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Life history traits, age profile, and conservation of the panther chameleon, *Furcifer pardalis* (Cuvier 1829), at Nosy Be, NW Madagascar

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The morphometry, age structure, and abundance of the panther chameleon *Furcifer pardalis* (Cuvier 1829) were studied at Nosy Be (NW Madagascar). Males were larger and heavier than females (SVL, 138.38 ± 35.94 vs 91.92 ± 18.48 mm; mass, 61.06 ± 39.86 vs 22.62 ± 13.17 g). The age, assessed by skeletochronology, was usually less than one year, with a maximum of 2 years. The density estimate for adult individuals was higher along roads (42.21/ha) than in agricultural habitats far from roads (17.43/ha). Compared to other species of Malagasy chameleons, *F. pardalis* is infrequent in pristine and close forests, while, like other *Furcifer* species, it is more closely associated with riverine habitats. The higher concentration of individuals in forest-like bands along roads is explained by the presence of a suitable vegetation band along roads and the similarity of this habitat to the riverine and ecotonal forests preferred by chameleons of the genus *Furcifer*. The life history traits, high fecundity and short life span indicate that the current collecting rate does not affect the abundance of *F. pardalis*. Measures of chameleon conservation at Nosy Be should consider the preservation of the anthropogenic forest band.

KEY WORDS: *Furcifer pardalis*, chameleons, Madagascar, conservation, density, population structure, trade.

INTRODUCTION

With three chameleon genera and about half of the world's 138 species, Madagascar is depicted as the family diversity centre, from where it likely radiated via oceanic dispersal (Raxworthy et al. 2002). These genera have different life styles and morphology, with the large-bodied and sexually dimorphic *Furcifer* Fitzinger 1834 mainly living in dry areas and deciduous forests and only rarely penetrating close rainforests, the smaller and less dimorphic *Calumma* Gray 1865, almost typical of the eastern rainforests, and the dwarf and terrestrial *Brookesia* Gray 1865, inhabiting both rain and deciduous forests (Nečas 2004, Nečas & Schmidt 2004).

Since the Malagasy chameleons are in high demand in the international pet-trade (Raxworthy & Nussbaum 2000, Andreone 2003, Carpenter et al. 2005) they have been included in CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) lists, regulating the trade of endangered animals and plants (Wijknstekers 2001, Vasquez 2003). Beside this regulation, a ban was established in 1994: thus with the exception of *F. lateralis* (Gray 1831), *F. pardalis* (Cuvier 1829), *F. oustaleti* (Mocquard 1894) and *F. verrucosus* (Cuvier 1829), which were considered non-threatened and whose exportation is allowed, the Malagasy species cannot be commercialized (Brady & Griffiths 1999, Jenkins et al. 1999, Raselimanana 2003). The number of exported specimens for each of these species reached a maximum of about 15000 individuals per year until 1998, after which it dropped to 2000 individuals (Carpenter et al. 2005).

Furcifer pardalis is certainly the most sought after chameleon species of Madagascar, due to a combination of attractive colouration, large size and readiness to breed in captivity (Müller et al. 2004, Nečas 2004, Affre et al. 2005). It is fairly widely distributed and locally abundant on the eastern (central-northern area) and north-western coasts of Madagascar, and was introduced to La Réunion (Glaw & Vences 1994). Although Brady & Griffiths (1999) provided a general overview and population data for many forest chameleons (mainly *Calumma* and *Brookesia*), they did not deal with *F. pardalis* and most of the *Furcifer* species, which are generally less frequent in forest habitats. Yet, given the local abundance and high commercial demand, data on the life history of *F. pardalis* are badly needed, since they are currently limited to scattered notes (Bourgat 1968) and physiological and captive breeding observations (Ferguson et al. 2004).

Trade in rare species is a potential threat for their local population conservation (Affre et al. 2005). However, the abundance of some species may allow a certain level of capture and collection that will not harm the population (Jenkins 2000). This might be the case for the four legally traded *Furcifer* species, although it should be stressed that their exportation quotas were established mainly upon a political decision, without solid scientific knowledge. As for other exportation aspects regarding the amphibians and reptiles of Madagascar, there is an urgent need to revise the quotas using a scientific approach, also because the export of

Malagasy chameleons represents a considerable economic resource for local populations (Carpenter et al. 2004). A change in the quotas will only be possible after the wild populations have been monitored, and basic life history information has been collected. Thus, data on the ecology and abundance of *F. pardalis* may be useful tools for its conservation and for the establishment of reliable capture and exportation parameters.

The aim of this paper is to provide data on the morphometry and population traits of *F. pardalis* at Nosy Be, as well as information about the species' life span, obtained by estimating the age via skeletochronology (Castanet 1994). Moreover, we provide information gathered during a series of field surveys in several forests to highlight the ecological preferences of other species of the three Malagasy genera, which might be useful to national and international authorities for future decisions and to assure sustainable management of these chameleon species.

