# Habitat use and abundance of a low-altitude chameleon assemblage in eastern Madagascar

Jeanneney Rabearivony<sup>1</sup>, Lee D. Brady<sup>2</sup>, Richard K.B. Jenkins<sup>3,4</sup> & Olga R. Ravoahangimalala<sup>1</sup>

<sup>1</sup>Département de Biologie Animale, Université d'Antananarivo, Madagascar <sup>2</sup>Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, UK <sup>3</sup>School of Biological Sciences, University of Aberdeen, UK <sup>4</sup>Madagasikara Voakajy, Antananarivo, Madagascar

We studied the density and abundance of chameleons in a lowland Malagasy rainforest during the austral summer and winter. Nocturnal searches for chameleons were conducted along transects within relatively intact forest and vegetation on abandoned agricultural land adjacent to the forest. Four chameleon species were encountered during the study, *Brookesia superciliaris*, *Calumma parsonii parsonii*, *Calumma nasutum* and *Furcifer pardalis*. *Brookesia superciliaris* was most common inside relatively intact forest and the few individuals located in the regenerating forest on abandoned agricultural land were found in tiny, isolated patches of degraded rainforest next to rivers. *Calumma p. parsonii* was only encountered on three occasions in relatively intact forest and was a rare member of the community. The abundance of *C. nasutum* was highest in relatively intact forest but this species also occurred in vegetation on abandoned agricultural land. *Furcifer pardalis* was only found on the abandoned agricultural land, where it was observed laying eggs in sandy soil in August. The abundance of all species in habitats alongside rivers was higher in January than July–August, with the exception of *C. p. parsonii*, which was not detected during the former period. Additional investigations into habitat preference of chameleons and surveys in other forests in region are needed to establish whether the low abundance of *C. p. parsonii* and the absence of the *Brookesia minima* group at this site are related to 1) abiotic factors associated with altitude, 2) physical barriers that have prevented dispersal, or 3) the selective logging that occurred at the site until 1993.

Key words: Brookesia, Calumma, deforestation, Furcifer, seasonality

### INTRODUCTION

The remaining humid forests of eastern Madagascar are of international conservation importance as the last refuges for many forest-dependent vertebrates. These forests have high herpetofaunal diversity and many threatened species have restricted ranges within the remaining intact vegetation (Raxworthy, 2003). New species continue to be discovered in these forests and the amphibian fauna has received particular attention from herpetologists (e.g. Glaw & Vences, 2002; Vences & Glaw, 2004; Vences et al., 2005).

Interest in the taxonomy and evolution of Malagasy reptiles (e.g. Raxworthy & Nussbaum, 1995; Raxworthy et al., 2002, 2003) has yet to be complemented by similar advances in ecology, and basic information on habitat preferences, natural history and population structure remains poorly documented for many forest reptiles. Whilst some forest reptile groups are notoriously difficult to study in the field (e.g. Andreone & Randrianirina, 2000), conservation-relevant ecological information is comparatively straightforward to obtain for chameleons (e.g. Jenkins et al., 1999; Andreone et al., 2005; Metcalf et al., 2005; Randrianantoandro et al., 2007).

There are 66 species of chameleon in Madagascar and all are endemic (Raselimanana & Rakotomalala, 2003).

Chameleons from the genus Calumma Gray 1865 are chiefly restricted to the eastern and northern part of the island and are usually associated with intact humid forest (Andreone et al., 2005). Calumma are found across a wide altitudinal range, from around sea level to 2800 m above sea level (Raxworthy & Nussbaum, 1996). Brookesia Gray 1865 occupies a broadly similar distribution to Calumma, although some species are also found in the deciduous dry forests in the west, at sites where no Calumma occur (Raselimanana & Rakotomalala, 2003). Like Calumma, Brookesia are usually associated with intact forest (Raxworthy, 1991; Raxworthy & Nussbaum, 1995; Jenkins et al., 2003), but some species have been recorded from degraded habitats (Glaw et al., 1999). Furcifer Fitzinger, 1834 chameleons mainly occur in dry areas and in the east are restricted to open habitats, whilst in the west they are found inside deciduous forest (Jesu et al., 1999; Andreone et al., 2005).

