Montane Amphibian and Reptile Communities in Madagascar

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Abstract: *Two habitats in Madagascar, secondary, montane heathland and high plateau prairie, are considered artificial, having been created by human-set fires soon after the island was colonized less than 2000 years ago. These prairie and secondary heathland habitats are also thought to be degraded and faunistically depauperate. To test the depauperate fauna hypothesis we measured levels of herpetofaunal (amphibian and reptile) endemicity between primary forest, montane secondary heathland, and high plateau prairie. We found no species endemic to high plateau prairie, but a significant percentage of the montane herpetofauna is restricted to post-fire secondary heathland. These results support the human-origin hypothesis for prairie, but secondary heathland appears to be a natural, post-fire successional stage that leads to a climax of sclerophyllous forest. This suggests that careful management of montane heathland could establish new dispersal corridors between currently isolated montane forest blocks and, therefore, could offer new opportunities for conservation in Madagascar. Despite widespread burning, the montane heathlands of Madagascar have diverse herpetofaunal communities, demonstrating that these montane communities are not as seriously degraded as previously believed, and that they may be naturally resistant to fire.*

Comunidades de Anfibios y Reptiles de Montaña en Madagascar

Resumen: *En Madagascar los hábitats de brezal secundario de montaña y los de la pradera alta (High Plateau) son considerados como artificiales debido a que se originaron por incendios provocados por humanos poco después de la colonización de la isla menos de 2000 años a.C. También se piensa que estos hábitats están degradados y la fauna se encuentra en condiciones paupérrimas. Para evaluar la hipótesis de pauperización de la fauna, medimos los niveles de endemismo de la herpetofauna (anfibios y reptiles) entre bosque primario, brezal secundario y la pradera High Plateau. No encontramos especies endémicas a la pradera High Plateau, pero un procentaje significativo de la herpetofauna de montaña está restringido a tierras de post-incendio secundario. Estos resultados soportan la hipótesis de origen-humano para las regiones de pradera, pero los hábitats de brezal secundarios parecen presentar un estado seral natural post-incendio que conducen a un clímax de bosque esclerófilo. Esto sugiere que un manejo cuidadoso de los brezales de montaña puede permitir nuevos corredores de dispersión entre bloques de bosque de montaña actualmente aislados y de esta manera ofrecer nuevas oportunidades de conservación en Madagascar. A pesar de los tan comunes incendios, los brezales de montaña de Madagascar poseen comunidades diversas de herpetofauna que demuestran que estas áreas no se encuentran seriamente degradadas como previamente se había pensado, además de que pueden presentar resistencia natural al fuego.*

Introduction

The High Plateau of Madagascar (Fig. 1) was once assumed to have been almost completely forested before the arrival of humans (Perrier de la Bâthie 1921; Humbert 1927), but it was actually a dynamic mosaic of heathland, grassland, and forest during the Holocene, 11,000-1240 years ago (MacPhee et al. 1985; Burney 1987*a*, 1987*b*). The current prairies of the high plateau are believed to be artificial habitats created by clearing, burning, and cattle grazing (Humbert 1927; Koechlin 1972; Dewar 1984). In support of this interpretation, these prairies appear to have an impoverished fauna