MATERIAL AND METHODS

Study site and periods

Nosy Be Island (Fig. 1), about 12 km from the mainland of NW Madagascar (13°09'-13°30'S and 47°58'-48°27'E) and about 25200 ha in area, falls within the Sambirano Domain, which has vegetation similar to that of the eastern rainforest, with humid and warm climate, an annual mean rainfall of 2250 mm, and a mean annual temperature of 26 °C (Andreone et al. 2003).

Roads and paths cross the island and allow access to most of the tourist destinations (beaches, hotels). Although a small portion of the original forest at Nosy Be is now protected (Réserve Naturelle Integrale de Lokobe), the forest coverage has mostly disappeared. A large proportion of its surface area has been converted for agricultural purposes, with a mosaic of croops, including rice, sugar cane, and ylang-ylang. Forest relicts consist of scattered trees and degraded shrubs, and vegetation belts along rivers and roads for a width of about 5-10 m. This vegetated belt is a mix of trees originally present on the island, exotic species and fruit trees, which reach 5-10 m in height.

The study was conducted in 2000 and 2001 during the warm, wet period, between November and March, when most of the animals are active, due to a combination of good climatic and trophic availability.

The chameleon trade

A general overview of the trade in Malagasy chameleons is given by Carpenter et al. (2004, 2005). For *F. pardalis* the major collecting sites during the years of the present study were Nosy Be and the areas around the towns of Ambanja and Antsiranana (north-western and northern Madagascar), Sambava, Maroantsetra and Tamatave (north-eastern Madagascar). One of the most requested colour morphs was the "blue panther chameleon", which is the commercial name for the populations from Nosy Be (Ferguson et al. 2004). For this reason and the general ease in collecting chameleons on this island, most traded individuals (up to 50%, i.e. 1000 individuals/year) came from Nosy Be.

At Nosy Be the chameleons were usually collected at night, by car along the asphalted road connecting the main town (Hellville) to the island's airport, where lengthy sections are bordered by forest-like vegetation. Other sites and habitats (agricultural fields, isolated bushes, residual forest fragments) were only seldom visited for regular collecting. The annual peaks of demand were in November-December and February-March, the collecting usually not exceeding 100-200 animals at any one time (pers. obs).

Population estimate

We selected 21 transects, nine of which in the vegetation along roads (hereafter called "road transects"), and the other 12 in agricultural fields and secondary vegetation randomly chosen at a distance > 50 m from the road ("external transects").

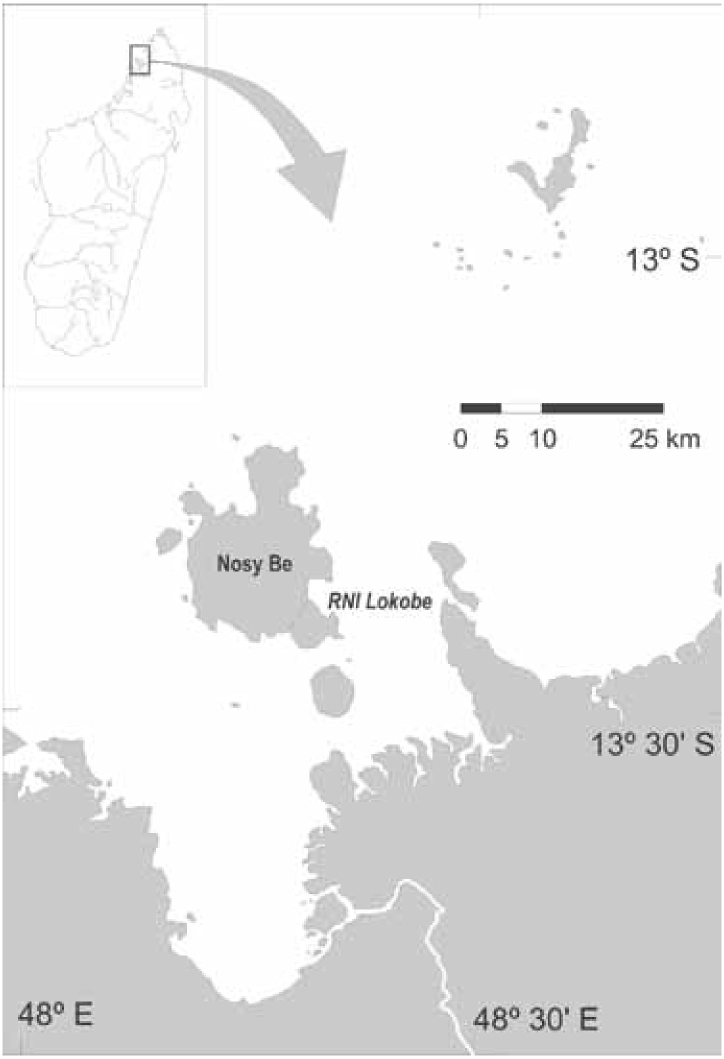

Fig. 1. — Location of Nosy Be and of the Réserve Naturelle Integrale (RNI) de Lokobe, and nearby islands. Map source: GIS Service of WWF-Antananarivo, based upon FTM (Foiben-Taosarintanin'i Madagascar / Institut Géographique et Hydrographique National) maps.