Lowland (<800 m) humid dense forest is one of the most threatened habitat types in Madagascar and its extent has been dramatically reduced by agricultural expansion in recent decades (e.g. Green & Sussman, 1990; McConnell et al., 2004). In this study we investigated the chameleon community in a lowland humid forest to determine which chameleons utilize secondary growth on abandoned agricultural land adjacent to relatively intact

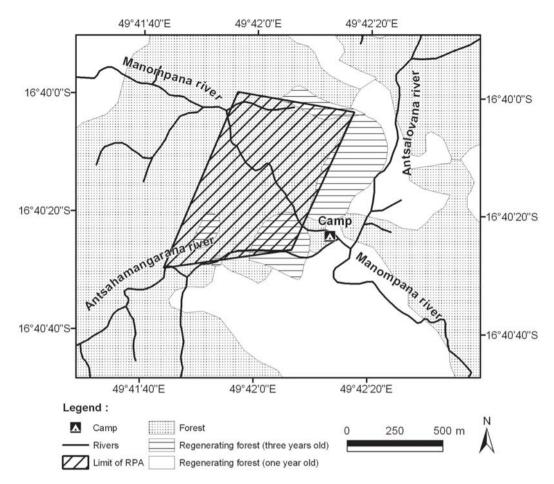


Fig. 1. Map of Ambodiriana forest showing major habitat types, rivers and extent of the private reserve.

forest. We also investigated the impact of seasonality on chameleon abundance in forests alongside rivers.

# MATERIALS AND METHODS

The Réserve Privée (R.P.) d'Ambodiriana (16°40'S, 49°42'E) is within the forest of Ambodiriana, approximately 6 km north-west of the Rural Commune of Manompana (16°41'S, 49°45'E) and 40 km north of the town of Soanierana-Ivongo, in the province of Toamasina. It is flanked by the Antsahamangarana River to the south and by the Antsalovana River to the east; altitude varies from 45 to 230 m a.s.l. and the total area is 67 ha. It is divided into two sections by the river Manompana (Fig. 1).

Field work was conducted in two seasons, the first during the austral winter (24 July – 25 August 2001) and the second during the austral summer (5–27 January 2002). The climate in R.P. d'Ambodiriana is tropical and humid with rain in every month; during the surveys, a total of 116 mm of rain occurred over 29 days in winter, and 115 mm over 23 days in summer. Average daily temperature is around 25 °C in the summer and 20 °C during the winter. Average daily precipitation is approximately 5 mm per day during the summer and 4 mm per day in the winter.

We selected two main types of habitat within the reserve. The first was relatively intact humid forest (Dufils, 2003), which had been selectively logged before 1993.

Logging was mainly for commercial purposes to supply the local demand for timber products for the construction of pirogues and houses, and mature individuals of the preferred tree species, such as *Calophyllum* spp., *Ocotea* spp., *Dalbergia* spp. and *Sideroxylon* spp., are now relatively rare in the reserve. *Uapaca* spp. are infrequently used by people and are now the most common canopyforming tree. The area at the edge of and outside the reserve is subject to chronic degradation and humid forest is removed, using the slash and burn technique (*tavy* in Malagasy), and replaced with agriculture for three to

**Table 1.** ANOVA results on vegetation characteristics of relatively intact forest and tavy, winter 2001. Values are means  $\pm$  SE.

		Habitat type	
	Relatively	Forest on	
	intact	regenerating	
Vegetation	forest	agricultural	
characteristics	(n=20)	land ( <i>n</i> =20)	P
Trees (>1.0 m dbh)	1.5±0.29	0.0±0.00	< 0.001
Trees (<1.0 m dbh)	$15.3\pm2.01$	$0.2\pm0.11$	< 0.0001
Small trees (0.5–2 m)	$31.4\pm3.25$	2.0±0.56	< 0.0001
% vegetation ground			
cover (<0.5 m)	62.9±4.88	91.7±3.27	< 0.0001

**Table 2.** Abundance (mean±SE) and density (individuals per ha, coefficient of variation in parentheses) of four chameleon species from R.P. d'Ambodiriana, eastern Madagascar during the austral winter. Density calculations were only performed for species with  $\geq 10$  individuals. Sample effort was 32 transects (4.6 km) in the relatively intact forest and 26 (4.1 km) in the forest on regenerating agricultural land. ANOVAs performed on log-transformed abundance counts.

Species	Habitat type	n	Density ha <sup>-1</sup> (CV)	Abundance	One-way ANOVA (habitat comparison)
Brookesia superciliaris	Relatively intact forest Forest on regenerating agricultural land	19 2	7.0 (23.5) n/a	0.42±0.11 0.05±0.05	$F_{1,56}$ =6.2 P=0.02
Calumma p. parsonii	Relatively intact forest Forest on regenerating agricultural land	3 0	n/a n/a	0.06±0.04 0	n/a
Calumma nasutum	Relatively intact forest Forest on regenerating agricultural land	17 5	4.2 (38.6) n/a	0.37±0.15 0.13±0.05	$F_{1,56} = 0.9$ P = 0.76
Furcifer pardalis	Relatively intact forest Forest on regenerating agricultural land	0 10	n/a 2.0 (63.1)	0 0.26±0.16	$F_{1,56}$ =3.4 $P$ =0.07

five years before being abandoned. After abandonment, the land cover is replaced by a thick herb layer and a few small trees and low shrubs, mainly *Lantana camara* to a height of 1.5 m. We therefore compared the chameleon community in the relatively intact forest inside the reserve with that from the secondary growth in abandoned (1–3 years ago) agricultural land adjacent to, or just inside, the reserve boundary.