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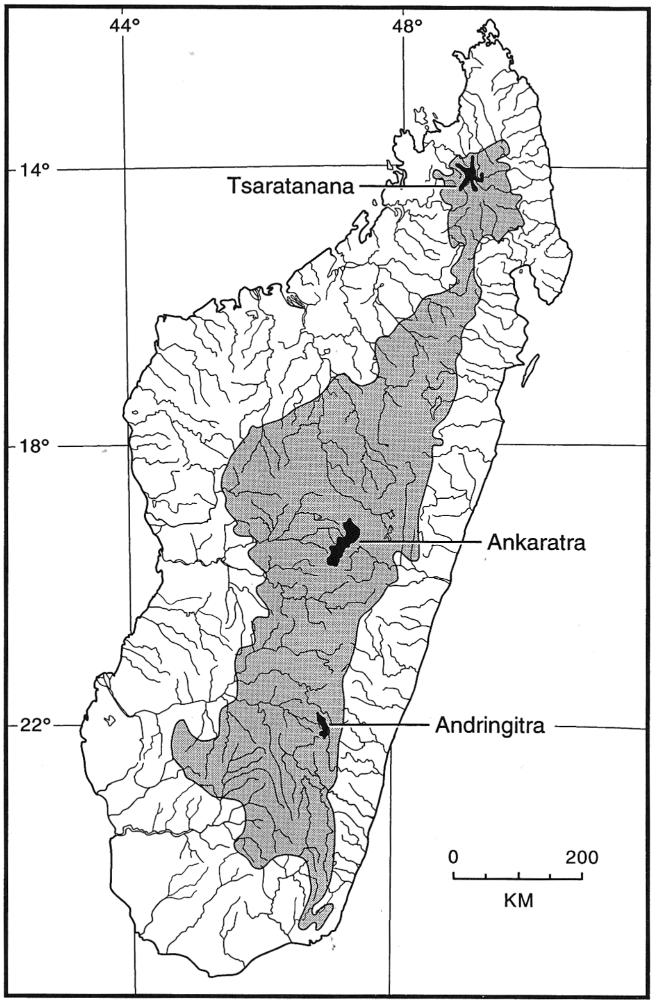

Figure 1. The high plateau of Madagascar (shaded > 800 m elevation) and associated major massifs (black > 2000 m). In Madagascar montane habitats above 1500 m elevation are confined to the high plateau.

(Perrier de la Bâthie 1936; Jenkins 1987), suggesting insufficient time since the creation of the prairies for the evolution of endemic species or subspecies.

The primary montane vegetation of the three highest massifs in Madagascar—Tsaratanana (2876 m), Ankaratra (2642 m), and Andringitra (2658 m)—is also thought to be badly degraded or destroyed because of burning by humans (Jenkins 1987; Nicoll & Langrand 1989). Four primary montane (above 1500 m) vegetation types are recognized currently: moist montane (moss) forest in less exposed areas; sclerophyllous (lichen) montane forest; montane heathland (bushland) in isolated patches on exposed ridges above 2000 m; and rupicolous shrubland restricted to rocky outcrops (Perrier de la Bâthie 1927; White 1983). No primary heathland survives at Ankaratra and Tsaratanana; both massifs have been burned frequently during this century (Perrier de la Bâthie 1927; Humbert 1928; Guillaumet 1984). The frequency of fires at Andringitra (Jenkins 1987) and our personal observations suggest that almost all extant heathland at this site is also secondary.

The large areas of extant, secondary montane heathland, typically dominated by *Philippia* and grasses, are usually interpreted as anthropogenic habitats (produced by human burning of sclerophyllous forest or primary heathland) that are faunistically depauperate (Humbert 1927, 1928; Perrier de la Bâthie 1927). Therefore, these secondary heathlands are considered analogous to the pseudo-steppe prairies of the high plateau. In montane regions, however, there is evidence of natural wildfires occurring throughout the Holocene (Burney 1987*a*), which in addition to recent reports of lightning-caused fires (Jenkins 1987), suggests that secondary heathland is a natural, post-fire successional stage.

The Madagascan herpetofauna, with about 550 total endemic species (Raxworthy & Nussbaum, unpublished data), represents about 65% of the endemic vertebrate species of Madagascar. This diverse group is well-suited for analyzing patterns of endemism within Madagascar because herpetofaunal species typically have restricted elevational and regional distributions, reflecting considerable habitat specialization (Raxworthy & Nussbaum 1994, 1995). None of these 550 island endemic species is restricted to obvious anthropogenic habitats (such as agricultural or urban areas), despite the widespread occurrence of anthropogenic habitats throughout Madagascar. Herpetofaunal species that occur in anthropogenic habitats appear to have invaded from adjacent natural habitats and probably have broad ecological tolerances.