The density of *F. pardalis* was estimated by means of "distance" transects, i.e. by measuring the perpendicular distance from the transect line to the observed individual, as described by Jenkins et al. (1999) and Brady & Griffiths (1999). Transect positions were set in place 1 day before the survey. Surveys began 2 hr after sunset, when chameleons lose their colours and are identifiable by torchlight (Brady & Griffiths 1999). The observers searched for chameleons using hand-torches (Maglite) and head-lamps (Petzl). Each transect was followed once, and the chameleons were detected on the right and left sides. According to Jenkins et al. (1999), we established a "detection ceiling" of 6 m, since any ground-based census of arboreal chameleons is obviously confounded by a decreasing vertical detection. Since juveniles are small and generally have cryptic colouration, their detection probability is not the same as for adult individuals. Moreover, their abundance is variable according to the birth periods and consequent presence of newborns. Therefore, we only considered adult chameleons for the population estimate, although we also collected data on habitat preferences and general abundance of juveniles.

The density analysis was performed with the program DISTANCE (version 4.2) and the variance was calculated empirically. The program fit a series of functions to the distance data and the model best fitting the data was selected by the Akaike Information Criterium (Buckland et al. 2001).

For each encountered individual (both adults and juveniles) we measured the perpendicular distance from the transect line (named "horizontal distance"), and the elevation above the ground. Males were recognised by their bright green-turquoise colouration, large size, and swollen basis of the tail, due to the presence of the hemipenes (Fig. 2A). Females were identified as being more uniformly greenish-reddish, smaller, with a thinner tail base, and sometimes with eggs detectable through the body walls (Fig. 2B). Individuals without evident external secondary sexual characters, and usually with a SVL < 50 mm, were classified as juveniles. We also measured the snout-vent length (SVL, to the nearest mm, with a flexible tape) and body mass (to the nearest 0.5 g, with a spring balance) of captured animals. After the measurements, the chameleons were released at their original capture site. Due to their remote positions, some individuals were only spotted with a binocular and sexed by sight; we calculated their position with respect to the transect.

Abundance of chameleons in natural forests

To identify and compare the habitat preferences of *F. pardalis* we also provided an abundance index (AI) of this and other chameleon species found during former biodiversity surveys in: (1) the Sambirano Lokobe forest at Nosy Be (Andreone et al. 2003); (2) the transitional Sambirano-dry forest at Sahamalaza Peninsula (Andreone et al. 2001); (3) five low-altitude rainforest sites at Masoala (Andreone & Greer 2002); (4) two mid-altitude rainforests at Ambolokopatrika (Andreone et al. 2000). At each site we alternated a research night along rivers and streams within a distance < 50 m from the river (named "riverine habitats"), with an other night at greater distance (named "forest habitats"). For all the localities we counted the number of chameleons encountered during predefined walks across the studied territories, and then calculated the number of individuals per meter.

Age assessment

We applied the skeletochronological method to a preserved sample previously collected at Nosy Be (Andreone et al. 2003) and housed in the herpetological collections of Parc Botanique et Zoologique de Tsimbazaza (PBZT, Antananarivo) and Museo Regionale di Scienze Naturali (MRSN, Torino). These specimens (6 adult males, 6 adult females, and 5 juveniles) were chosen to obtain a wide body size range. Following the method indicated by Andreone & Guarino (2003) we decalcified the left femur in 5% nitric acid for 3 hr. Then, serial 15 µm thick cross

