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Reptile, amphibian, and lemur diversity of the Malahelo Forest, a biogeographical transition zone in southeastern Madagascar

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Abstract. Ambatorongorongo Mountain lies at the historical intersection between humid, spiny, and littoral forests in southeastern Madagascar. We report the results of surveys of the herpetofauna and lemurs occurring in Malahelo Forest, a small (<25 ha) forest fragment lying on the western slope of Ambatorongorongo Mountain. There are at least 41 reptile, 11 amphibian, and 7 lemur species in this forest, including several that are endemic to southeastern Madagascar and are at severe risk of extinction. The species richness of the Malahelo fauna is comparable to that of even the largest forest reserves in the region. We also evaluate the similarity of the Malahelo herpetofauna to that of nearby humid, spiny, and littoral forests to assess the biogeographic affinities of its amphibians and reptile assemblages. Both groups contain species characteristic of each of the three surrounding forest types, but the biogeographic patterns appear to differ for amphibians and reptiles. Overall, the herpetofauna and lemurs of the Malahelo Forest indicate that it is a remnant of a biogeographic transition zone between the major forest types of southeastern Madagascar. The combination of high species richness, regional endemics, and unique herpetofaunal and lemur assemblages should make Malahelo Forest a high conservation priority, and we give recommendations for protecting what remains of this important transitional forest.

Introduction

Where large blocks of different types of habitat intersect, there often exist transitional zones with physical characteristics and biological communities intermediate between those of the adjacent habitats (Brown and Gibson 1983; Williams 1996). These transitional habitats may host representative species from each of the surrounding major habitats, resulting in unusual combinations of species. In addition, conditions in transitional zones may be sufficiently unique to facilitate the evolution of their own endemic species. By combining species from the neighboring communities and hosting their own endemics, transitional habitats may have higher species richness than the adjacent major habitat types (Gelderblom and Bronner 1995; Gottfried et al. 1998; Hamann et al. 1999). These characteristics suggest that

protection of transitional habitats may support conservation goals in at least four ways. First, transitional habitats may host an unusually large number of species from different habitat types, thus protecting them may be an efficient way to achieve species-level conservation in some areas. Second, the composition of communities in transitional zones will usually be unique, and unusual assemblages may be of conservation value in their own right (Schwartz 1999). Third, transitional habitats may harbor species of particular conservation concern, either their own endemics or rare species from the adjacent habitats (Gelderblom and Bronner 1995; Hamann et al. 1999). Finally, surviving transitional habitats provide a natural starting point for restoring connections between major habitat types that have become isolated through human activities.

Southeastern Madagascar, under the influence of the Anosyenne Mountain chain and the Indian Ocean, encompasses representative segments of most major forest types found on the island (Goodman et al. 1997). Fragments of the littoral forest lie along the coast, montane and lowland humid forests are found on the slopes of the Anosyenne and Vohimena mountain ranges, and the spiny dry forest of western Madagascar dominates to the west and southwest of the Anosyenne chain. The forests lying at the boundaries between these dominant types have been identified as a high conservation priority for southern Madagascar (Nicoll and Langrand 1989; Ganzhorn et al. 1997). The Ranopiso region, which includes our study site, has been identified as a particular priority for the conservation of amphibians and reptiles because it hosts many endemic species (Ganzhorn et al. 1997).

Southeastern Madagascar's forests have been under ever-increasing pressure from human demands for fuel, crop land, and pasture (Goodman et al. 1997). The ongoing removal and degradation of forests makes it necessary to rapidly prioritize areas for protection. Regardless of whether conservation efforts focus on particular species, overall richness, or endemicity, species-level information from surveys is required to delineate the areas of greatest interest. The flora and fauna of the area at the intersection between the major forest types of southeastern Madagascar have received little investigation, and only one area at the boundary between the humid and spiny forests has been protected as parcel 3 of the Réserve Naturelle Intégrale (RNI) d'Andohahela. Given the potential historical and conservation importance of this transitional zone, biodiversity inventories are needed. Fragments of forest can be found on Ambatorongorongo and Ambohimisampana (Petit Lavasoa) Mountains, and their proximity to humid, dry, and littoral forests suggests that these might be of particular biogeographic and conservation interest.

Here, we present the results of surveys of the reptiles, amphibians, and lemurs found in Malahelo Forest (Nussbaum and Raxworthy 1994a), a small forest fragment located on the western slope of Ambatorongorongo Mountain. Using data from earlier surveys in the nearby humid, spiny, and littoral forests, we demonstrate that Malahelo Forest lies in a zone of faunal transition that serves as one of the last refuges for several species endemic to southeastern Madagascar. We analyze the biogeographic affinities of its reptile and amphibian assemblages, and conclude by discussing some possible approaches to protecting this important transitional forest.

