
POPULATION ASSESSMENTS OF CHAMELEONS FROM TWO MONTANE SITES IN MADAGASCAR

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Abstract.—The highest peaks of Madagascar contain relatively little native forest vegetation but they have a remarkably high endemism and diversity of reptiles and amphibians for their surface area. Many chameleons are associated with these highland habitats in Madagascar and we assessed the population status of five species at Itremo-Ambatofinandrahana and Ankaratra, including three with restricted ranges (*Calumma hilleniusi*, *Furcifer campani* and *Furcifer minor*). *Calumma* species occurred at relatively high densities and were restricted to humid forest with the occasional occurrence of *C. hilleniusi* in savanna. *Furcifer minor* and *Furcifer lateralis* were common in both tapia (*Uapaca* spp.) forest and agricultural land while *F. campani* was restricted to savanna and heathland. *Calumma hilleniusi* is of conservation concern because of its restricted range and dwindling habitat. *Furcifer campani* and *F. minor* are currently listed as Vulnerable on the IUCN Red List of Threatened Species; they have restricted ranges but there are no obvious threats to their habitat at the moment. These species are subject to continued collection pressure even though import of these, and indeed most chameleon species, from Madagascar is currently prohibited by CITES. Itremo-Ambatofinandrahana and Ankaratra have potential to become legally protected areas and management of these sites needs to consider the future possibility of legalized collection of *F. campani* and *F. minor* for international trade.

Key Words.—Ankaratra, *Calumma*, conservation, density, *Furcifer*, Itremo

INTRODUCTION

The island of Madagascar is considered a global biodiversity hotspot because of its high levels of endemism and the significant threats to its species and habitats (Myers 1988; Brooks et al. 2002). Madagascar has significant amounts of native forest remaining, but threats to the integrity of this vegetation continue (Harper et al. 2007). Native montane vegetation occurs above 1,500 m elevation but only three massifs extend beyond 2,500 m. These highland areas probably acted as montane refugia during glacial periods of the Pleistocene and presently the biodiversity of these sites show exceptionally high levels of endemism and many species are restricted to single massifs (Raxworthy and Nussbaum 1996a, b; Raxworthy et al. 2008). Frequent fires in these montane sites shape the composition and structure of the vegetation and the herpetofaunal communities appear to withstand these regular events (Raxworthy and Nussbaum 1996a).

Madagascar has approximately 70 species of endemic chameleons and they occupy a wide range of vegetation

types and altitudes (Raselimanana and Rakotomalala 2003; Glaw and Vences 2007). Members of the *Calumma* genus are found in humid forest from sea level to at least 2,800 m, while *Furcifer* chameleons occupy a similar altitudinal range but occur in many types of forest vegetation in addition to heathland and urban areas (Glaw and Vences 2007). The dwarf chameleons, *Brookesia*, are associated with forest vegetation, occurring in both humid and deciduous formations from sea level to elevations of up to 1,875 m (Rakotomalala and Raselimanana 2003). Madagascar's biodiversity is characterized by high levels of microendemism (Vences et al. 2009), and a number of chameleon species are only known from a single montane locality, or occupy small areas of suitable montane habitat (Glaw and Vences 2007). The survival of these species is potentially of concern because herpetofaunal communities at these sites are isolated abiotically by climate and biotically by the lack of suitable forest vegetation at lower elevations (Raxworthy and Nussbaum 1995, 1996b). These communities are also potentially at risk from up-slope displacement because of climate warming and the effects

