Chapter 2.3
A Perspective on the Paleo-ecology and Biogeography of Extreme Southeastern Madagascar, with Special Reference to Animals

Steven M. Goodman[1] and Jean-Baptiste Ramanamanjato[2]

Abstract

The southeastern portion of Madagascar contains a remarkable number of natural forest habitats overlaid on considerable topographic variation, including evergreen littoral, montane, sclerophyllous formations, transitional forests, and spiny bush. Associated with this habitat and variation in elevation, is a diverse and unique biota with a considerable number of micro-endemic forms. The north-south aligned Anosyenne Mountains act as a barrier for weather systems reaching the island from the east, and this rain shadow gives rise to very abrupt ecotones on the western flank of this chain. Given the biotic clines across southeastern Madagascar, with increasing aridity towards the west, the waning and waxing of different climatic shifts during the Pleistocene would certainly have had an important bearing on the biogeography of the region. Data from several different fields are used in this review chapter to interpret some of these patterns. Remains of plants and animals found at paleontological and archaeological sites across southern Madagascar, including the Andrahomana Cave in the Tolagnaro region, provide important insights into the timing and degree of these climatic shifts. Available information from these different deposits is summarized. Details are presented on the biogeography of a variety of land animal groups, including details on patterns of geographic variation, species turnover, phylo-geography, and aspects of the systematics of these organisms within the different natural formations of the region. One consistent pattern is the much greater species turnover within the short ecotone between humid forest and spiny bush than in the entire 1200 km eastern humid forest.

Résumé

Une perspective de la paléoécologie et de la biogéographie dans l'extrême sud-est de Madagascar, avec référence particulière aux animaux. La partie sud-est de Madagascar abrite un nombre étonnant d'habitats forestiers naturels distribués sur un gradient topographique remarquable en allant de la forêt sempervirente littorale et de montagne aux formations sclérophylles, aux forêts de transition et au fourré épineux. Un biote unique et diversifié est associé à cette variation de l'habitat et de l'altitude qui abrite souvent un grand nombre de formes marquées par le microendémisme. La chaîne des montagnes anosyennes qui s'étend sur un axe nord-sud joue un rôle de barrière sur les systèmes météorologiques qui affectent l'île depuis l'est et les effets orographiques sont extrêmement marqués avec des écotones abrupts sur les versants occidentaux de cette chaîne. Compte tenu des clines biotiques rencontrés dans le sud-est de Madagascar avec une aridification croissante vers l'ouest et en considérant les hauts et les bas des divers changements climatiques qui ont eu cours pendant le Pléistocène, la biogéographie de la région doit sans aucun doute être marquée. Des données issues de diverses spécialités sont utilisées dans ce chapitre de revue pour interpréter certains de ces schémas. Des restes de plantes et d'animaux trouvés dans les sites paléontologiques et archéologiques de la région méridionale de Madagascar, dont la grotte d'Andrahomana dans la région de Tolagnaro, fournissent des informations importantes sur le degré et la chronologie des changements climatiques. L'information disponible

1 Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA. Email: sgoodman@fieldmuseum.org

2 QIT Madagascar Minerals, BP 225, Tolagnaro 614, Madagascar. Email: jeanbaptiste.ramanamanjato@riotinto.com

de ces différents dépôts est résumée. Des éléments sur la biogéographie d'un certain nombre de groupes d'animaux terrestres sont présentés avec des détails sur les schémas de variation géographique, les remplacements d'espèces, la phylogéographie et certains aspects de la systématique de ces organismes dans les différentes formations naturelles de la région. Le schéma général qui ressort montre que le remplacement des espèces est bien plus important sur l'étroit écotone entre la forêt humide et le fourré épineux qu'il ne l'est sur l'ensemble des 1200 km de long de la forêt humide orientale.

Introduction

The southeastern portion of Madagascar, often referred to as the Anosy Region, holds exceptional biotic diversity with few parallels to any other region of the island. Within relatively short distances of Tolagnaro, there are several remarkably different natural forest habitats. These include the coastal littoral forests resting on sandy substrates, humid forest habitats ranging from lowland to montane formations, and spiny bush. Further, ecotones between these habitats are often pronounced, particularly the transition from humid forest to spiny bush on the western side of the Anosyenne Mountains. It is here that biotic turnover is greater for certain plant and animal groups than the 1200 km length of the eastern humid forests. In this chapter, we review Quaternary climate shifts that certainly had pronounced impacts on the current composition and evolutionary history of the regional biota, discuss general aspects of the local biogeography, and summarize current information for the different terrestrial animal groups.

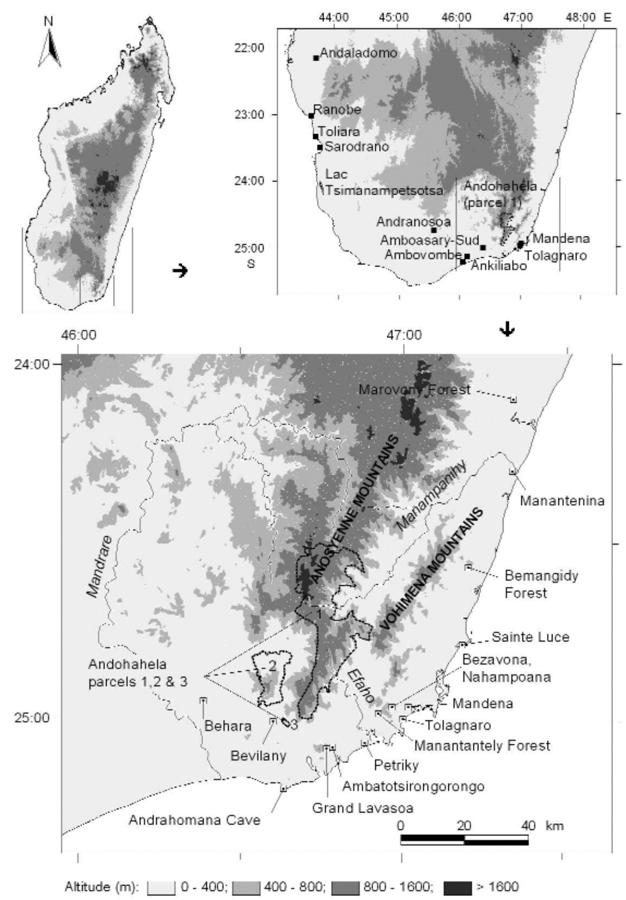

Figure 1. Map of southeastern Madagascar.

Paleoecology

Pollen cores

As far as we are aware, no cores of subfossil pollen from lake deposits have been published from sites in the extreme southeastern portion of Madagascar. These types of data provide a means to examine vegetational changes during the Quaternary, and have been extremely informative with regards to climatic change in other areas of the island (e.g., Burney 1993, 1997). Such paleontological "looking glasses" provide a remarkable window into the dynamics of ecological change in recent geological time, and the understanding of current local and regional biogeographical patterns. Further, when these types of data are combined with faunistic reconstructions based on excavated subfossil animals, aspects of the vicissitudes a given area has undergone in recent geological time can be elaborated upon.

The closest site to Tolagnaro from which a pollen core sample has been analyzed is the Ranobe area, north of Toliara (Fig. 1), where Burney (1993) obtained a 5000-year before present stratigraphic sequence. An interpretation of this core provides clear evidence of vegetational shifts before human occupation of the region, and shows how dynamic ecological change can be on a short geological time scale. While this site is about 400 km from Tolagnaro, associated interpretations of climatic change are presumably applicable to the portion of southeastern Madagascar west of the Anosyenne Mountains. This is a zone within the rain shadow of the eastern mountain range. However, given the distance between Toliara and the zone to the west of the Anosyenne Mountains, it is probable that the effects of these climatic shifts may have been dampened in the latter area most notably in moist and warm periods of the Quaternary.

About 5000 years ago, the area close to Ranobe contained a relatively large freshwater lake, surrounded by a mixture of woodlands with more deciduous elements than currently exist in the region. At a nearby subfossil site with deposits contemporary to this period, important collections of animal bones have been excavated, including those of species that are now extinct (e.g., land tortoises, elephant birds, hippos, and giant lemurs). These animals, all of which were of large body size, are often referred to as the megafauna. Based on an interpretation of the types of pollen found in the core and their frequency, it can be postulated that sometime between 3500 and 2500 years ago the Ranobe region experienced a reduction in rainfall, water levels fell, and the local vegetation contained fewer forest trees. This is a period, that falls just before the first colonization of Madagascar by people (Burney *et al*. 2004), is one of widespread drying-up of freshwater bodies in the southern portion of the island and the extinction of numerous animal species requiring more mesic conditions (Goodman and Rakotozafy 1997). The next stage within the Ranobe core, about 2000 years before present, demonstrates a notable increase of charcoal in the deposits, presumably associated with anthropogenic modifications of the environment, as well as the increasing presence of modern spiny bush plant taxa that typify the region today. Thus, during a relatively short sequence of time there was a very pronounced aridification of the zone, which would have had considerable impact on the regional biota, particularly to the western side of the Anosyenne Mountains.