Methods

Description of Malahelo Forest

Ambatorongorongo Mountain (25°04′47″ S, 46°46′51″ E) is located approximately 25 km to the west–southwest of Tolagnaro (Fort-Dauphin) near the village of Manambaro. It is isolated, but can be viewed as the southernmost extension of the Anosyennes Mountains (Nussbaum and Raxworthy 1994a). The entire region was once completely forested, but today only a few isolated forest fragments remain between valleys of rice paddies and various forms of dry-field agriculture and pasturage. The largest fragment, Malahelo Forest, lies on the western slope of Ambatorongorongo Mountain and covers less than 25 ha between 200 and 430 m elevation. The forest is surrounded by agriculture fields and cattle pastures, and its conversion for manioc (cassava) and banana production continues. Most of what remains is in a large block near the top of the mountain, while a narrower strip extends westward downhill toward the valley. The eastern slope and summit of Ambatorongorongo Mountain are completely deforested, although small patches of secondary forest occur along the eastern stream courses. Another small forest fragment, Ambohimisampana, lies to the west on the other side of a small tributary of the Makazary River.

A preliminary botanical survey suggests that the plant species composition of the Malahelo Forest is intermediate between that of nearby humid, spiny, and littoral forests, containing species characteristic of each forest type (J. Rabenatoandro and L. Randrihasipara, personal communication). The typical canopy height is approximately 10–14 m, with a few emergent trees. Granitic rock outcrops are common, and there are no permanent streams within Malahelo Forest. At present, no climatological data are available, but rainfall at the nearby transitional forest of Andohahela (parcel 3) is 700–800 mm per year (Nicoll and Langrand 1989).

Historical land cover maps indicate that the Malahelo and Ambohimisampana Forests have not been directly connected to other forests for more than 40 years (Foiben-Taosarintanin'i Madagasikara 1979). However, they lie in the region where humid, spiny, and littoral forests once converged. Today, the nearest representatives of each type are: the humid forests of RNI d'Andohahela (parcel 1; 22 km north in the Anosyenne Range) and Manantantely (20 km east in the Vohimena Range); the littoral forests of Petriky (5 km east), Mandena (30 km east), and Ste Luce (40 km east–northeast); and the spiny forests at Ranopiso (10 km west) and Ankodida (25 km west).

Based on a map of forest cover (Foiben-Taosarintanin'i Madagasikara 1979), we estimate that the forest on and around Ambatorongorongo Mountain covered approximately 300 ha in 1957. An aerial photograph produced by the QIT Madagascar Minerals project showed that ca. 25 ha remained in 1989, yielding a mean annual rate of forest cover loss of 8.6 ha/year between 1957 and 1989. Had that rate been maintained from 1989 to the present time, no forest would remain on Ambatorongorongo Mountain. Nussbaum and Raxworthy (1994a) predicted that Malahelo

Forest would not survive more than 3 years at the rate of degradation observed by them. The survival of Malahelo Forest clearly indicates that there has been some reduction in deforestation rate since 1994. Clearing continues, however, in the center and edges of the forest, and there has been selective tree removal throughout the fragment.

Faunal inventories in southeastern Madagascar

The vertebrate faunas of many forests in southeastern Madagascar have been inventoried during the last decade as part of conservation and development efforts. Several of the littoral forests nearest to Ambatorongorongo, including those at Petriky, Mandena, and Ste Luce, were surveyed intensively in 1989–1990 as part of the environmental impact assessment study for a proposed major mining project (Creighton 1992). The herpetofauna and lemurs of the humid (parcel 1) and spiny (parcel 2) portions of RNI d'Andohahela were surveyed in 1995 (Feistner and Schmid 1999; Nussbaum et al. 1999) as part of a broader inventory of its flora and fauna. Finally, survey teams have studied the herpetofauna of many of the forest fragments in southeastern Madagascar, including Malahelo Forest (Nussbaum and Raxworthy 1994a, b). In biogeographic analyses, the forests of southeastern Madagascar make up a distinct area of vertebrate endemism within eastern Madagascar (Raxworthy and Nussbaum 1996).

1999 Survey of Malahelo Forest

The team, composed of six technicians and two herpetologists, inventoried the reptiles, amphibians, and lemurs of Malahelo Forest from 1 to 9 February 1999. This was during the rainy season, and it rained daily during the survey period. We also sampled small mammals (see Appendix), and marked *Phelsuma antanosy* geckos as part of a study of their population size. In total, our team spent 72 person-days surveying the forest. We worked approximately 10 h every day and 3–4 h per night, recording observations of both the herpetofauna and lemurs at all times. We searched the entire forest fragment, and we also collected along a small stream in a freshly deforested area adjacent to the remaining forest.

Lemurs were recorded during visual searches of the canopy along altitudinal transects and at random during the day and night. They were identified on sight, and no individuals were captured. We searched for reptiles and amphibians along two altitudinal transects from the lowest to the highest parts of the forest fragment, and at random during the day and night, capturing all individuals encountered and preserving voucher specimens for each species (deposited at the Université d'Antananarivo, Madagascar). We also established a 100 m pitfall line (45 cm high plastic curtain; 10 m between buckets; bucket dimensions 30 cm top diameter, 29 cm deep), which was left in place for seven full days and checked each morning. Finally, we searched specific microhabitats (rotten logs, tree holes, loose bark, *Pandanus* axils, streambeds) for cryptic or sedentary reptile and amphibian species.