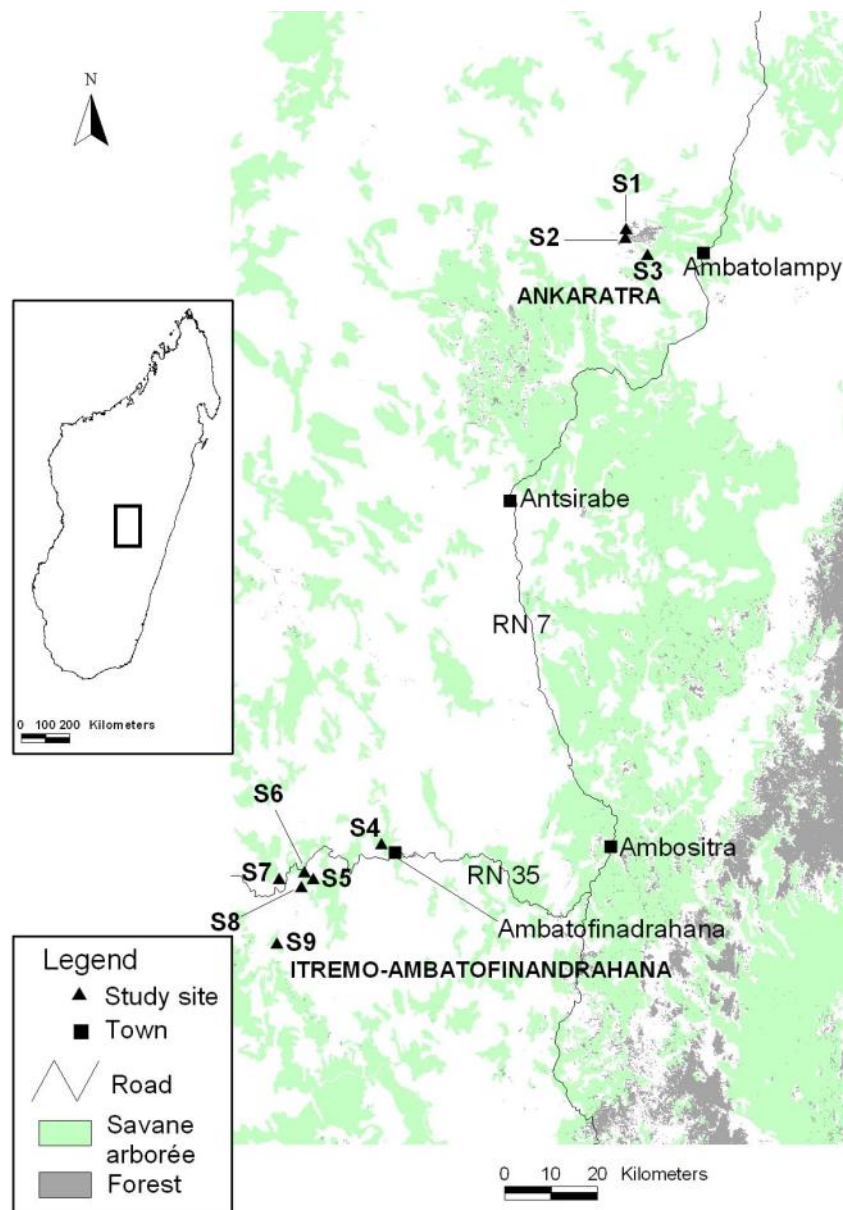


FIGURE 1. Map of the two study areas showing sites at Ankaratra [Ambohimirandana (S1), Analamilona (S2), Analatsama (S3)] and Itremo-Ambatofinandrahana [Ringorano (S4), Itremo (S5), Hazofotsy (S6), Beapombo (S7), Ampangabe (S8), Antsirakambiaty (S9)]. Forest cover is in grey and wooded savanna in green. National Roads (RN) are also marked.

of habitat loss and degradation (Raxworthy et al. 2008). Careful consideration needs to be given therefore to understanding the biology of species that are restricted to these montane habitats.

In this paper we report on the chameleons at two high elevation sites in central Madagascar that are currently being developed as protected areas. The two focal taxa, *Furcifer campani* and *Furcifer minor*, are listed as threatened on the IUCN Red List and were present in international trade before the 1994 CITES suspension (Carpenter et al. 2004). Their IUCN Red List assessments, however, need to be updated, and a recent

evaluation by CITES indicates that both species are potential candidates for a resumption in exports. The objective of our study was therefore to obtain information on these chameleons regarding population density, broad-scale habitat use, and threats.

MATERIALS AND METHODS

Study sites.—We surveyed two sites in the central highlands of Madagascar (Fig. 1), the Ankaratra Massif in the Vakin'Ankaratra Region and Itremo-Ambatofinandrahana in the Amoron i'Mania Region.