During the periods of climatic shifts in southern Madagascar, such as dry and cool epochs of northern and southern hemisphere glacial maxima, the specific placement of the ecotone between humid and dry forests would have fluctuated, providing dispersal routes across the Anosyenne Mountains for certain organisms and vicariant separation for others. Associated with these glacial maxima, montane vegetation would have covered larger elevational swaths and lowland flora would have been reduced in extent as compared to modern times. One of the keys in explaining the biogeography of the littoral forests surrounding Tolagnaro is deciphering patterns of exchange across the Anosyenne Mountains during periods of climatic vicissitude.

Animal subfossils

Another aspect in understanding changes in the regional biota in recent geological time is the study of subfossils excavated at sites in the southern portion of the island. Many such locations are known to the west of the Anosyenne Mountains (Goodman and Rakotozafy 1997, Godfrey and Jungers 2002). The site with closest proximity to Tolagnaro and falling within the region covered by this book is the Andrahomana Cave (Fig. 1), which is located on Cap Andavaka within the modern transitional zone between humid and dry forests. Subfossils from this site have been excavated by early paleontological teams, including those of Sikora in 1899, Alluaud in 1900 - 02, Geay in 1906, and Decary in 1926 (Walker 1967, Chanudet 1975), during a period when care was rarely given to stratigraphic order of excavated material, which is paramount for the reconstruction of the sequence of events represented in the deposits. David Burney and colleagues reopened the site in 2003 under controlled excavation techniques. The new material is currently under study, and should provide important details on the waning and waxing of different environmental conditions in the region in recent geological time.

A number of very interesting vertebrate taxa have been identified from Andrahomana Cave, including giant lemurs and elephant birds. Grandidier (1902) reported that the remains of a bizarre extinct species of endemic waterbird, *Centrornis majori*, were found in the cave deposits. Based on osteological characters this bird is best placed in the shelduck tribe Tadornini (Livezey 1997). *Centrornis* would not have been a strong swimmer, but with its disproportionately long legs was adapted for wading, presumably in freshwater. Several lakes and estuaries occur in this portion of southeastern Madagascar, which would have been more extensive and had a greater percentage of freshwater before the Quaternary climatic shifts described above. Further, remains of elephant birds of the extinct Family Aepyornithidae have been found in this cave (Grandidier 1902). The largest of the elephant birds are estimated to have reached heights of 3 - 4 m and had a mass approaching 400 kg. Their eggs had dimension of 32 x 24 cm, which is equivalent in volume to 150 - 170 chicken eggs (Cauderay 1931, Amadon 1947).

Grandidier (1903) described a large species of extinct rodent, *Hypogeomys australis*, from subfossil remains found in the Andrahomana Cave. This animal is the larger congener of an extant forest-dwelling species, *H. antimena*, now confined to the central Menabe region north of Morondava, and whose continued existence is uncertain due to genetic bottlenecks, reduced habitat, and low recruitment rates of young into the breeding population, probably associated with high predation rates (Sommer 2003). Radiocarbon dates of *H. australis* remains from the cave include (calibrated range at 2σ in parentheses): 4440 ± 60 years BP (5640-4420 cal yr BP) and 1536 ± 35 years BP (428-618 cal yr AD) (Goodman and Rakotondravony 1996, Burney *et al.* 2004). Bone remains of the extant *H. antimena* have been found at subfossil sites much further south than its current range, including the extreme portion of the island. Thus, members of this genus are excellent examples of the impact of Quaternary climatic shifts had on the distribution of certain animals.

Remains of the endemic, extant rodent *Macrotarsomys petteri* have been identified from Andrahomana Cave. This is a species only recently described as new to science from the Forêt d'Andaladomo (Fig. 1), within an area known as the Mikea Forest, north of Toliara (Goodman and Soarimalala 2005), and some 450 km northwest from the cave and close to Burney's (1993) Ranobe pollen core site. Radiocarbon dates of *M. petteri* remains obtained in Andrahomana Cave yielded the dates of 2480 ± 40 yr BP (790-410 cal yr BC) and 1760 ± 40 yr BP (150-390 cal yr AD; Goodman *et al*. 2006). These dates overlap with a period of climatic desiccation in the region (Burney 1993; see above). This species has also turned up in other subfossil deposits in the Tsimanampetsotsa region of southwestern Madagascar and formerly had an even broader geographical range (Goodman *et al*. 2006). We hypothesize that the notable shift in this species' distribution is associated with climatic shifts.

Other small mammal remains recovered from the cave include those of *Microgale principula* (Grandidier 1928, MacPhee 1987), a small insectivorous Tenrecidae that is confined to humid forest formations (Jenkins 2003) and is known from the nearby parcel I of the Parc National (PN) d'Andohahela (Goodman *et al.* 1999a). Grandidier (1928) described a new species of a presumed extinct tenrecid, *Cryptogale australis*, from bone remains recovered in Andrahomana Cave. Subsequent analysis of this material revealed that they refer to *Geogale aurita* (Heim de Balzac 1972), a small terrestrial extant mammal found in the Petriky and spiny forest regions (see section 3.6 below). A large number of small mammal bones excavated by David Burney and colleagues under stratigraphic control from Andrahomana Cave are currently under study. Amongst these remains is a species of *Microgale*, which is extinct and based on current information only known from this site (Goodman *et al.* 2007). The ongoing study of the subfossil small animal remains should provide an interesting window into the types and degree of climatic shifts that the zone to the west of the Anosyenne Mountains underwent in recent geological time.

An assortment of extinct subfossil lemurs has been identified from the cave, including *Archaeolemur majori*, *A. edwardsi*, *Hadropithecus stenognathus*, *Megaladapis edwardsi*, *M. madagascariensis*, and *Pachylemur insignis* (Godfrey and Jungers 2002, Godfrey *et al.* 2006a). Available radiocarbon dates for different extinct primate bones from the cave include bones of *Hadropithecus stenognathus* at 6724 ± 54 BP (7660-7490 cal yr BP) and a *Megaladapis* sp. at 4566 ± 35 BP (5436-5059 cal yr BP; Burney *et al*. 2004). A study of stable carbon isotopes of the *H. stenognathus* bones from this cave indicate that this animal had a mixed diet of C3 and C4 plants (or some combination of plants and animals, such as snails, consuming C4 plants), perhaps indicative of current ecological conditions of the region (Godfrey *et al*. 2006b). In contrast, the $\triangle^{13}C$ determinations for the *M. edwardsi* bones show that this species consumed C3 (generally closed forest) plants (Godfrey *et al*. 2006b). Given that the *Hadropithecus* remains are older than those of *Megaladapis*, this might indicate climatic shifts during the Holocene or a zone of considerable ecological transition, similar to that occurring in this zone today.

During the Quaternary, presumably Holocene, a species of large-bodied Carnivora went extinct in the drier portions of Madagascar, including the south. This animal, *Cryptoprocta spelea*, was distinctly bigger than the extant species *C. ferox*, which is the largest extant Carnivora on the island (Goodman *et al*. 2004). *Cryptoprocta spelea* was originally named based on material collected in the Andrahomana Cave (Grandidier 1902). Since its extinction, aspects of predator-prey relationships on the island have changed dramatically. Presumably it was this animal that would have predated on the large subfossil lemur species, as well as some of the other large animals only known today from subfossil remains.

Archeological sites

An analysis of animal remains recovered from archaeological sites, rather than the largely paleontological site of Andrahomana Cave, provides an excellent means to understand nearly modern distributions of animals, as well as some early interactions between people and the natural environment. A large number of archaeological sites have been excavated in the southern portion of the island and an assortment of animal remains has been identified from them. Radimilahy (1980) worked at a series of sites near Ambovombe that date from historical times. At one of these sites, Ankiliabo (Fig. 1), eggshell fragments were found of an elephant bird, presumably *Aepyornis maximus* (Rakotozafy and Goodman 2005), the largest of this extinct lineage. This would indicate that populations of elephant birds remained extant in southeastern Madagascar until relatively recent, which would corroborate information noted in the chronicles of Flacourt (1658; see Wright and Rakotoarisoa Chapter 2.2). At the archaeological site of Andranosoa, in the central Androy and dating from the 13th -17th centuries, remains of a now extinct species of dwarf *Hippopotamus* were recovered; further evidence of the remarkable and dramatic level of faunistic change that has taken place within recorded history.

