Habitat use by chameleons in a deciduous forest in western Madagascar

Christian Randrianantoandro[1], Bertrand Razafimahatratra[2], Mathilde Soazandry[3],

Jonah Ratsimbazafy[3,4], Richard K.B. Jenkins[1,5,6,*]

Abstract. Information on the distribution and abundance of chameleons in Madagascar is required to develop conservation plans that integrate protected area management and sustainable use. We surveyed chameleons in eight sites in deciduous forest in Menabe, western Madagascar. *Brookesia brygooi* was the most frequently detected species, with a population density of 35 ha^{-1}. *Furcifer* species were less common, with calculated densities of 7.2 ha^{-1} (*F. labordi*), 3.0 ha^{-1} (*Furcifer* sp.) and 1.3 ha^{-1} (*F. oustaleti*). Chameleon abundance varied according to altitude (*B. brygooi*) and no clear effect from logging was detected (all species). A lack of information on chameleon diurnal habitat requirements impedes a fuller assessment of the extent to which these species are tolerant to forest degradation. There were interspecific differences in the height of nocturnal perches and additional studies are needed to determine whether these are related to diurnal resource partitioning. *Furcifer labordi* and *Furcifer* sp. are of conservation concern because they are restricted to native forests in western Madagascar.

Keywords: *Brookesia*, chameleon, *Furcifer*, Madagascar, Menabe, reptile.

Introduction

The Menabe region has one of the largest remaining tracts of dry deciduous forests in Madagascar (Nelson and Horning, 1993; Woolaver et al., 2006) and the central part has recently been declared as new protected area. The forests of central Menabe contain a number of locally endemic species, including the giant jumping rat *Hypogeomys antimena* (Sommer, 2003), narrow-striped mongoose *Mungotictis decemlineata* (Woolaver et al., 2006) and the

flat-tailed tortoise *Pyxis planicauda* (Young et al., 2008). Certain species of herpetofauna have a large proportion of their global distribution in the forests of Menabe and these include the amphibians *Scaphiophryne menabensis* (Glos et al., 2005), *Aglyptodactylus laticeps* (Glaw et al., 1998) and the reptiles *Paroedura vahiny*, *Stenophis citrinus* and *Furcifer labordi* (Glaw and Vences, 2007).

Furcifer labordi is a sexually dimorphic chameleon species that occurs in the dry forest habitats of western and south-western Madagascar (Glaw and Vences, 2007). It is considered a threatened species by the IUCN Red List, although this is in need of a re-assessment (IUCN, 2008). Little is known about the ecology of *F. labordi* although a recent study from the south-west of Madagascar reported an annual life history (Karsten et al., 2008), making this species of evolutionary as well as of conservation interest.

Many chameleon species in Madagascar have small geographic ranges and seem to require relatively intact forest for survival (Raxworthy and Nussbaum, 1995; Schimmenti and Jesu, 1996; Jesu et al., 1999; Andreone et al., 2001; Raxworthy and Nussbaum, 2006).

1 - Madagasikara Voakajy, B. P. 5181, Antananarivo (101), Madagascar

2 - Département de Biologie Animale, Faculté des Sciences, Université d'Antananarivo, Antananarivo (101), Madagascar

3 - Ecole Supérieure des Sciences Agronomiques, Département des Eaux et Forêt, Université d'Antananarivo, Antananarivo (101), Madagascar

4 - Durrell Wildlife Conservation Trust, Antananarivo, Madagascar

5 - School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ

6 - Current address: Durrell Institute of Conservation and Ecology, University of Canterbury, Kent, United Kingdom