Herpetological Conservation and Biology

TABLE 1. The abundance (mean \pm SE) and density of chameleons from two highland sites in central Madagascar (Ankaratra and Itremo-Ambatofinandrahana). Density was calculated using the program DISTANCE (N = number of observations used in the calculations, C.V. = coefficient of variation; C.I. = confidence interval) and the recommended models (Thomas et al. 2004). Sample size for *Calumma nasutum* was too small to estimate population density.

Species	Abundance (100 m ⁻¹)	Density (ha ⁻¹)	N	C.V.	95% CI	Model
Itremo-Ambatofinandrahana						
<i>Calumma crypticum</i>	3.0 \pm 0.40	39.7	180	21.2	26.1–60.4	Half-normal
<i>C. nasutum</i>	0.0 \pm 0.03	-				
<i>Furcifer lateralis</i>	2.0 \pm 0.40	27.3	365	13.1	21.1–35.3	Half-normal
<i>F. minor</i>	1.0 \pm 0.21	16.4	174	14.9	21.2–21.9	Hazard
Ankaratra						
<i>C. hilleniusi</i>	1.5 \pm 0.80	19.7	63	56.6	6.6–58.0	Hazard
<i>F. lateralis</i>	0.5 \pm 0.20	5.1	21	47.9	2.0–12.8	Uniform
<i>F. campani</i>	1.1 \pm 0.30	12.2	47	26.6	7.1–20.9	Uniform

The Ankaratra massif is volcanic in origin and the summit, at 2,643 m, is the third highest peak in Madagascar (Goodman et al. 1996). Mixed forest occurs on the eastern slope at the Manjakatempo Forest Station between 1,700 m and 2,000 m elevation and includes remnants of native forest (both humid and sclerophyllous), and planted woodland dominated with *Weinmannia bojeriana* and pine plantations (Goodman et al. 1996). The surveys spanned an elevational range of between 1,601 m and 2,643 m above sea-level. The vegetation changes above 2,000 m into a secondary montane heathland, with scattered ericoid bushes and grassland (Vences et al. 2002). There is a greater variety of vegetation types at Itremo-Ambatofinandrahana, including mid-altitude humid forest, *Uapaca boejeri* dominated tapia forest and savanna heathland. Areas near to human settlements have been converted into rice and maize cultivation. We visited eight sites, five at Itremo-Ambatofinandrahana and three at Ankaratra (Table 1), the former between January and March 2008 and the latter during November and December 2008.

Nocturnal surveys.—We searched for chameleons along randomly placed line transects at night in the main habitats at each study site. Transects were placed at least 24 hours before the survey commenced. Each transect consisted of three parallel lines, each 50 m long, and separated by approximately 30 m. Search teams consisted of two experienced herpetologists equipped with a Petzl Myo XP LED head torch (Petzl, Crolles, Grenoble, France). Each observer walked slowly along a transect and searched only on the right or left of the line respectively. Only chameleons detected from the transect line were counted and the perpendicular distance from the roost location to the line was measured with a tape measure to the nearest centimeter. Individuals of each taxon were preserved as voucher specimens at the Department of Animal Biology, University of Antananarivo. Because we focused on *Furcifer* species, which rarely occurred in closed humid forest, the survey

effort in different habitat types was not always proportional to their occurrence in the site, and there was a numerical bias towards transects in savanna, tapia forest, and agricultural land. This was particularly the case at Ankaratra where relatively few surveys were undertaken in humid forest compared to the heathland. We undertook additional nocturnal visual encounter surveys at Ankaratra towards the end of the study in the heathland to determine the elevational range of *F. campani* at the site.

Density and abundance estimation.—We estimated the abundance of chameleons by converting the counts on each transect into values per 100 m. Chameleon density was calculated using the program DISTANCE (Buckland et al. 2001; Thomas et al. 2004), which uses a detection function based on the perpendicular distances from the chameleon to the transect line and has been used in previous studies to assess the density of chameleons (e.g. Brady and Griffiths 1999; Karsten et al. 2009).