To fully represent the herpetofaunal diversity at Ambatorongorongo, we consoli-

dated the records from our 1999 survey with those presented by Nussbaum and Raxworthy (1994a) and unpublished records from the University of Michigan Museum of Zoology collection. Records from the latter two sources were collected in 1992–1995, and we compare our results to these earlier surveys where appropriate.

Faunal comparisons

To evaluate whether Malahelo Forest is in a biogeographical transition zone, we compare its herpetofauna with that of the three adjacent forest types. Comparisons are made between Malahelo and the nearest surveyed humid forests (Andohahela parcel 1, Manantantely), littoral forests (Petriky, Mandena, Ste Luce), and spiny forest (Andohahela parcel 2). Figure 1 shows the distribution of the three major forest types relative to Ambatorongorongo Mountain, and the location of each site in our analysis. Our comparisons are based upon both species richness and Jaccard's coefficient of faunal similarity. Jaccard's coefficient is calculated as the number of species found at both sites divided by the total number of species found at one or both of the sites (Krebs 1999). The Malahelo Forest data used in the biogeographic analysis included only species found within the forest itself, and we combined the lists of species from the 1999 survey and earlier surveys in order to represent the assemblage found at Ambatorongorongo historically and at present. To elucidate the biogeographical relationships between sites, we performed cluster analysis using the unweighted pair-group method using arithmetic averages (UPGMA) method applied to matrixes of Jaccard's coefficients for the amphibian and reptile faunas, respectively (Krebs 1999).

Results

Our 1999 survey yielded 35 reptile, 10 amphibian, and 7 lemur species in Malahelo Forest. The herpetofauna data from surveys in 1992–1995 indicated the presence of an additional 7 reptile and 1 amphibian species, for a total of 42 reptile and 11 amphibian species dwelling in the forest. An additional 3 reptile and 4 amphibian species are known from the cleared areas near the forest. Table 1 summarizes species diversity for all sites in our comparison, and Table 2 lists every species found in Malahelo Forest and its occurrence at other sites.

The vertebrate fauna of Malahelo Forest is very rich, given that less than 25 ha of forest remains. It contains more reptile species than any other nearby site, and only one fewer lemur species than the large humid forest at Andohahela (parcel 1). It retains approximately the same total numbers of amphibians and reptiles as the littoral forests at Petriky, Mandena, and Ste Luce, and many more than the spiny forest of Andohahela (parcel 2), yet it is less than 3% of the size of these forests during the respective surveys (Table 1).

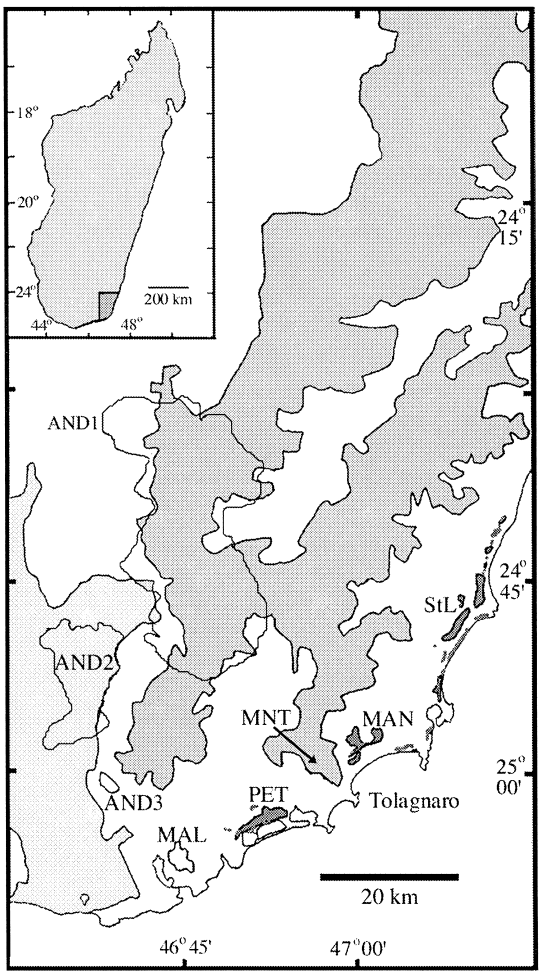

Figure 1. Map of southeastern Madagascar, showing each site used in our zoogeographic comparisons. Based on 1989 satellite photos, we indicate the location and extent of spiny forest (light grey), humid forest (medium grey), littoral forest (dark grey), and transitional forest (uncolored, adjacent to MAL and AND3 labels). The present extent of each of these forest types is reduced. The three parcels of RNI Andohahela are outlined, and the site abbreviations are: Malahelo Forest (MAL), Petriky (PET), Mandena (MAN), Ste Luce (StL), Manantantely (MNT), Andohahela parcel 1 (AND1), parcel 2 (AND2), and parcel 3 (AND3).

Reptiles

Three of the reptile species found in Malahelo Forest are unique to southeastern Madagascar: *P. antanosy*, *Paragehyra gabriellae*, and *Pseudoxyrhopus sokosoko*. The known distribution of these species appears to truly reflect their geographical ranges rather than inadequate sampling; despite intensive surveys of the herpetofauna of southeastern Madagascar in the last decade, they have been found only

Table 1. Summary of the sites compared in this study.