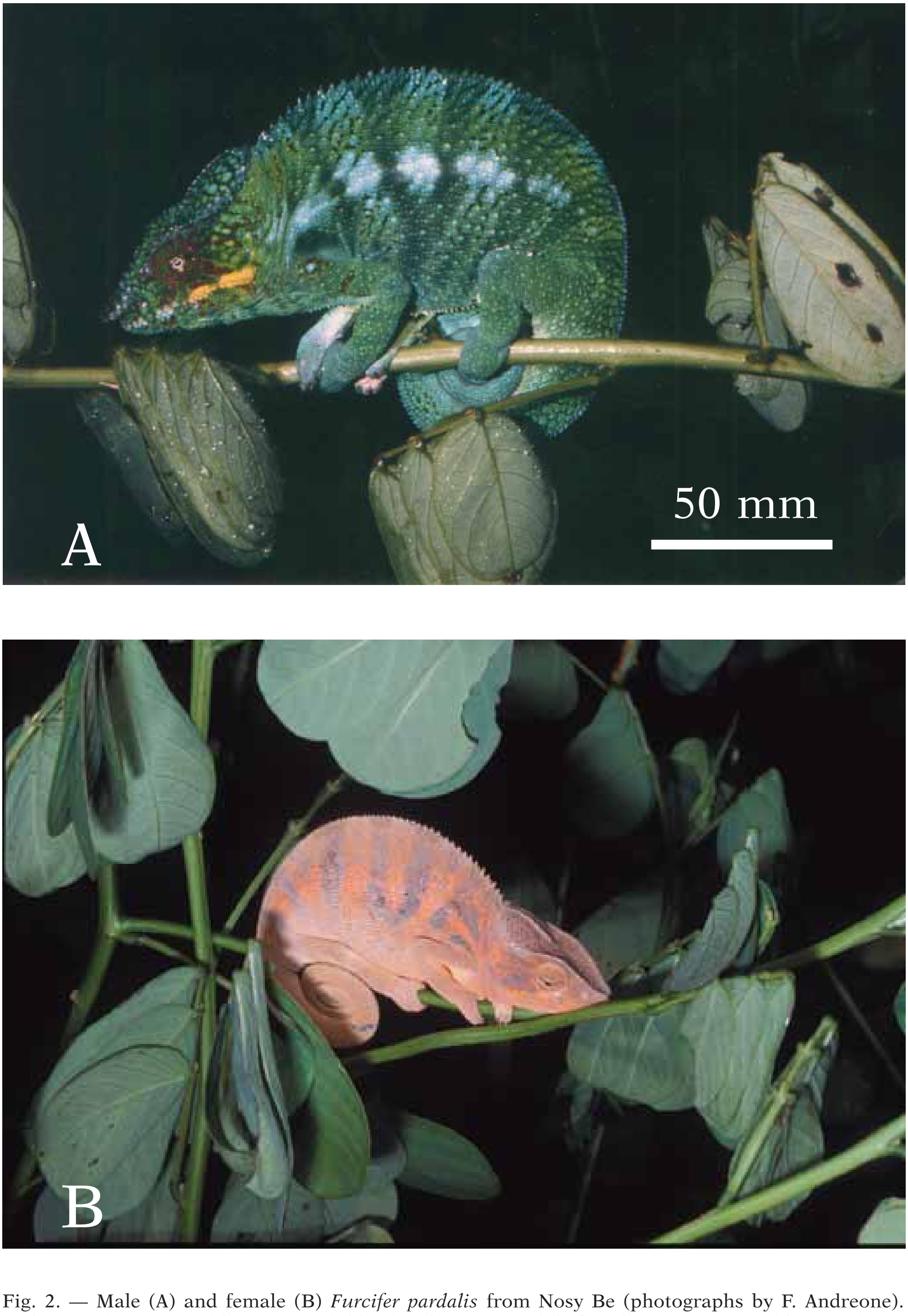

Fig. 2. — Male (A) and female (B) *Furcifer pardalis* from Nosy Be (photographs by F. Andreone). Males are characterised by a greenish-bluish colouration, while females are tawny and brownish.

sections were obtained with a cryostat from the diaphysis, and stained with Ehrlich's haematoxylin for 25 min. At least 20 serial cross sections were analysed under transmitted light microscope. We identified the haematoxylinophilic growth rings in the bone tissue corresponding to the lines of arrested growth (LAGs). The LAG counting was performed by one of us (FMG), and confirmed by a second person. To evaluate the rate of bone remodelling, which often destroys the inner LAGs, we also carried out an osteometric analysis according to Guarino et al. (2004).

RESULTS

Body size and sexual dimorphism

The mean SVL ± SD is 138.4 ± 35.9 mm in males (n = 83; range: 59.0-229.0 mm) and 91.9 ± 18.5 mm in females (n = 102; 57.0-134.7 mm), while the mean body mass ± SD is 61.1 ± 39.9 g in males (n = 70, 4.5-155.0 g) and 22.6 ± 13.2 g in females (n = 103, 3.0-60.0 g). Both variables differ significantly between the sexes (SVL, unpaired t = 11.35; $P < 0.01$; body mass, t = 9.09, $P < 0.01$) (Fig. 3). Data were Log-transformed to conform to assumptions of normality and homogeneity of variance. Significant linear relationships, on a Log-Log scale, were evident between body mass and SVL (males, r = 0.94, df = 65, $P < 0.001$; females, r = 0.81, df = 95, $P < 0.001$) (Fig. 4). Single-factor analysis of covariance, with sex as the factor and Log(mass) as the covariate, shows that, at the same body mass, male and female *F. pardalis* do not differ in SVL (ANCOVA, F = 0.683, df = 1,160, $P = 0.409$). This indicates a non-significant slope divergence between the two lines.

Population traits and abundance in different habitats

In total, we detected 262 *F. pardalis* (93 males, 106 females, and 63 juveniles) over an overall transect length of 9.25 km, giving a sex ratio (SR) of 0.88, not sig-

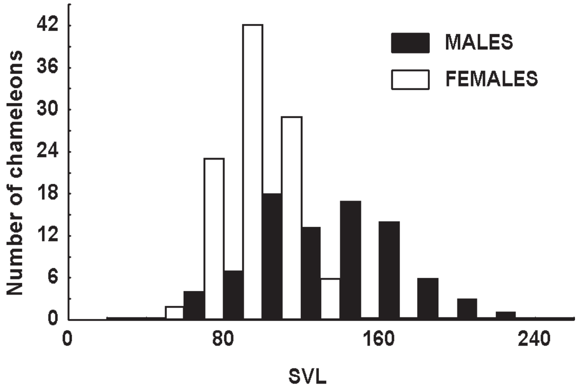

Fig. 3. — Size distribution of snout-vent length (SVL at 1 mm) in male and female *Furcifer pardalis* measured at Nosy Be.