The first possible evidence of humans in southern Madagascar is from the archaeological site of Sarodrano, south of Toliara (Fig. 1). Here a charcoal radiocarbon dated 1460 ± 90 BP (410-710 cal yr BP) was obtained in a context probably derived from human activities (Battistini and Vérin 1971, see Wright and Rakotoarisoa Chapter 2.2). Based on temporal extrapolations, humans were in contact with now extinct animals for a considerable period, and the disappearance of the latter was a slow process that continued into historical times rather than a punctuated event, as proposed by the "Blitzkrieg" hypothesis associated with drastic climatic shifts or human colonization of the region (see Burney 1999 for a review of these points). On the basis of currently available data, the best explanation of the disappearance of the megafauna is a synergy of factors linked with climatic change and human pressure associated with habitat modification and hunting.

Biogeography

As presented in other chapters within this volume, southeastern Madagascar has a varied geological history, a range of vegetational formations, soil types, and climatic conditions, as well as an assorted history of human habitat modification. These factors, when overlaid on recent climatic shifts of the region, make a broad overall synopsis of the biogeographic patterns of this region extremely complex. In order to understand these patterns, finer analyses are necessary, including pollen cores in the eastern and western foothills of the regional mountain chains. In this section, we first examine in a broad sense the biogeography of the region and then focus specifically on the zoogeography of different land animal groups.

To the east of the Anosyenne Mountains lay the Vohimena Mountains, and these two massifs are separated by a relatively deep valley containing the Manampanihy River. Little is known about the biota of the Vohimena Mountains and most of the extrapolations presented here on the biota of upland humid forest formations are derived from the Anosyenne Mountains. Given the very recent formation of the geological deposits on which the littoral forests rest, this information gap may pose a serious problem for the interpretation of certain biogeographic patterns, as sufficient time may not have passed for the evolution of littoral forest endemics. Biological inventories of the remaining relatively intact forests of the Vohimena Mountains will almost certainly uncover some of the littoral forest "endemics," and hence modify our interpretations of the regional biogeography.

The timing of speciation in the modern biota

A current axiom in the literature is that the period of speciation on Madagascar for many organisms, particularly land vertebrates, occurred during the climatic vicissitudes of the Quaternary. This aspect is at least in part a by-product of the fact that there is no important fossil record on the island between the Late Cretaceous and the Late Pleistocene/Holocene, a gap of 65 million years. Thus, current knowledge of biotic and abiotic changes that took place over the last 26,000 years, milliseconds in the context of geological history through time, provides an extremely narrow and perhaps inaccurate window into the history of speciation of the modern flora and fauna. Recent models using nucleotide data indicate that in some cases the period of rapid speciation, or cladogenesis, may have been earlier in geological history than this axiom would indicate and more appropriately associated with the Pliocene (Yoder *et al*. 2003, 2005, Poux *et al*. 2005). Until fossil-bearing deposits on Madagascar associated with the Pliocene-early Pleistocene period are located and studied, it will be difficult to directly address this question.

General overviews of regional biogeography

Until very recently, the major syntheses on the biogeography of Madagascar were based on plant distributions or floristic units, which at some level for animals has inhibited new advances in understanding the overall patterns of the island's unique biota. There is growing evidence that the island's phytogeographic and zoogeographic patterns are not necessarily in parallel and examples of co-evolution between them are notably more limited than in other continental tropical settings (e.g., Bollen *et al.* 2005).

One of the first major analyses, with regards to the phytogeographic divisions of the island, was that of Perrier de la Bâthie (1921, 1936). He divided the island into two separate zones: "Flore sous le Vent" (or leeward flora), the zone under the rain shadow of the eastern mountains and central highlands, with rainfall limited to the seasonal monsoon and with deciduous vegetation, and "Flore du Vent" (or windward flora) that included all areas with a rainfall regime under the permanent influence of trade winds and with non-deciduous vegetation. Within each of these zones, five different regions were proposed. Based on this classification, the portion of southeastern Madagascar to the west of the Anosyenne Mountains falls within the leeward flora (Southern Region), and to the east within the windward flora (Eastern Region). Subsequently, there were various tests of this phytogeographic classification with some modifications (see Lowry *et al*. 1997 for an excellent review).

Humbert (1955) redelimited Perrier de la Bâthie's regions into domains and added a sixth domain to accommodate a distinct vegetational zone in areas above 2000 m on the higher mountains, which would include the higher summital zones within parcel I of the PN d'Andohahela (Rakotomalaza and Messmer 1999). Several more recent phytogeographic classifications have been proposed for the island, but in most cases these are refinements of the Humbert system (e.g., White 1983, Faramalala 1995, Du Puy and Moat 1996, 1998). One of the drawbacks of the Humbert model is that certain biogeographic aspects applicable to plants may not be for animals, such as the importance of edaphic characteristics or the role of vicariance. Recent studies mapping the biogeographic patterns of different animal groups using the Humbert system have found a lack of concordance (Raxworthy and Nussbaum 1996, 1997, Raherilalao and Goodman 2005). Thus, for the purpose of explaining zoogeographic patterns on Madagascar, it is becoming increasingly clear that the Humbert system is not applicable in many cases.

Another approach to explain the biogeographic patterns on Madagascar was proposed by Cornet (1974) based on a bioclimatic classification using data from 198 meteorological stations. Here the principal variables were hydric deficit (precipitation minus potential evapotranspiration) and the mean minimum temperature in the coldest month. The map resulting from this analysis delineates 29 different bioclimate zones grouped in five main categories ("étages," or stages): humid, subhumid, dry, subarid, and montane. These stages are divided into a series of "sous étage" or sub-stages. Within Cornet's classification the montane areas of southeastern Madagascar (the Anosyenne and Vohimena Mountains) are placed within the humid stage (sub-stage perhumid), the eastern lowland portions within the humid stage (substage humid), and areas to the west of the Anosyenne Mountains as subarid stage (divided into different substages). Thus, once again, the major division in the biogeographic zones of southeastern Madagascar was to the east and west of the Anosyenne Mountains.

The Cornet (1974) bioclimatic system provided several important improvements of the Humbert (1965) classification (see Schatz 2000), although there are numerous limitations associated with portions of the island not covered by meteorological data and the associated difficulties of certain inferences, such as the fact that not a single station is within a forested area. Furthermore, vegetational cover is dependent on certain soil characteristics which the bioclimatic system cannot capture. As explained in a previous section, the southern portion of Madagascar has undergone considerable climatic change in recent millennia, towards desiccation, specifically the zone to the west of the Anosyenne Mountains. Given that different vegetational types can persist after certain levels of climatic change, the bioclimatic model would not be able to predict "refuge" zones of remnant vegetation. This is certainly the case for some of the more relict humid forested areas to the west of the Anosyenne Mountains, such as Grand Lavasoa and the Ambatotsirongorongo forests (Ramanamanjato *et al.* 2002, Hapke *et al.* 2005).

Wilmé *et al.* (2006) recently proposed a new biogeographic hypothesis to explain the evolution of the high levels of microendemism on the island. Using an analysis of watersheds in the context of recent climatic shifts, they provide a mechanistic approach to elucidate the process of explosive regional speciation on the island. River catchments with sources at relatively low elevations were zones of isolation, as during climatic vicissitudes organisms could not find refuge along riverine forest corridors to higher elevations, and hence led to the speciation of locally endemic taxa. This is in contrast to zones with river sources at higher elevations, which served as areas of retreat and dispersion; hence containing proportionately lower levels of microendemism. Amongst the zones of exceptional microendemism defined by Wilmé *et al.* (2006), is one that falls within southeastern Madagascar, the "South Mananara Zone," which is defined as the area south of the Mananara watershed along the eastern slopes of the Anosyenne and Vohimena Mountains (Fig. 2). Further, the Mandrare River basin has a complex history and whether it belongs in the large "South Mangoky Zone" or should be considered a retreat-dispersal watershed remains ambiguous. It is interesting to note that several species known from subfossil and modern remains, with very limited modern distributions (e.g., *Macrotarsomys petteri*), have distributions fitting with this latter zone of endemism.