Habitat use.—We used each 150 m transect as independent replicates in tests to compare the abundance of chameleons between broad habitat types. Survey effort in the different habitats was as follows: Itremo-Ambatofinandrahana (humid forest transects n = 30, agricultural land n = 30, tapia forest n = 30) and Ankaratra (humid forest n = 4, savanna n = 23). To further explore other differences in abundance, we tested for linear relationships with elevation at each site.

Threat identification.—Through the course of the surveys, we interviewed people at each site to obtain information on collection pressure. This was not a systematic assessment, but we used the responses from different sources to establish a broad assessment of recent collection pressure. We also noted any major disturbances to the habitat at each site.

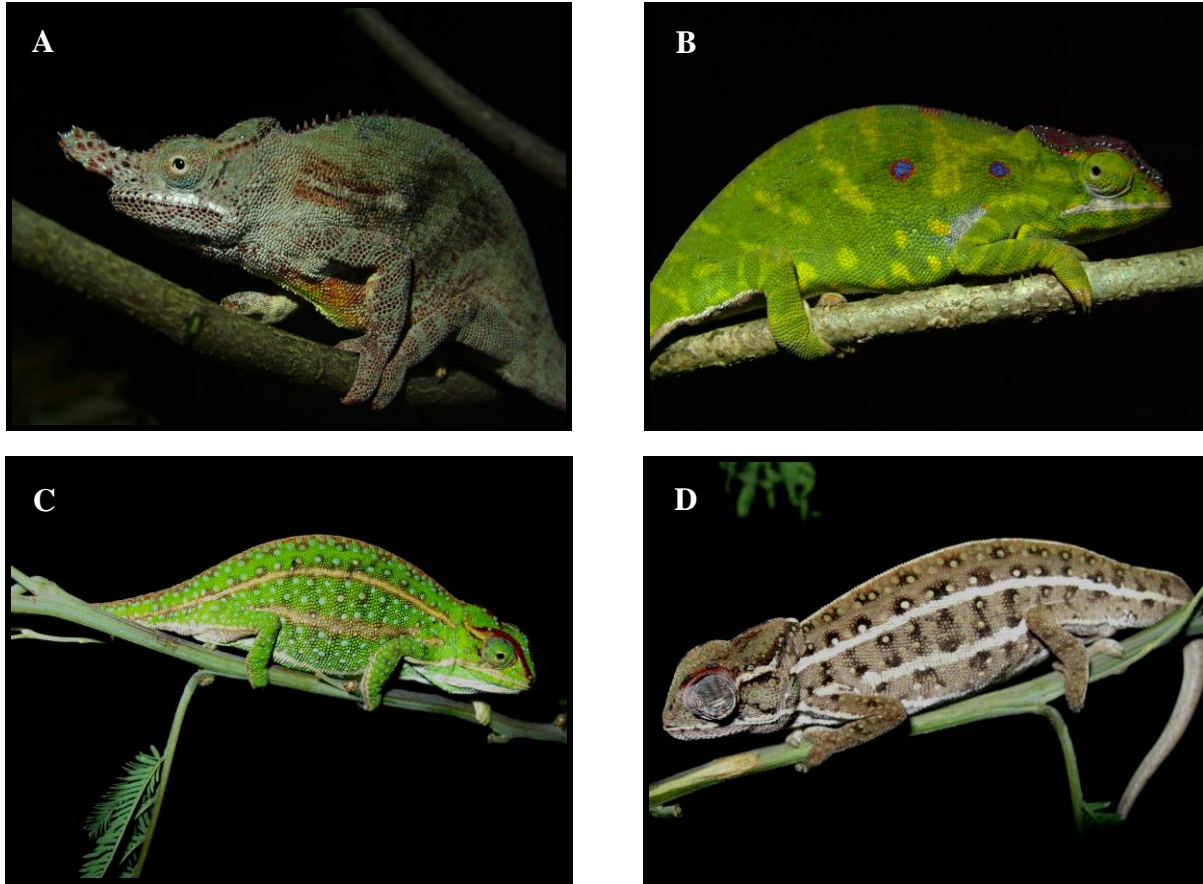


FIGURE 2. (A) *Furcifer minor*, adult male (B) *F. minor*, adult female: Itremo-Ambatofinandrahana; (C) *F. campani* adult female; (D) *F. campani* adult male: from Ankaratra.