Site	Forest type	Coordinates	Area (ha)	Elevation (m)	Amphibians	Reptiles	Lemurs
Malahelo Forest	Transitional	25°04′ S, 46°46′ E	<25	200–430	11[a,b,c]	41[a,b,c]	7[a]
Petriky	Littoral	25°04′ S, 46°53′ E	1180	0–40	5[c,d,e]	31[c,d,e]	4[g,h]
Mandena	Littoral	24°58′ S, 47°00′ E	1103	0–20	21[c,d,e]	32[c,d,e]	6[g,h]
Ste Luce	Littoral	24°45′ S, 47°11′ E	1947	0–20	22[c,d,e]	38[c,d,e]	4[s]
Manantantely	Humid	24°59′ S, 46°55′ E	>10000	50–600	21[d]	33[d]	5[d]
Andohahela 1	Humid	24°42′ S, 46°11′ E	63100	400–1950	45[f]	33[f]	8[i]
Andohahela 2	Spiny	24°53′ S, 46°06′ E	12420	120	4[f]	29[f]	5[j]

The name, forest type, coordinates, surface area at the time of study, elevational range, and species diversity of amphibians, reptiles, and lemurs are given for each site. Sources of diversity data are footnoted. [a]This study; [b]Nussbaum and Raxworthy (1994a); [c]Nussbaum et al. (unpublished data); [d]Creighton (1992); [e]Ramanamanjato (in preparation); [f]Nussbaum et al. (1999); [g](Ganzhorn 1998); [h]Ramanamanjato (unpublished data); [i]Feistner and Schmid (1999).

in a few southeastern localities. A fourth reptile species, *Uroplatus malahelo*, was originally thought to be restricted to Malahelo Forest (Nussbaum and Raxworthy 1994a), but it has subsequently been found in other southwestern and southeastern fragments (R.A. Nussbaum and C.J. Raxworthy, unpublished data).

Phelsuma antanosy was discovered in the littoral forest at Petriky and Ste Luce (Manafiafy) in 1989–1990, and described by Raxworthy and Nussbaum (1993). It is endemic to the littoral forests of the southeast, where it is found exclusively on the endemic palm *Dypsis saintlucei*. By 1994, its habitat at Petriky had been destroyed for manioc cultivation, and that population disappeared. The species was first reported in Malahelo Forest by Nussbaum and Raxworthy (1994a), and the population at Ste Luce is now the only other one remaining. We found *P. antonosy* living only on palms (*Dypsis* sp.), and laying its eggs almost exclusively in the axil of *Pandanus leptopodus*.

Pseudoxyrhopus sokosoko was discovered in 1990 in the rain forests of the Anosyenne and Vohimena mountains, and lives at altitudes from 75 to 800 m (Raxworthy and Nussbaum 1994). It is generally confined to primary forest, but it persists in Malahelo Forest. Among the localities where it is known, only Andohahela receives legal protection (Andreone and Randriamahazo 1997); all other populations are at risk due to habitat degradation. In particular, Manantantely Forest has been exploited heavily during the last decade.

Paragehyra gabriellae is known only from the primary humid forests of southeastern Madagascar (Manantantely, Nahampoana, Manangotry, Andohahela parcel 1) (Nussbaum and Raxworthy 1994b; Andreone and Randriamahazo 1997). With the exception of Andohahela, all of these sites are unprotected and are disappearing at a rapid rate due to slash-and-burn agriculture and timber collection. This species hunts on large rocks at night and seems to survive only in closed-canopy forest, so it is probably very vulnerable to habitat modification or loss.

Uroplatus malahelo was discovered in and described from Malahelo Forest in 1994 (Nussbaum and Raxworthy 1994a). It is endemic to southern Madagascar, and has also been found in RNI d'Andohahela (parcel 1) (Nussbaum et al. 1999), the

Table 2. Reptiles, amphibians, and lemurs of the Malahelo Forest, and their presence at nearby sites.