Recently, in the context of a regional development program in the Anosy Region, southeastern Madagascar was divided into two separate areas that are applicable both culturally and biologically (Charmont 2006). The Anosy Zone, falling within the sub-prefecture of Tolagnaro, is defined as the area from the ocean, west to the Anosyenne Mountains, north to the Manampanihy River, and south to the Efaho River. The second zone, known as the Androy East Zone, within the sub-prefecture of Amboasary-Sud, is delimited by the western side of the Anosyenne Mountains west to the Androy volcanic zone (Vohidava and Vohitsiombe), south by the sea, and to the north by the Manamby Rim.

General biogeographic patterns of vertebrates occurring in the littoral forests

A number of studies have been conducted across an assortment of animals to examine the biogeographic affinities of the littoral forest fauna with respect to other habitats on the island. In many cases, the faunistic communities occupying the remaining and highly fragmented littoral forest are more closely related to one another and form a subset to those occurring in nearby humid forest habitats on lateritic soils. These are the general conclusions reached for several different vertebrate groups including birds, amphibians, and certain small mammals (Goodman *et al*. 1997, Raxworthy and Nussbaum 1996, 1997, Ganzhorn *et al*. 2003). However, certain animal groups, such as ants, contain endemic species not found in adjacent forests resting on lateritic soils (Fisher and Girman 2000). Thus, an overall synthesis of the zoogeography of the littoral forests may be inappropriate, as a variety of different factors at varying temporal and geographic scales may have come into interplay in giving rise to these patterns. Hence, here we examine separately a number of different vertebrate groups. Further, little is known about the fauna inhabiting the natural forests of the Vohimena Mountains, which lie close to the coastal littoral forests, and the biogeographic relationships between this chain, the littoral forests, and the Anosyenne Mountains.

The role of local extirpations resulting from the fragmentation of the remaining littoral forest habitats must be taken into consideration as fragment size, edge effects, and species diversity are closely correlated (e.g., Ganzhorn *et al*. 2000, Ramanamanjato 2000, Lehtinen *et al*. 2003, Lehtinen and Ramanamanjato 2006, see Watson Chapter 4.6). Given the massive variation in the home range of large diurnal lemur taxa and small body ants, for example, and that the largest remaining littoral forest fragment in the Tolagnaro region is approximately 275 ha, certain biogeographic patterns maybe masked due to differential extinction. Finally, it should be kept in mind that in a geological sense the alluvial soils of the littoral forest are more recent than those occurring further inland, and inherently the littoral forest biota has had less time for local differentiation. The history of Pleistocene climatic changes has had a major bearing on this process.

Reptiles and amphibians

The herpetofauna of southeastern Madagascar is remarkably varied, reflecting the wide variety of habitats across the region and the considerable specificity amongst these animals in the vegetational communities they occupy. It is currently estimated that about 168 species occur within the Anosy

Table 1. List of amphibians and reptiles endemic to the Anosy Region. Details are also presented on their IUCN red data book status (IUCN 2004) and if they are known to occur in a protected area.

Form	IUCN status	Present in protected area
Family Hyperolidae		
Heterixalus boettgeri	Least concern	YES
Family Mantellidae		
Mantella haraldmeieri	Vulnerable	YES
Mantidactylus microtympanum	Endangered	YES
Boophis andohahela	Data deficient	YES
Family Chamaeleonidae		
Calumma capuronnii	Threatened	YES
Family Gekkonidae		
Lygodactylus sp.	Not evaluated	NO
Paragehyra gabriella	Threatened	YES (400 m)
Phelsuma antanosy	Seriously threatened	NO
Phelsuma malamakibo	Not evaluated	YES
Uroplatus malahelo	Threatened	YES
Family Gerrhosauridae		
Zonosaurus anelanelany	Not evaluated	YES
Family Scincidae		
Amphiglossus anosyensis	Not evaluated	YES
Family Colubridae		
Pseudoxyrhopus kely	Threatened	NO
Pseudoxyrhopus sokosoko	Not evaluated	YES
Mabuya elegans delphinensis	Not evaluated	YES

Table 2. Geographic distribution of threatened amphibian species occurring in the Anosy Region. DD = data deficient, EN = endangered, LC = least concern, and VU= vulnerable.

	Mantella haraldmeieri VU	*Boophis haematopus* VU	*B. andohahela* DD	*Mantidactylus brunae* EN	*M. guibei* EN	*M. microtis* EN	*M. microtympanum* EN	*Heterixalus boettgeri* LC	*Anodonthyla rouxae* EN	*A. nigrigularis* DD	*Stumpffia tridactyla* DD
PN d'Andohahela	X	X	X	X	X	X	X	X			
Anosyenne Mountains north of parcel I of Andohahela									X		
Tsitongambarika	X	X	X	X			X	X		X	X
Sainte Luce								X			X
Mandena								X			X
Marovony		X					X			X	
Ambatotsirongorongo							X	X		X	
Dry forest sites											
Petriky											

Region (Ramanamanjato unpublished data), which is approximately one-third of the island's herpetofauna. Across the western flank of the Anosyenne Mountains, there is remarkable species turnover, and perhaps more than any other locally occurring vertebrate group, the reptiles and amphibians can really be divided in wet and dry forest taxa.

In an elevational transect of five zones on the slopes of the humid forest parcel I of the PN d'Andohahela, Nussbaum *et al*. (1999) found very pronounced patterns of species turnover as a function of elevation. In total, 87 species of reptiles and amphibians were documented in this parcel. Subsequent taxonomic revisions of certain genera and species among these animals, as well as other inventories, render this figure to be conservative (e.g., Andreone and Randriamahazo 1997). Amongst these five zones, 38 species were recorded at 440 m (lowland humid forest), 45 species at 810 m (towards upper limit of lowland humid forest), 42 species at 1200 m (montane forest), 23 species at 1500 m (montane forest), and 14 species at 1875 m (ecotone between upper montane forest and sclerophyllous forest). In all of the possible pairwise comparisons between these sites, the coefficients of community similarity are relatively low, not greater than 0.50 in any case. This can be interpreted that there is considerable species turnover and replacement across this gradient. However, the herpetofauna of the region shows close biogeographical affinities, particularly when comparing the same elevational zones to other regions of eastern humid forest. Thus, many elements of this fauna are altitudinally restricted, but with broad latitudinal distributions.

In contrast, parcel I and parcel II (spiny bush) of this park, separated by a few kilometers, show remarkably different herpetological communities. Of the four species of amphibians and 30 species of reptiles documented by Nussbaum *et al*. (1999) in parcel II, only one species, *Amphiglossus ornaticeps*, is shared between the two parcels. Hence, there is much greater species turnover across the short ecotone between humid forest and spiny bush than over the entire 1200 km length of the eastern humid forest. This pattern is repeated across different animal groups.

On a finer scale, in the Anosy Region, 15 species of reptiles and amphibians are microendemics (Table 1), that is to say they are not found elsewhere on the island. In many cases, the natural history of these animals is very poorly known and their conservation status has not been assessed, while the future survival of several taxa is uncertain. Amongst the 11 species of amphibians that occur in the Anosy Region that are considered threatened across their Madagascar distribution (Table 2), eight are found in the forests of parcel I of the PN d'Andohahela and Tsitongambarika, and notably fewer in the forests of Sainte Luce, Mandena, Marovony, and Ambatorongorongo. Interestingly, none of these threatened species occur in the regional dry forests