RESULTS

We encountered 934 chameleons along 117 transects over a total distance of 17 km. The most frequently encountered species across all sites was *Furcifer lateralis* ($n = 398$), followed by *Calumma crypticum* ($n = 219$), *F. minor* ($n = 199$), *F. campani* ($n = 47$), *C. hilleniusi* ($n = 63$), and *C. nasutum* ($n = 8$).

Distribution.—*Furcifer lateralis* was the only species found at both Itremo-Ambatofinandrahana and Ankaratra, with *Furcifer campani* (Fig. 2) and *Calumma hilleniusi* restricted to Ankaratra, and *Furcifer minor*, *Calumma crypticum* and *Calumma nasutum* only found at Itremo-Ambatofinandrahana.

Population and habitat.—*Furcifer lateralis* and *F. campani* were the most abundant species we recorded across all vegetation types in the two sites, while *C. crypticum* occurred at the highest density (Table 1). Sample sizes of *C. nasutum* from Itremo-Ambatofinandrahana were too small to perform density calculations, while the coefficient of variation for *F.*

lateralis and *C. hilleniusi* at Ankaratra were greater than 30%, and these results should be treated with caution (Brady and Griffiths 1999).

Calumma species occurred at a higher density than *Furcifer* species in both areas (Table 1). The density of *Furcifer* species varied notably, both between and within species, with highest densities reported for *F. lateralis* at Itremo-Ambatofinandrahana. At Itremo-Ambatofinandrahana the abundance of *F. lateralis* and *F. minor* was significantly different between three habitat types (Kruskal Wallis, $H = 51$, $P < 0.001$ *F. lateralis*; $H = 15$, $P < 0.005$ *F. minor*). The chameleons were frequently found in tapia forest and agricultural land but rarely in humid forest. We detected a few individual *F. minor* and *F. lateralis* on humid forest transects near to the edge of the forest. *Furcifer* species were therefore only found in heathland, while the *Calumma* species were mostly restricted to closed humid forest, although there were occasional discoveries of *C. hilleniusi* in savanna grassland at Ankaratra (Fig. 3). At Itremo-Ambatofinandrahana *F. minor* occurred throughout the elevational range that we surveyed, but