A total of 32 and 26 transects were installed in relatively intact forest and regenerating agricultural land respectively during the winter. This constituted the main part of our study and we focused on the comparison of chameleon abundance and density between these two habitats. Because small rivers can influence chameleon abundance in humid forest (Jenkins et al., 2003) we stratified our transects into riparian (≤50 m from rivers) and non-riparian habitats, and 37% and 46% of transects in relatively intact forest and regenerating agricultural land were undertaken next to rivers, respectively.

Because of resource constraints we were not able to repeat the same transects during the summer months. We therefore decided to focus on riparian habitats and our seasonal comparisons, between summer and winter, are therefore only from relatively intact forest or regenerating agricultural land within 50 m of rivers.

For each habitat type, chameleons were surveyed following the transect methodology developed by Jenkins et al. (1999). Existing trails and river banks were used to localize transects (Jenkins et al., 2003) and transects were least 100 m apart (Brady & Griffiths, 1999). Each transect consisted of three 50 m-long parallel lines placed perpendicular to the river or trail and spaced 25 m from each other. Their parallel layout and separation meant that individuals were unlikely to be counted twice on neighboring lines (Brady & Griffiths, 1999). To minimize disturbance to chameleons in the study area, transect lines were installed at least 24 hours before the surveys were run.

Two people equipped with headlamps (Petzl Mega®, standard bulb, 4.5 volts) walked the length of each transect once per season, one surveying to the left, the

other to the right, taking care to look backwards and to locate chameleons concealed by foliage from the front. The perpendicular distance between the transect line and the chameleon was measured with a 5 m or 10 m tape measure to the nearest 0.5 cm. Species name and age class (adult, juvenile, hatchling) were also recorded. Vegetation characteristics in the transect zone were taken the day following the surveys. No voucher specimens were collected during the study.

To assess vegetation structure in the study site, a single 5 m  $\times$  5 m quadrat was placed on each 50 m transect line at distances of 5, 20 and 35 m from the origin (Jenkins et al., 2003). In each quadrat, the number of large trees in two categories (dbh  $\geq$ 1m; dbh  $\leq$ 1m) as well as small trees (height 0.5–2 m) were counted. The percentage cover of ground vegetation ( $\leq$ 0.5 m) was also estimated in each quadrat.

"Distance sampling", described by Buckland et al. (1993), allows the estimation of absolute density based on the detection curve obtained from a series of perpendicular distances between the transect line and the target objects. This method is appropriate for estimating chameleon densities (Brady & Griffiths, 1999; Reisinger et al., 2006) and has been used in previous studies in Madagascar (Jenkins et al., 1999, 2003; Andreone et al., 2005). We also calculated the abundance of each species per transect (number of animals/transect length × 100 m) and used this in statistical comparisons.

We tested the hypothesis that there were no differences in chameleon abundance between relatively intact forest and regenerating agricultural land using one-way ANOVA (habitat as the factor) on each species. Each transect  $(3 \times 50 \text{ m})$  line was considered as an independent replicate in this and subsequent analyses. We assumed that there was insignificant overlap of area covered between adjacent transects and that individual chameleons rarely occupied the habitat traversed by more than one transect line. Furthermore, we assumed that relative detectability of each species was the same for each habitat. We also sought to determine whether there was a

**Table 3.** Mean ( $\pm$ SE) abundance (animals/100 m) of four chameleon species from R.P. d'Ambodiriana, eastern Madagascar during the austral winter and summer within 50 m of rivers. Sample effort was 13 transects (1.9 km) in the relatively intact forest and 5 (0.8 km) in the forest on regenerating agricultural land during the summer.

Species	Habitat type	n	Winter	n	Summer	ANOVA
Brookesia superciliaris	Relatively intact forest Forest on regenerating	10	0.56±0.24	31	1.59±0.55	One-way $F_{1,23}$ =1.73, $P$ =0.20
	agricultural land	2	$0.50\pm0.50$	0	0	n/a
Calumma p. parsonii	Relatively intact forest Forest on regenerating	1	0.06±0.06	0	0	n/a
	agricultural land	0	0	0	0	n/a
Calumma nasutum	Relatively intact forest Forest on regenerating	10	0.55±0.34	53	2.72±0.88	Two-way Habitat $F_{1.32}$ =0.25, $P$ =0.62
	agricultural land	4	$0.44\pm0.34$	19	2.53±1.34	Season $F_{1,32}^{1,32}$ =2.76, $P$ =0.11
Furcifer pardalis	Relatively intact forest Forest on regenerating	0	0	0	0	n/a
	agricultural land	10	1.11±0.61	15	2.00±1.67	One-way $F_{1.9}$ =1.01, $P$ =0.34

significant seasonal effect on the chameleon abundance in the two habitats. We therefore conducted another one-or two-way ANOVA on chameleon abundance, using either season or season and habitat as the factors from the riparian transects only. Small sample sizes often precluded two-way ANOVA comparisons.