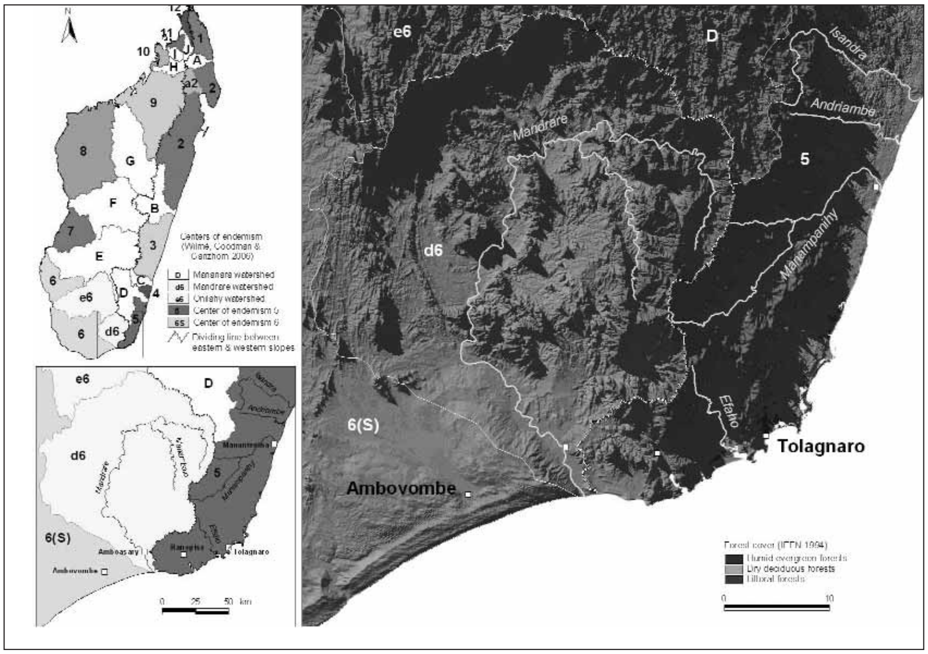

Figure 2. Map showing the delimitation of the zones of microendemism in southeastern Madagascar as defined by Wilmé *et al.* (2006). Definitions of zones include: D = Mananara watershed, d6 = Mandrare watershed, e6 = Onilahy watershed, 5 = center of endemism # 5, and 6S = southern portion of center of endemism # 6.

or Petriky. Precise details of the distribution and faunal relationships, and the conservation status of species occurring in the littoral forest areas are presented in Ramanamanjato (Chapter 4.4).

A recent study was conducted at Sainte Luce on two sympatric species of endemic frogs, *Mantidactylus bicalcaratus* and *M. punctatus*, which spend virtually their entire life cycles among the leaves of *Pandanus* (Lehtinen 2005). Within the leaves of these plants are permanent water bodies, known as phytotelmata. Results of various experiments indicate asymmetric competitive interactions between these taxa in favor of *M. punctatus* at the larval stage. Thus, *M. bicalcaratus* tends to avoid plants with individuals of *M. punctatus* (Lehtinen 2004).

Scott *et al*. (2006) studied the effects of habitat fragmentation on lizards in the spiny bush forest of Bevia, near Behara, to the west of the Anosyenne Mountains. These animals were notably sensitive to habitat fragmentation. Of the 14 endemic species examined, 12 showed negative responses to habitat fragmentation with only 41% of the species occurring in "cleared" areas.

Recent phylogeographic research has helped resolve questions on the origin of several different organisms thought to have been introduced by humans to Madagascar. A nucleotide study on *Hemidactylus* geckos, animals often associated with synanthropic settings and thought to have been widely dispersed by human agents, indicates that the species occurring in the Tolagnaro region, *H. mercatorius*, shows considerable phylogeographical structure (Vences *et al*. 2004a). Moreover, this population is differentiated from that on the African continent at a level that indicates that its dispersal history predates that of human settlement of Madagascar. A similar pattern has been found for the frog *Ptychadena mascareniensis*. This taxon is the only presumed native Malagasy species shared in common with Africa, as well as other western Indian Ocean islands, and it was uncertain if indeed it was naturally occurring on Madagascar. Based on genetic analysis, populations of this frog were introduced on the Mascarene and Seychelles islands from Madagascar, but populations from Madagascar, including those from Tolagnaro and Nahampoana, are notably differentiated from

African populations (Vences *et al*. 2004b). Hence, it is concluded that the African and Malagasy populations have been separated from one another for considerable periods, certainly superceding human intervention in their distribution patterns.

Birds

Given the exceptional habitat diversity in the Anosy Region, the number of locally occurring bird species within 50 km of Tolagnaro is without parallel elsewhere on the island in such a geographically confined zone. In their review of the regional avifauna, including the area south of Manantenina and to the east of the Mandrare River, Goodman *et al*. (1997) listed 189 locally occurring bird species, which represented 68% of the island's known avifauna at that time. The only possible regional endemic is a vanga, *Hypositta perdita,* named by Peters (1996), but for which the specific status remains unclear (Goodman *et al*. 1997). Subsequently, a number of bird species have been recorded in the littoral forests of the region (see Watson Chapter 4.6) that were not documented in this habitat by Goodman *et al*. (1997).

The ecotonal divide on the western flank of the Anosyenne Mountains between the humid areas to the east and the dry areas to the west, shows a remarkable shift in species richness. Whether based on biological or phylogenetic species concepts, betadiversity turnover across this zone is extraordinary. The differences in the birds occurring between parcels I and II of the PN d'Andohahela, separated by approximately 5 km, are many times greater than those occurring between the species of the entire 1200 km length of the eastern humid forest, from parcel I of the PN d'Andohahela to the Réserve Spéciale d'Anjanaharibe-Sud (Goodman *et al*. 1997).

Several dry forest and spiny bush bird species occur in the littoral forests of Mandena and Sainte Luce. An excellent example is the large terrestrial Giant Coua (*Coua gigas*) that occurs across the dry western deciduous forests of the island to the extreme south and over to the western edge of the Anosyenne Mountains. This species was able to pass over the Anosyenne threshold and colonize the eastern littoral forest zones of Mandena and Sainte Luce, a narrow band of habitat. However, it is not known to occur on the more upland forests (e.g., at Nahampoana), which rest on lateritic soils. This may be best explained by certain edaphic parameters of the sand based littoral forests that parallel dry forests, regardless of meteorological regimes and the associated biotas of these two littoral forests.

A study was conducted by Scott *et al*. (2006) near Behara, to the west of the Anosyenne Mountains, on the effects of habitat fragmentation on spiny forest birds. These animals were notably sensitive to habitat fragmentation. In general, species classified as forest dependent show a negative relationship with regard to forest fragmentation, being particularly notable among endemic and insectivorous species. Interestingly, these endemic, spiny forest-dwelling species were replaced in the smaller fragments by endemic open area species.

A recent Parsimony Analysis of Endemism (PAE) of bird biogeography was conducted with special reference to the Malagasy Central Highlands (Raherilalao and Goodman 2005). One aspect of the analysis, which included data from parcel I of the PN d'Andohahela, was to determine if the biogeographic distribution of birds followed the phytogeographic classification of Humbert (1965). In general, the PAE analysis failed to corroborate Humbert's hypothesis on several levels, including the montane and upper montane forests of the PN d'Andohahela. This lack of concordance is probably associated with the different evolutionary histories of birds and vascular plants.

There is evidence of a local, modern extinction within the Anosy Region avifauna. Milon (1950) described a new subspecies to science, *Coua cristata maxima*, based on a single specimen found in the environs of Tolagnaro. This holotype is clearly different from other named forms of *C. cristata*, one of which occurs in the Anosy Region (*C. c. pyropyga*), based on external measurements and pelage characteristics (Goodman *et al*. 1997) and should be considered a full species (*C. maxima*). In August 1988, an individual of *C. cristata* was observed in the last vestige of littoral forest near Lac Lanirano, 2 km north of Tolagnaro (Goodman *et al*. 1997). At that time, it was not noted whether the bird showed plumage characteristics typical of *C. c. pyropyga* or *C. maxima*. A search for this animal the following year was unsuccessful. Given that the Tolagnaro region is well known ornithologically, and frequented by numerous bird-watchers, a bird of this size, form, and coloration could probably not go undetected for over 50 years. *Coua* spp. are forest-dwelling birds, although *C. cristata* can exist in heavily degraded zones. Thus, it is assumed that a combination of habitat destruction and hunting lead to the extinction of *C. maxima*, which weighed approximately 175-200 g. Other large-bodied birds are being exploited for meat, and are becoming increasingly rare in the zone (e.g., Madagascar Crested Ibis, *Lophotibis cristata*).

Several recent studies have been conducted on Malagasy birds, and have included individuals from southeastern Madagascar. Warren *et al*. (2005) examined the phylogeography of *Hypsipetes madagascariensis*, a species of bulbul that occurs in open disturbed habitats as well as forest. Due to its life history, geography was not strongly correlated to patterns of haplotypic variation.

