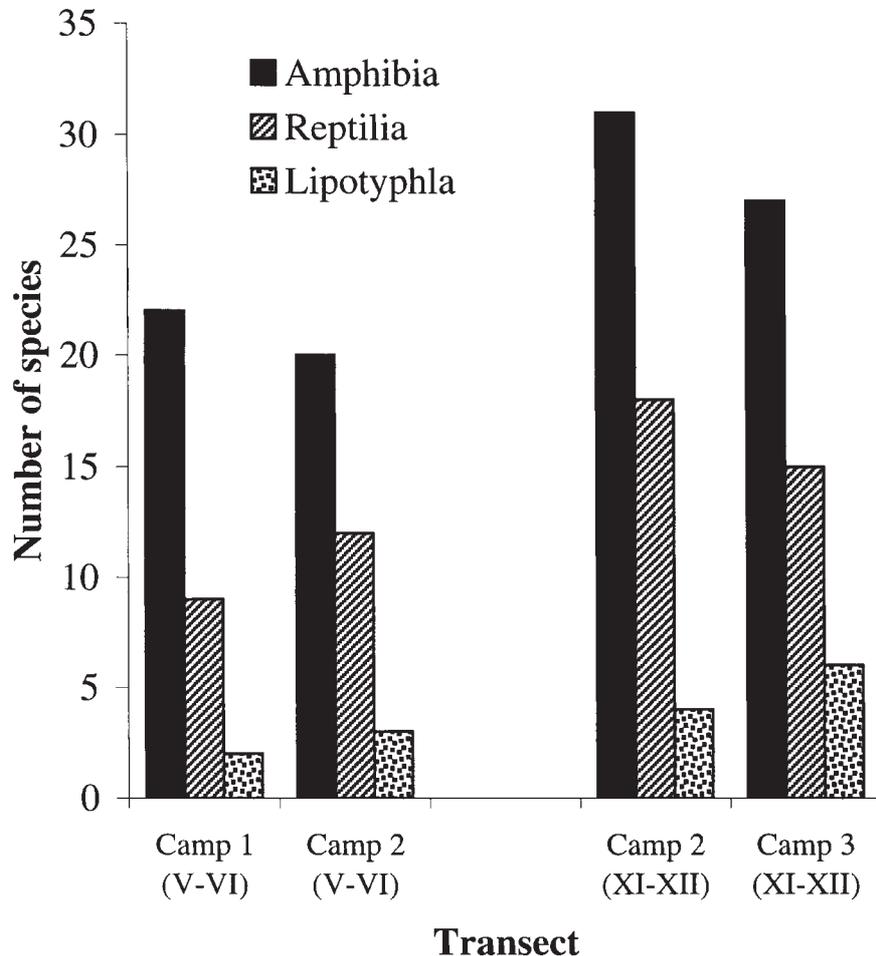


Figure 3. Histograms showing the species diversity at three sites (two study periods) of Ambolokopatrika Forest for amphibians, reptiles, and lipotyphlan mammals.

The results of the pitfall trapping are given in Tables 2 and 3. The 91 individuals captured (13 amphibians, 24 reptiles, and 54 tenrecs) during 1089 trap days (495 during winter, and 594 during summer), were six amphibian, six reptile, and nine lipotyphlan species. The overall mean daily pitfall capture rate of small vertebrates was 8.4% (1.2% for amphibians, 2.2% for reptiles, and 5.0% for lipotyphlans).

The highest species diversity for amphibians and reptiles was found at Site 2 during the December 1997 (31 and 18 species, respectively), while the highest lipotyphlan diversity was found at Site 3 (December 1997), with six species. During the winter survey the capture of amphibians and reptiles with pitfalls was extremely low, with only one amphibian and three reptile individuals at Site 1, representing 26.7% of

Table 2. Characteristics and captures (Amphibia, Reptilia, Lipotyphla) for all pitfall lines during May–June 1997 (cold season) in the Ambolokopatrika Forest.

	Sites						Total
	Andemakatsara (Site 1)			Andranomadio (Site 2)			
	Elevational range of the site (m)						
	800–900			800–900			
	Dates						
	27 May–9 June 1997			10–17 June 1997			
Pitfall lines	1	2	3	4	5	6	
Mean altitude of the pitfall line (m)	810	820	840	809	825	840	
Trap position	Valley	Slope	Ridge	Valley	Slope	Ridge	
Number of nights	7	7	7	8	8	8	
Pitfall number	11	11	11	11	11	11	
Trap-nights	77	77	77	88	88	88	
Total bucket-nights	231			264			495
	Number of captured specimens						
Amphibia							
<i>Mantidactylus asper</i>	1						1
Total	1						1
Reptilia							
<i>Amphiglossus melanopleura</i>		1	2				3
Total		1	2				3
Mammalia – Lipotyphla							
<i>Microgale parvula</i>			1	1			2
<i>Microgale talazaci</i>	4	1		3	2		10
<i>Oryzorictes hova</i>	2	1		2	1	1	7
<i>Suncus murinus</i>	2						2
Total	8	2	1	6	3	1	21
Overall total	9	3	3	6	1	3	25

the small vertebrates captured with pitfalls in this period, while at Site 2 lipotyphlans only were captured. At the four transects where pitfalls were used, species diversity and capture rate were greatest on valley forest and lowest in ridge and slope forests.

Discussion

Sampling methods

The herpetological capture rate during the winter (Table 2), with only four captures (one amphibian and three reptiles) in 495 bucket-days (0.2% for amphibians and 0.6% for reptiles) is far lower than during the summer (Table 3), with 33 captures (12 amphibians and 21 reptiles) in 594 bucket-days (2.0% for amphibians and 3.5% for

Table 3. Characteristics and captures (Amphibia, Reptilia, Lipotyphla) for all pitfall lines during November–December 1997 (warm season) in the Ambolokopatrika Forest.

	Sites						Total
	Andranomadio (Site 2)			Antsinjorano (Site 3)			
	Elevational range of the site (m)						
	800–900			950–1250			
	Dates						
	29 November–9 December 1997			9–20 December 1997			
	4	5	6	7	8	9	
Pitfall lines	4	5	6	7	8	9	
Mean altitude of the pitfall line (m)	809	825	840	1025	1040	1060	
Forest type	Valley	Slope	Ridge	Valley	Slope	Ridge	
Number of nights	8	8	8	10	10	10	
Pitfall number	11	11	11	11	11	11	
Trap-nights	88	88	88	110	110	110	
Total bucket-nights	264			330			594
	Number of captured specimens						
Amphibia							
<i>Mantidactylus asper</i>					2		2
<i>Mantidactylus redimitus</i>						1	1
<i>Plethodontohyla laevipes</i>				2			2
<i>Plethod. serratopalpebrosa</i>			1			1	2
<i>Stumpffia</i> sp. 1	4			1			5
Total	4	0	1	3	2	2	12
Reptilia							
<i>Amphiglossus melanopleura</i>	3	1					4
<i>Amphiglossus mouroundavae</i>			4	8	1	2	15
<i>Androngo crenni</i>	2						2
<i>Geodipsas boulengeri</i>				1			1
<i>Liopholidophis epistibes</i>				1			1
<i>Liopholidophis rhadinaea</i>	1						1
Total	6	1	4	10	1	2	24
Mammalia – Lipotyphla							
<i>Microgale cowani</i>	5	2	2				9
<i>Microgale fotsifotsy</i>	1	1					2
<i>Microgale longicaudata</i>	1						1
<i>Microgale parvula</i>	3	3	3				9
<i>Microgale soricoides</i>	1	2	1				4
<i>Microgale taiva</i>		1					1
<i>Microgale talazaci</i>		1					1
<i>Oryzorictes hova</i>		2	1	3			6
Total	11	12	7	3	0	0	33
Overall total	21	13	12	16	3	4	69

reptiles). Similar results were obtained with lipotyphlans with regard to a lower rate of captures during the winter, although the differences between the seasons were not so obvious as for amphibians and reptiles: 21 small mammal captures during the May–June period (4.2% daily success) and 33 individuals during the November–December period (5.6% daily success). These results indicate that during the winter, when rainfall and temperatures are lower, especially the small mammals and some terrestrial amphibians and reptiles, such as microhylids, skinks, gerrhosaurids, and some colubrid snakes, are much less active.

Data for amphibians and reptiles collected during the warm season are comparable to those collected during the other field surveys (Table 4). The capture success of 5.6% is higher than that obtained by Raxworthy et al. (1998) and Raselimanana et al. (in press) for the pitfall lines in comparable elevational zones at Anjanaharibe-Sud (2.9% overall; 0.7% for amphibians, and 2.2% for reptiles) and at Marojejy (3.8% overall; 2.2% for amphibians, and 1.6% for reptiles).