Species	MAL	PET[d,e,f]	MAN[d,e,f]	StL[d,e,f]	MNT[f]	AND1[g,h]	AND2[g,h]
Reptiles							
Boa dumerili	x[a]	x	x	x			x
Bo. manditra	x[b]		x	x	x	x	
Dromicodryas bernieri	x[a,c]	x		x	x		x
Langaha madagascariensis	e[c]	x	x		x		
Liophidium torquatus	x[a]	x	x	x			
Liopholidophis epistibes	x[a,c]			x	x	x	
L. lateralis	x[a]	x	x	x	x	x	
Lycodryas arctifasciatus	x[a,c]			x	x		
Ly. gaimardi	x[a,b,c]	x		x	x		
Ly. variabilis	x[c]						
Madagascarophis colubrinus	x[a,b,c]	x	x	x	x		x
Mimophis mahfalensis	x[a],e[c]	x	x	x			x
Pseudoxyrhopus sokosoko	x[a,b,c]				x	x	
Typhlops decorsei	x[a]						x
Calumma nasuta	x[a,b,c]			x	x	x	
Furcifer lateralis	x[c],e[a,c]		x	x			x
F. oustaleti	x[a]	x	x	x	x		
F. verrucosus	x[a,c]						x
Zonosaurus karsteni	x[a]	x					
Z. laticaudatus	x[a,c]	x					x
Blaesodactylus sakalava	x[a,c]	x					x
Ebenavia inunguis	x[a,b,c]	x	x	x	x		
Geckolepis maculata	x[a,b,c]		x	x	x		
G. typica	x[a]	x					x
Hemidactylus mercatorius	x[a,b,c]	x	x	x	x		x
Lygodactylus miops	x[a]			x	x	x	
Lyg. tolampyae	x[c]	x	x				
Lyg. tuberosus	x[a,c]	x					
Paragehyra gabriellae	x[a,b,c]				x		
Paroedura androyensis	x[a]	x					x
Par. bastardi	x[a,b,c]						x
Phelsuma antanosy	x[a,b,c]	x		x			
P. modesta	x[c],e[a,c]	x	x	x	x		
Uroplatus malahelo	x[a,b,c]					x	
U. sikorae	x[a,b,c]			x	x	x	
Chalarodon madagascariensis	e[a,c]	x					x
Oplurus quadrimaculatus	x[a],e[c]	x	x		x	x	x
Amphiglossus macrocercus	x[a,c]		x	x	x	x	
A. melanopleura	x[a,b,c]	x	x	x	x	x	
A. melanurus	x[b,c]			x			
A. ornaticeps	x[c]	x	x	x	x	x	x
A. splendidus	e[c]						
Mabuya elegans	x[a,c]	x	x	x	x		x
M. gravenhorsti	x[a,c]	x	x	x	x		x
M. vato	x[a],e[c]	x					x
Amphibians							
Heterixalus boettgeri	e[a,c]	x	x	x	x		
Mantidactylus betsileanus	x[a,c]		x	x	x	x	

Table 2. (*continued*)

Species	MAL	PET[d,e,f]	MAN[d,e,f]	StL[d,e,f]	MNT[f]	AND1[g,h]	AND2[g,h]
Ma. boulengeri	x[a]					x	
Ma. decaryi	x[a,c]		x	x		x	
Ma. femoralis	x[a,c]				x	x	
Ma. ulcerosus	x[a,c]	x	x	x		x	
Ptychadena mascarenensis	x[a],e[a,c]	x	x	x	x		x
Anodonthyla boulengeri	x[a,b,c]		x	x		x	
An. nigrigularis	x[a]					x	
Plethodontohyla alluaudi	e[c]		x	x	x		
Pl. bipunctata	x[a]		x	x	x	x	
Scaphiophryne calcarata	e[c]	x	x				x
Aglyptodactylus madagascariensis	x[c]		x	x		x	
Boophis majori	e[c]				x	x	
B. tephraeomystax	x[a,c]		x				
Lemurs							
Microcebus murinus	x[a]	x	x		x		x
Cheirogaleus medius	x[a]	x	x	x	x		
Lepilemur sp.	x[a]					?	?
Hapalemur g. griseus	x[a]		x		x	x	
Lemur catta	x[a]	x					x
Eulemur fulvis collaris	x[a]		x	x	x	x	
Propithecus v. verreauxi	x[a]					x	x

Site abbreviations follow Figure 1. Records are designated as from forest (x) or nearby edges (e). Sources are footnoted. [a]This study; [b]Nussbaum and Raxworthy (1994a); [c]Nussbaum et al. (unpublished data); [d]Ganzhorn (1998); [e]Ramanamanjato (in preparation); [f]Creighton (1992); [g]Nussbaum et al. (1999); [h]Feistner and Schmid (1999).

Réserve Spéciale de Kalambatritra (R.A. Nussbaum, unpublished data), and at Analavelona in southwestern Madagascar (R.A. Nussbaum and C.J. Raxworthy, unpublished data). At all four sites, it appears to occur at low density: during 72 person-days of surveying at Malahelo Forest we found two individuals, three individuals were found during 65 person-days at Kalambatritra, and two individuals were found during 120 person-days in Andohahela (Nussbaum et al. 1999).

These four species are endemic to southern Madagascar and are threatened with extinction from destruction of their habitat. *Phelsuma antanosy* is particularly vulnerable since neither of its remaining populations is found within a protected area. *Pseudoxyrhopus sokosoko* and *Pa. gabriellae* are protected only in the RNI d'Andohahela, while *U. malahelo* is protected in Andohahela and Kalambatritra. We are especially concerned about the possible impact of collecting these species for sale in the pet trade, which is a significant industry in Madagascar (Stuart et al. 1990).

Amphibians

One species of frog found in Malahelo Forest is of special concern due to its apparently limited distribution. *Anodonthyla nigrigularis* is known primarily from a few primary forest sites near Tolagnaro (Glaw and Vences 1994) and in Andohahela

parcel 1 (Andreone and Randriamahazo 1997). It is a small, climbing microhylid typically found on trees and rocks, but little else is known of its ecology. We found four young individuals in a bird's-nest fern (*Asplenium* sp.) on top of a large boulder, suggesting that they were oviposited there rather than in tree holes (Glaw and Vences 1994). Recently, the species also has been reported from a rainforest reserve in the central highlands (Vallan 2000), therefore it may be more widely distributed than previously thought (Glaw and Vences 1994).