Classically, only one species of Scops owl, *Otus rutilus* (e.g., Langrand 1995), was recognized on Madagascar. A recent study on the patterns of morphological variation of this taxon concluded that it should be divided into two separate species: *O. rutilus* in the eastern humid zones, and *O. madagascariensis* in the drier western areas (Rasmussen *et al*. 2000). This two-species hypothesis was tested by Fuchs *et al*. (2007) using mitochondrial DNA sequence data. They found that individuals of populations assigned to these forms showed low levels of differentiation (maximum sequence divergence was 0.6 %), which might best be explained by recent genetic isolation. The greatest difference found across a short geographical distance was in extreme southeastern Madagascar, between the slopes of the Anosyenne Mountains and areas to the west. These authors rejected the two-species hypothesis and concluded that *Otus*, on Madagascar, may have started to diverge in recent geological time, perhaps associated with Quaternary climatic shifts.

Non-volant small mammals (rodents and tenrecs)

Here we examine non-volant small mammals, which in Madagascar consist of several different groups. First, Order Afrosoricida (e.g. Lipotyphla, Insectivora), which includes the Family Tenrecidae, with three endemic Subfamilies, Geogalinae, Oryzorictinae, and Tenrecinae (Bronner and Jenkins 2005). Second, Order Soricomorpha, or shrews, which contains two species of the Family Soricidae, one native, *Suncus madagascariensis*, and the other the introduced, *S. murinus* (Hutterer 2005). Lastly, Order Rodentia, or rodents, composed of the endemic Subfamily Nesomyinae (within the Family Nesomyidae) and the introduced Subfamily Murinae (within the Family Muridae; Musser and Carleton 2005). The volant mammal group, which includes bats of the Order Chiroptera, is discussed in Jenkins *et al*. (Chapter 4.7).

The southeastern portion of the island possesses a rich, small mammal fauna attributable to the varied habitats occurring in the region and the high elevations of the Anosyenne and Vohimena Mountains. No endemic species of extant small mammal is known from the Anosy Region. As with other groups of organisms, there are two principal gradients that show high levels of species turnover within this region: the east-west gradient from humid forests to dry forests, and the elevational gradient, particularly in parcel I of the PN d'Andohahela, from lowland habitats to sclerophyllous forest in the summital zones.

The east-west habitat gradient is best examined by comparing the small mammals occurring in parcels I and II of the PN d'Andohahela (Table 3). Other than spiny tenrecs of the Subfamily Tenrecidae, which are widespread generalists, there is no native species of small mammal shared between these sites. Thus, within a short distance there is total replacement.

On the slopes of the PN d'Andohahela in parcel I, notable shifts in the species of small mammals occur along the elevational gradient. The following figures are presented for tenrecs and native rodents, respectively: 440 m, 5 and 1 species; 810 m, 5 and 4 species; 1200 m, 7 and 5 species; 1500 m, 7 and 3 species; and 1875 m, 8 and 2 species (Goodman *et al*. 1999a, 1999b). Certain species are restricted to the lower end of the elevational transect (e.g., *Eliurus webbi*), some have broad elevational distributions (e.g., *Microgale thomasi*, *E. minor*), while others are limited to the high mountain zone (e.g., *M. gracilis*, *Monticolomys koopmani*). Hence, both alpha- and beta-diversity change along the continuous forest in these mountains.

There is also notable contrast in the small mammal faunas in humid forest habitats resting on lateritic soils and those on alluvial sands. This shift is well illustrated by a comparison of the non-volant small mammals known from parcel I of the PN d'Andohahela, a humid forest site resting on lateritic soils, and the littoral forest sites of Sainte Luce and

Table 3. List of living, non-volant mammal species known from the extreme southeastern portion of Madagascar. Taxonomy based largely on Bronner and Jenkins (2005) for the Afrosoricida [=ex Lipotyphla and Insectivora], Hutterer (2005) for the Soricomorpha [= shrews], Musser and Carleton (2005) for the Rodentia [=rodents], and Wozencraft (2005) for the Carnivora [=carnivorans]. For the primates we have used several different sources and have tended not to except recently described species based exclusively on molecular data. Specific details on the distribution of these different mammal species are derived from Goodman and Pidgeon (1999), Goodman *et al.* (1999a, 1999b), Olson *et al.* (2004), Ramanamanjato and Ganzhorn (2001), as well as some unpublished museum specimen records [FMNH = Field Museum of Natural History, Chicago; USNM = National Museum of Natural History, formerly United States Museum of Natural History, Washington, D.C.]. Non-native species are preceded by an asterisk (*).

Species	**Sainte Luce**	**Mandena**	**Petriky**	**PN d'Andohahela (parcel I)**	**PN d'Andohahela (parcel II)**
Afrosoricida					
Family Tenrecidae					
Subfamily Tenrecinae					
Echinops telfairi	-	-	+	-	+
Setifer setosus	+	+	+	+	+
Tenrec ecaudatus	+	+	+	+	+
Subfamily Geogalinae					
Geogale aurita	-	-	+	-	+
Subfamily Oryzorictinae					
Microgale cowani	-	-	-	+	-
Microgale dobsoni	-	-	-	+	-
Microgale fotsifotsy	-	-	-	+	-
Microgale gracilis	-	-	-	+	-
Microgale gymnorhyncha	-	-	-	+	-
Microgale longicaudata	-	-	-	+	-
Microgale majori	-	-	-	+	-
Microgale parvula	-	-	-	+	-
Microgale principula	-	-	-	+	-
Microgale pusilla	+	-	-	-	-
Microgale soricoides	-	-	-	+	-
Microgale talazaci	-	-	-	+[1]	-
Microgale thomasi	-	-	-	+	-
Oryzorictes hova	-	-[2]	-[3]	+	-
Species totals (native)	**3**	**2**	**4**	**15**	**4**
Soricomorpha					
Family Soricidae					
Subfamily Crocidurinae					
Suncus madagascariensis	+	+	+	-	+
**Suncus murinus*	-	+	-	-	-
Species total (native)	**1**	**1**	**1**	**0**	**1**

[1] This species was not recorded in this parcel during an intensive 1995 survey, but is known from lowland forests immediately surrounding the park. It is included herein as occurring in this zone.

[2] There is a specimen (USNM) taken at Bezavona, near the base of Pic Saint Louis, 1 km west of Tolagnaro.

[3] There is a specimen (FMNH) taken at Ambatotsirongorongo [=Ambatorongorongo].

[4] This species presumably occurs in urban areas such as Tolagnaro, as well as other towns and villages within the region.

[5] This species was captured within parcel III of the PN d'Andohahela (FMNH 156536).

Table 3. *Continued.*

Species	**Sainte Luce**	**Mandena**	**Petriky**	**PN d'Andohahela (parcel I)**	**PN d'Andohahela (parcel II)**
Rodentia					
Family Muridae					
Subfamily Murinae					
**Mus musculus*	+	+	+		
**Rattus norvegicus*	-	-[4]	-	-	-[5]
**Rattus rattus*	+	+	+	+	+[6]
Family Nesomyidae					
Subfamily Nesomyinae					
Brachytarsomys albicauda	-	-	-	-[7]	
Eliurus majori	-	-	-	+	-
Eliurus minor	-	-	-	+	-
Eliurus myoxinus	-	-	+	-	+[8]
Eliurus tanala	-	-	-	+	-
Eliurus webbi	+	+	-	+	-
Gymnuromys roberti	-	-	-	+	-
Macrotarsomys bastardi	-	-	+	-	-[9]
Monticolomys koopmani	-	-	-	+	-
Nesomys rufus	-	-	-	+	-[10]
Species total (native)	**1**	**1**	**2**	**7**	**1**
Carnivora[11]					
Family Viverridae					
Subfamily Viverrinae					
**Viverricula indica*	+	+	+	-[12]	+
Family Eupleridae					
Subfamily Euplerinae					
Cryptoprocta ferox	+	+	+	+	+
Eupleres goudotii	-	-	-	+[13]	
Fossa fossana	+	+	-	+	-
Subfamily Galidiinae					
Galidia elegans	-	+	-	+[14]	-[15]
Galidictis fasciata	-	-	-	+	-
Species total (native)	**2**	**3**	**1**	**5**	**1**

[6] Also known to occur in parcel III.

[7] Reports of an animal fitting the description of this species are known from parcel I of the PN d'Andohahela.

[8] Also known to occur in parcel III of the PN d'Andohahela.

[9] This species is known from the Bevilany region and it presumably occurs in parcels II and III of the PN d'Andohahela.

[10] There are records of *Nesomys audeberti* in southeastern Madagascar at the sites of Bemangidy, Marovony and Manantantely forests.

[11] We have not included here dogs (*Canis lupus*) and cats (*Felis catus* [=*F. sylvestris*]), which include partially and completely feral populations in the region.

[12] This species can presumably be found in disturbed areas and at the forest edge within this parcel.