Based on this observation, we predict that if secondary montane heathland and high plateau prairie are anthropogenic, with no history prior to human colonization, there should be no herpetofaunal species endemic to just these habitats. To test the working hypothesis that these habitats are of anthropogenic origin, we measured levels of herpetofaunal (amphibian and reptile) endemicity in primary forest, secondary heathland, and prairie habitats.

Methods

Surveys were completed during the rainy seasons of 1993 (January-March, October-December) when most species are breeding and activity is at its highest. Field techniques used to sample animals were (1) opportunistic day and night searching; (2) refuge examination (under and in fallen logs and rotten tree stumps, under bark, under rocks, in leaf litter, in root-mat and soil, and in leaf axils of screw palms of the genus *Pandanus*); and (3) pitfall trapping with drift fences. Opportunistic searching and refuge examination were done throughout the full elevational range of habitats available. Night

Table 1. Habitat distribution of species of amphibians and reptiles endemic to the high plateau (800–1500 m elevation).[a]

	High plateau habitat				
Species[b]	*Prairie*	*Forest*	*Wetland*	*Rupicolous*	*Unknown*
Amphibia					
Hyperoliidae					
Heterixalus rutenbergi Boettger 1881	+[c]		+		
Microhylidae					
Plethodontohyla A		+			
Scaphiophryne gottlebei Busse & Böhme 1992					+[d]
Mantellidae					
Mantella aurantiaca Mocquard 1900		+			
Mantella cowani Boulenger 1882					+[e]
Mantidactylus ambohimitombi Boulenger 1919		+			
Rhacophoridae					
Boophis idae Steindachner 1867		+[f]			
Boophis goudoti Tschudi 1838		+			
Boophis mandraka Blommers-Schlösser 1979		+			
Boophis rhodoscelis Boulenger 1882		+[f]			
Boophis erythrodactylus Guibé 1953		+			
Boophis hillenii Blommers-Schlösser 1979		+[f]			
Boophis A		+			
Boophis B		+			
Boophis C		+			
Reptilia					
Opluridae					
Oplurus grandidieri Mocquard 1900				+[g]	
Chamaeleonidae					
Brookesia thieli Brygoo and Domergue 1969		+			
Brookesia therezieni Brygoo and Domergue 1970		+			
Calumma brevicornis tsarafidy Brygoo & Domergue 1970		+[h]			
Calumma fallax Mocquard 1900		+			
Calumma globifer Günther 1879		+[i]			
Calumma malthe Günther 1879		+			
Calumma A		+			
Cordylidae					
Zonosaurus ornatus Gray 1845	+		+		
Zonosaurus A		+			
Typhlopidae					
Typhlops domerguei Roux-Estève 1980		+			
Colubridae					
Brygophis coulangesi Domergue 1988		+[j]			
Geodipsas vinckei Domergue 1988		+[j]			
Geodipsas A		+			
Liopholidophis pinguis Parker 1925			+		
Liopholidophis sexlineatus Günther 1882			+		
Pseudoxyrhopus ankafinaensis Raxworthy and Nussbaum 1994		+			

[a] *Data from Raxworthy and Nussbaum, unpublished unless otherwise indicated.*
[b] *Taxa not assigned specific names were considered undescribed and are the subject of ongoing taxonomic studies to be published elsewhere.*
[c] *Blommers-Schlösser (1982).*
[d] *Busse & Böhme (1992).*
[e] *Boulenger (1882).*
[f] *Blommers-Schlösser (1979).*
[g] *Blanc (1977).*
[h] *Brygoo (1971).*
[i] *Seguier-Guis (1988).*
[j] *Domergue (1988).*

searches were made using headlights. Pitfall trapping proceeded as described by Raxworthy and Nussbaum (1994). Date, time, longitude and latitude, altitude, habitat, and microhabitat were recorded at the time of capture of each individual.

Voucher specimens were fixed in 10% buffered formalin and later transferred to alcohol. Liver and muscle were removed from representatives of almost all species and frozen in liquid nitrogen for genetic studies. Representative live individuals of most species were photographed to record color, which fades in preservative. Voucher specimens were deposited either in the Museum

Table 2. Habitat and elevational distribution of montane endemic (> 1500 m elevation) species of amphibians and reptiles.