The trap success for lipotyphlans during the November–December period was 5.6%, thus identical to that obtained for the herpetofauna. This rate is comparatively lower than that obtained at Anjanaharibe-Sud and Marojejy. At Anjanaharibe-Sud the capture rate (583 accrued bucket-days) in pitfall lines placed between 850 and 1240 m was 6.0% (Goodman and Jenkins 1998), while at Marojejy the capture rate (583 bucket-nights) in pitfall lines at a comparable altitude (850–1250 m) was 9.3% (Goodman and Jenkins in press). The differences in pitfall captures between sites are difficult to explain, although differences in rainfall rates, microhabitats and survey times may be taken into account.

At Ambolokopatrika Forest the pitfall trapping for amphibians did not provide any species not collected by other methods, and in general we can affirm that in eastern humid forest pitfall devices are not particularly important for obtaining information on the presence of frogs. On the other hand, the use of this trapping system is quite productive for reptiles and small mammals. Of the six reptile species collected at Ambolokopatrika with this method, only two snakes (the colubrids *Liopholidophis epistibes* and *Geodipsas boulengeri*) were also found with opportunistic searching. One skink, *Androngo crenni*, is very secretive: at several sites the only evidence of this species was obtained with pitfall devices (e.g., Raselimanana 1998; Raxworthy et al. 1998).

The species accumulation curves for amphibians are given in Figure 4. The increase in previously unrecorded species during May–June is relatively continuous throughout the survey, indicating that the eight day survey was not sufficient to give a complete estimate of species diversity during this season. On the other hand, during the warm and wet months of November and December, there is an indication of a saturation point being reached for the Site 2 and Site 3, with no new species captured in the last three days of the survey. This seasonal difference in the measures of local species diversity is important to bear in mind when interpreting the survey data. Differences between winter and summer transects for amphibians may be

Table 4. Distribution of the Tsararano, Anjanaharibe-Sud, Ambolokopatrika Forest, and Marojejy amphibians.

Taxa	Sites			
	Tsararano	Anjanaharibe-Sud	Ambolokopatrika	Marojejy
	Altitude (m)			
	600–850	800–1350	810–1250	550–1350
Elevational range (m)				
	250	550	440	850
Microhylidae				
<i>Anodonthyla boulengeri</i>		+		
"Microhylid sp." ^a	+			
<i>Platypelis grandis</i>	+	+	+	+
<i>Platypelis occultans</i>		+	+	+
<i>Platypelis barbouri</i>			+	+
<i>Platypelis pollicaris</i>		+		
<i>Platypelis tsaratananaensis</i>	+			
<i>Platypelis tuberifera</i>	+	+	+	+
<i>Platypelis</i> sp. 1		+		
<i>Platypelis</i> sp. 2		+	+	
<i>Platypelis</i> sp. 3	+		+	
<i>Platypelis</i> sp. 4			+	
<i>Plethodontohyla alluaudi</i>	+		+	
<i>Plethodontohyla coudreaui</i>				+
<i>Plethodontohyla inguinalis</i>	+			
<i>Plethodontohyla laevipes</i>		+	+	
<i>Plethodontohyla minuta</i>		+		
<i>Plethodontohyla notosticta</i>		+	+	+
<i>Plethodontohyla serratopalpebrosa</i>		+	+	+
<i>Plethodontohyla</i> sp. 1		+		
<i>Plethodontohyla</i> sp. 2	+			
<i>Stumpffia grandis</i>		+		+
<i>Stumpffia psologlossa</i>				+
<i>Stumpffia roseifemoralis</i>	+	+	+	+
<i>Stumpffia</i> sp. 1			+	
<i>Stumpffia</i> sp. 2	+	+	+	
Ranidae – Raninae				
<i>Aglyptodactylus madagascariensis</i>	+	+		
<i>Ptychadena mascareniensis</i>		+		
Ranidae – Rhacophorinae				
<i>Boophis albilabris</i>		+	+	
<i>Boophis albipunctatus</i>	+	+		
<i>Boophis anjanaharibeensis</i>	+	+	+	+
<i>Boophis brachychir</i>	+	+	+	+
<i>Boophis englaenderi</i> ^b				+
<i>Boophis erythrodactylus</i>	+	+		
<i>Boophis lichenoides</i>	+			
<i>Boophis luteus</i>				+
<i>Boophis madagascariensis</i>	+	+	+	+
<i>Boophis</i> cf. <i>mandraka</i>	+	+	+	
<i>Boophis marojezensis</i>	+	+	+	+

Table 4. Continued.

Taxa	Sites			
	Tsararano	Anjanaharibe-Sud	Ambolokopatrika	Marojejy
	Altitude (m)			
	600–850	800–1350	810–1250	550–1350
	Elevational range (m)			
	250	550	440	850
<i>Boophis rappiodes</i>	+	+		
<i>Boophis reticulatus</i>	+	+	+	+
<i>Boophis</i> cf. <i>burgeri</i>			+	
<i>Boophis</i> cf. <i>septentrionalis</i>		+	+	
Ranidae – Mantellinae				
<i>Mantella laevigata</i>	+			+
<i>Mantella nigricans</i>	+	+		+
<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 cornutus</i>	+	+		+
<i>Mantidactylus curtus</i>				+
<i>Mantidactylus femoralis</i>	+	+	+	+
<i>Mantidactylus fimbriatus</i>	+		+	
<i>Mantidactylus flavobrunneus</i>		+		
<i>Mantidactylus grandidieri</i>	+	+		+
<i>Mantidactylus</i> cf. <i>grandisonae</i>	+	+	+	
<i>Mantidactylus guttulatus</i>		+	+	
<i>Mantidactylus klemmeri</i>	+		+	+
<i>Mantidactylus leucomaculatus</i> ^c		+	+	+
<i>Mantidactylus liber</i>	+	+		+
<i>Mantidactylus</i> cf. <i>lugubris</i>	+			
<i>Mantidactylus luteus</i>		+	+	+
<i>Mantidactylus malagasius</i>	+			+
<i>Mantidactylus opiparis</i>	+	+	+	
<i>Mantidactylus peraccaae</i>		+		+
<i>Mantidactylus phantasticus</i>		+	+	
<i>Mantidactylus pseudoasper</i>	+		+	
<i>Mantidactylus pulcher</i>	+	+	+	+
<i>Mantidactylus</i> cf. <i>punctatus</i>			+	
<i>Mantidactylus redimitus</i>	+	+	+	+
<i>Mantidactylus rivicola</i>	+	+	+	+
<i>Mantidactylus ulcerosus</i>				+
Total number of species	42	50	42	39

^a Unidentified microhylid.

^b We here follow the specific attribution given by Raselimanana et al. (in press) for the treefrogs of the *Boophis luteus* group from Marojejy. See the text for further explanations.

^c On the occasion of an analysis of specimens collected at Anjanaharibe-Sud (western slope), we identified *Mantidactylus leucomaculatus*, a species which was not previously quoted by Raxworthy et al. (1998).