[13] This species has been observed in this parcel.

[14] This species is also known from numerous forest parcels on lateritic soils in southeastern Madagascar such as Bemangidy, Marovony, Nahampoana, and Manantantely.

[15] This species is not specifically recorded in this parcel of the park, but has been reported in surrounding areas.

[16] The specific status of this population is unclear, but is assigned here to *M. rufus*.

[17] Animals referred to *C. crossleyi* have been reported from the Grand Lavasoa region (Hapke *et al.* 2005).

Table 3. *Continued.*

Species	Sainte Luce	Mandena	Petriky	PN d'Andohahela (parcel I)	PN d'Andohahela (parcel II)
Primates					
Family Cheirogaleidae					
Microcebus griseorufus	-	-	-	-	+
Microcebus murinus	-	+	+	-	+
Microcebus rufus	+[16]	-	-	+	-
Cheirogaleus medius	+	+	+[17]	-	-
Cheirogaleus major	+	+	-	+	-
Phaner furcifer	-	-	-	-	+[18]
Family Lepilemuridae					
Lepilemur leucopus	-	-	-	-	+
Lepilemur mustelinus	-	-	-	+[19]	-
Family Lemuridae					
Hapalemur griseus meridionalis	-	+	-	+	-
Lemur catta	-	-	+	-	+
Eulemur collaris	+	+	-	+	-
Family Indridae					
Avahi meridionalis	+	+	-	[+]	-
Propithecus v. verreauxi	-	-	-	+	+
Family Daubentoniidae					
Daubentonia madagascariensis	-	-	-	+	-
Species total	**5**	**6**	**3**	**8**	**6**
SUMMARY					
Total species	**15**	**17**	**14**	**36**	**15**
Total native species	**12**	**13**	**10**	**35**	**13**

[18] The specific status of this population is unclear, but is assigned here to *P. furcifer*.

[19] On the basis of a recent molecular revision of this genus, the population at this site is referred to as *L. fleuretae* (Louis *et al.* 2006).

Mandena (Table 3). Twenty-two native small mammal species (rodents and tenrecs) are known from parcel I of the PN d'Andohahela as compared to five from Sainte Luce and four from Mandena. The Petriky Forest shows closer small mammal faunistic affinities to spiny bush sites, such as parcel II of the PN d'Andohahela, presumably associated with edaphic and climatic parameters, and may not be appropriate in comparisons with Sainte Luce and Mandena.

Among small mammals belonging to the Afrosoricida, particularly small species in the genera *Microgale* and *Oryzorictes* that feed extensively on soil invertebrates, certain biotic and abiotic variables would have a direct impact on the density, diversity, and seasonality of their prey. No species of these genera is shared by parcel I of the PN d'Andohahela and Sainte Luce and Mandena. By contrast, species of spiny tenrecs of the Subfamily Tenrecinae, which are dietary generalists, have a broad distribution in southeastern Madagascar including littoral forest sites. Another way to examine this question is by comparison of the *Microgale* and *Oryzorictes* fauna of Mandena and Nahampoana. The latter site rests on lateritic soils less than 1 km from Mandena, and before human degradation of the native forested habitat between these parcels, it was presumably continuous, although not necessarily floristically homogenous. Four species of these genera (*M. dobsoni*, *M. parvula*, *M. talazaci* and *O. hova*,) are known to occur in Nahampoana, but not in Mandena (Noe database: L. Wilmé and S.M. Goodman). Finally, the biogeographic affinities of the small mammal fauna occurring in littoral forests, as compared to the forests on lateritic soils across the eastern portion of the island, provide further insight into this inquiry. An analysis of the Afrosoricida fauna conducted by Ganzhorn *et al*. (2003) clearly shows that sites on sandy soils and at lower elevation across the 1200 km long eastern portion of the island have closer biogeographic affinity to one another than to nearby sites resting on lateritic soils. Thus, the question of dispersal and distance is clearly secondary to aspects of adaptation to local environments.

In general, the native rodent fauna of southeastern Madagascar shows the same basic biogeographic pattern as that of the tenrecs. Species diversity is notably higher in forests resting on lateritic soils than those on alluvial substrates. The only native rodent species shared between parcel I of the PN d'Andohahela and Sainte Luce and Mandena is *Eliurus webbi*. This species broadly distributed in a variety of lowland forest habitats of eastern Madagascar. While for the small tenrecs of the Family Oryzorictinae the explanation for this difference is associated with pedological aspects of the soil and the density and diversity of their invertebrate prey, for the rodents it is presumed to be associated with fruit and nut availability, which are the principal components of their diet. In this case, edaphic and seasonal variables are presumed to be related to the phenology of the littoral forests (Bollen and Donati 2005). An additional two species of *Eliurus* occur in the Nahampoana Forest, *E. minor* and *E. tanala*, not known to occur at Mandena (Noe database: L. Wilmé and S.M. Goodman). Thus, once again, there is an important shift in species diversity across the narrow divide from the littoral forest of Mandena to a nearby forest resting on lateritic soils.

It has previously been observed on Madagascar that when introduced *Rattus* invade natural forest habitats there is a reduction in the density and species diversity of native rodents (Goodman 1995, Goodman *et al*. 1996). Several different explanations for this relationship have been proposed, two of which are the introduction of diseases, and the creation of direct or indirect competition. Ramanamanjato and Ganzhorn (2001) tested this observation in the littoral forests of Mandena, and its relation to native forest fragmentation. Capture rates of *E. webbi*, the only native rodent occurring in this forest, were not found to be correlated with the number of *R. rattus* at a given site, and there was no evidence of replacement. Hence, the proposed hypothesis associated with negative effects on native rodents, does not hold for littoral forests.

Scott *et al*. (2006) studied the effects of habitat fragmentation on small mammals in the spiny bush forest of Bevia, near Behara, to the west of the Anosyenne Mountains. They found a strong negative correlation with forest size for specialists such as *Geogale aurita*, and none or positive correlations for generalists such as *Echinops telfairi*.

A recent morphological and molecular study conducted on long-tailed shrew tenrecs of the genus *Microgale* (Olson *et al*. 2004) included specimen material from parcel I of the PN d'Andohahela. Three different species occur in the humid forests of the Anosyenne Mountains: *M. longicaudata*, *M. majori*, and *M. principula*. On the basis of the molecular analysis, members of the widespread clade [=*M. majori*] demonstrated little genetic differentiation. The Andohahela individuals showed no clear differentiation from a large number of samples coming from various eastern moist forest sites. In contrast, samples from Andohahela of the highland form [=*M. longicaudata*] showed some genetic differentiation from other populations of this form. This may well be associated with shifts in vegetational zonation during the climatic vicissitudes of the Quaternary, and associated vicariant separation of populations, which are presumed to be more pronounced for species occurring in montane habitats.

Carnivores

Other than observations and a few captured animals, little is known about the native Carnivores of southeastern Madagascar. However, the fauna appears to be complete with regards to the species expected to occur in the region. This monophyletic group (Yoder *et al.* 2003), which represents a fascinating radiation of mammals, is now placed in the endemic Family Eupleridae, and divided into Subfamilies Euplerinae and Galidininae (Table 3). Other than domestic feral dogs and cats, the other introduced species of carnivore occurring in the area is *Viverricula indica* of the Family Viverridae.

There is no species of Carnivora endemic to southeastern Madagascar, and all of the locally occurring species have broad geographical ranges. These can be divided into two separate groups: species that are found in both the dry and humid forest biomes (*Cryptoprocta ferox*), and those that have broad distributions in the humid forest. Given the home range size of many of these animals, ranging from 7.3 ha to 26.2 km^2 (Goodman *et al.* 2003), it is possible that they could move across a relatively narrow zone that would encompass, for example, the forest of Nahampoana resting on lateritic soils and the forest of Mandena on sandy alluvial soils. Hence, such habitat divisions might not be important for carnivores as compared to small mammals, as they could fall within the home range of an individual. Interestingly, until recently there was no evidence of *C. ferox* in the Mandena forest (see Donati *et al.* Chapter 4.9).

With the extinction of the subfossil species *Cryptoprocta spelea*, which is known from the deposits of Andrahomana Cave to the west of the Anosyenne Mountains (Goodman *et al.* 2004), predator-prey relationships have certainly changed in the region. This would include a relaxation of predator pressure on extant medium to large land vertebrates, which were presumably this animal's prey base.