Species[b]	*Massif*[a] *Tsaratanana*	*Ankaratra*	*Andringitra*	*Massif endemic*	*Elevation (m)* *min*	*max*
Amphibia						
Microhylidae						
Anodonthyla montana Angel 1925			F, H	+	1700	2300
Platypelis tsaratananaensis Guibé 1974	F			+	2350	2350
Platypelis A	F			+	2350	2350
Plethodontohyla guentherpetersi Guibé 1974	F			+	2300	2300
Plethodontohyla tuberata Millot and Guibé 1954		F, H		+	1700	2550
Plethodontohyla A	H			+	2700	2700
Plethodontohyla B	F			+	2050	2050
Plethodontohyla C	F			+	2050	2050
Scaphiophryne A	F			+	1900	1900
Stumpffia A	F			+	2050	2050
Mantellidae						
Mantidactylus aerumnalis Peracca 1893		F	H		1700	2150
Mantidactylus alutus Peracca 1893		F, H			1700	2500
Mantidactylus domerguei Guibé 1974		F	F, H[c]		1500[d]	2150
Rhacophoridae						
Boophis microtympanum Boettger 1881		H	H		1850	2550
Reptilia						
Gekkonidae						
Lygodactylus montanus Pasteur 1964			R	+	2000	2250
Millotisaurus mirabilis Pasteur 1962		R		+	2400	2640
Phelsuma barbouri Loveridge 1942		R	R		1600	2640
Phelsuma lineata punctulata Mertens 1970	R			+	2700	2870
Chamaeleonidae						
Brookesia lolontany Raxworthy and Nussbaum 1995	F			+	1650	2050
Calumma brevicornis hilleniusi Brygoo, Blanc, and Domergue 1973		F, H	F, H		1550	2550
Calumma guibe Hillenius 1959	F			+	1600	2100
Calumma tsaratananaensis Brygoo, Blanc, and Domergue 1969	H			+	2700	2800
Calumma A	F			+	2550	2550
Calumma B	F			+	1630	2350
Furcifer campani Grandidier 1872		H	H		1850	2500
Scincidae						
Amphiglossus tsaratananaensis Brygoo 1981	F, H			+	2050	2870[e]
Amphiglossus A		F, H	H		1700	2640
Mabuya boettgeri Boulenger 1887		H	H		1600	2400
Mabuya madagascariensis Mocquard 1908		H			1650	2400
Colubridae						
Geodipsas B	F			+	1620	2050

[a] *F, montane moist and sclerophyllous forest; H, secondary heathland; R, rupicolous habitats.*
[b] *Taxa not assigned specific names were considered undescribed and are the subject of ongoing taxonomic studies to be published elsewhere.*
[c] *Millot & Guibé (1950).*
[d] *Blommers-Schlösser & Blanc (1991).*
[e] *Brygoo (1981).*

of Zoology, University of Michigan, or in the collections of the Service de Zoologie, Université d'Antananarivo.

A list of amphibians and reptiles endemic to the High Plateau and their habitat associations was compiled from our field work and from the literature (cited in Table 1). These data are based on studies made in the regions of Ambatondrazaka, Ambatolampy, Ambositra, Ambohitantely, Andringitra, Antananarivo, Isalo, Mandraka, Mantady, Perinet, Ranomafana, Tsarafidy, and Zahamena. Coordinates and further information of these sites are given by the U.S. Department of the Interior (1955) and by Nicoll and Langrand (1989).

The three montane systems surveyed were Ankaratra, 10–24 February, 19°21′S, 47°18′E; 19°22′S, 47°19′E; Tsaratanana, 18 March–4 April, 14°09′S, 48°58′E; 14°06′S, 48°59′E; 14°11′S, 48°57′E; and Andringitra, 8–17 December, 22°12′S, 46°58′E; 22°10′S, 46°56′E. Montane habitats were classified and identified as follows: (1)