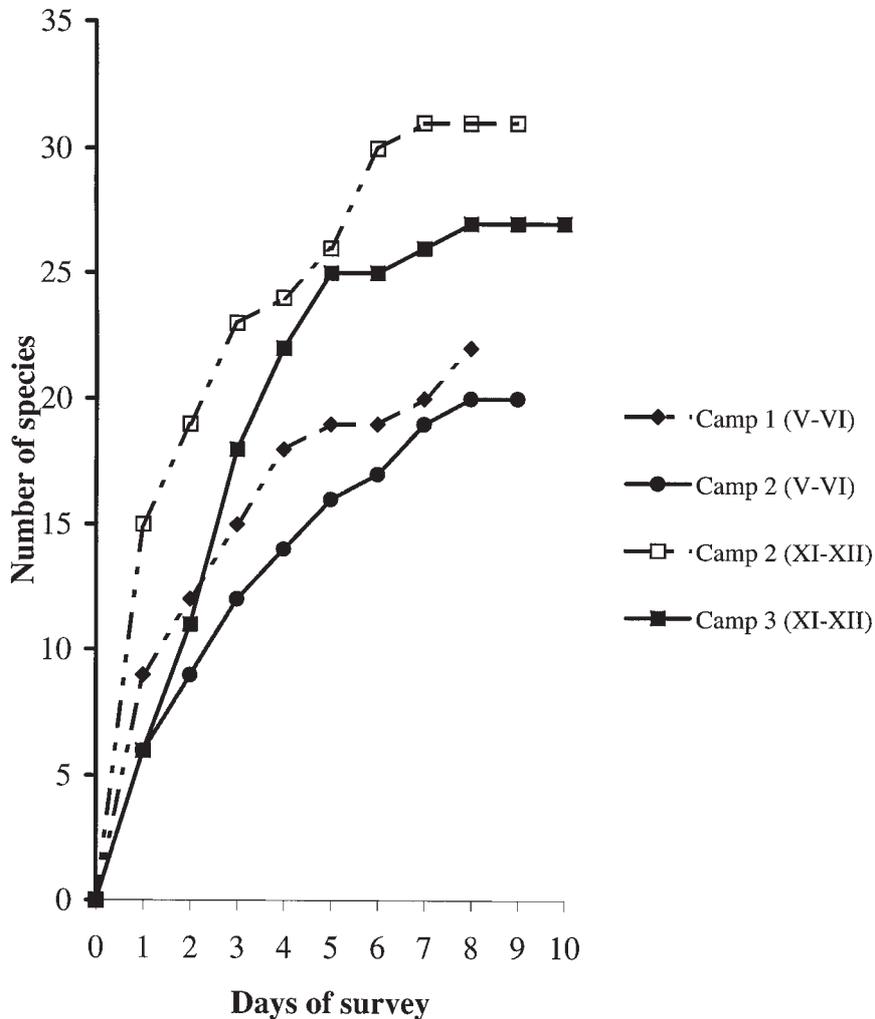


Figure 4. Species accumulation curves for all techniques combined amphibian species at Ambolokopatrika Forest.

explained by taking into consideration that the abundance of amphibians is significantly lower during the winter, with recording of additional species continuing until the last days of surveys. In contrast, during the summer specimens are far more abundant and therefore higher numbers of species are found within a few days, reaching a 'plateau' after 7–8 days.

The situation for reptiles is quite different (Figure 5), as no new species were captured after four to five days during the summer. During the winter a 'plateau' was reached only at Site 1, with no species increase in the last three days of the inventory. More than amphibians the reptiles appear difficult to find, being present in low densities, and not localised at particular habitats.

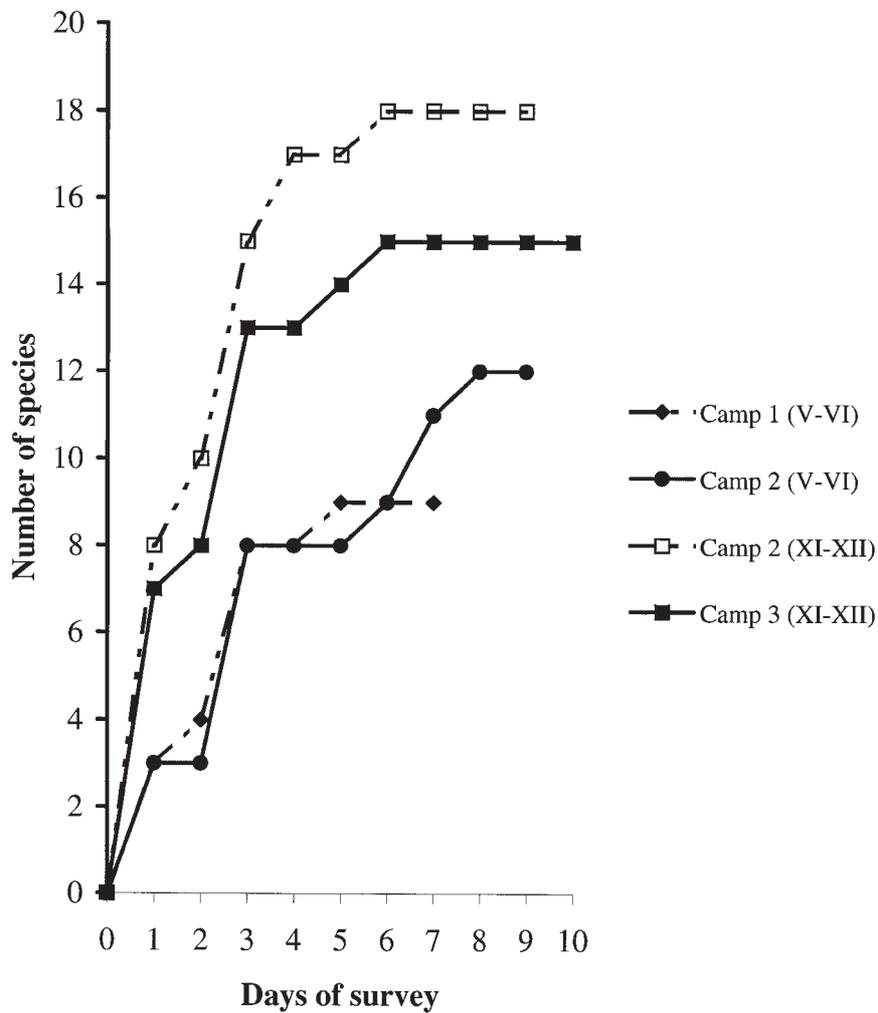


Figure 5. Species accumulation curves for all techniques combined reptile species at Ambolokopatrika Forest.

The accumulation curves for lipotyphlans indicate that in general the pitfall devices are effective for capturing a wide range of species and that rarely after seven nights are any new species obtained (Figure 6). The number of lipotyphlan species collected at Ambolokopatrika (9) represents a significant proportion (75.0%) of those expected to occur in the region at similar altitudes, since Goodman and Jenkins (1998, in press) found a total of 12 species at Anjanaharibe-Sud and Marojejy, 14 if we include two species (*Hemicentetes semispinosus* and *Oryzorictes hova*) found at the western slope of Anjanaharibe-Sud.

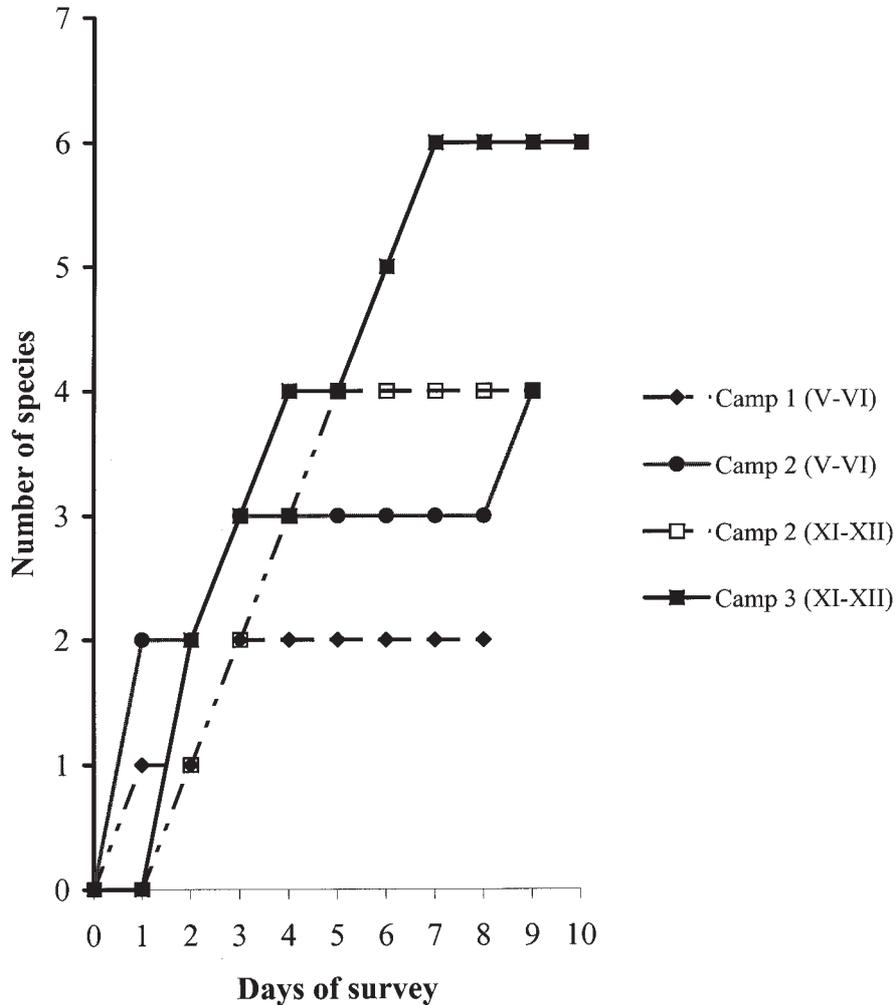


Figure 6. Species accumulation curves for pitfall trapping of lipotyphlans at Ambolokopatrika Forest.