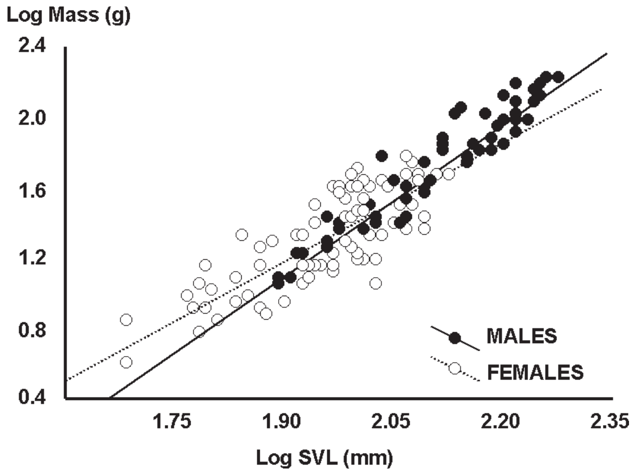

Fig. 4. — Regression of SVL logarithm against body mass logarithm in *Furcifer pardalis* from Nosy Be.

nificantly different from the expected 1 : 1 primary ratio ($\chi^2 = 0.72$; $P > 0.05$). We found 193 individuals along roads and 69 in external habitats. Most of the juveniles were found along the road (52 of 63 specimens).

Considering the different length of surveyed transects (4.4 km of road transects and 4.85 km of external transects), there was a significant preference and a higher abundance of adult chameleons along the roads. The detection rate at Nosy Be was 0.032 chameleons per meter on roads and 0.012/m in external transects (Table 1). These values are significantly different ($\chi^2 = 41.45$, $P < 0.01$).

The selected models give a density value of 42.21 individuals per ha (95% Confidence Interval CI, 25.54-69.78) along roads and 17.43 per ha in the external transects (95% CI, 8.08-37.60). By drawing the roads on Nosy Be, we roughly, but realistically, estimated that 5% of the island's total surface area is occupied by road vegetation bands. Considering this habitat proportion and applying the calculated densities on the two main habitats we obtained an overall Nosy Be chameleon population of 451720 adult individuals (95% CI, 21664-941860).

Horizontal and vertical distribution

The horizontal detection distances did not differ significantly between sexes, although males were observed at a somewhat greater distance than females both along roads (3.20 ± 3.49 versus 2.47 ± 0.94 m) and in external transects (2.28 ± 2.15 vs 1.35 ± 1.48 m) (Table 2). Males also differed significantly from females in elevation above the ground along roads (1.82 ± 0.94 vs 1.47 ± 0.96 m; $t = 2.16$, $P < 0.05$), but not in the external habitats (1.52 ± 0.62 vs 1.47 ± 0.90 m). Differences in the horizontal detection distance were not observed between adults and juveniles (adults: 2.50 ± 3.00 m; juveniles: 1.85 ± 1.26 m; $t = 1.60$; $P = 0.111$). Juveniles were not found at a significantly different elevation above the ground with respect to adults (adults: 2.08 ± 7.02 m; juveniles: 2.32 ± 1.44 m; $t = -0.262$; $P = 0.794$).

Table 1.

Number of males, females and juveniles of *Furcifer pardalis* observed at Nosy Be in two different kinds of habitats.

Transect number	Transect length (m)	Males	Females	Juveniles
Road transect				
1	400	6	7	7
2	500	10	19	21
3	500	10	19	18
4	500	2	2	1
5	500	1	4	0
6	500	5	4	1
7	500	11	1	0
8	500	4	9	0
9	500	12	15	4
Total road transects	4400 m	61	80	52
Total of adults		141		
Abundance index		0.032 adult chameleons /m		
External transect				
10	300	2	0	0
11	250	2	5	2
12	300	7	5	0
13	400	3	3	2
14	500	0	0	0
15	300	2	5	3
16	500	0	0	0
17	500	2	0	1
18	300	8	6	2
19	500	0	0	1
20	500	2	1	0
21	500	4	1	0
Total external transects	4850 m	32	26	11
Total of adults		58		
Abundance index		0.012 adult chameleons /m		

Road transect = vegetation band along roads; External transect = external habitats at about 50 m from the road.

Abundance and distribution of chameleons in close forests

Data on chameleon abundance at forest sites are given in Table 3. At the two sites of Lokobe (Nosy Be) and Sahamalaza (respectively a Sambirano and a transitional dry deciduous – Sambirano forest) we observed 18 adult *F. pardalis* individuals along a 9699 m transect, with a consequent detection rate of 1.86/km. These values are much lower than the number of adult panther chameleons per meter observed along the roads (AI = 0.032, $\chi^2 = 102.01$, $P < 0.01$) and in the external

Table 2.