*Corresponding author; e-mails:
rkbjenkins@gmail.com, jenkins@moov.mg

Chronic habitat degradation in south-western Madagascar (Seddon et al., 2000; Ganzhorn et al., 2001) is a major threat to species that are dependent on the remaining relatively intact forest. *Furcifer* chameleons are often considered to prefer open or degraded habitats and are therefore probably of lower conservation concern than species which rely on relatively intact forest vegetation (Andreone et al., 2005). However, there have been few attempts to study the habitat requirements of *Furcifer* chameleons, especially in the west of Madagascar where forests are naturally more open and drier than in the east. Metcalfe et al. (2005) reported higher densities of *Furcifer rhinoceratus* from high-canopy deciduous forest compared to low-canopy forest. Furthermore, there is some evidence that *Furcifer nicosiai* is strongly associated with relatively intact deciduous forest (Jesu et al., 1999; Randrianantoandro et al., 2008). Karsten et al. (in press) provided population densities of three *Furcifer* species from the spiny forest in the south-west and concluded that *Furcifer antimena* in particular was threatened by habitat loss. Thus, whilst some *Furcifer* species have large geographic distributions and can survive in heavily modified habitats, others are restricted in range and appear to require forest vegetation. The habitat use of the latter species needs to be described to better understand the impact of forest degradation and fragmentation. In this study we compared the abundance, density and ecology of four sympatric chameleon species in forests subject to different levels of disturbance and assessed the conservation status of each species. The main objective was to identify priority species for conservation within the new protected area.

Materials and methods

Study site

Our study was conducted in forests of the Menabe Region in western Madagascar between 21 January and 1 April 2006. Study sites were located between 7 km and 20 km east of the Mozambique Channel and 30 km to 70 km northeast of Morondava town (fig. 1). The dry tropical climate of the

Menabe Region has two distinct seasons; a hot wet season between November and April and a cooler dry season from May to August. Most of the rain falls between January and March, and the mean annual rainfall averaged 767 mm/year between 1906 and 1993 (Sorg et al., 2003). Eight different forest areas within central Menabe were selected to cover a range of vegetation types and disturbance levels.

1. *Kirindy Centre de Formation Professionnelle Forestiére* (CFPF): A relatively dense deciduous forest that has undergone a selective logging regime principally for *Dalbergia* spp. (Sorg et al., 2003). Baobabs *Adansonia* spp. are common canopy trees. Elevation above sea-level: 49-76 m.
2. *Tsitakabasia*: This forest was subject to selective logging (*Dalbergia greveana*, *Givotia madagascariensis* and *Gyrocarpus americanus*) in the past. Recently burned areas were found during the study but some areas remain relatively intact. Elevation above sea-level: 102 m.
3. *Kiboy*: This forest is subject to selective logging and has numerous clearings where bamboo liana thickets have developed. Elevation above sea-level: 113 m.
4. *Ampataka*: This forest in the western part of the study site is rather degraded with a more open canopy than other sites. Elevation above sea-level: 20 m.
5. *Kirindy*: A highly disturbed forest that is now characterized by open clearings and baobab *Adansonia* spp. Elevation above sea-level: 29 m.
6. *Ankoraobato*: Degraded forest at the edge that gives way to a more intact interior. Elevation above sea-level: 67 m.
7. *Marofandilia*: A degraded forest left with a low canopy and dense vegetation. Elevation above sea-level: 57 m.
8. *Bedo*: Baobabs are noticeably abundant in this lakeside forest that has highly degraded areas but also some relatively intact patches. Elevation above sea-level: 20 m.