Seasonal differences

At Ambolokopatrika during the May–June (cold season) survey we found 27 of the total 42 amphibian species (corresponding to 64.3%), 13 of the total 23 reptiles (56.5%) and 4 of the total 9 lipotyphlans (44.4%). These numbers, although lower during the winter, do not differ significantly either between seasons (amphibians, $\chi^2 = 1.83$; reptiles, $\chi^2 = 1.44$; lipotyphlans, $\chi^2 = 0.75$, $P > 0.05$), or among vertebrate classes ($\chi^2 = 0.05$, $P > 0.05$).

Limiting the analysis at Site 2, which was the only site visited during both seasons, during the winter we found only *Boophis anjanaharibeensis*, *B. madagascari-*

ensis (amphibians), *Ebenavia inunguis*, *Uroplatus ebenau*, *U. sikorae* (reptiles), and *Suncus murinus* (lipotyphlans). Some of these taxa (such as *B. anjanaharibeensis*, *U. ebenau*, and *U. sikorae*), were found during the summer too, but at Site 3, thus showing that their absence from Site 2 might be due to research deficiencies. *Boophis madagascariensis* and *Ebenavia inunguis* were missed during the warm season, but we believe anyway that this, together with the case of *Suncus murinus*, did not refer to a real absence. Most likely this is due to the lower density and abundance during the cold season, which makes more difficult the observation of some species, for which a longer study period should be practised.

Different is the case of species found during the summer only and missed during the cold season, and which therefore show a true seasonality. They were respectively: amphibians – *Platypelis barbouri*, *P. occultans*, *P. tuberifera*, *P. sp. 1*, *P. sp. 2*, *P. sp. 4*, *Plethodontohyla notosticta*, *P. serratopalpebrosa*, *Stumpffia sp. 2*, *Mantidactylus aglavei*, *M. betsileanus*, *M. bicalcaratus*, *M. cf. punctatus*; reptiles – *Furcifer willsii*, *Phelsuma quadriocellata*, *Zonosaurus madagascariensis*, *Amphiglossus mouroundavae*, *Androngo crenni*, *Geodipsas boulengeri*, *G. laphystia*, *Liopholidophis epistibes*, *L. rhadinaea*; lipotyphlans – *Microgale fotsifotsy*.

In general, the frogs which were found in all the study periods and sites (such as *Boophis cf. mandraka*, *B. marojezensis*, *Mantidactylus asper*, *M. femoralis*, *M. fimbriatus*, *M. guttulatus*, *M. klemmeri*, *M. luteus*, and *M. redimitus*) are arboreal (*Boophis* spp.), semi-arboreal or semi-aquatic *Mantidactylus* species, which live along the forest streams. The latter amphibians take advantage of the riverine habitat, which can be considered quite stable throughout the seasons in respect to temperature and humidity ranges, and for this they can be found also during the winter. On the contrary, most of the species found only during the warm season are not so closely tied to aquatic habitats. This is the case of the cophyline microhylids (genera *Platypelis*, *Plethodontohyla*, and *Stumpffia*), which represent 69.23% of the amphibians found only during the summer. Indeed they are among the most specialised amphibians of Madagascar, and almost all reproduce in phytotelms, and are therefore active when they are filled up with water in the rainy season (Andreone 1999). A similar biology is shared by *Mantidactylus bicalcaratus* and *M. cf. punctatus* too, which live beneath the leaves of *Pandanus*. The apparent absence of *M. betsileanus* might be explained taking into account the scarcity of still water bodies at the analysed site, and therefore to a local rarity of this species, elsewhere almost abundant (Andreone 1993, 1994).

Among the reptiles the absence of some species may be explained taking into account their low abundance as well. *Furcifer willsii*, which was found during the summer only consisted of a single specimen, represented the unique finding during the whole survey. In fact, all the other chameleonids which were quite abundant (*Brookesia* and *Calumma* spp.) were found during both study periods. The only other exception is represented by *Calumma parsonii*, which was found as a single specimen at Site 2 during the winter only. For this species too the apparent seasonality might reflect its low abundance and difficulty of observation. The absence of other reptiles

during May–June suggests instead a real absence or at least a decrease during the cold season, since none of these species was found at Site 1 as well. Skinks, excepting for *Amphiglossus melanopleura* (which is quite adaptable and locally abundant), were found only during the hot season. Snakes appear quite sensitive to seasonal variations and difficult to contact during the cold months. We attribute the absence of snakes during this season to the fact that they, more than other reptiles, need high temperatures and sun exposure to become active.

Amongst the lipotyphlans, four of the nine species were found during the winter: *Microgale parvula*, *M. talazaci*, *Oryzoricetes hova* and *Suncus murinus*. Except for *M. parvula*, the activity of the other species during the cold season is already known, and most likely depends on the capacity to store lipidic reserves in their body (S. Goodman, pers. comm.).

Comparison with other areas of NE Madagascar

The number of amphibian species recorded within the analysed 550–1350 m elevation range is 42 at Tsararano, 50 at Anjanaharibe-Sud, 42 at Ambolokopatrika, and 39 at Marojejy; for reptile species diversity is 30 at Tsararano, 33 at Anjanaharibe-Sud, 23 at Ambolokopatrika, and 43 at Marojejy; the number of lipotyphlan species are 7 at Tsararano, 11 at Anjanaharibe-Sud, 9 at Ambolokopatrika, and 11 at Marojejy (Tables 4–6).

Although the species diversity is higher at Anjanaharibe-Sud for amphibians, and at Marojejy for reptiles, the number of species found at the four sites is not significantly different either for amphibians ($\chi^2 = 1.54$, $P > 0.05$), or reptiles ($\chi^2 = 6.40$, $P > 0.05$). For lipotyphlans too these figures are not significantly different ($\chi^2 = 1.16$, $P > 0.05$).

One major problem for the faunal comparisons is that, while for Anjanaharibe, Ambolokopatrika, and Tsararano the members of the surveys were co-ordinated by F. Andreone (and therefore warranting homogeneity in searching and identifying methods), at Marojejy the surveys were carried out by a different team (Raselimanana et al. in press), which, although following a common and standardised research protocol, may have given different taxonomic attributions. We quote, as an example, the occurrence at Marojejy (according to Raselimanana et al. in press) of three species of *Boophis* belonging to the *B. luteus* group (*B. anjanaharibeensis*, *B. englaenderi*, and *B. luteus*), while, according to our opinion, it is likely that *B. luteus* is absent from N. Madagascar. Moreover, the specific attribution of these *Boophis* is virtually impossible upon preserved specimens only, since data about the acoustic repertoire and life colouration are necessary. In considering differences and similarities between Marojejy and the other rainforests caution therefore should be taken into consideration.

At each of the analysed localities there are apparently exclusive taxa: for the amphibians *Platypelis tsaratananaensis*, *Plethodontohyla inguinalis*, *P. sp. 2*,

Table 5. Distribution of the Tsararano, Anjanaharibe-Sud, Ambolokopatrika, and Marojejy reptiles.

Taxa	Sites			
	Tsararano	Anjanaharibe-Sud	Ambolokopatrika	Marojejy
	Attitude (m)			
	600–850	800–1350	810–1250	550–1350
Elevational range (m)				
	250	550	440	850
Gekkonidae				
<i>Ebenavia inunguis</i>		+	+	
<i>Homopholis antongilensis</i>	+			
<i>Lygodactylus cf. miops</i>	+		+	+
<i>Paroedura gracilis</i>	+	+	+	+
<i>Phelsuma guttata</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>	+	+	+	+
Chamaeleonidae				
<i>Brookesia betschi</i>		+	+	+
<i>Brookesia griveaudi</i>	+			+
<i>Brookesia karchei</i>				+
<i>Brookesia cf. minima</i>				+
<i>Brookesia superciliaris</i>			+	
<i>Brookesia therezieni</i>		+		
<i>Brookesia vadoni</i>	+			+
<i>Calumma boettgeri</i>			+	+
<i>Calumma brevicornis</i>		+		
<i>Calumma cucullata</i>	+			
<i>Calumma guillaumeti</i>		+		+
<i>Calumma cf. malthe</i>				+
<i>Calumma marojezensis</i>		+		+
<i>Calumma nasuta</i>		+	+	+
<i>Calumma parsonii</i>		+	+	
<i>Calumma n.sp. 1</i>	+		+	
<i>Calumma n.sp. 2</i>	+			
<i>Furcifer pardalis</i>		+		+
<i>Furcifer willsii</i>			+	
Scincidae				
<i>Amphiglossus astrolabi</i>	+			
<i>Amphiglossus frontoparietalis</i>	+			+
<i>Amphiglossus macrocercus</i>				+
<i>Amphiglossus melanopleura</i>	+		+	+
<i>Amphiglossus melanurus</i>	+	+		+
<i>Amphiglossus minutus</i>		+		+
<i>Amphiglossus mouroundavae</i>	+		+	+
<i>Amphiglossus punctatus</i>	+	+		
<i>Amphiglossus sp. 1</i>	+			

Table 5. Continued.