Horizontal transect distance and vertical elevation in adult males and females of *Furcifer pardalis* along road and external transects at Nosy Be.

		Males	Females	t	*P*
Road transects	Horizontal	3.20 ± 3.49 (62)	2.47 ± 0.94 (78)	1.288	0.200
	Vertical	1.82 ± 0.94 (61)	1.47 ± 0.96 (77)	2.164	0.032 *
External transects	Horizontal	2.28 ± 2.15 (31)	1.35 ± 1.48 (27)	1.844	0.070
	Vertical	1.52 ± 0.62 (32)	1.47 ± 0.90 (27)	0.252	0.802
	t	1.338	1.700		
		1.631	– 0.009		
	P	0.184	0.092		
		0.106	0.992		

Mean values ± standard deviation, with number of individuals between parentheses (in meters); t = Student's t value, *P* = probability value; the asterisks indicates a significant difference at $P < 0.05$.

habitats (AI = 0.012, $\chi^2 = 34.99$, $P < 0.01$). At the only other forest with *F. pardalis* (Masoala, a rainforest) we found only 4 individuals over 3420 m of transect (AI = 1.17/km).

Considering all the studied forests, we found 25 *Furcifer,* 138 *Calumma* and 68 *Brookesia* individuals along a 41645 m river transect, versus 59 *Calumma*, 62 *Brookesia* and no *Furcifer* in 24826 m of forest transects. As an interesting annotation, all the *Furcifer* species (3) and individuals in these forests were detected only along rivers. Some preference was also shown by the *Calumma* species (4), which were more abundant along rivers than in forests (AI = 3.31 and 2.38 chameleons/km, $\chi^2 = 4.23$, $P < 0.05$). In contrast, the terrestrial *Brookesia* dwarf chameleons (4 species) were more frequently found in forest than along rivers (AI = 2.56/km vs 1.63/km) ($\chi^2 = 5.33$, $P < 0.05$).

Age structure

In *F. pardalis* the femur has a layer (cortex) of compact avascular bone delimiting the marrow cavity. This layer, equivalent to the periosteal bone described for other lizards (De Buffrénil & Castanet 2000), consists mainly of parallel fibres. We observed endosteal bone around the medullar cavity only in the adults, while in juveniles it was totally lacking.

Two types of haematoxylinophilic lines were found. A first line was recognised as a typical LAG, since it was strongly chromophilic, well defined, and had a continuous profile. We observed a maximum of two LAGs in the male PBZT 207, which had a SVL of 166 mm (Fig. 5). A few other specimens (two males and one female) had a single LAG, while the others (including all the juveniles) did not show any

Table 3.

Chameleon species in various forests and several transects during field surveys and number of specimens in different habitat types.

	Nosy Be	River transects										Forest transects								
		LB	S	M1	M2	M3	M4	M5	A2	A3		LB	M1	M2	M3	M4	M5	A2	A3	
Forest type	SF	SF	TDS	RF	RF	RF	RF	RF	RF	RF	Tot.	SF	RF	RF	RF	RF	RF	RF	RF	Tot.
Transect length (m)	9250	2333	7366	3420	4480	2720	4680	4773	5020	6853	41645	2333	2713	2120	4140	2107	3300	3080	5033	24826
Furcifer bifidus							1				1									
Furcifer pardalis (adults)	199	5	13	4							22									
Furcifer willsii					1			1			2									
Total *Furcifer* species	199	5	13	4	1		1	1			25									
Calumma boettgeri	11	11							29		40						1			1
Calumma cucullata								3		28	31			1			4			5
Calumma gastrotaenia					16	3	1	2	5	22	49		3	13	5	6	1	4	4	36
Calumma nasuta		2		2	6	3	1	2		2	18			3	5	2	3	3	1	17
Total *Calumma* species	11	13		2	22	6	2	7	34	52	138		3	17	10	8	9	7	5	59
Brookesia betschi										5	5								4	4
Brookesia stumpffi	2	12	24						2		38							4		4
Brookesia superciliaris				3	4	11		1	1	4	24		4	4	26	3		2	11	47
Brookesia vadoni								1			1					1	3			4
Total *Brookesia* species	2	12	24	3	4	11		2	3	9	68		4	4	26	4	3	6	15	62
Overall total	274	30	37	9	27	17	3	10	37	61	206		7	21	36	12	12	13	20	121

River transects = forest at a distance < 50 m from the river; Forest transects = forest at a distance > 50 m from the river. Nosy Be, Nosy Be transect, data obtained during the abundance study along road and external transects; LB, Lokobe, Nosy Be; S, Sahamalaza; M1-M5, Masoala, campsites 1-5; A2-A3, Ambolokopatrika, campsites 2-3. SF = Sambirano forest; TDS = transitional deciduous-Sambirano forest; RF = rainforest.

Table 4.

Number of lines of arrested growth (LAG) among 17 *Furcifer pardalis* from Nosy Be.