Lemurs

Of the seven lemur species in Malahelo Forest, four are diurnal and three are nocturnal. Given that the forest is somewhat degraded and covers less than 25 ha, it is remarkable that it supports seven species. Also, there are few localities where *Eulemur fulvus collaris*, *Propithecus verreauxi verreauxi* and *Lemur catta* are syntopic (Mittermeier et al. 1994).

Lemur catta typically inhabits spiny forests (Mittermeier et al. 1994), but is also found in several transitional forests and in the littoral forest at Petriky (S. Goodman, personal communication; J.B. Ramanamanjato, personal observation). At Ambatorongorongo, we found it only near the edges of Malahelo Forest, and it probably travels across the deforested areas between forest fragments. Its sleeping sites were situated 15–20 m high in trees near the forest edge. *Lemur catta* is a high priority species for conservation efforts (Mittermeier et al. 1992).

Eulemur fulvus collaris is a humid forest species found in southeastern Madagascar from the Mananara River near Vangaindrano south to Tolagnaro (Mittermeier et al. 1994). Its presence at Ambatorongorongo constitutes the southern limit of its distribution. We noted two small social groups composed of 4–7 members active in the canopy near the center of the forest fragment. We observed *L. catta* and *E. f. collaris* both feeding on the large fruits of an unidentified liana during the survey.

Propithecus verreauxi verreauxi occurs in dry, semi-arid spiny vegetation, bush-and-scrub thickets, and deciduous gallery forest along watercourses (Mittermeier et al. 1994), and is found in the humid and transitional forests of Andohahela (Feistner and Schmid 1999). We often heard it calling within Malahelo Forest during the day, but no individuals were seen.

Hapalemur griseus griseus, a specialized consumer of bamboo, is present in the Malahelo Forest despite the complete absence of bamboo. It is also found in the Mandena littoral forest (Ganzhorn et al. 2000), where bamboos are absent and it consumes fruit and leaves.

The nocturnal lemurs (*Cheirogaleus medius*, *Microcebus* cf. *murinus*, and *Lepilemur* sp.) at Ambatorongorongo are typical of the dry forests of southern Madagascar (Mittermeier et al. 1994). These genera are also present in some littoral forests (Ganzhorn et al. 2000), but further research is needed to determine whether the species are the same.

Biogeographic affinities

The reptile, amphibian, and lemur assemblages of Malahelo Forest contain species

that are characteristic of each of the three dominant, nearby forest types. This suggests that Malahelo Forest indeed lies in a zone of faunal transition. For instance, the reptiles *Amphiglossus macrocercus*, *Calumma nasuta*, *U. sikorae*, and *Ps. sokosoko* are typically found only in eastern rainforests. Representatives of the western spiny forest fauna include *Paroedura androyensis*, *Par. bastardi*, *Furcifer verrucosus*, and *Typhlops decorsei*. Littoral forest species include *Zonosaurus karsteni* and *P. antanosy*. Despite their lower overall species diversity, the lemur and amphibian assemblages at Malahelo also include representatives from each of the surrounding forest types.

Table 3 shows Jaccard's coefficients of similarity for the reptile and amphibian faunas of all sites, and Figure 2 presents the results of the cluster analysis. There were few high values of Jaccard's coefficient for either group, indicating that the herpetofauna at all sites is at least moderately differentiated. The highest similarities among both amphibian and reptile assemblages were between the littoral forest sites at Ste Luce and Mandena, but the third littoral forest site (Petriky) did not cluster with them in either case.

The reptile assemblage at Malahelo Forest is most similar to that of the relatively dry littoral forest at Petriky, but shares many species with the other littoral forests, Manantantely humid forest, and the spiny forest of Andohahela (parcel 2). Despite the occurrence of several southeastern rainforest endemics at Malahelo Forest, its reptile fauna is very different from that of the humid forest of Andohahela (parcel 1). The similarity of the Malahelo amphibian assemblage to that at other sites was somewhat lower than the similarity of the Malahelo reptiles to those at other sites. Malahelo amphibians were most similar to those from the littoral forests at Mandena and Ste Luce, followed by the humid forests. The more arid-adapted amphibian faunas of the spiny forest and Petriky littoral forest form a distinct grouping that is quite different from that of all other sites. Overall, the patterns of similarity in the amphibian faunas reflect the influence of the rainfall gradient in southeastern Madagascar. In contrast, similarity of the reptile faunas corresponds more closely to the distances between sites than their respective climates. At a broader scale, reptiles and amphibians in eastern Madagascar show parallel biogeographical histories (Raxworthy and Nussbaum 1996), but the affinities among the reptile and amphibian assemblages in our analysis showed little concordance.