Taxa	Sites			
	Tsararano	Anjanaharibe-Sud	Ambolokopatrika	Marojejy
	Attitude (m)			
	600–850	800–1350	810–1250	550–1350
Elevational range (m)				
	250	550	440	850
<i>Androngo cremi</i>		+	+	
<i>Mabuya gravenhorstii</i>		+		
<i>Paracontias hildebrandti</i>	+	+		
<i>Paracontias holomelas</i>				+
<i>Pseudacontias angelorum</i>				+
Gerrhosauridae				
<i>Zonosaurus brygooi</i>	+			
<i>Zonosaurus madagascariensis</i>	+	+	+	+
<i>Zonosaurus rufipes</i>				+
<i>Zonosaurus subunicolor</i>				+
Boidae				
<i>Sanzinia madagascariensis</i>		+		+
Typhlopidae				
<i>Typhlops mucronatus</i>	+	+	+	
<i>Typhlops ocularis</i>				+
<i>Typhlops</i> sp. 1				+
<i>Typhlops</i> sp. 2	+			
Colubridae				
<i>Geodipsas boulengeri</i>			+	+
<i>Geodipsas infralineata</i>		+		
<i>Geodipsas laphystia</i>	+		+	
<i>Langaha madagascariensis</i>	+			
<i>Liophidium rhodogaster</i>	+	+		+
<i>Liophidium</i> sp. 1		+		
<i>Liophidium</i> sp. 2		+		
<i>Liopholidophis epistibes</i>	+	+	+	+
<i>Liopholidophis rhadinaea</i>			+	
<i>Liopholidophis stumpffi</i>				+
<i>Liopholidophis</i> sp. 1				+
<i>Pseudoxyrhopus analabe</i>		+		
<i>Pseudoxyrhopus microps</i>	+	+		+
<i>Pseudoxyrhopus tritaeniatus</i>		+		
<i>Stenophis arctifasciatus</i>	+			+
<i>Stenophis betsileanus</i>		+		
<i>Stenophis gaimardi</i>				+
Total number of species	30	33	23	43

Table 6. Distribution of the Tsararano, Anjanaharibe-Sud, Ambolokopatrika, and Marojejy lipotyphlans.

Taxa	Sites			
	Tsararano	Anjanaharibe-Sud	Ambolokopatrika	Marojejy
	Attitude (m)			
	600–850	800–1350	810–1250	550–1350
Elevational range (m)				
	250	550	440	850
Tenrecidae				
<i>Hemicentetes semispinosus</i> ^a	+	+		
<i>Microgale brevicaudata</i>				+
<i>Microgale cowani</i>	+	+	+	+
<i>Microgale dobsoni</i>		+		+
<i>Microgale fotsifotsy</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 taiva</i>		+	+	
<i>Microgale talazaci</i>	+	+	+	+
<i>Oryzorictes hova</i>	+	+	+	
<i>Setifer setosus</i>		+		+
Soricidae				
<i>Suncus murinus</i> ^b			+	
Total number of species	7	11	9	11

^a *Hemicentetes semispinosus* and *Microgale taiva* were found by F. Andreone, H. Randriamahazo, and J.E. Randrianirina at Anjanaharibe-Sud, western side (Goodman et al. 1998). *Microgale principula*, and *Oryzorictes hova* were found at different altitudes at Marojejy (Goodman et al. in press).

^b Species introduced to Madagascar.

'Microhylid sp.', *Mantidactylus* cf. *lugubris*, and *Boophis lichenoides* at Tsararano; *Anodonthyla boulengeri*, *Platypelis pollicaris*, *P.* sp. 1, *Plethodontohyla minuta*, *P.* sp. 1, *Ptychadena mascareniensis*, and *Mantidactylus flavobrunneus* at Anjanaharibe-Sud; *Platypelis* sp. 4, *Plethodontohyla laevipes*, *Stumpffia* sp. 1, *Boophis* cf. *burgeri*, and *Mantidactylus* cf. *punctatus* at Ambolokopatrika; *Plethodontohyla coudreaui*, *Stumpffia psologlossa*, *Boophis englaenderi*, *B. luteus*, *Mantidactylus curtus*, and *M. ulcerosus* at Marojejy. The site exclusive reptiles are: *Homopholis antongilensis*, *Calumma cucullata*, *C.* n.sp. 2, *Amphiglossus astrolabi*, *A.* sp. 1, *Zonosaurus brygooi*, *Typhlops* sp. 2, and *Langaha madagascariensis* at Tsararano; *Brookesia therezieni*, *Calumma brevicornis*, *Mabuya gravenhorsti*, *Geodipsas infralineata*, *Liophidium* sp. 1, *L.* sp. 2, *Pseudoxyrhopus analabe*, *P. tritaeniatus*, and *Stenophis betsileanus* at Anjanaharibe-Sud; *Brookesia superciliaris*, *Furcifer willsii*, and *Liopholidophis rhadinaea* at Ambolokopatrika; *Brookesia karchei*, *B.* cf. *minima*, *Calumma* cf. *malthe*, *Phelsuma pusilla*, *Uroplatus fimbriatus*, *U. lineatus*, *Amphiglossus macrocerus*, *Paracontias holomelas*, *Pseudoacontias angelorus*, *Zonosaurus rufipes*, *Z. subuni-*

color, *Typhlops ocellaris*, *T. sp. 1*, *Liopholidophis stumpffi*, *L. sp. 1*, and *Stenophis gaimardi* at Marojejy.

The mean coefficient of exclusivity $E \pm SD$ is 0.14 ± 0.01 for amphibians, 0.26 ± 0.13 for reptiles, and 0.10 ± 0.07 for lipotyphlans. The difference between amphibian and reptile E values is significant (Student's t -test, $t = 2.46$, $P < 0.05$), as well as that between reptiles and small mammals ($t = 2.67$, $P < 0.05$), but not that between amphibians and lipotyphlans ($t = 1.13$, $P > 0.05$).

It is worth stressing that most of the species 'exclusive' to only one of the four analysed sites, are anyway known from elsewhere. *Boophis lichenoides* was found at Tsararano only, but is also known at 'Ambatolaidama' and 'Menamalona', two sites within the PN de Masoala (Andreone and Randrianirina, unpubl.), and from much further south next to Andasibe and Vondrozo (Vallan et al. 1998). Furthermore, this species is also known from Marojejy (as based upon tadpoles found by Glaw and Vences 1994, and quoted by Vallan et al. 1998). Likely, *Furcifer willsii* has been found at Ambolokoparika, with other findings in central-eastern Madagascar, and in the north-east of the island it has been recently found at the two Masoala sites (Andreone and Randrianirina, unpubl.). For this reason, only a few of the site exclusive species may actually be really endemic to a single locality. On the evidence available to date examples of such presumed endemics are *Platypelis sp. 1*, *Plethodontohyla sp. 1*, *Liophidium sp. 1*, *L. sp. 2* and *Pseudoxyrhopus analabe* (Anjanaharibe-Sud), *Pseudoacontias angelorum*, *Liopholidophis sp. 1* and *Typhlops sp. 1* (Marojejy), *Amphiglossus sp. 1*, *Calumma n.sp. 2*, and *Typhlops sp. 2* (Tsararano). The only amphibian species of Ambolokopatrika which has not been found elsewhere, and which might be endemic is *Platypelis sp. 4*. No reptile species found at Ambolokopatrika may be considered as endemic.

As it is stressed by Andreone and Randrianirina (2000) the higher E values observed in reptiles may probably be due to objective difficulty in finding them during a short term survey. The number of exclusive species, in this case, would mirror the missed species at each site. If this turns out to be true, it would mean that the saturation point reached for reptile species is only apparent, and that therefore to get a sufficiently exhaustive list of reptiles at each analysed site it would be necessary for a longer survey. Unluckily, most of the recent surveys on the Malagasy herpetofauna (e.g., Raxworthy and Nussbaum 1996; Raselimanana 1998; Raselimanana et al. in press) show accumulation curves where data for amphibians and reptiles are pool together, hiding therefore the differences between these two vertebrate classes.

Concerning small mammals *Microgale brevicaudata* is apparently exclusive to Marojejy, but no endemic species were found at the elevational range under consideration. The species from Ambolokopatrika also occur at both Anjanaharibe-Sud and Marojejy, with the exception of *Microgale taiva* and *Oryzorictes hova*, which were found only at Anjanaharibe-Sud, and *Microgale fotsifotsy* and *M. parvula* shared with Marojejy only. *Suncus murinus* was found only at Ambolokopatrika (but this is generally a difficult species to capture in forest habitats: S. Goodman 1998, pers.