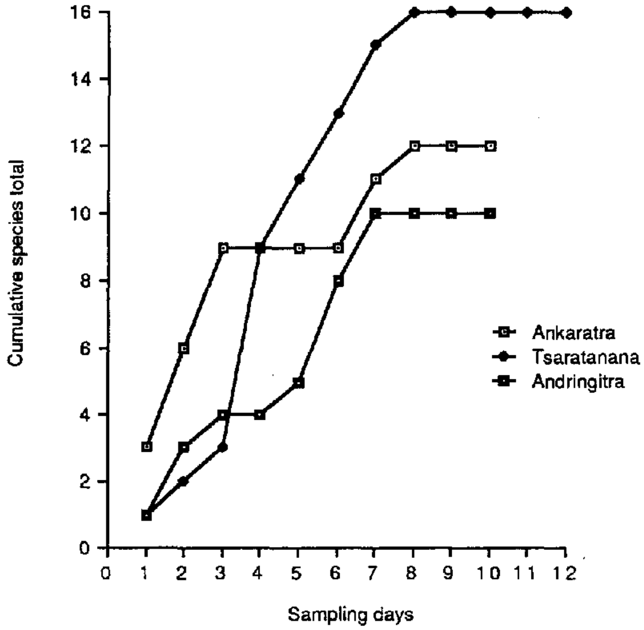

Figure 2. Accumulation curves illustrating the rate of discovery of new species of amphibians and reptiles at each montane site.

montane moist and sclerophyllous forest, trees forming a continuous canopy; (2) secondary heathland, vegetation dominated by ericoid shrubs and grasses with evidence of former burning (blackened tree trunks, stems, or roots); (3) rupicolous habitats, areas of rock surface and crevices. Montane moist forest was not distinguished from sclerophyllous forest because the two types proved to intergrade over broad areas.

Results

Of the herpetofauna surveyed, nine species of amphibians and seven species of reptiles appear to be undescribed taxa. This reflects the general lack of herpetological survey work that has been conducted in the interior of Madagascar. These new species are in the process of being described and in all cases are represented by voucher specimens. Because these new species represent such a sizeable fraction of the surveyed herpetofauna, we have chosen to include them in this analysis.

We identified 32 species of amphibians and reptiles as high plateau endemics (restricted to elevations between 800 and 1500 m on the high plateau). These endemics and their habitat types are listed in Table 1. Of these, 25 (78%) are restricted to forest habitat. Just two species (6%) occupy prairie, and neither is confined to this habitat. The complete absence of endemism in the high plateau prairie supports the current belief that this habitat is artificial and of recent origin.

Our surveys of the three major massifs (Andringitra, Ankaratra, Tsaratanana) yielded 30 amphibians and reptiles restricted to 1500 m elevation or higher (Table 2). No additional species were found during the final 3-5 survey days at each site (Fig. 2), which indicates that these species lists are nearly complete. Four geckos (Gekkonidae) are restricted to montane rupicolous habitats. All other montane species (Microhylidae, Mantellidae, Rhacophoridae, Chamaeleonidae, Scincidae, and Colubridae) occur only in heathland and/or forest.

The herpetofaunal species diversity for secondary montane heathland is eight species at Andringitra, eight at Ankaratra, and three at Tsaratanana. Five species are restricted to secondary montane heathland at Andringitra, four at Ankaratra, and two at Tsaratanana. At Tsaratanana, 12 species are restricted to moist or sclerophyllous forest, compared to just two at Ankaratra and none at Andringitra (Table 3). Secondary heathland is occupied by 54% of the nonrupicolous montane herpetofauna (all three massifs combined), and 23% of the species are found only in this montane secondary habitat. The significant percentage of montane endemic species restricted to secondary heathland contrasts sharply with the results for the high plateau prairie, where no endemic species were identified. We therefore reject the hypothesis that montane secondary heathland is artificial and faunistically depauperate.