Discussion

Despite the miniscule size of Malahelo Forest, the species richness of its herpetofauna and lemurs is high. All of the nearby sites in our comparison are at least 40 times larger than Malahelo Forest in surface area (Table 1), yet only the large rainforest tract in Andohahela (parcel 1) contains substantially greater species diversity of lemurs or amphibians, and Malahelo Forest has more species of reptiles than any other site. Preliminary surveys of a few other forest fragments in the transitional zone (Ankodida and Vohidava/Bekinana) have revealed neither the overall diversity nor the rare species found at Ambatorongorongo (R.A. Nussbaum and J.B. Ramanamanjato, unpublished data). The relatively low amphibian diversity

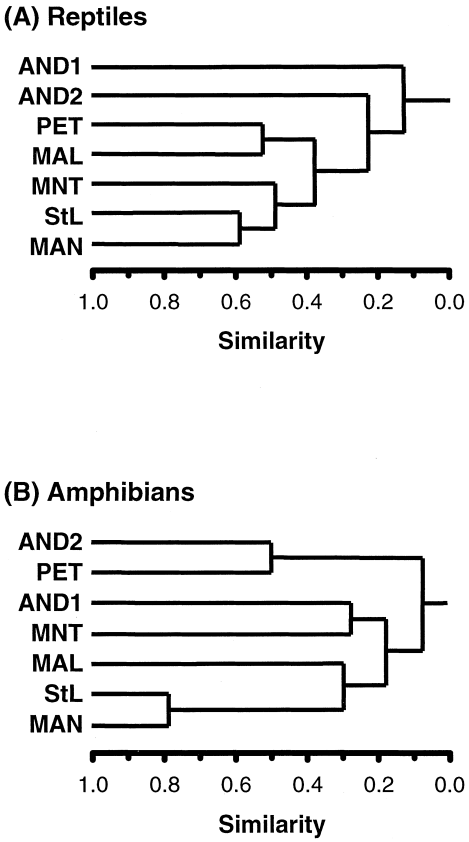

Figure 2. Tree diagrams produced by cluster analysis of Jaccard's similarity coefficients for seven forests in southeastern Madagascar. The UPGMA was used to produce these trees, but the nearest neighbor method yielded the same topologies. The relationships between reptile assemblages and between amphibians are depicted in the trees in (A) and (B), respectively; see Figure 1 for site abbreviations.

Table 3. Jaccard's similarity index comparing the herpetofauna of sites in southeastern Madagascar. Similarities of reptile assemblages are shown above the diagonal; amphibians are shown below the diagonal. See Figure 1 for explanation of site abbreviations.

	MAL	PET	MAN	StL	MNT	AND1	AND2
MAL	×	0.52	0.35	0.48	0.44	0.17	0.34
PET	0.14	×	0.40	0.33	0.28	0.05	0.33
MAN	0.33	0.18	×	0.59	0.44	0.12	0.17
StL	0.27	0.13	0.79	×	0.54	0.18	0.16
MNT	0.14	0.08	0.20	0.23	×	0.25	0.13
AND1	0.19	0.02	0.16	0.18	0.29	×	0.03
AND2	0.07	0.50	0.09	0.04	0.04	0.00	×

at Malahelo Forest may reflect the lack of permanent streams within the forest fragment; even very small highland rainforest fragments containing streams usually maintain populations of most amphibian species found at much larger sites nearby (Vallan 2000).

In addition to its high diversity, Malahelo Forest contains a significant number of animal species whose distribution is limited to southeastern Madagascar. Three reptiles and one amphibian species are endemic to the region and are found at only a few other sites, most of which are not legally protected. All of these species should be considered at risk of extinction, and several will soon be under consideration for endangered status by the IUCN (J.B. Ramanamanjato, in preparation). The presence of these species alone should make Malahelo Forest a conservation priority among unprotected sites in southeastern Madagascar.

Our analysis of the biogeographic affinities and species composition of the herpetofauna of Malahelo Forest provides strong evidence that this forest is a remnant of the transitional zone between the three major forest types in southeastern Madagascar. The herpetofauna has elements from the faunas of all three surrounding ecosystems, constituting the range limit of some species. The lemur assemblage comprises species from humid and dry forests in a combination rarely found elsewhere, and also includes most species found in the littoral forests.

We cannot rule out the possibility that the present occurrence of these taxa together at Ambatorongorongo is an artifact of habitat destruction elsewhere in the region. If so, Malahelo Forest may be acting as a last refuge for many displaced populations. However, we think this unlikely since this forest fragment has been isolated from all other forests for at least 40 years, and it is improbable that so many species have colonized Malahelo Forest in the years since its isolation. Instead, we suggest that most of these species are a natural part of forest fauna of this region, and that Malahelo is truly a transitional forest in biogeographic terms. Thus, it would be an ideal starting point for restoration of the natural connections between the larger forest reserves in southeastern Madagascar in the future. In any case, it is rare to find so many species typical of very different habitats in a single forest, and we believe that this unusual characteristic enhances the conservation value of Malahelo Forest.