Nocturnal chameleon surveys

Within each forest site we searched for chameleons at night along transects that were placed randomly in the forest. Each of the transects consisted of 150 m (3 parallel lines × 50 m) and the starting point was located 5-8 m into the forest from the nearest trail (Brady and Griffiths, 1999). Each transect was visited only once and the lines were set up the day preceding the nocturnal survey to minimize disturbance to the chameleons. Survey teams consisted of two people moving slowly along each transect searching opposite flanks for roosting chameleons with the aid of Petzl Myo XP LED head torches. All field personnel were experienced and trained in chameleon surveys and the team consisted of three biologists (JCR, BR, MS) and two local guides (Rasolonandrasana, J.-C. and Sambiravo). For each animal encountered we measured the perpendicular distance from the transect line, roosting (perch) height and the maximum height of the plant. Each chameleon was placed in a cloth bag and measured the following morning. Body mass (Pesola balance)
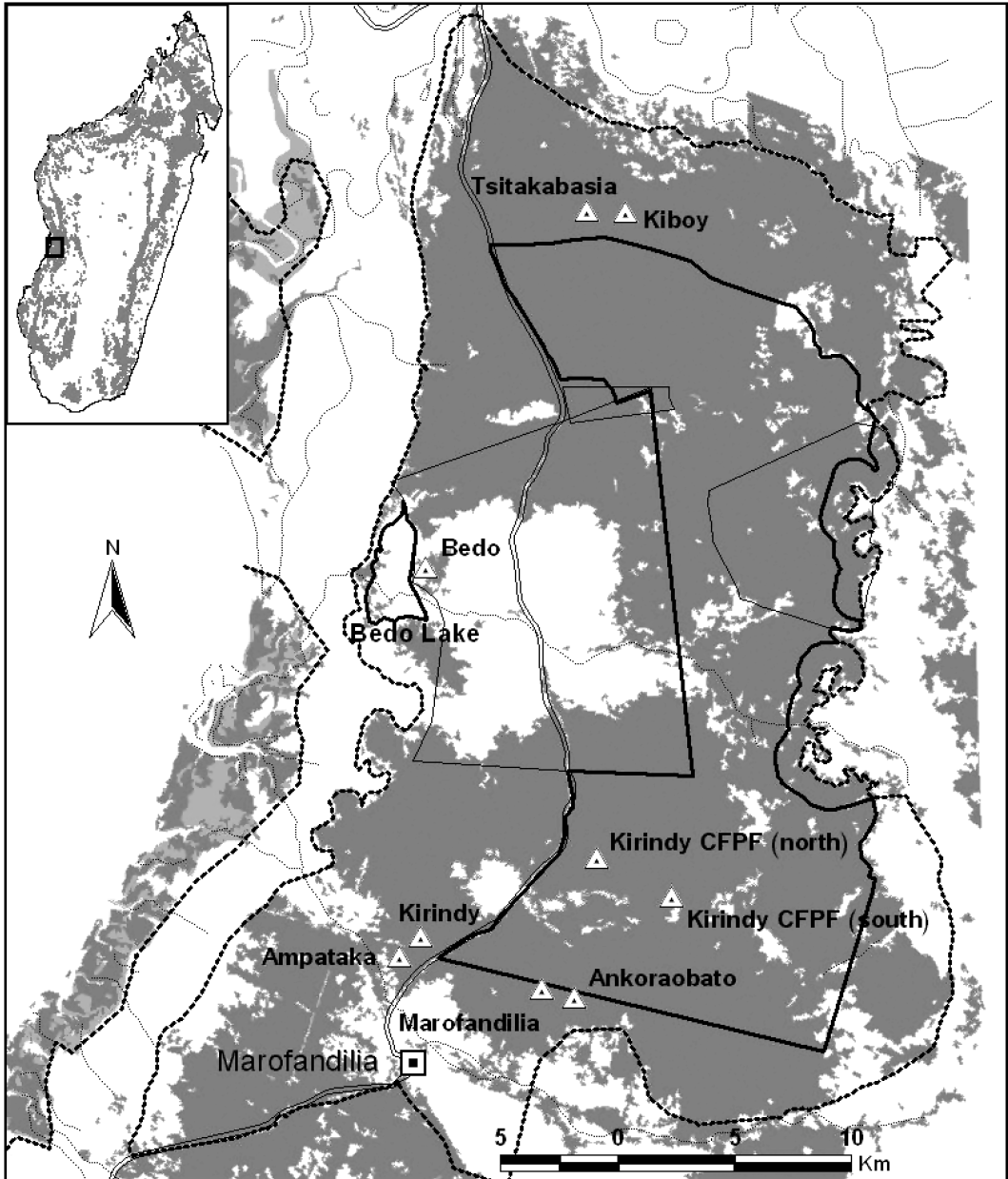
Figure 1. Map of central Menabe depicting the eight locations where we surveyed chameleons (triangles) and remaining forest cover (grey).

and snout-vent length (calipers) were recorded, as well as age and sex. Chameleons were released at the exact point of capture the afternoon after the nocturnal transect.