Table 7. Similarity coefficients (*S*) for the herpetofauna (Amphibia, Reptilia), and small mammals (Lipotyphla) in the four analyzed rainforests.

Sites	Tsararano	Anjanaharibe-Sud	Ambolokopatrika
Anjanaharibe-Sud ^a	0.46 0.26 0.50		
Ambolokopatrika ^b	0.46 0.29 0.33	0.51 0.30 0.43	
Marojejy ^c	0.42 0.31 0.29	0.51 0.31 0.47	0.40 0.27 0.43

^a Values for amphibians.

^b Values for reptiles.

^c Values for lipotyphlans.

comm.), while *M. fotsifotsy* was found at the western slope of Anjanaharibe-Sud Massif, but at a higher elevation (Goodman and Jenkins 1998). *Setifer setosus* was found at Marojejy and Anjanaharibe-Sud, but was missed at Ambolokopatrika. Thus the lipotyphlan diversity in the Ambolokopatrika region is slightly lower, but generally in line with that occurring in parallel elevational ranges in the neighbouring reserves.

In order to place the level of similarity between the four analysed forests into a clearer context, we also analysed the similarity coefficient. The values are given in Table 7. Mean values \pm SD are respectively 0.46 ± 0.05 (amphibians), 0.29 ± 0.02 (reptiles), 0.41 ± 0.08 (lipotyphlans). The difference in the mean values of *S* between amphibians and reptiles is significant ($t = 8.36$, $P < 0.01$), as well as between reptiles and lipotyphlans ($t = 3.44$, $P < 0.05$), but not between amphibians and lipotyphlans ($t = 1.36$, $P = 0.20$). For amphibians and reptiles *S* was higher for the Ambolokopatrika/Anjanaharibe-Sud comparison (0.51 for amphibians and 0.30 for reptiles) than for Ambolokopatrika/Marojejy (0.40 for amphibians and 0.27 for reptiles). For the lipotyphlans, if we exclude *Hemicentetes semispinosus*, which was cited as occurring at Marojejy by Nicoll and Langrand (1989) and by Duckworth (1990), but not found by Goodman and Jenkins (in press), the Ambolokopatrika Forest shares six species with both Marojejy and Anjanaharibe-Sud, with a *S* coefficient of 0.43. The highest value for the small mammals is 0.50 for the comparison Anjanaharibe-Sud/Tsararano, and the smallest index value is 0.29 for Marojejy/Tsararano. We interpret these values to indicate that the Ambolokopatrika Forest – at least for amphibians and reptiles – is more similar to Anjanaharibe-Sud than to Marojejy.

Biogeographical considerations

The surveys we carried out at Ambolokopatrika, added to information gathered at Anjanaharibe-Sud, Marojejy, and Tsararano, allow us to draw some preliminary

conclusions about the biogeography of these forest systems in north-eastern Madagascar, especially concerning the faunal composition at low and mid altitudes.

The Marojejy Massif, although not much higher than Anjanaharibe-Sud (2132 and 2064 m respectively), appears to have played a remarkable role as a biogeographic refuge and endemism center for some taxa. The amphibians and reptiles retained as endemics at this massif (at the whole 300–2133 m elevational range studied by Raselimanana et al. in press) turn out to be nine (*Mantella manery*, *Mantidactylus* sp., *Boophis* sp. 1, *B.* sp. 2, *Uroplatus* sp., *Pseudoacantias angelorum*, *Brookesia karchei*, *Calumma* cf. *brevicornis*, and *Liopholidophis* sp. 1), representing a conspicuous percentage of the overall herpetofauna of the massif (7.5%). Among the studied sites the Marojejy Massif (at least for the analysed elevational range) shows a greater number of exclusive reptile species when compared to the other sites ($E = 0.37$). The same tendency is not clearly apparent for amphibians and lipotyphlans for which values are comparable to those of the other sites (0.15 and 0.18 respectively).

At Anjanaharibe-Sud four species (*Platypelis* sp. 3, *Plethodontohyla* sp. 2, *Liophidium* sp. 2, and *Pseudoxyrhopus analabe*) were until now not found elsewhere and are possible endemics of this massif, corresponding to 4.3% of its herpetofauna. *Platypelis* sp. 2 and *Boophis anjanaharibeensis*, given by Raxworthy et al. (1998) as Anjanaharibe-Sud endemics, have been found subsequently at other sites.

The small mammal survey conducted at Marojejy by Goodman and Jenkins (in press) did not confirm the presence of *Microgale taiva*, a species known to occur on the western slopes of Anjanaharibe-Sud, in the Ambolokopatrika Forest, and at Ambatolaidama in the Masoala Peninsula (Andreone and Randrianirina, unpubl.). The previous northernmost records for *M. taiva* were from Ambositra and Périnet-Analamazaotra region in central-eastern Madagascar (Nicoll and Rathbun 1990; Goodman et al. 1998; Garbutt 1999). Similar distributions are known for several amphibian and reptile species, with records around the Andapa Basin and in north-eastern Madagascar, and then from areas in the central-eastern portion of the island: *Boophis lichenoides* (Vallan et al. 1998), *B.* cf. *burgeri* (if indeed *B. burgeri* and *B.* cf. *burgeri* – as from Glaw and Vences 1997a – are conspecific), *Mantidactylus phantasticus* (Glaw and Vences 1997b; Andreone et al. 1998), *Furcifer willsii* (Glaw and Vences 1994), and *Brygophis coulangesi* (Andreone and Raxworthy 1998). It is unclear if all these species really have a disjunct distribution in central-eastern and northern Madagascar or if, as we suspect, they are widely distributed throughout the eastern rainforest belt, but observational data are missing for northernmost areas.

Some species were not found at Ambolokopatrika, but are present on both the Anjanaharibe-Sud and Marojejy massifs (at the altitudes considered): *Stumpffia grandis*, *Mantella nigricans*, *Mantidactylus grandidieri*, *M. liber*, *M. peraccae*, *M. ulcerosus*, *Phelsuma guttata*, *Amphiglossus melanurus*, *A. minutus*, *Liophidium rhodogaster*, and *Pseudoxyrhopus microps*. Disregarding the snakes, which are often present in low densities (and therefore not easily observed in a comparatively short survey period), and the amphibians *Stumpffia grandis* and *Mantidactylus ulcerosus* (which

are difficult to identify), we attribute the absence of species elsewhere abundant, or usually easily captured by pitfall traps, like *Mantella nigricans* and *Mantidactylus grandidieri*, *Phelsuma guttata*, *Amphiglossus melanurus* and *A. minutus* to research deficiency, and possibly to scarcity of suitable habitats in the study areas.

Zonosaurus rufipes and *Z. subunicolor* present at Marojejy previously were not found at the other areas around Andapa. *Zonosaurus brygooi* occurs in both the forests of Tsararano and Besariaka-Amponaomby (a rainforest between the Anjanaharibe-Sud and Tsararano massifs visited briefly by F. Andreone and J.E. Randrianirina during the 1996 winter season: see Figure 1), but is apparently absent at Marojejy (Vences et al. 1999b). Other species of reptiles present at Marojejy but not found at the other sites are *Brookesia* cf. *minima*, and *Calumma* cf. *malthe*.

If we take into consideration the altitudinal range analysed (250 m at Tsararano, 550 m at Anjanaharibe-Sud, 440 m at Ambolokopatrika, and 850 m at Marojejy), the number of amphibian and reptile species turned out to be significantly different (amphibians: $\chi^2 = 33.33$; reptiles: $\chi^2 = 14.60$, $P < 0.01$), which is not the case for lipotyphlans ($\chi^2 = 2.78$, $P > 0.05$). In particular, at the Marojejy's 850 m band only 39 amphibian species are known (versus an expected number of 68), while the number of reptile species at this site is 43. Marojejy is also unique among the analysed sites in having more reptiles than amphibians. This is true also for the overall herpetological survey as reported by Raselimanana et al. (in press), where, for the overall 1833 (300–2133 m) studied elevation, they give 52 species of amphibians and 61 of reptiles.

Possible explanations for the differences between Marojejy and the other sites should take into account: (i) the higher number of persons involved in the research at Marojejy (7 versus 1–3 for the other sites), which might have positively influenced the discovery of a larger number of reptiles; (ii) a greater attention of the Marojejy team to reptiles than to amphibians; (iii) differences in climatic conditions being more favourable for reptiles when searches were carried out; (iv) a truly greater diversity of reptiles for Marojejy.

