THE INFLUENCE OF HABITAT TYPE AND STRUCTURE ON THE ABUNDANCE OF *PHELSUMA MADAGASCARIENSIS GRANDIS* (GEKKONINAE) IN NORTHERN MADAGASCAR

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Abstract.—During a nine week period, we studied the abundance of the gecko *Phelsuma madagascariensis grandis*, using visual encounter surveys conducted along 75 transects within each of three habitat types in a semi-humid dry deciduous forest in the north of Madagascar. We observed 91 *P. m. grandis* during our study. Capture rates in village orchards were higher than in clear cut and forest areas. Structural habitat parameters on transects differed significantly between habitats. The orchards and the clear cut areas showed lower structural diversity than forests. Multiple regression analyses showed that the habitat parameters that we measured significantly influence the abundance of *P. m. grandis*. The best regression model explained 57% of the variation in the abundance of *P. m. grandis*. We conclude that high structural diversity is not important for this species. Our results suggest that abundance is positively influenced by higher numbers of trees (perch sites and associated cover) and increases in food resources within orchard habitats. Herein, we discuss the conservation implications of our study for this gecko.

Key Words.—conservation; degradation; Gekkonidae; habitat structure; Montagne des Français; Reptilia

INTRODUCTION

Madagascar has a fascinating fauna with an extraordinary degree of endemism, particularly reptilian species (93%; Glaw and Vences 2000; 2007). Madagascar supports 12 genera representing approximately 90 species of the sub-family Gekkoninae (Bauer 2003; Glaw and Vences 2007), which is one of the most diverse reptile families found on the island (Ikeuchi et al. 2005). *Phelsuma* is the most diverse Malagasy lizard genus (Ikeuchi et al. 2005) and is



FIGURE 1. A Madagascar Giant Day Gecko, *Phelsuma madagariensis grandis*, from the calcareous massif known as Montagne des Français in the extreme north of Madagascar (D'Cruze et al. 2007). (Photographed by Neil D'Cruze).

composed of over 20 species (Glaw and Vences 2007). The majority of *Phelsuma* are endemic to Madagascar (Ikeuchi et al. 2005; Glaw and Vences 2007). However, endemic species and radiations also occur on other islands of the Indian Ocean; especially the Seychelles, Comoros and Mascarene Islands (Glaw and Vences 2007). In Madagascar, reptiles are threatened by a range of different anthropogenic activities that all result in various degrees of habitat destruction (Bauer 2003; Vallan 2003; D'Cruze at al 2007; Glaw and Vences 2007). Furthermore, members of this genus are also subject to additional pressure from collection for the international pet trade due partly to their attractive coloration. Consequently all species currently receive protection on the CITES Appendices (Bauer 2003).

We investigated the abundance and natural history of *P. m. grandis* ([Madagascar Giant Day Gecko], Glaw and Vences 2007; Fig. 1), one of four subspecies currently recognised by Glaw and Vences (2007): *P. m. madagascariensis* (east coast), *P. m. boehmei* (Andasibe region), *P. m. kochi* (northwest and west) and *P. m. grandis* (north). It is important to note that initial analysis indicates that *P. madagascariensis* populations from different localities differ strongly from each other genetically, but the patterns of differentiation do not conform fully to this subspecies division (Glaw and Vences 2007). Furthermore some researchers (based upon the results from ecological niche modelling, mtDNA, and morphology) propose that *P. m. boehmei*

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should be considered a junior synonym of the nominate form *P. madagascariensis*, and that three of these subspecies (*P. m. madagascariensis*, *P. m. grandis*, and *P. m. kochi*), should be elevated to species rank (Raxworthy et al. 2007). In summary, it is clear that a comprehensive taxonomic revision is necessary (Glaw and Vences 2007). All four subspecies inhabit a range of different habitats including both primary forest (rainforest and dry deciduous forest) and anthropogenically altered habitats (banana plantations, palms, and buildings) (Glaw and Vences 2007; Bauer 2003).