Density estimation

Population densities were calculated using the computer program *Distance* version 4.1 Release 2 (Thomas et al., 2004). The program fits a series of functions to the distance

data and the model best fitting the data was selected by the Akaike Information Criterion (Buckland et al., 2001). There are a number of important assumptions regarding the use of *Distance* sampling and key one is that all animals on the line (i.e., at 0 m) are detected. We did not test this empirically (Young et al., 2008) but made every effort to locate chameleons through careful searching of all vegetation on the transect line. As noted in other studies (Jenkins et al., 1999; Jenkins et al., 2003), nocturnal surveys of chameleons

are limited by reduced detectability of animals roosting high in the canopy. In this study we used a vertical ceiling of 7 m, rather than 6 m as used in other studies (Jenkins et al., 1999, 2003; Andreone et al., 2005) because the vegetation is more open in the dry deciduous forests allowing greater penetration by torch light. The horizontal, or perpendicular, distance data were truncated at 5 m for *Brookesia* sp. and 6 m for *Furcifer* spp., which has a larger body size, and can be easily found at this distance from the line in the forest at Menabe. Hatchling chameleons were excluded from the analysis.

Microhabitat assessment

A sample of the chameleon roost perches was marked each night with a colored tag and we returned to the site the following morning where a plot of 5 × 5 m was placed on the ground with the perch at the centre.

Within these plots we recorded 14 microhabitat variables: the abundance of trees in three categories (sub canopy < 1.5 m height; canopy-forming < 1.0 m dbh; canopy-forming > 1.0 m dbh), the number of trees cut by humans or felled by natural causes (e.g., cyclones) and leaf litter depth (cm). Using a 1 m stick marked with centimeter gradations, we recorded whether there was contact with ground vegetation in four height categories (0-0.24 m, 0.25-0.49 m, 0.50-0.74 m and 0.75-1.0 m) every 25 cm along two 5 m lines with the perch at the centre in the plot. The percentage canopy, understory and leaf litter cover was estimated by eye in, or above, each quadrat by four people and the mean value was used in subsequent analyses. A liana index was used to assess the abundance of this plant and ranged from 0 to 3.

Statistical analysis

For species with a coefficient of variation < 30% for the density estimate we calculated an abundance index to control for detectability (Brady and Griffiths, 1999; Jenkins et al., 2003). Principal Component Analysis was used to summarize the main variation in the 14 habitat variables. The resulting parametric data (principal component scores) were compared between quadrats with and without each species using ANOVA. The scores were also compared between sites classed as relatively intact or disturbed using ANOVA based on the presence or absence of trees cut by humans. Inter-specific differences in the height of roosting chameleons were investigated using ANOVA. In assessing the influence of abiotic factors on chameleon abundance we used ANCOVA with altitude as the covariate and survey date as the independent variable. Statistical comparisons of abundance and habitat use were not possible for two species because of small sample sizes.

Results

A total of 533 chameleons from four species were detected along 13.8 km of transects;

Brookesia brygooi was the most abundant with 406 observations, followed by *F. labordi* (59), *Furcifer* sp. (52) and *Furcifer oustaleti* with 16 observations. The morphology of *Furcifer* sp. in central Menabe was different to *F. nicosiai* from Parc National Tsingy de Bemaraha to the north (Randrianantoandro et al., 2008) and we therefore follow Raselimanana (2008) and attribute this taxon to an undescribed species, but recognize that this is tentative and subject to taxonomic verification.

Density and abundance of chameleons

Brookesia brygooi occurred in highest density during the study, followed by *F. labordi*, *Furcifer* sp. and *F. oustaleti* (table 1). The density of all *Furcifer* chameleons together was 12.7 ha^{-1} (coefficient of variation 11.8%). The abundance of *B. brygooi* and *Furcifer* sp. was noticeably higher in Kiboy and Tsitakabasia than the other sites (table 2). In contrast, the highest abundance of *F. labordi* was from Bedo and Kirindy-CFPF. *Furcifer oustaleti* was only found in three of the sites and was most abundant in Bedo.

Biotic factors

Principal component analysis of the 14 habitat variables produced three factors with Eigenvalues over 1.0 and these accounted for 54% of the variation in the data. The first principal component (PC) represented 25% of data variation and was positively correlated with a dense lower vegetation layer and negatively correlated with tree abundance and leaf litter cover. The second PC (16%) was positively correlated with dense vegetation < 0.25 m, lianas

Table 1. Chameleon densities calculated using DISTANCE along random forest transects in central Menabe, Madagascar, during January to April 2007.