So as to investigate the major vegetative and structural difference between the two habitats we tested the hypotheses that there were no differences in the specific habitat characteristics that we recorded between relatively intact forest and regenerating agricultural land using one-way ANOVA.

We were unable to calculate abundance indices, a measure that allows for statistical comparison whilst controlling for detectability (Jenkins et al., 2003), because sample sizes were too low to produce density estimates using DISTANCE. We therefore give (detectability-controlled) density estimates and abundance values. We assumed that intraspecific differences in detectability were negligible between seasons.

#### **RESULTS**

We found four chameleon species during our study, the terrestrial *Brookesia superciliaris* and three arboreal species, *Calumma parsonii parsonii*, *Calumma nasutum* and *Furcifer pardalis*. The vegetation structure in the forest on regenerating agricultural land was significantly different from the relatively intact forest. The former had few trees but high vegetation cover because of a thick herb layer and *L. camara* plants (Table 1).

# Chameleon use of different habitats in the winter

Brookesia superciliaris occurred at highest densities inside relatively intact forest and only two individuals were found in the forest on regenerating agricultural land (Table 2). The abundance of *B. superciliaris* varied significantly between these habitats (Table 2). Calumma p. parsonii was also restricted to the relatively intact forest but was only encountered on three occasions (Table 2). Two of the three (one male and one female) *C. p.* 

parsonii were located in small canyons and were not associated with the major rivers in the reserve and a single male was found within 50 m of the Manompana River. Calumma nasutum was found in both habitats but sample sizes for density estimates were only high enough (> 10 animals) in the forest (Table 2). Furcifer pardalis was the only species found exclusively on the regenerating agricultural land.

On 19 August 2001 egg-laying behaviour by *F. pardalis* was observed on regenerating agricultural land. In moist and sandy soil the female started to excavate a hole using both front legs at 1230 and by 1400 had made a hole approximately 90 mm in depth, which was about the same as the snout–vent length of the animal. Egg deposition commenced at 1410 and at 1520 the chameleon started to refill the hole. By 1605 the eggs were completely buried and a dead leaf and a dead fern frond were moved into place over the nest.

At the camp site a single female *C. nasutum* was observed on an *Albizia* sp. tree that was isolated from the surrounding vegetation. Over a period of 10 consecutive days it was observed roosting (2.0–2.5 m height) in the same tree each night, but used different branches. It was also regularly seen on its roosting perch during the day, giving us the impression that it was not very active during this period.

# Chameleon use of riparian forests in different seasons

Transects conducted during both seasons within riparian zones yielded sample sizes that were too small for reliable estimates of chameleon density (Brady & Griffiths, 1999).

Although none of the differences in chameleon abundance between seasons were statistically significant, three species (*B. superciliaris*, *C. nasutum* and *F. pardalis* were most abundant in the summer (Table 3). No *C. p. parsonii* were found during summer, perhaps because only riparian transects were used.

## Population structure

As only a single *C. p. parsonii* was observed, it was excluded from seasonal demographic comparisons. Adults

**Table 4.** Population structure of three chameleon species from eastern Madagascar in relatively intact forest alongside rivers during the austral summer and winter. Animals of unknown age or sex are omitted from the table.

Species	Season	Proportion by sex				Proportion by stage class			
		$\overline{n}$	Male	Female	$\overline{n}$	Adult	Juvenile	Hatchling	
B. superciliaris	Winter	12	0.58	0.42	12	0.75	0.25	0.00	
	Summer	30	0.43	0.57	31	0.87	0.10	0.03	
C. nasutum	Winter	12	0.25	0.75	13	0.92	0.08	0.00	
	Summer	47	0.40	0.60	70	0.74	0.16	0.10	
F. pardalis	Winter	9	0.44	0.56	10	0.30	0.70	0.00	
•	Summer	1	1.00	0.00	15	0.13	0.00	0.87	

comprised the majority of individuals found during both seasons in the riparian forest for *B. superciliaris* and *C. nasutum* (Table 4). This was in contrast to observations of *F. pardalis*, which were represented mainly by hatchlings during the summer and juveniles in the winter. *Calumma nasutum* samples showed a female bias, but *F. pardalis* and *B. superciliaris* had broadly similar sex ratios consisting of 42–56% females.