Specimen	SVL (mm)	Development	Sex	LAG Number	False lines
PBZT 206	174	Adult	Male	1	+
PBZT 207	166	Adult	Male	2	–
PBZT 186	118	Adult	Male	0	+
PBZT 185	108	Adult	Male	0	–
PBZT 194	102	Adult	Male	1	–
PBZT 195	85	Adult	Male	0	–
PBZT 170	120	Adult	Female	1	–
MRSN R2318	113	Adult	Female	0	–
PBZT 10723	105	Adult	Female	0	–
MRSN R2319	102	Adult	Female	0	–
PBZT 173	91	Adult	Female	0	–
PBZT 189	85	Adult	Female	0	–
PBZT 223	61	Juvenile	undetermined	0	+
PBZT 225	51	Juvenile	undetermined	0	+
PBZT 196	49	Juvenile	undetermined	0	+
MRSN R2892	47	Juvenile	undetermined	0	–
PBZT 10727	37	Juvenile	undetermined	0	–

PBZT, specimen housed in the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo; MRSN, specimen housed in the Museo Regionale di Scienze Naturali, Torino.

LAG. In five femora we also observed less defined lines with an incomplete profile, sometimes associated with the lamellae of the bone matrix (Table 4). As observed for other species (Zug & Rand 1987), we consider such lines as "false" or "supernumerary" lines, without useful meaning for the age estimation.

In the adults showing no LAG (Fig. 5A) the widening of the marrow cavity due to bone remodelling was never larger than the perimeter of the first LAG observed in four adults. This excluded a LAG destruction due to endosteal resorption.

DISCUSSION

Differential habitat partitioning and abundance

One of the most important results of our study is confirmation that the panther chameleon is less abundant in close forests than in open areas and anthropogenic habitats, such as forest borders, river edge or road vegetation. At the Nosy Be sites we found *F. pardalis* in very high numbers along roads, while it was much rarer in external habitats and in natural forests.

The lack of difference in the horizontal detection distances between male and female *F. pardalis* indicates that both the sexes are equally visible during nocturnal inspections, not with standing the males' greater size and brighter colouration dur-

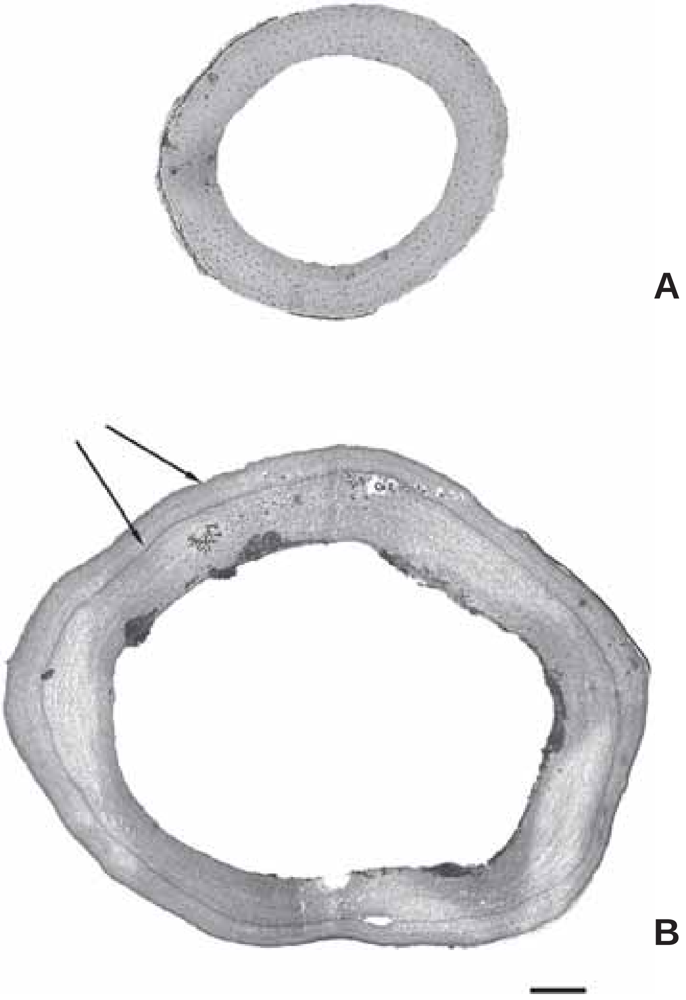

Fig. 5. — Representative femur cross sections (at the diaphyseal level) of *Furcifer pardalis*. (A) female (PBZT 189), SVL = 85 mm, absence of lags; (B) male (PBZT 207), SVL = 166 mm, two LAGs (arrows). Scale bar: 170 μm.

ing the day. As with most chameleons, the animals become pale during the night, and are easily spotted by electric light. On the other hand, the different vertical distribution, with males found at higher elevation than females, suggests that males prefer more elevated posture sites, likely for territorial reasons. Juveniles do not show a significantly different distribution. However, given the relatively small number of juveniles found during our research in relation to the high fecundity in *F. pardalis*, we believe that the overall number of detected juveniles is underestimated.