Species	Model	D (ha^{-1})	n	% C.V.	95% CI
B. brygooi	Uniform	35.5	460	15.1	26.4-47.8
F. labordi	Uniform	7.2	60	16.7	5.2-9.9
Furcifer sp.	Uniform	3.0	27	38.4	1.4-6.3
F. oustaleti	Uniform	1.3	17	57.9	0.4-3.9

Table 2. Mean $\pm$ SE (n) abundance per 100 m for four chameleon species in eight forests in central Menabe, western Madagascar.

Study site	*Brookesia brygooi*	*Furcifer labordi*	*Furcifer* sp.	*Furcifer oustaleti*
Ampataka	0.44 ± 0.3 (6)	0.29 ± 0.1 (4)	0.07 ± 0 (1)	0.14 ± 0.1 (2)
Ankoraobato	1.4 ± 0.4 (19)	0.14 ± 0.1 (2)	0.22 ± 0.1 (3)	0
Bedo	0.55 ± 0.3 (10)	0.94 ± 0.2 (17)	0	0.61 ± 0.1 (11)
Kiboy	8.44 ± 0.6 (152)	0.33 ± 0.1 (6)	0.94 ± 0.2 (17)	0.16 ± 0.1 (3)
Kirindy	0.66 ± 0.3 (9)	0.22 ± 0.1 (3)	0.44 ± 0.2 (6)	0
Kirindy-CFPF	2.21 ± 0.4 (68)	0.71 ± 0.1 (23)	0.38 ± 0.1 (12)	0
Marofandilia	0.74 ± 0.2 (10)	0.29 ± 0.1 (4)	0.14 ± 0.1 (2)	0
Tsitakabasia	7.44 ± 1.0 (134)	0.16 ± 0.1 (3)	0.62 ± 0.1 (11)	0

and fallen trees, and negatively correlated with logged trees. The third PC (13%) was positively correlated with dense vegetation < 0.25 m and leaf litter and canopy cover and negatively with the abundance of trees. All three PC scores differed significantly between quadrats with and without *B. brygooi* (ANOVA PC1 $F_{1,88} = 5.14$, $P = 0.03$; PC2 $F_{1,88} = 9.26$, $P = 0.003$; PC3 $F_{1,88} = 5.36$, $P = 0.02$) but no significant differences were found for *F. labordi* (ANOVA PC1 $F_{1,88} = 2.82$, $P = 0.89$; PC2 $F_{1,88} = 0.08$, $P = 0.78$; PC3 $F_{1,88} = 0.02$, $P = 0.89$). There was a significant difference in scores for PC1 and PC3 for quadrats with and without *Furcifer* sp. (ANOVA PC1 $F_{1,88} = 4.47$, $P = 0.04$; PC2 $F_{1,88} = 0.12$, $P = 0.73$; PC3 $F_{1,88} = 10.16$, $P = 0.002$). *Brookesia brygooi* were therefore associated with habitat patches characterized by dense layers of ground vegetation that were located in areas subject to disturbance from timber extraction but were also represented in sites with a closed canopy. *Furcifer* sp. presence was associated with well vegetated habitat patches in areas with many lianas and a relatively closed canopy. PC2 scores were significantly different between relatively intact and disturbed forest ($F_{1,88} = 59.20$, $P = <0.001$) but the other PCs were not related to logging.

Abiotic factors

We used ANCOVA with log abundance index as the dependent variable, survey date (divided into five periods) as the factor and altitude as covariate for *B. brygooi* and *F. labordi*. Survey date was not significantly related to the abun-

dance of *B. brygooi* ($F_{5,78} = 1.17$, $P = 0.33$) once the effect of altitude had been accounted for ($F_{1,78} = 5.90$, $P = 0.02$). *Brookesia brygooi* was most abundant in the higher altitude forest sites at Kiboy, Tsitakabasia, Ankoraobato and Kirindy CFPF, and were rarely encountered in the lower altitude sites at Bedo and Kirindy. Neither survey date ($F_{5,78} = 1.25$, $P = 0.28$) nor altitude were significantly related to the abundance of *F. labordi* ($F_{1,78} = 0.20$, $P = 0.64$).