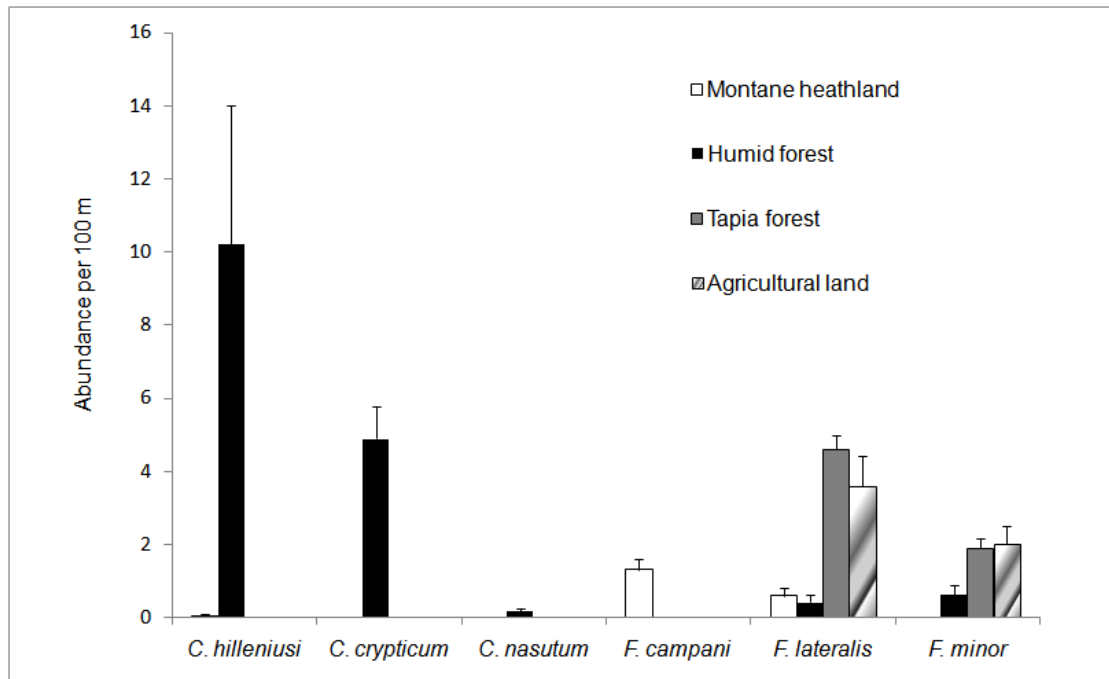


FIGURE 3. The abundance of six Malagasy chameleon species in four different habitat types in the central highlands. Data for *Furcifer lateralis* was pooled from two sites (Itremo-Ambatofinandrahana and Ankaratra).

C. crypticum was not observed higher than 1,515 m, which is the upper elevational limit of the humid forest. At Ankaratra, *C. hilleniusi* occurred in a relatively narrow elevational range spanning 300 m (Table 2). The limit of *F. lateralis* appeared to be at 1,925 m above sea level. *Furcifer campani* was not found at elevations lower than 1,700 m but was present to 2,643 m above sea-level (Table 2). We detected no significant relationship between log *Furcifer* abundance and transect elevation (*F. minor*, $r = -0.01$; *F. lateralis*, $r = 0.19$; *F. campani*, $r = 0.07$), although *F. campani* abundance exhibited a positive linear relationship with elevation but was not significant because of the absence

of chameleons at three high altitude transects that had been recently burned.

Threats and conservation.—We obtained convincing reports from local collectors at Itremo-Ambatofinandrahana of ongoing collection of *F. minor*. However, community leaders reported a decline in the number of collectors operating in the community-managed tapia forest and stated that most chameleons were collected from agricultural land. We were also informed that *F. campani* collection continues at Ankaratra. There are a number of human activities that negatively impact the habitats at Itremo-

TABLE 2. Survey sites in two highland areas of Madagascar (Ankaratra¹ and Itremo-Ambatofinandrahana²) indicating geographical coordinates and potential threats.

Locality	Geographical position (S, E)	Recent collection of chameleons	Expanding agriculture	Invasive species (<i>Pinus</i> sp.)	Wildfire	Timber extraction	Mineral extraction	Soil erosion	Over-grazing
Beapombo ²	20°43'110.7''				X				
Antsirakambiaty ²	46°33'35.6''	X	X			X		X	
Ampangabe ²	20°35'39.8''				X		X		
Itremo-Ambatofinandrahana ²	46°33'47.3''				X	X			
Ringorano ²	20°36'37.6''	X	X		X			X	
Ambohimirandana ¹	46°36'35.4''								
Analamilona ¹	20°35'43.4''			X	X				X
Analatsama ¹	46°37'58.7''			X	X				X
	20°31'20.6''	X		X	X				X
	46°45'51.0''								
	19°20'08.9''								
	47°14'41.0''								
	19°21'19.3''								
	47°16'01.1''								
	19°21'19.3''	X		X	X				X
	47°16'01.1''								

TABLE 3. Elevational (m above sea level; ASL) range of chameleon surveys and species presence from two highland sites in central Madagascar.

Site / Species	Lowest ASL	Highest ASL
Ankaratra	1,601	2,643
Itremo-Ambatofinandrahana	1,311	1,696
<i>C. crypticum</i>	1,515	1,572
<i>C. hilleniusi</i>	2,102	2,408
<i>C. nasutum</i>	1,515	1,518
<i>F. campani</i>	1,793	2,489
<i>F. lateralis</i>	1,317	1,925
<i>F. minor</i>	1,311	1,696

Ambatofinandrahana and Ankaratra but these appear to threaten *Calumma* more than *Furcifer* chameleons because of their dependence on the small amount of remaining humid forest at the sites (Table 3).