#### DISCUSSION

This assessment of chameleon habitat use in a lowland humid forest in eastern Madagascar found that *C. p. parsonii* was rare and restricted to relatively intact forest. Two other species, *B. superciliaris* and *C. nasutum*, were more abundant in relatively intact forest vegetation but were also located in vegetation on nearby regenerating agricultural land. *Furcifer pardalis* was found to exclusively inhabit the vegetation on the regenerating agricultural land. There was a strong seasonal influence with the highest abundance of all species except *C. p. parsoni* found during the summer.

#### Species composition

The chameleon community at R.P. d'Ambodiriana contains two common and widespread species, *B. superciliaris* and *C. nasutum*. These are found in humid forests throughout much of the island (Raselimanana & Rakotomalala, 2003). *Furcifer pardalis*, meanwhile, is only found in central-eastern and northern Madagascar (Brygoo, 1971; Raselimanana & Rakotomalala, 2003). *Calumma p. parsonii* is restricted to the remaining humid forests from Fianarantsoa in the south to the Masoala peninsula in the north. The only populations in protected areas are *C. parsonii cristifer* in Parc National de Mantadia and Reserve Specialé d'Analamazaotra (Raselimanana & Rakotomalala, 2003; Rakotondravony, 2004).

The *B. minima* group is widely distributed in Madagascar (e.g. Schimmenti & Jesu, 1996; Glaw et al., 1999), and its absence from R.P. d'Ambodiriana is not easily explained because its altitudinal range falls within that of our study site (Glaw et al., 1999). *Brookesia* species usually occupy distinct altitudinal zones (Glaw et al., 1999), and forest reserves spanning lowland and mid-altitude vegetation have the highest species richness (Raxworthy, 1991; Raxworthy & Nussbaum, 1995). However, within sites that encompass a similar range of

altitudes there appears to be a latitudinal decline in *Brookesia* species richness. For example, P.N. de Montagne d'Ambre in the north has five species (Raxworthy & Nussbaum, 1994), P.N. de Mantadia in the centre-east has three species (Rakotondravony, 2004) and P.N. d'Andohahela in the south has only one species (Nussbaum et al., 1999). However, as Tampolo littoral forest, situated adjacent to the Indian Ocean, just south of R.P. d'Ambodiriana, has *Brookesia superciliaris* and *B. minima* (Raselimanana et al., 1998), a latitudinal decline probably does not explain the low *Brookesia* diversity at our site.

Several authors have noted that species of the *B. minima* group are usually found in intact forests (Raxworthy, 1991; Raxworthy & Nussbaum, 1995; Glaw et al., 1999; Jenkins et al., 2003), and even though there are a few observations from more degraded habitats (Glaw et al., 1999), levels of forest disturbance at R.P. d'Ambodiriana may have rendered the area studied unsuitable for the *B. minima* group. Another concept that may explain the absence of the *B. minima* group is that the rivers to the north and south of the site have prohibited dispersal and colonization. It has been noted previously that even small forest streams may act as barriers to the dispersal of terrestrial reptiles (Tam-Alkis, 1997; Raxworthy et al., 1998).

#### Seasonal effects

Seasonality in Malagasy herpetofauna is thought to be stronger for species of mid-altitudes than those from low altitudes (Raxworthy, 1988). Herpetologists are strongly seasonal too, and most surveys and studies in Madagascar have been conducted during the austral summer, with few data available for the winter period. We observed egg deposition during August and hatchlings of three species were found in January. In our study, C. nasutum abundance in relatively intact forest alongside rivers was highest during the summer, as reported for larger chameleons in mid-altitude forests (Brady & Griffiths, 1999), but the reverse of this is reported for C. nasutum at Parc National de Ranomafana (Brady & Griffiths, 1999, 2003). Seasonal patterns may therefore be less extreme in lowland forest and further ecological studies of species that occur across a wide altitudinal range are needed.

#### Habitat use

Brookesia superciliaris was most abundant in the relatively intact forest and its occasional detection on

transects in the regenerating agricultural land was because it occurred in small patches of humid forest there; we never observed it roosting in non-forest vegetation. In Parc National de Ranomafana *B. superciliaris* is absent from certain areas of relatively intact forest but present in the more disturbed patches closer to human habitation and the main road (Tam-Alkis, 1997). Similarly, *B. superciliaris* was absent from the intact forests of P.N. de Mantadia and R.S. d'Analamazaotra, but was recorded in degraded plantations close to the reserve boundary of the latter site (Rakotondravony, 2004). *Brookesia superciliaris* therefore appears to be an obligate forest dweller but can survive in a wide range of vegetation types and tolerates moderate disturbance.