Roosting

There was a significant difference in the height of perches (ANOVA $F_{3,259} = 74.7$, $P = <0.001$) and vegetation (ANOVA $F_{3,258} = 52.2$, $P = <0.001$) used by the four species for roosting at night (fig. 2). *Brookesia brygooi* usually used vegetation < 1 m in height whilst *Furcifer* species generally used vegetation > 2 m in height (fig. 2). Post-hoc tests revealed that interspecific differences in perch height were all significant, with *F. oustaleti* roosting in the highest locations, followed by *Furcifer* sp. and *F. labordi*. The height of vegetation used by roosting chameleons also differed significantly with the exception of *F. oustaleti* and *Furcifer* sp. which roosted in trees of similar height (fig. 2).

Discussion

This study found interspecific differences in the abundance, density and use of nocturnal perches by four endemic species of Malagasy
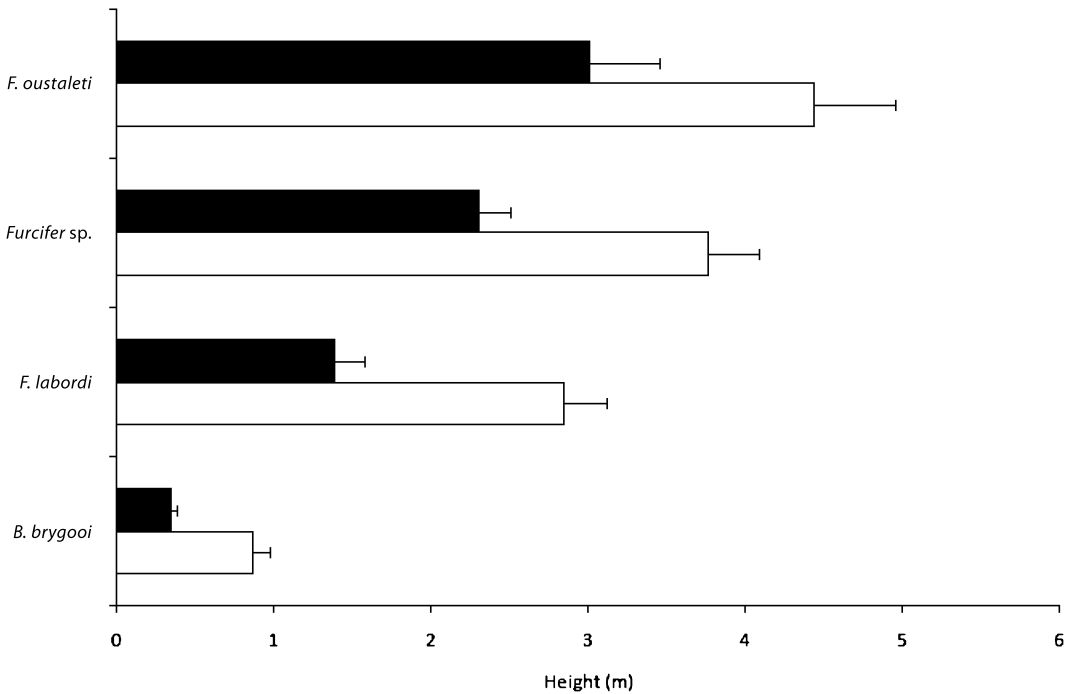
Figure 2. Mean (+SE) of the plant height (white) and perch height (black) used by four species of chameleons in deciduous forest in western Madagascar.

chameleon in deciduous forest. There was also an important altitudinal effect for one species which could explain variation in abundance between the different sites.

Chameleon density

The density of the large bodied *Furcifer* chameleon species was notably lower than for the dwarf chameleon *B. brygooi*. This is consistent with results from the dry deciduous forest in Parc National Tsingy de Bemaraha to the north (Randrianantoandro et al., 2008). Densities of *Brookesia* species in the eastern humid forests are also higher than large-bodied *Calumma* species (Jenkins et al., 1999, 2003). *Brookesia* are usually found near the forest floor and are assumed to forage in, or just above, the leaf litter (Raxworthy, 1991; Raxworthy and Nussbaum, 1995; Glaw et al., 1999; Jenkins et al., 2003; Randrianantoandro et al., 2007) and are therefore members of a different guild to the larger bodied *Calumma* and *Furcifer* species

that forage mainly on shrubs and trees. Differences in the density of terrestrial and arboreal chameleons may therefore be related to the availability of suitable prey and microhabitats.