Primates

In accordance with the considerable variation of natural forest types in southeastern Madagascar, the zone holds an interesting composition of primate species (Table 3). The fauna is diverse given the mixture of dry and moist habitats. However, several eastern humid forest species do not reach the southeastern portion of the island. The reason for this interesting absence almost certainly lies in the biogeographic history of the region.

Etienne de Flacourt, based in Fort Dauphin (now Tolagnaro), was the representative of the French Compagnie des Indes Orientales in the latter half of the 17th century, and wrote extensively on cultural and biological aspects of the region (Flacourt 1658, reprinted edition 1995). Flacourt's account contains the now famous description of the "Tretretretre ou Tratratratra:" "C'est un animal grand comme un veau de deux ans qui a la tête ronde et une face d'homme, les pieds de devant comme un singe et les pieds de derrière aussi. Il a le poil frisoté, la queue courte et les oreilles comme celles d'un homme. . . . C'est un animal fort solitaire, les gens du pays en ont grand peur et s'enfuient à sa vue tout comme lui aussi d'eux" [This animal is the size of a two-year-old calf. It has a round head, a face like a human being, and hands and feet like a monkey. It has curly hair, a short tail, and ears like a man. . . .The animal is solitary. Peasants as well as the animal are afraid of one another and run away when there is an encounter between them]. This beast has been interpreted as possibly a subfossil lemur, perhaps *Megaladapis* or *Palaeopropithecus*, or a completely strange or fantastic animal (Decary 1950, Mittermeier *et al.* 2006, Simons 1997). Based on Flacourt's description and the facial osteology of subfossil lemurs, *Palaeopropithecus* might be the best candidate for the identification of this beast (Godfrey and Jungers 2002).

Several locally occurring lemur species appear to be endemic to the extreme portion of southeastern Madagascar. Warter *et al*. (1987) proposed a new subspecies of *Hapalemur griseus*, *H. g. meridionalis*, based on karyological differences, and the Station Forestière de Mandena was subsequently named as the type locality of this animal (Warter and Tattersall 1994). Until recently, knowledge of the distribution of *H. meridionalis* was incomplete, and it was not clear whether it occurred on higher ground in the Vohimena and Anosyenne Mountains or was restricted to the littoral zone. A recent molecular study showed that populations from Andohahela and Mandena were closely related, but that individuals from Ranomafana (Ifanadiana) also occur within this clade (Fausser *et al*. 2002). Further, the measurements of individuals referred to as *H. meridionalis* fall within the range of the widely distributed eastern form *H. g. griseus* (Mutschler and Tan 2003). Thus, there is no conclusive evidence that *meridionalis* is a form restricted to the southeastern region of the island.

In extreme southeastern Madagascar, there is another unique form of lemur, *Eulemur* (*fulvus*) *collaris*. This animal occurs in several different forest types. Two recent molecular studies of this form and *E. f. albocollaris*, occurring further north, found clear sister relationships between these two taxa (Pastorini *et al*. 2000, Wyner *et al.* 2000), indicating that some vicariant event has separated these populations. The molecular data is somewhat ambiguous as to whether these animals should be considered separate species (cf. Wyner *et al.*

1999, Pastorini *et al*. 2000). Based on chromosomal arrangements of different hybrid *Eulemur* spp., there is evidence that *albocollaris* and *collaris* should be regarded as two different species and we follow their separation herein (Djeltati *et al.* 1997).

Given the slightly detached distribution of populations of *Microcebus murinus* in the littoral forests of Mandena from the main distribution of this taxon further to the west, questions on its phylogeographic relationships are potentially interesting (see Hapke *et al*. Chapter 4.12). In studies on the phylogeographic relationships of members of this genus (Yoder *et al*. 2000, Pastorini *et al*. 2001), the Mandena population showed only slight differentiation from more westerly populations. This may indicate that this population has only recently colonized this zone or retains some genetic contact with populations to the west of the Anosyenne Mountains.

Recent field and genetic studies of the genus *Cheirogaleus* in southeastern Madagascar reveled that three species occur locally: *C. medius, C. major*, and *C. crossleyi* (Hapke *et al*. 2005). *C. major* is found in the Anosyenne and Vohimena Mountains, *C. medius* in lowland areas, often littoral forest, from Sainte Luce south and then west to Grand Lavasoa, and *C. crossleyi* only being presented at Grand Lavasoa. Within *C. medius* and *C. major* samples from the region showed little haplotypic variation that could be correlated with geography.

There are several lemur genera and species that have broad distributions across much of eastern Madagascar, but are not known to occur in the extreme southeastern portion of the island. These include the genera *Varecia* and *Indri*, and a variety of species (e.g., *Propithecus diadema*, *Hapalemur simus*, *H. aureus*, *Eulemur rubriventer*). Several hypotheses have been presented to explain such patterns including the role of rivers as dispersal barriers (Goodman and Ganzhorn 2004a), aspects of historical geology associated with the breakup of India and Madagascar (Goodman and Ganzhorn 2004b), and the role of hydrology and recent climatic shifts (Wilmé *et al*. 2006). The possibility that these factors did not play an important role in the distribution of these animals, but there has simply been differential extinction in the southeast should also be considered. It is interesting to note that *Propithecus verreauxi*, a taxon generally occurring in dry forest formations, occurs in the humid forest of parcel I of the PN d'Andohahela. Perhaps this is associated with the disappearance of a local *Propithecus* within the humid forests of the region. With the reopening of the Andrahomana Cave (see above) and the recovery of considerable primate material, numerous hypotheses of lemurs of this region should be testable.

One of the most endangered palm species on Madagascar is *Dypsis decaryi*, which is restricted to a narrow zone to the west of the Anosyenne Mountains, largely in parcel III of the PN d'Andohahela. There appears to be no seed dispersal of this plant and most seeds that germinate are found within a 3 m radius of the parent tree (Ratsirarson 2003). There appears to be no viable disperser in the modern local vertebrate community (Ratsirarson and Silander 1997), and it has been proposed that one of the extinct lemur species that lived in the region may have been an important disperser of the seeds of this plant (Ratsirarson 2003).

Conclusion

Virtually all of the remaining forested regions of Madagascar contain locally endemic plants and animals, and in many cases unique ecosystems that, in a strict biological sense, warrant protection. However, for many reasons, including time and socio-economic factors, this is not a tangible possibility. As witnessed by the level of habitat destruction currently taking place in certain areas, including that of the Tolagnaro region, the clock is ticking at an alarming rate. The actions to be taken to prioritize the conservation of specific sites, are also limited by available data, and human and financial resources. Important strides have been made by the Malagasy Government and associated partners in this regards in the context of the "Plan Durban", which seeks to increase the area within the protected area system to 10% of the surface area of the island before late 2008.

When aspects of human livelihood and economic sustainability are overlaid on the importance of conservation action, few areas of the island are more important than the region of Tolagnaro. First, as described in detail in this chapter and others in this monograph, this is a zone of remarkable biotic turnover, particularly with regards to elevational variation and transitions between the extremes of mesic and dry forests. The zone holds a number of locally endemic plants and animals, as well as a substantial portion of the island's unique biota. Second, the remaining forested habitats play an important role in the future functioning of the region's terrestrial and marine ecosystems, as well as the agricultural landscape. Without safeguarding the forest and the role it plays in protecting these watersheds, the future of the region, in both biological and economic terms, is bleak.

An important negative example of this paradigm is the inability of local organizations in the private and public sectors to properly protect the Bezavona Forest, which formed the watershed of the Nahampoana water pumping station, one of the major sources of potable water for Tolagnaro a few kilometers to the south. Before the 1990s, the hills above the station, a few kilometers from the Mandena site had extensive forest cover, but within a few years this had largely been destroyed by slash-and-burn agriculture, timber extraction, charcoal production, and, to a lesser extent, cattle pasture. This destruction has had an important bearing on local farmers, with regards to irregular water sources for their rice fields, and shortages to the residents of Tolagnaro.

In this case, the negative aspects of the destruction of the forest in the Nahampoana watershed do not rest in abstract notions of the value of biodiversity or aesthetics, but in clearly measurable economic terms of agricultural output and human welfare. Given the pronounced population growth Tolagnaro will soon experience with regard to the installation and advancement of the QMM mining project and the associated infrastructure, it is paramount that the various sectors working in the region take a greater role in protecting the remaining forests, whether or not the zone is an immediate economic interest. Without this, they are taunting with an impeding biological catastrophe in the region that will have major impacts on people, the forest biota, the marine fisheries, and ongoing commercial financial investments.

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