One forest transect was located in a small fragment (50 × 50 m) of vegetation, approximately 150 m from the nearest continuous forest and surrounded by regenerating agricultural land. In each season, this single transect yielded the highest number of B. superciliaris, four in the winter and seven in the summer. This high abundance in a small fragment may be explained by the unusually high humidity caused by spray from a nearby cascade providing the moist conditions that some *Brookesia* species are thought to prefer (Jenkins et al., 2003; Rabearivony, 1999). An alternative explanation is that the remaining vegetation in the fragment is acting as a refuge for the chameleons as the surrounding forest habitats recede. Given the apparent lack of association between rivers and B. superciliaris at this site, we propose the latter hypothesis as the more likely.

Calumma nasutum is variously considered to be a primary forest species (IUCN/SSC, 1993), a colonizer of secondary habitats (Glaw & Vences, 1994) and a forest edge species (Brady & Griffiths, 2003), and has been found in a Pinus sp. plantation (Raxworthy & Nussbaum, 1994). As in our study, Jenkins et al. (2003) found C. nasutum present, but at a lower abundance in the most disturbed forest habitats. Calumma nasutum used the regenerating forest in our study during both months but it would be profitable for future studies to investigate whether such use of degraded sites is dependent on the close proximity of relatively intact forest.

Calumma p. parsonii and F. pardalis had very different habitat preferences, with the former found in relatively intact forest and the latter in regenerating agricultural land. As the agricultural land adjacent to the reserve was forested with dense, humid vegetation until relatively recently (three years ago), it appears that F. pardalis may benefit from the expansion of agriculture and transformation of forested habitats. Human-impacted habitats appear to provide suitable conditions for F. pardalis and all hatchlings of this species in our study were found roosting on the dicotyledon Emilia amplexicaulis (Asteraceae) in abandoned manioc (cassava) fields. A similar case was reported from Nigeria, where three chameleon forest-dependent (Chamaeleo owenii, C. cristatus and Rampholeon spectrum) disappeared locally after a period of intensive forest exploitation and were replaced by C. gracillis, a species with broader habitat requirements (Akani et al., 2001). Our results concur with those of Andreone et al. (2005), which indicate that *F. pardalis* prefers open areas of scattered regenerating forest to dense, mature forests, and is therefore not a species of immediate conservation concern, except perhaps in areas where collection levels are reportedly high.

#### Conservation

Although the area around Soanierana-Ivongo was reported by Brady & Griffiths (1999) to be one of the key locations for chameleon collection for the pet trade, we have no evidence of collection, past or present, from R.P. d'Ambodiriana. Furthermore, legal trade in *C. parsonii* was suspended by CITES in 1995 (Carpenter et al., 2005) and the impact of collection and trade on wild populations has declined. Nevertheless, *Calumma p. parsonii* is a species of conservation concern because of its restricted range, probable dependence on relatively intact forest and an apparent low population density in the sites where it occurs (Brady & Griffiths, 1999; this study).

Furcifer pardalis is a highly sought-after chameleon in the pet trade and is collected from a number of sites in northern and eastern Madagascar (Andreone et al., 2005; Carpenter et al., 2005). Current CITES quotas (2006) permit the live export of 2000 F. pardalis per year. Andreone et al. (2005) noted that current export quotas for Malagasy chameleons are set without access to information on their ecology or natural history. More field research on relative density, habitat preference, reproduction and seasonality are now required to provide better information to the Malagasy CITES scientific and management authorities. Also, given that only four chameleon species are currently listed on the IUCN Red List (Furcifer minor, Furcifer campani, Furcifer labordi and Brookesia perarmata; www.redlist.org, accessed 10 February 2007) field surveys need to be accompanied by a chameleon conservation review and an updated Red List assessment

## **ACKNOWLEDGEMENTS**

We thank the management association at R.P. d'Ambodiriana (ADEFA) and in particular Chantale Misendeau and Annie-Claude for permission to conduct the work and for the facilities provided. Data collection was assisted by members of Malagasy (Augustin Kaloloha, Adolphe Sully Totobe, Claude Drongo) and British (Rosie Lord, Andrew Willis, Rhona Barr, Anna Gibson) teams. Funding for the field work was provided by the Wellcome Trust (U.K.) and the University of Edinburgh, whilst WWF's Education for Nature funded the early part of the analysis and data preparation. The Peregrine Fund was generous in allowing J.R. time away from his duties to prepare this paper. Marius Rakotondratsima prepared Figure 1. Dr Richard Griffiths has provided support and guidance for many years, as well as helpful comments on the manuscript, and we are extremely grateful to him. An earlier version of the manuscript in French was swiftly and kindly translated by Dr Jessica Metcalf. Franco Andreone, Chris Raxworthy and an anonymous referee made helpful comments on the original submission.