In 2005 and early 2006, we spent approximately 12 months studying the herpetofauna in the calcareous massif known as Montagne des Français in the extreme north of Madagascar (D'Cruze et al. 2007). conducted a nine week study focused on the abundance of geckos because: (1) they commonly occur in all habitats throughout a variety of strata and microhabitats; (2) there is limited detailed ecological information about gecko species in Madagascar (Henkel and Schmidt 2000; Bauer 2003; Ikeuchi et al. 2005; Glaw and Vences 2007); and (3) Malagasy reptiles are threatened with extinction (Raxworthy 1988; Raxworthy 2003; Glaw and Vences 2007). By preliminary sampling with visual encounter surveys (VES), we observed seven species of gecko in the study area. Blaesodactylus boivini, Geckolepis maculate (Golden Fish Scaled gecko), Lygodactylus heterurus (Boettger's Ground Gecko) and an unknown species of Uroplatus (Leaf Tailed Gecko) are all nocturnal and predominantly arboreal species (Table 1). Paroedura stumpffi is a nocturnal and predominantly terrestrial species. Phelsuma abbotti checkei (Northwestern Day Gecko) and Phelsuma madagascariensis grandis are diurnal and predominantly arboreal species. These seven species represent half of the 14 species of gecko known from this site (D'Cruze et al. 2007). The largest and most conspicuous diurnal gecko, P. m. grandis commonly occurred at various heights on the trunks and branches of trees of all sizes in all surveyed habitat types. Phelsuma m. grandis was the only species observed in sufficient numbers by VES during this nine week study to allow correlations with habitat characteristics.

MATERIALS AND METHODS

Site description.—The study took place from March to May 2005 in Montagne des Français, a calcareous massif that recently garnered semi-protected status (D'Cruze et al. 2007). It covers approximately 6,114 ha located 12 km south of Antsiranana (12°19.78'S, 49°22.05'E) and is part of the dry bioclimatic zone (Cornet 1974). This zone is subject to marked seasonal variation with a distinct and relatively long dry season followed by a wet season lasting from December to

The annual precipitation of this location is April. usually higher than that received by Antsiranana, which has a mean of 980 mm (Nicoll and Langrand 1989). Consequently, the vegetation therein is characteristic of a more mesic environment and is transitional between mid-altitude rainforest and dry deciduous western forest (Ramanamanjato et al. 1999; D'Cruze et al. 2007). A variety of habitats occur at Montagne des Français as past and recent human activities have altered the landscape. Recent examples outlined by D'Cruze et al. (2007) include: (1) agricultural clearance for maize, rice and orchard fruit cultivation; (2) charcoal production; (3) timber production; and (4) zebu grazing. These activities degrade or clear large areas of forest. For comparison, we chose several forest areas subject to minimal anthropogenic disturbance, several clear cut sites, and several orchard areas located close to human habitation.

Sampling procedures.—We collected data using VES (Campbell and Christman 1982; Corn and Bury 1990). We used teams of five trained volunteer observers led by an experienced researcher to conduct the VES. Each team hiked every designated transect for one hour, searching within an area 10 m x 100 m along each of the transect lines for geckos. We recorded the number of geckos encountered along with time elapsed during the survey. We distributed 25 line transects in each of the three habitat types to total 75 transects across all three habitats. In most cases, we separated line transects by at least 100 m, but six of them in the forest areas were less than 50 m apart. We regularly observed and briefly handled geckos in the field.

Habitat Parameters.—We recorded structural habitat characteristics along all transects. These parameters included (1) the number of anthropogenic structures (e.g., small wooden structures, meeting halls, sleeping quarters, etc); (2) termitarias; (3) dead wood fragments on the ground (diameter > 10 cm and length > 50 cm = logs); (4) shrubs (saplings and vegetation height < 1 m and diameter of main trunk where identifiable < 10 cm); and (5) trees (height > 3 m and diameter of main trunk > 10 cm). We collected six litter samples of 1 m² in each of the 75 transect areas. We estimated the amount of litter in each sample by pressing the litter samples in a bucket of known circumference and then measuring the height of the column. We used this data to mathematically calculate the volume of litter. measured foliar cover for each of the 75 transects by placing ten 0.1 m² (20×50 cm) microplots centered on equidistant points along each transect at least 5 m from the beginning and end of the transect (Daubenmire 1959). We estimated foliar cover in each microplot in 10% cover classes. We gave microplots with an estimated cover < 1% a cover value of 0.5%.

TABLE 1. Natural history of the seven gecko species encountered during this study in Northern Madagascar (Glaw and Vences 2007).