Some authors depicted the large *Furcifer* species, such as *F. oustaleti* and *F. verrucosus* (Nečas 2004) or *F. pardalis* (Raxworthy 1988), as forest canopy specialists, only secondarily adapted to edge habitats. During our work at Nosy Be and our biodiversity surveys in Sambirano and eastern rainforests we regularly searched for large chameleons on the forest canopy, but only very rarely found them. As further confirmation that the panther chameleon is not a canopy specialist we report that a ten-day study carried out in the forest canopy at Masoala in 1998 yielded only one detected individual (M.E. Walvoord pers. comm.).

In the close forests *F. pardalis* was found only along rivers, as with all the other *Furcifer* species. These chameleons apparently prefer more open habitats and likely follow the vegetation associated with rivers to penetrate the forests. At Nosy Be the ecological conditions and vegetation along roads mimic to a certain extent the situation observed along rivers, and are more favourable for chameleons than in the anthropogenic habitats dedicated to agriculture. We interpret this preference for riverine or "road" vegetation as the effect of a generalised life style and conspicuous sexual dimorphism in *Furcifer*, and the consequent need to colonise open spaces where they may bask and use visual signals directed to females (during courtship) or to males to establish territories.

Unlike the *Furcifer* chameleons the smaller and less sexually dimorphic *Calumma* species appear more related to close forests, although they too show a general trend to aggregate along water bodies. This is in agreement with the observations by Jenkins et al. (2003), who stated that the arboreal chameleons (*Furcifer* and *Calumma*) are generally associated with water bodies and forest streams. The habitat preferences are different for the dwarf and terrestrial *Brookesia* chameleons, which are small and lack remarkable sexual dimorphism (Necas & Schmidt 2004): the studied species were independent of the presence of water bodies and were equally found in riverine and forest habitats. This is evidence of a major niche segregation in these three chameleon genera**.**

Size and life span

Our previous studies demonstrated the applicability of skeletochronology to tropical amphibians and reptiles, and provided further evidence on the utility of this method in assessing natural history traits (Guarino et al. 1998, Andreone et al. 2002, Andreone & Guarino 2003). This is confirmed by the present study on *F. pardalis*¸ for which we were able to detect the lines of arrested growth.

Although an unequivocal correspondence between body size and LAG number is not always evident, other studies have confirmed that the largest specimens are usually also the oldest. The morphometric data indicate that *F. pardalis* at Nosy Be is characterised by a large sex difference in body size, the males being much larger and heavier than females. Within the examined *F. pardalis* sample the only individual with two LAGs was a large male (PBZT 207). This confirms the observation by Jenkins (2000) and Ferguson et al. (2004) that sexual maturity and maximum size is reached within one year, before the formation of the first LAG. Since we did not find LAGs in the analysed females, we argue that they seldom live in nature for longer than one year, while males can surpass this threshold, attaining a much larger size. We interpret the greater male size as an advantage for territorial defence and increased mating success (Stamps 1983).

Conservation

The high densities of panther chameleons observed along the roads and rivers at Nosy Be contrast with the scarcity of individuals in the external habitats and forests. This highlights the conservation value of the buffer vegetation along the studied transects. The importance of riverine vegetation and other marginal habitats has been stressed as being of benefit for many organisms (Burbrink et al. 1998): since large tracts of these habitats still persist at Nosy Be, their management may assure — wherever the original habitats have vanished — the survival of a quite diversified zoological community (Andreone et al. 2003).

Assessing the impact of harvesting of natural amphibian and reptile populations in Madagascar is often hazardous (Raselimanana 2003), since most of the conservation actions were based on distribution, rather than on demographic parameters (Andreone et al. 2005). Indeed, limited selective removal would be counterbalanced to some extent by decreasing natural mortality caused by density-dependent factors. Furthermore, the removal of a component of the population may promote immigration from adjacent populations (Jenkins 2000).

Other life history traits suggest the implementation of management actions at Nosy Be, based upon the species' adaptability and r-oriented strategy: *F. pardalis* prefers edge habitats, has a rapid growth rate and a short life span, confirmed by our age estimates. Furthermore, the females have high fecundity (our counting in three preserved females revealed 16-24 eggs, a number supported by observations by Schmidt (1987) and Müller et al. (2004).

From this evidence, we argue that the allowed collecting rate for *F. pardalis* (2000 individuals per year) has little influence, and likely does not represent *per se* a significant risk to the conservation of the species or, on a lesser scale, to the Nosy Be population. If we consider that around 1000 individuals could be exported each year from Nosy Be, they correspond to about 0.22% of the estimated adult population. Finally, since most of the chameleons were found in the residual vegetation along roads and rivers and that most of the island's agriculture is increasingly oriented towards monoculture (in which biodiversity is constantly reduced), we recommend that the buffer vegetation band along Nosy Be roads be carefully preserved and that the captures of panther chameleons throughout the island be regularly monitored.

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