#### REFERENCES

- Akani, G.C., Ogbalu, O.K. & Luiselli, L. (2001). Life-history and ecological distribution of chameleons (Reptilia, Chamaeleonidae) from the rain forests of Nigeria: conservation implications. *Animal Biodiversity and Conservation* 24, 1–15.
- Andreone, F., Guarino, F.M. & Randrianirina, J.E. (2005). Life history traits, age profile and conservation biology of the panther chameleon (*Furcifer pardalis*) at Nosy Be, NW Madagascar. *Tropical Zoology* 18, 209–225.
- Andreone, F. & Randrianirina, J.E. (2000). Biodiversity, rainforests and herpetological communities in Madagascar: what about the differences between amphibians and reptiles. In *Diversité et Endémisme à Madagascar*, 217–228. Lourenco, W.R. & Goodman, S.M. (eds). Paris: Société de Biogéographie.
- Brady, L.D. & Griffiths, R.A. (1999). *Status Assessment of Chameleons in Madagascar*. Cambridge: IUCN Species Survival Commission.
- Brady, L.D. & Griffiths, R.A. (2003). Chameleon population density estimates. In *The Natural History of Madagascar*, 970–972. Goodman, S.M. & Benstead, J.P. (eds). Chicago: University of Chicago Press.
- Brygoo, E.R. (1971). Reptiles sauriens Chamaeleonidae. Genre *Chamaeleo*. Faune de Madagascar 33, 1–318.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993). Distance Sampling. London: Chapman and Hall
- Carpenter, A.I., Robson, O., Rowcliffe, J.M. & Watkinson, A.R. (2005). The impacts of international and national governance changes on a traded resource: a case study of Madagascar and its chameleon trade. *Biological Conservation* 123, 279–287.
- Dufils, J.-M. (2003). Remaining forest cover. In *The Natural History of Madagascar*, 88–96. Goodman, S.M. and Benstead, J.P. (eds). Chicago: University of Chicago Press.
- Glaw, F. & Vences, M. (2002). Two new tree frogs of the Boophis rappiodes group from eastern Madagascar (Amphibia Mantellidae). Tropical Zoology 15, 141–163.
- Glaw, F. & Vences, M. (1994). A Fieldguide to the Amphibians and Reptiles of Madagascar, 2<sup>nd</sup> edn. Köln:
   M. Vences and F. Glaw.
- Glaw, F., Vences, M., Ziegler, T., Böhme, W. & Köhler, J. (1999). Specific distinctness and biogeography of the dwarf chameleons *Brookesia minima*, *B. peyrierasi* and *B. tuberculata* (Reptilia: Chamaeleonidae): evidence from hemipenal and external morphology. *Journal of Zoology* 247, 225–238.
- Green, G.M. & Sussman, R.W. (1990). Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science* 248, 212–215.
- IUCN/SSC (1993). A Preliminary Review of the Distribution and Status of Reptile and Amphibian Species Exported from Madagascar. Peterborough: Joint Nature Conservation Committee.
- Jenkins, R.K.B., Brady, L.D., Huston, K., Kauffmann, J.L.D., Rabearivony, J., Raveloson, J. & Rowcliffe, M.J. (1999). The population status of chameleons within

- Ranomafana National Park, Madagascar. <u>Oryx 33, 38–</u> 47
- Jenkins, R.K.B., Brady, L.D., Bisoa, M., Rabearivony, J. & Griffiths, R.A. (2003). Forest disturbance and river proximity influence chameleon abundance in Madagascar. *Biological Conservation* 109, 407–415.
- Jesu, R., Mattioli, F. & Schimmenti, G. (1999). On the discovery of a new large chameleon inhabiting the limestone outcrops of western Madagascar: Furcifer nicosiai sp. nov. (Reptilia, Chamaeleonidae). Doriana 12, 1–14.
- McConnell, W.J., Sweeney, S.P. & Mulley, B. (2004). Physical and social access to land: spatio-temporal patterns of agricultural expansion in Madagascar. *Agriculture, Ecosystems and Environment* 101, 171–184.
- Metcalf, J., Bayly, N., Bisoa, M., Rabearivony, J. & Stewart-Jones, A. (2005). Edge effect from paths on two chameleon species in Madagascar. *African Journal of Herpetology* 54, 99–102.
- Nussbaum, R.A., Raxworthy, C.J., Raselimanana, A.P. & Ramananjato, J.-B. (1999). Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. In A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With Reference to Elevational Variation. Fieldiana: Zoology 94, 155-173.
- Rabearivony, J. (1999). Conservation and Status