Discussion

The absence of endemic amphibians and reptiles in the high plateau prairie strongly suggests that the modern prairie is recent and artificial, and that the original vegetation (and its endemic herpetofauna) has been lost. Claims that the original vegetation was extremely susceptible to fire and that it was therefore destroyed by the very first human-set fires (Morat 1973) cannot be supported because wildfires were common the high plateau throughout the Holocene (Burney 1987*a*, 1987*b*). It is also unlikely that such a large area of natural vegetation, 22,350-36,000 km^2 (Jenkins 1987), was destroyed by clearing, because the original human population must have been small (MacPhee et al. 1985). Grazing by introduced domestic bovids also has been proposed to explain the destruction of the natural vegetation of the

Table 3. Number of montane endemic (> 1500 m elevation) herpetological species in different habitats.

	Habitat			
Massif	*Rupicolous*	*Forest*	*Heathland*	*Forest and heathland*
Tsaratanana	1	12	2	1
Ankaratra	1	2	4	4
Andringitra	2	0	5	3

high plateau (Dewar 1984). We suspect that the modern practice of yearly burning for improved grazing (widespread throughout the high plateau) originated when pastoralists first settled in Madagascar, and that regular, repeated burning, rather than grazing per se, ultimately destroyed the original high plateau vegetation. Unlike prairie, the montane habitats have not been frequently burned; therefore, their natural, post-fire successional stages have not yet been destroyed.

We propose the following revised montane vegetational model for Madagascar. Prior to human colonization, a mosaic of sclerophyllous forest and heathland was maintained by natural wildfires within each of the major massifs of Madagascar. Secondary heathland developed as a post-fire successional stage leading to a climax of sclerophyllous forest, except on the most exposed ridges, plateaus, and summits, where heathland was the climax vegetation. The rupicolous montane habitats, largely protected from fire, remained stable.

At the northern massif, Tsaratanana, 75% of the montane herpetofauna is restricted to moist or sclerophyllous forest, a much higher percentage than on the two central massifs, Ankaratra and Andringitra, with just 17% and 0% respectively. This contrast may result from differences in the size of the montane forest refugia that existed at each massif during glacial periods of the Pleistocene. In East Africa, glacial periods of the Pleistocene had much drier climates, which caused the montane forests to contract during these periods (Hamilton 1982). Current rainfall is considerably higher at Tsaratanana (mean monthly rainfall 200–250 mm) than at the two central massifs (mean monthly rainfall 100–150 mm) (Donque 1972). If rainfall was also higher at Tsaratanana during glacial periods than on the central massifs, then montane forest would have been much more extensive at Tsaratanana than Ankaratra or Andringitra. The larger (and probably more stable) montane forest refuge at Tsaratanana would, therefore, be expected to have a greater diversity of montane forest specialists than either Ankaratra or Andringitra.

The secondary montane habitats in Madagascar are obviously not depauperate of endemic vertebrates, a result that has important implications for conservation. Despite frequent burning at Ankaratra and Andringitra, the secondary heathlands of both massifs still have diverse herpetofaunas. The montane vegetation of Tsaratanana, frequently reported to have been completely destroyed by fire (Guillaumet 1984; Jenkins 1987; Nicoll & Langrand 1989), also has a secondary heathland that supports an endemic herpetofauna. The sclerophyllous forest at Tsaratanana, claimed in 1924 to have been completely burned above 2200 m elevation (Perrier de la Bâthie 1927), has actually regenerated or survived in some areas to an elevation of 2600 m (Raxworthy, personal observation).

The widely held view that the Madagascan montane habitats have been destroyed or degraded has been largely responsible for the lack of research and conservation programs in these regions. At Tsaratanana (the most diverse massif with probably the highest degree of local endemicity of any site in Madagascar) our survey was the first scientific study made at the summit in almost 30 years, and there are no conservation programs currently active within the Tsaratanana Reserve. Although conservation programs have recently been established at Andringitra and Ankaratra, the lack of research on the high-elevation habitats is preventing their effective management.

Our results suggest that montane communities in Madagascar may be more resistant to fire than currently realized. Post-fire secondary heathland is a valuable habitat with a diverse endemic fauna. If protected from further burning or cattle grazing, it may develop into climax sclerophyllous forest. This offers the possibility that careful management of heathland could establish new dispersal corridors between montane forest blocks. This conclusion, if confirmed, offers new challenges and opportunities for conservation management in Madagascar.

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