Several interesting contrasts may be made between the results of the 1999 survey of Malahelo Forest and earlier surveys. Three species of mantellid frogs (*sensu* Vences and Glaw 2001) were collected from in and near the forest in 1992, but only *Boophis tephraeomystax* was collected in 1994–1995. In 1999, we found only a single juvenile *Boophis*, which we tentatively assign to *B. tephraeomystax*. This may reflect reduction or disappearance of *Aglyptodactylus madagascariensis* and *B. majori* populations in Malahelo Forest, as these species are typically extirpated from forest fragments smaller than 200 ha due to fragmentation effects (Ramanamanjato 2000). Earlier surveys also recorded four species of *Amphiglossus* skinks in the forest, whereas we found only two, possibly signifying loss of species due to competitive displacement or habitat loss. Finally, the earlier surveys yielded *P. modesta* in and near the forest from 1993 to 1995, yet the only individuals found in 1999 were in mango trees near the village at the base of the mountain. We searched

diligently for *Phelsuma* and other geckos during our 1999 survey, so if *P. modesta* still occurs in Malahelo Forest, it is very rare.

Conservation recommendations

We are not aware of any plans to give legal protection to Malahelo Forest. A local permit for harvesting timber or creating new fields is supposed to be required, but the steep slope of the remaining forest and its distance from villages may be the strongest constraint on its rate of destruction.

As is the case for most of Madagascar, protecting this unique habitat and its diverse fauna depends upon the goodwill and cooperation of the local people. The ongoing destruction and degradation of Malahelo Forest results from people trying to improve their low standard of living. Our discussions with the community suggest that relatively few individuals are actively removing forest for slash-and-burn agriculture; the majority are silent observers who prefer to use their current lands closer to the village. Some are even aware of the threat to their water supply posed by the continued destruction of Malahelo Forest, but the social structure of the village inhibits protests against traditional activities such as forest conversion.

We believe that targeted, relevant educational efforts could convince the local people to protect Malahelo Forest in order to ensure an adequate supply of water for rice production and personal consumption in the future. Training in manure fertilization of rice fields, fuel-efficient cooking stoves, and re-use of agricultural clearings might also relieve pressures on the remaining forest. Other options include developing an ecotourism site associated with Malahelo Forest to create an incentive for its protection, or establishing a guarded preserve from which harvest of food, fuel, or materials is prohibited.

Though some species may do well in a reserve as small as Malahelo Forest (Cowling and Bond 1991; Turner and Corlett 1996; Schwartz 1999; Ramanamanjato 2000; Vallan 2000), others are less likely to persist. The lemurs will probably experience problems associated with small population size, and the small area of forest remaining may be insufficient to provide enough food resources for them throughout the year (Ganzhorn et al. 2000). In addition, during our survey, we encountered villagers using dogs to track lemurs. Regardless of future protection of the forest habitat, the lemur fauna will soon diminish unless hunting ceases.

To ameliorate the problems caused by small habitat area and population size, we recommend that any conservation strategy for Malahelo Forest includes the Ambohimisampana forest fragment on the other side of the Makazary River valley. The forest there begins at a lower elevation and includes several permanent streams. The presence of these streams may be especially important for protecting amphibian diversity (Vallan 2000); a brief exploration of the Ambohimisampana fragment at the conclusion of our 1999 survey revealed two stream-dependent frog species that are not present in Malahelo Forest (*B. luteus* and *Mantidactylus lugubris*). We recommend that both fragments be considered in a unified conservation plan that designates a protected corridor for forest regeneration between them.

Though there is a clear need to continue floral and faunal inventories in

southeastern Madagascar, the existing data are sufficient to begin to establish conservation priorities in the region. In this paper, we have summarized and analyzed data on the herpetofauna and lemurs of the three dominant forest types, and we conclude that Malahelo Forest is an important transition zone between these habitats. This site should be a target for conservation efforts because it holds high diversity, several rare species, and an unusual combination of species, but these features must be weighed against the small area of the remaining forest and the likely small population sizes of many of its species. We believe that many of the reptiles and amphibians, and at least some of the lemurs, could persist in a reserve comprising both the Malahelo and Ambohimisampana forest fragments.

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Appendix

We recorded observations of non-primate mammals during day and night transect walks and during other work, and we also identified tracks and fecal material when found. To capture small mammals, we set 80 Sherman traps ($10 \times 10 \times 25$ cm) daily along six transects and baited them with banana. They were left in place both day and night, and checked and rebaited every morning and evening. Half of the traps were on the ground, and half were 1–2 m above ground on rocks and trees. We found only three small mammal species: one insectivore (*Tenrec ecaudatus*), one native rodent (*Eliurus* sp.), and one introduced rodent (*Rattus rattus*). *Rattus* was the only species captured in the Sherman traps and constituted the majority of our small mammal records; only one individual of each *Eliurus* and *Tenrec* were observed during field work. The *Eliurus* was not captured, so further identification was not possible. No mammals were captured in our pitfall traps. We believe that the low number of small mammal species captured was not the result of poor sampling, but rather reflects their low diversity at the site. This may be related to the small size of the remaining forest fragment. We also found a dead bat (*Hipposideros commersoni*), and evidence of the carnivores *Cryptoprocta ferox* and *Fossa fossana*, and the bush pig *Potamochoerus larvatus*.

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