In particular, to comment on the last point we should take into account the position of Marojejy, which constitutes the easternmost portion of the mountains around the Andapa Basin. This massif is mostly encircled by low altitude areas and by the Androranga and Lokoho rivers, which may contribute to its isolation from the other rainforests (Raxworthy et al. 1998). The only access to the Anjanaharibe-Sud Massif is the Betaolana Ridge (where the Ambolokopatrika Forest is sited); the narrow 500–1000 m forest band at the western part of Marojejy Massif along the Lokoho River (Figure 2) may have limited the spread of some species from the eastern slope. Reptiles are possibly sensitive to these slope differences, being more dependant on sun exposure and variation in daily temperature, and they may also have a smaller distribution than amphibians and lipotyphlans. At Marojejy (Raselimanana et al. in press) the mean elevational range (\pm SD) of the amphibian species ($n = 51$) is 505.20 ± 407.73 m, while it is 360.25 ± 338.68 m in reptiles ($n = 59$); these values

are significantly different (Mann–Whitney $U = 1211.50$, $P < 0.05$). Probably, the study conducted at Andringitra Massif (Raxworthy and Nussbaum 1996) revealed a similar trend, with a mean elevational range of 287.02 ± 301.66 m for amphibians ($n = 57$), and 143.43 ± 193.45 for reptiles ($n = 35$); these values too are significantly different ($U = 748.50$, $P < 0.05$). Eight of the 12 lipotyphlans (66.7%) found at Andringitra by Goodman et al. (1996), and 8 of the 11 species (72.7%) found at Anjanaharibe-Sud by Goodman and Jenkins (1998) were found at two or more altitudes. Amphibians and lipotyphlans may therefore be more successful in colonising the low- and mid-altitude rainforests, possibly depending less on the general climate of the area (and therefore on west-east slope differences), and can disperse following the network of forest streams, where the ecological conditions (e.g., humidity, food, and temperature) are generally more stable.

Conservation

The conservation aspects facing the Ambolokopatrika Forest are similar to those already invoked for Anjanaharibe-Sud and Marojejy massifs by Berner (1995), Raxworthy et al. (1998) and Raselimanana et al. (in press). However, it is worth stressing that the latter two sites are already in the protected areas program, and thus, the lack of any protection at Ambolokopatrika poses more urgent action. Virtually nothing is known about the history of forest destruction and alteration at Ambolokopatrika: this forest has already been severely altered in several places and currently consists of a patchwork of pristine and degraded parcels. Grazing pressure does not seem to be particularly severe at present since the people of the neighbouring villages of Miandampona and Ambodivoara, for example, do not intensively exploit the forest for cattle pasture as is the case of Besariaka–Amponaomby and Tsararano forests. On the other hand the ‘tavy’ (slash and burn agriculture) is a common practice at Ambolokopatrika, and represents, as for many other Malagasy forests, the main problem for ecological conservation.

Other human activities should be carefully managed at Ambolokopatrika: at the edges of areas of ‘savoka’ many lemur traps were found. Local people use temporary camps to hunt lemurs (*Eulemur* spp.) and wild pigs (*Potamochoerus larvatus*), and to collect the bark of *Evodia* trees (‘bilahy’), used to fabricate the ‘betsa’, a popular alcoholic beverage. The fishing activity is mainly upon eels (*Anguilla* spp.) and river crabs. Anyway, the capture of large frogs, such as *Mantidactylus guttulatus* (locally known as ‘radaka’ or ‘radakabe’) is rather occasional, and does not seem to affect the local populations of these amphibians.

There is little doubt that the human pressure will increase in the next years, especially in non-protected areas, like Ambolokopatrika and Tsararano. These forests are therefore particularly important in assuring biotic exchanges, since Ambolokopatrika connects the Anjanaharibe-Sud and the Marojejy forests, while Tsararano ties the Anjanaharibe-Sud forests to the PN de Masoala, one of the largest remaining forest

blocks on Madagascar. In this sense we agree with considerations made by Raselimanana (1999) in a similar context for the rainforest connecting the RS du Pic d'Ivohibe and the PN d'Andringitra.

Given the faunal similarities between various forest blocks surrounding the Andapa watershed, it is evident that the forests of Ambolokopatrika and Tsararano are important for dispersal of forest dwelling animals and important means of genetic exchange, and may indeed act as real corridors. Taking into account the criticisms of the 'corridor' notion (e.g., Noss 1987; Simberloff et al. 1992) we recommend that these forests should be given important consideration for conservation actions. We also consider it important that with the development of new management practices of the two neighbouring reserves, particularly after the recent upgrading of Marojejy from a Réserve Naturelle Intégrale to Parc National, a certain degree of protection should be given at least to the Ambolokopatrika Forest. In particular the fragmentation of forest parcels due to human activity represents a real problem for the persistence of viable animal populations: special attention should be given to assuring the persistence of sufficiently wide forest habitats between the protected areas of Anjanaharibe-Sud and Marojejy, which, otherwise, may become isolated in a near future. For the herpetofauna and small mammals the persistence of forests ribbons along the main water courses may assure a certain biotic exchange and the persistence of riverine populations (Andreone and Randrianirina 2000). Of course this might not be the case for other animals, and in particular for other vertebrates (such as birds and larger mammals). This observation supports the necessity for further research on other zoological groups to be carried out urgently to understand more clearly if there are real biological differences between the sites and elucidate the biogeographic history of north-eastern Madagascar. This will be useful to assess the importance of these sites in the context of the creation of a complex of linked reserves that allow protection of the rich and remarkable biota of north-eastern Madagascar.

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Note

¹The Malagasy toponyms for sites were given by local people, and must be regarded as unofficial names.

References

- Andreone F (1993) Kommentierte Liste von Amphibienfunden auf Madagaskar. *Salamandra* 29(3/4): 200–211
- Andreone F (1994) The amphibians of Ranomafana rain forest, Madagascar – preliminary community analysis and conservation considerations. *Oryx* 28(3): 207–214
- Andreone F (1996a) Seasonal variations of the amphibian communities in two rainforests of Madagascar. In: Lourenço WR (ed) *Biogéographie de Madagascar*, pp 397–402. Orstom, Paris
- Andreone F (1996b) Another new green treefrog, *Boophis anjanaharibeensis* n.sp. (Ranidae: Rhacophoridae), from northeastern Madagascar. *Aqua Journal of Ichthyology and Aquatic Biology* 2(2): 25–32
- Andreone F (1999) Madagascar amphibians. In: Yamagishi S (ed) *Madagascar Animals – Its Wonderful Adaptive Radiations*, pp 213–261. Shoukabou Co. Ltd., Tokyo
- Andreone F, Glaw F, Vences M and Vallan D (1998) A new *Mantidactylus* (Ranidae: Mantellinae) from south-eastern Madagascar, with considerations a review of *Mantidactylus peraccae* (Ranidae: Mantellinae). *Herpetological Journal* 8: 149–159
- Andreone F and Randriamahazo H (1997) Ecological and taxonomic observations on the amphibians and reptiles of Andohahela low altitude rainforest. *Revue française d'Aquariologie* 3/4: 95–128
- Andreone F and Randrianirina JE (2000) Biodiversity, rainforests and herpetological communities in Madagascar: what about differences in amphibians and reptiles? In: Lourenço WR and Goodman SM (eds) *Diversity and endemism in Madagascar*. Mémoires de la Société de Biogéographie
- Andreone F and Raxworthy CJ (1998) The colubrid snake *Brygophis coulangesi* (Domergue 1988) rediscovered in north-eastern Madagascar. *Tropical Zoology* 11: 249–257
- Berner PO (1995) Préparation d'un volet forestier d'un projet de conservation et développement intégré de la région est de Madagascar: le cas du complexe des réserves de Marojejy et d'Anjanaharibe-Sud. *Akon'ny Ala* 17: 28–39
- Blommers-Schlösser RMA (1993) Systematic relationships of the Mantellinae Laurent 1946 (Anura Ranioidea). *Ethology, Ecology and Evolution* 5: 199–218
- Blommers-Schlösser RMA and Blanc Ch P (1991) Amphibiens (première partie). Paris: Faune de Madagascar 75(1): 1–379
- Böhme W (1997) Eine neue Chamäleonart aus der *Calumma gastrotaenia*-Verwandschaft Ost-Madagaskars. *Herpetofauna* 19(107): 5–10