Furcifer density was lower in Parc National Tsingy de Bemaraha (2.3 ha^{-1}; J.C. Randrianantoandro, unpubl. data) than Menabe (12.7 ha^{-1}). As *Furcifer* species in humid areas are found outside of closed forest in habitats that are drier and warmer (Andreone et al., 2005), the low density in the forest in Parc National Tsingy de Bemaraha may be because of the higher humidity associated with the peculiar geological formations at this site. Metcalfe et al. (2005) reported densities of *F. rhinoceratus* and *F. oustaleti* combined to vary between 5.8 ha^{-1} and 13.9 ha^{-1} at Parc National d'Ankarafantsika in western Madagascar. Karsten et al. (in press) calculated *F. labordi* densities in the south-western spiny forest to range between 30.8 ha^{-1} (late breeding season) and 4.0 ha^{-1} (early dry season). It therefore appears that the density of *F. labordi* varies consid-

erably within its range. This could be because of differences in vegetation type (e.g., deciduous vs. spiny forest) or habitat quality (impact of disturbance). The differences could also be artifacts of methodology and related to the timing of the surveys in relation to life cycle development (Karsten et al., in press) or the number of observations; relatively large confidence intervals accompanied the Karsten et al. (in press) density estimates because of the small number of chameleons observed in each period.

Roosting ecology

There were interspecific differences in the roosting height of *Furcifer* chameleons and *F. labordi* used perches closer to the ground, but still well above those of *B. brygooi*. Perch selection by chameleons is poorly understood but may be related to foraging opportunities the following day, as well as nocturnal predator avoidance. Additional data are needed on feeding ecology and behaviour to develop a better understanding of whether differences in the roosting heights of *Furcifer* sp. and *F. labordi* are related to diurnal resource partitioning.

The impact of forest disturbance

The forests of central Menabe have been subject to different levels of exploitation, ranging from the selective removal of timber to the removal of forest vegetation for agriculture (Sorg et al., 2003). Reptiles respond to changes in the availability of suitable microhabitats when forest structure is changed and can undergo local increases or decreases in abundance accordingly (e.g., Lima et al., 2001; Shine et al., 2002; Todd and Andrews, 2008). A number of studies have reported differences in chameleon density and abundance between relatively intact and degraded forests (Brady and Griffiths, 1999; Akani et al., 2001; Jenkins et al., 2003). These differences are presumably because of interspecific habitat requirements for roosting, foraging and breeding and changes to vegetation structure and abiotic characters when closed canopy

forest becomes more open and degraded. There was no clear relationship between forest degradation and *Furcifer* spp. in the present study although there was notable variation between sites subject to different disturbance regimes. It is not clear therefore how habitat change influences the suitability of dry forest for chameleons with respect to predator-free space, prey availability, roosting habitats, egg-laying sites or overwintering habitats. Significant changes in habitat suitability for reptiles can occur on a very small scale (e.g., Shine et al., 2002) and more detailed investigations of the diurnal behaviour and habitat use of chameleons are needed.

Abiotic factors are important for chameleons, and precipitation and humidity, are likely to influence species composition and abundance. Glos and Volahy (2004) for example noted that the Bedo forest was probably too dry for *B. brygooi* and we detected a low density of this species at this site as well as relationship with altitude. Taxa that have specific abiotic requirements are often restricted to particular habitats or narrow elevation ranges and are the most susceptible to the impacts of deforestation and climate change (Raxworthy et al., 2008). Most previous studies on the micro-distribution of chameleons have focused on changes in species composition and abundance between different vegetation types and elevations without addressing changes in thermal properties at different sites. The removal of large trees, through logging or cyclone passage, will likely have a profound effect on the thermal environment.

Habitat conservation

Furcifer labordi is restricted to the lowland western forests of western Madagascar from Soalala in the north-west to Ranobe in the south-west (Glaw and Vences, 2007; Karsten et al., 2008). There are no recent records from north of the Manambolo River (Raselimanana, 2008) and it is therefore important to determine whether it still occurs in the north of its reported range. The main threat to *F. labordi* is from the destruction, fragmentation and degradation

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