DISCUSSION

Madagascar's native montane vegetation covers a relatively small surface area but contains an exceptionally high diversity and elevated levels of endemism. Species restricted to these isolated habitat patches are threatened by habitat loss, reduced dispersal opportunities, and the potential effects of climate change. A number of chameleon species are known to occur in montane habitats but there is little known about their abundance or habitat use.

We encountered six chameleon species, three *Calumma* and three *Furcifer*, during our study. Raxworthy and Nussbaum (2006) drew attention to the fact that in addition to their small ranges, many of the montane *Calumma* species were also restricted to relatively intact humid forest and are therefore threatened by habitat degradation and fragmentation. In our study both *C. hilleniusi* and *C. crypticum* were most common in humid forest. While *C. crypticum* has a relatively wide distribution across Madagascar and is known from a number of protected areas (Raxworthy and Nussbaum 2006), *C. hilleniusi* occupies a relatively small area of montane forest that is divided between two sites (Raxworthy and Nussbaum 1996a; Raselimanana 1999; Vences et al. 2002); Parc National d'Andringitra (31,160 ha) – Reserve Spéciale d'Ivohibe (3,453 ha) in the south and at Ankaratra (< 650 ha). The specific status of the *C. hilleniusi* at Andringitra, though, requires additional verification (Vences et al. 2002). This species is of conservation concern because it only occurs in a few small fragments of humid forest.

Furcifer campani is reported to occur mainly in savanna grasslands and montane heathland habitat (Vences et al. 2002). The results from our study support this observation and we did not detect *F. campani* in forest vegetation. *Furcifer campani* is reported to occur

at a number of high peaks between Ankaratra in the north and Parc National d'Andringitra in the south (Brygoo 1971; Raxworthy and Nussbaum 1996a), although a number of these are historic localities and need to be verified because of a meager voucher specimen collection (Vences et al. 2002). The actual area occupied by this species may therefore be relatively small and limited to a few isolated high peaks. Historical records from lower elevation sites near Lake Mantasoa and Antoetra are particularly interesting because the habitat used by *F. campani* is unlikely to have undergone major changes and the species may still occur in these areas (Andreone et al. 2007). A rejuvenated effort is therefore needed to survey the isolated peaks in central Madagascar.

Furcifer minor appears to be restricted to the southern highlands, although there is a single, unusual record from Bélo-sur-mer on the west coast (Brygoo 1971; Glaw and Vences 2007). It is only known to occur within one protected area at the Réserve Spéciale d'Ambohijanahary (Raselimanana 1998). Aside from the record on the west coast, *F. minor* is reported to occur within an elevational range of between 1,060 m and 1,360 m above sea level (Raselimanana 1998), but we have extended this to 1,696 m in our study. *Furcifer minor* was most abundant during our study in tapia forest and agricultural land, which indicates that degradation of humid forest vegetation is not a major threat to this species. However, further studies on the ecology of *F. minor* are needed to describe its use of these different vegetation types, and in particular to determine if breeding occurs outside of tapia forest.

Furcifer lateralis is distributed throughout much of Madagascar and is associated with open forest, edges of closed forest, savanna grasslands, and urban areas (Glaw and Vences 2007). It is one of only four chameleon species that can be legally exported from Madagascar (Carpenter et al. 2005). During our survey it was sympatric with both *F. minor* and *F. campani* at elevations below 2,000 m above sea-level.

Chameleon abundance in Madagascar varies according to vegetation type, disturbance level, and forest structure (e.g. Jenkins et al. 2003). In this study we noted the presence of *F. minor* and *F. lateralis* on the edge of humid forest. These species, like most *Furcifer*, are usually found in open areas and can be associated with edges and paths (Metcalf et al. 2005; Rabearovony et al. 2008). Forest edges may provide suitable protection from predators or elevated prey availability (Metcalf et al. 2005).