- Butler PM (1988) Phylogeny of the insectivores. In: Benton MJ (ed) *The Phylogeny and Classification of the Tetrapodes*, Vol 2, pp 117–141. Clarendon Press, Oxford
- Cadle JE (1996a) Snakes of the genus *Liopholidophis* (Colubridae) from eastern Madagascar: new species, revisionary notes, and an estimate of phylogeny. *Bulletin of the Museum of Comparative Zoology* 154(5): 369–464
- Cadle JE (1996b) Systematics of snakes of the genus *Geodipsas* (Colubridae) from Madagascar, with descriptions of new species and observations on natural history. *Bulletin of the Museum of Comparative Zoology* 155(2): 33–87
- Duckworth JW (1990) Systematic list of mammals recorded in Marojejy. In: Safford R and Duckworth JW (eds) *A Wildlife Survey of Marojejy Nature Reserve, Madagascar*, pp 114–129. Study Report no. 40. International Council for Bird Preservation, Cambridge
- Garbutt N (1999) *Mammals of Madagascar*. Pica Press, Hong Kong
- Glaw F and Vences M (1994) *A Fieldguide to the Amphibians and Reptiles of Madagascar*. Second edition, including freshwater fish and mammals. Vences und Glaw Verlag, Köln
- Glaw F and Vences M (1997a) Neue Ergebnisse zur *Boophis goudoti*-Gruppe aus Madagaskar: Bioakustik, Fortpflanzungsstrategien und Beschreibung von *Boophis rufioculis* sp. nov. *Salamandra* 32(4): 225–242
- Glaw F and Vences M (1997b) Neue Daten über die *Mantidactylus*-Untergattung *Spinomantis* aus Madagaskar, mit Beschreibung einer neuen Art. *Salamandra* 32(4): 243–258
- Glaw F, Vences M and Böhme W (1998) Systematic revision of the genus *Aglyptodactylus* Boulenger, 1919 (Amphibia: Ranidae), and analysis of its phylogenetic relationships to other Madagascan ranid genera (*Tomopterna*, *Boophis*, *Mantidactylus*, and *Mantella*). *Journal of Zoological Systematic and Evolutionary Research* 36: 17–37
- Glaw F, Vences M, Ziegler T, Böhme W and Köhler J (1999) Specific distinctness and biogeography of the dwarf chameleons *Brookesia minima*, *B. peyrierasi* and *Brookesia tuberculata* (Reptilia: Chamaeleonidae): evidence from hemipenial and external morphology. *Journal of Zoology, London*, 247: 225–238
- Goodman SM and Jenkins PD (1998) The insectivores of the Réserve Spéciale d'Anjanaharibe-Sud. In: Goodman SM (ed) *A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: with Reference to Elevational Variation*, pp 139–161. *Fieldiana: Zoology, n.s.*, 90: 1–245
- Goodman SM and Jenkins PD (in press) The shrew tenrecs (Lipotyphla: Tenrecidae) of Parc National de Marojejy, Madagascar. In: Goodman SM (ed) *A Floral and Faunal Inventory of the Parc National de Marojejy, Madagascar: with Reference to Elevational Variation* *Fieldiana: Zoology, n.s.*, 92
- Goodman SM, Jenkins PD and Pidgeon M (1999) Lipotyphla (Tenrecidae and Soricidae) of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. In: Goodman SM (ed) *A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: with Reference to Elevational Variation* *Fieldiana: Zoology, n.s.*, 90: 1–296
- Goodman SM and Lewis BA (1998) Description of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. In: Goodman SM (ed) *A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: with Reference to Elevational Variation*, pp 9–16. *Fieldiana: Zoology, n.s.*, 90: 1–246
- Goodman SM, Raxworthy CJ and Jenkins PD (1996) Insectivore ecology in the Réserve Naturelle Intégrale d'Andringitra, Madagascar. In: Goodman SM (ed) *A Floral and Faunal Inventory of the Eastern Slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: with Reference to Elevational Variation*, pp 218–230. *Fieldiana: Zoology, n.s.* 85: 1–319
- Humbert H (1955) Les territoires phytogéographiques de Madagascar. Leur cartographie. *Annales Biologiques, troisième série* 31: 195–204
- Jenkins PD, Goodman SM and Raxworthy CJ (1996) The shrew tenrecs (*Microgale*) (Insectivora: Tenrecidae) of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. In: Goodman SM (ed) *A Floral and Faunal Inventory of the Eastern Slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: with Reference to Elevational variation*, pp 191–217. *Fieldiana: Zoology, n.s.* 85: 1–319
- Klaver C and Böhme W (1986) Phylogeny and classification of the Chamaelonidae (Sauria) with special reference to hemipenis morphology. *Bonner Zoologische Monographien* 22: 1–64
- Kluge AG (1991) Boine snake phylogeny and research cycles. *Miscellaneous Publications Museum of Zoology, University of Michigan* 178: 1–58

- Nicoll ME and Langrand O (1989) Madagascar: Revue de la Conservation et des Aires Protégées. WWF-Fonds Mondial pour la Nature, Gland
- Nicoll ME and Rathbun GB (1990) African Insectivora and Elephant-Shrews. An action plan for their conservation. International Union for the Conservation of Nature and Natural Resources, Gland
- Noss RF (1987) Corridors in real landscapes: a reply to Simberloff and Cox. *Conservation Biology* 1: 159–164
- Nussbaum RA, Andreone F and Raxworthy CJ (1998) A new rainforest species of *Pseudoxyrhopus* Günther (Squamata: Colubridae) from Northern Madagascar. *Copeia* 1998(1): 128–132
- Randriamaherisoa A, Binard M and Persoons E (1993) Use of G.I.S. and remote sensing in hydrological model for impact study of land cover change in a Malagasy rural basin. *ESRSeL Advances in Remote Sensing* 2(3): 154–164
- Raselimanana AP (1998) La diversité de la faune de reptiles et amphibiens. In: Rakotondravony D and Goodman S (eds) Inventaire Biologique Forêt d'Andranomay Anjozorobe, pp 43–59. Recherches pour le développement, Série Sciences Biologiques 13: 1–110
- Raselimanana AP (1999) Chapitre 4. Le herpétofaune. In: Goodman SM and Rasolonandrasana BPN (eds) Inventaire biologique de la réserve spéciale du pic d'Ivohibe et du couloir forestier qui la relie au Parc National d'Andringitra, pp 81–87. Recherches pour le développement, Série Sciences Biologiques 15: 1–181
- Raselimanana AP, Raxworthy CJ and Nussbaum RA (in press) Diversity and elevational distribution of the herpetofauna within the Parc National de Marojejy. In: Goodman SM (ed) A Floral and Faunal Inventory of the Parc National de Marojejy: with Reference to Elevational Variation. *Fieldiana: Zoology*, n.s. 92
- Raxworthy CJ, Andreone F, Nussbaum RA, Rabibisoa N and Randriamahazo H (1998) Amphibians and reptiles of the Anjanaharibe Massif: elevational distributions and regional endemism. In: Goodman SM (ed) A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: with Reference to Elevational Variation, pp 79–92. *Fieldiana: Zoology*, n.s. 90: 1–246
- Raxworthy CJ and Nussbaum RA (1995) Systematics, speciation and biogeography of the dwarf chameleons (*Brookesia*; Reptilia, Squamata, Chamaeleontidae) of northern Madagascar. *Journal of Zoology*, London 235: 525–558
- Raxworthy CJ and Nussbaum RA (1996) Amphibians and reptiles of Andringitra Massif: a study of elevational distribution and local endemism. In: Goodman SM (ed) A Floral and Faunal Inventory of the Eastern Side of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: with Reference to Elevational Variation, pp 158–170. *Fieldiana: Zoology*, n.s. 85: 1–319
- Richards CM and Moore WS (1998) A molecular phylogenetic study of the Old World treefrog family Rhacophoridae. *Herpetological Journal* 8: 41–46
- Simberloff DS, Farr JA, Cox J and Mehlman DW (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6: 493–504
- Vallan D, Glaw F, Andreone F and Cadle JE (1998) A new treefrog species of the genus *Boophis* (Anura: Ranidae: Rhacophorinae) with dermal fringes from Madagascar. *Amphibia-Reptilia* 19: 357–368
- Vences M, Glaw F and Andreone F (1997) Descriptions of two new frogs of the genus *Mantidactylus* from Madagascar, with notes on *Mantidactylus klemmeri* (Guibé 1974) and *Mantidactylus webbi* (Grandison 1953) (Amphibia, Ranidae, Mantellinae). *Alytes* 14: 130–146
- Vences M, Glaw F and Böhme W (1999a) A review of the genus *Mantella* (Anura, Ranidae, Mantellinae): taxonomy, distribution and conservation of Malagasy poison frogs. *Alytes* 17(1–2): 3–72
- Vences M, Ziegler T, Visser S and Andreone F (1999b) New data on the zoogeography and genital morphology of the lizards *Zonosaurus brygooi* and *Z. aeneus* from Madagascar (Reptilia: Squamata: Gerrhosauridae). *Tropical Zoology* 12: 145–155
- White F (1986) La végétation de l'Afrique. Mémoire accompagnant la carte de la végétation de l'Afrique. UNESCO/AETFAT/UNSO. Recherches sur les ressources naturelles 20. ORSTOM-UNESCO, Paris