  Assessment of Brookesia, the Dwarf Chameleons of

  Madagascar. Canterbury: Durrell Institute of

  Conservation and Ecology, University of Kent.
- Rakotondravony, H. (2004). Diversité des caméléons forestiers de la région d'Andasibe (Madagascar) et modèle de distribution de cette communauté selon différent types physionomiques. *La Terre et la Vie: Revue d'Écologie* 59, 529–544.
- Randrianantoandro, J.C., Randrianavelona, R., Andriantsimanarilafy, R.R., Fideline, H.E., Rakotondravony, D. & Jenkins, R.K.B. (2007). Roost site characteristics of sympatric dwarf chameleons (genus *Brookesia*) from western Madagascar. *Amphibia–Reptilia* 28, 577–581.
- Raselimanana, A.P., Rakotomalala, D. & Rakotondramparany, F. (1998). Les reptiles et amphibiens: diversité et conservation. In *Inventaire Biologique de la Forêt Littorale de Tampolo (Fenoarivo-Atsinanana)*, 183–195. Ratsirarson, J. & Goodman, S.M. (eds). Antananarivo, Madagascar: Recherche pour le Developpement, Série Sciences Biologiques, n° 14.
- Raselimanana, A.P. & Rakotomalala, D. (2003). Chamaeleonidae, chameleons. In *The Natural History of Madagascar*, 961–969. Goodman, S.M. & Benstead, J.P. (eds). Chicago: University of Chicago Press.
- Raxworthy, C.J. (1988). Reptiles, rainforest and conservation in Madagascar. *Biological Conservation* 43, 181–211.
- Raxworthy, C.J. (1991). Field observations on some dwarf chameleons (*Brookesia* spp.) from rainforest areas of Madagascar, with the description of a new species. *Journal of Zoology* 224, 11–25.
- Raxworthy, C.J. (2003). Introduction to the reptiles. In The

- Natural History of Madagascar, 934–949. Goodman, S.M. & Benstead, J.P. (eds). Chicago: University of Chicago Press.
- Raxworthy, C.J. & Nussbaum, R.A. (1994). A rainforest survey of amphibians, reptiles and small mammals of Montagne d'Ambre, Madagascar. <u>Biological</u> Conservation 69, 65–73.
- Raxworthy, C.J. & Nussbaum, R.A. (1995). Systematics, speciation and biogeography of the dwarf chameleons (*Brookesia*; Reptilia, Squamata, Chamaeleonidae) of northern Madagascar. *Journal of Zoology* 235, 525–558.
- Raxworthy, C.J. & Nussbaum, R.A. (1996). Montane amphibian and reptile communities. *Conservation Biology* 10, 750–756.
- Raxworthy, C.J., Meyer-Martinez, E., Horning, N.,
  Nussbaum, R.A., Schneider, G.E., Huerta-Ortega, M.A.
  & Peterson, T.A. (2003). Predicting distributions of known and unknown reptile species in Madagascar.
  Nature 426, 837–840.
- Raxworthy, C.J., Andreone, F., Nussbaum, R.A., Rabibisoa, N. & Randriamahazo, H. (1998). Amphibians and reptiles of the Anjanaharibe-Sud Massif, Madagascar: Elevational distribution and regional endemicity. In A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud: With Reference to Elevational Variation. Fieldiana: Zoology 90, 79–92.

- Raxworthy, C.J., Forstner, M.R. & Nussbaum, R.A. (2002). Chameleon radiation by oceanic dispersal. *Nature* 415, 784–787.
- Reisinger, W.J., Stewart-Fox, D.M. & Erasmus, B.F.N. (2006). Habitat associations and conservation status of an endemic forest dwarf chameleon (*Bradypodium* sp.) from South Africa. *Oryx* 40, 183–188.
- Schimmenti, G. & Jesu, R. (1996). *Brookesia exarmata* sp. nov. (Reptilia, Chamaeleonidae), a new dwarf chameleon from the limestone outcrops of western Madagascar. *Italian Journal of Zoology* 63, 193–197.
- Tam-Alkis, J.V. (1997). Factors Affecting the Abundance and Distribution of a Chameleon Assemblage in Ranomafana National Park, Madagascar. MSc thesis. Canterbury: University of Kent.
- Vences, M., Andreone, F. & Vieites, D.R. (2005). New tree frog of the genus *Boophis* Tschudi 1838 from the northwestern rainforest of Madagascar. *Tropical Zoology* 18, 237–249.
- Vences, M. & Glaw, F. (2004). Revision of the sub-genus *Chonomantis* (Anura: Mantellidae *Mantadactylus*) from Madagascar, with description of two new species. *Journal of Natural History* 38, 77–118.

Accepted: 14 December 2007