The density of *Furcifer* species in this study, with the exception of *F. lateralis* at Itremo-Ambatofinandrahana, was lower than those reported for *Furcifer verrocous*, *F. labordi*, and *F. antimena* in south-western Madagascar (Karsten et al. 2009). The population density of *F. campani* was lower than *F. lateralis* or *F.*

minor at Itremo-Ambatofinandrahana but higher than other *Furcifer* species in deciduous forests in the west (Randrianantoandro et al. 2008). Densities of *C. crypticum* and *C. hilleniusi* in this study were higher than for similar species elsewhere (Brady and Griffiths 1999; Jenkins et al. 2003). The relatively high population densities in highland humid forests may be supported because of low interspecific competition as these sites have notably lower species richness than forests at lower elevations (Brady and Griffiths 1999). The notable inter-site difference in density of *F. lateralis* is an important result because it emphasizes that managed collection of commercial species should be based on the attributes of the local population, and in this case, Itremo-Ambatofinandrahana could support higher harvests than Ankaratra.

Furcifer campani used to be collected in large quantities, and 10,324 were exported from Madagascar between 1977 and 1995 (Carpenter et al. 2004). Brady and Griffiths (1999) cite an unpublished study that reports Ankaratra as the main collection site for this species with harvests of up to 350 chameleons per day. Collection of *F. campani* from this site continues, but the final destination of the chameleons is unknown.

A total of 1,902 *F. minor* had been exported from Madagascar between 1977 and 1995 (Carpenter et al. 2004). Brady and Griffiths (1999) cite an unpublished study that reports collection from gallery forest and coffee plantations around Itremo-Ambatofinandrahana to meet the demand for orders that ranged between 30 and 150 pairs. As with *F. campani* at Ankaratra, collection of *F. minor* from this site continues but the final destination of the chameleons is unknown.

Export quotas and collection permits issued in Madagascar are not aligned with population densities at individual collection sites. If this could be altered and site-level collection quota agreed by commercial entities, conservation practitioners, and local communities, then both *F. minor* and *F. campani* could feasibly be sustainably collected. However, because *F. campani* occurs in two strictly protected areas, where commercial collection is prohibited, collection would therefore likely to be centered at a single site, Ankaratra.

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Herpetological Conservation and Biology



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GERMAIN RAZAFINDRAKOTO (left) is studying the population dynamics of *Furcifer lateralis* for his Ph.D. at the University of Antananarivo, but he is interested in the conservation and ecology of all Malagasy chameleon species. He has conducted a number of research projects on other taxa and is a Tropical Biological Association alumnus.

RAPHALI R. ANDRIANTSIMANARILAY obtained his Diplôme d'Etude Approfondies in 2007 from the University of Toliara during a Darwin Initiative funded project to conserve the biodiversity of Malagasy karst habitats. He studied chameleon ecology during his research degree and Madagasikara Voakajy recruited him in 2008 to work on its reptile ecology project. He is now working on projects to conserve *Furcifer* chameleons. (Photograph in Bora et al., this issue)

The late **OLGA R. RAMILJAONA** was a Professor at the Department of Animal Biology at the University of Antananarivo, Madagascar. She was a passionate biologist who received her doctoral degree at the Institute Pasteur in Paris studying parasitology. She had supervised many research students and was totally dedicated to supporting young Malagasy scientists. Her main interests in herpetology were related to international trade and mantella frogs, although she was involved in a whole range of other reptile and amphibian conservation projects. We dedicate this publication to her, for her tireless efforts in nurturing the next generation of research scientists in Madagascar. (Photograph in Bora et al., this issue)

APPENDIX: VOUCHER SPECIMENS

Ankaratra

Furcifer campani UADBA 49405; 49439; 49481; 49428; 49454; 49406; 49426; 49477; 49448; 49409; 49416; 49450; 49443; 49424; 49425; 49414, *Calumma hilleniusi* UADBA 49471; 49466; 49436; 49449, *Furcifer lateralis* UADBA 49413; 49415; 49401; 49460; 49437; 49431; 49432; 49418; 49444; 49434; 49410; 49451; 49402; 49473; 49457; 49447; 49490; 49462; 49412; 49427.

Itremo-Ambatofinandrahana

Calumma crypticum UADBA 49564, 49573, 49529, 49537; *Calumma nasutum* 49536, 49544, 49580, *Furcifer lateralis* 49552, 49561, 49565, 49511, 49538, 49527, 49567, 49513, 49555; *Furcifer minor* 49582, 49566, 49517, 49547.