Species	Max Total Length (mm)	Diurnal/ Nocturnal	Terrestrial/ Arboreal	Dorsal Coloration	Reproduction
Blaesodactylus boivini	300	Diurnal & Nocturnal	Arboreal	Dark	Oviparous
Geckolepis maculata	138	Nocturnal	Arboreal	Dark	Oviparous
Paroedura stumpffi	143	Nocturnal	Terrestrial	Dark	Oviparous
Lygodactylus heterurus	50	Diurnal	Arboreal	Cryptic	Oviparous
Phelsuma abbotti checkei	150	Diurnal	Arboreal	Bright	Oviparous
Phelsuma madagascariensis grandis	300	Diurnal	Arboreal	Bright	Oviparous
Uroplatus sp.	185	Nocturnal	Arboreal	Highly Cryptic	Oviparous

Afterwards, we calculated the average cover for each in the model. transect.

Statistical Analyses.—We conducted all statistical analyses with SYSTAT version 12 (SYSTAT Software Inc., Chicago, Illinois, USA). We used the Kruskal-Wallis test to test if the three habitat types (i.e., forest, clear cut and orchard) were significantly structurally different from each other. We explored associations between the abundance of *P. m. grandis* and the different habitat characteristics using the Pearson correlation coefficient (*r*). We tested all variables for normality using Shapiro-Wilk test (Shapiro and Wilk 1965; Royston 1982) and we log₁₀ transformed non-normal variables prior to analyses (Neter et al. 1996).

We developed P. m. grandis abundance models with and without habitat types considered as predictors using stepwise multiple regression analysis. We identified the best model from a set of candidate models using Akaike's Information Criterion (AIC) and information theoretic approaches; the model with the lowest AIC represented the best model (Burnham and Anderson 2002). Before conducting regression analyses, we tested predictor variables for multicollinearity (Neter et al. 1996) by examining cross-correlations among them (Table 2). We did not include highly correlated variables (i.e., $r > \pm 0.75$) in the same model. For example, tree number and foliar cover were highly correlated (r = 0.80; Table 2); therefore, we excluded tree number from the analysis and included foliar cover

in the model. In regression analyses, we coded categorical variables (e.g., habitat types) as zero/one dummy variables. We used an Alpha = 0.05 to test the significance in all cases.

RESULTS

We observed 141 geckos along the 75 visual encounter survey transects. *Phelsuma m. grandis* was the most abundant species (N = 91 specimens observed). We observed six of these in the forest areas, seven in the clear cut, and 78 in the village orchards. We saw between 0-9 *P. m. grandis* per transect among all 75 transects. Other species included *Blaesodactylus boivini* (N = 17), *Geckolepis maculata* (N = 7), *Lygodactylus heterurus* (N = 17), *Paroedura stumpffi* (N = 2), *Phelsuma abbotti checkei* (N = 5); and *Uroplatus* sp. (N = 2).

Differences in the number of *P. m. grandis* between the three habitats were significant (H = 36.49; Table 3). All habitat characteristics varied considerably within the three habitats but were also significantly different among habitats (Table 3), which suggests that habitat types are structurally different. The abundance of *P. m. grandis* was positively correlated with the number of anthropogenic structures, foliar cover, number of trees, and orchard habitat type. The abundance of *P. m. grandis* was negatively correlated with litter (Table 2). However, we detected no significant relationships between the abundance of *P. m. grandis* and logs,

TABLE 2. Cross-correlations (Pearson correlation coefficient; r) between response and predictor variables. Variables were \log_{10} transformed where appropriate. The correlations were significant at alpha = 0.05 unless otherwise stated; ns is non-significance (alpha > 0.05).

	Number of	Anthropogenic structure	Shrubs	Foliar cover (%)	Litter	Number of Logs	Termitarias	Number of trees	Forest	Clear
Anthropogenic	specimens 0.25	Structure	Siliuos	(70)	(cm)	of Logs	Termitarias	of tiees	rotest	cut
structure	0.23									
Shrubs	-0.19 ^{ns}	0.006^{ns}								
Foliar cover (%)	0.27	-0.01 ^{ns}	0.19^{ns}							
Litter (cm)	-0.53	-0.20 ^{ns}	0.16^{ns}	0.20^{ns}						
Logs	0.17^{ns}	$0.05^{\rm ns}$	0.31	0.67	0.30					
Termitarias	-0.20 ^{ns}	-0.10 ^{ns}	$0.20^{\rm ns}$	0.21^{ns}	0.55	0.45				
Number of trees	0.43	$0.06^{\rm ns}$	$0.10^{\rm ns}$	0.80	0.02^{ns}	0.73	0.29			
Forest	-0.33 ^{ns}	-0.24 ^{ns}	0.21^{ns}	0.63	0.77	0.59	0.57	0.46		
Clear cut	-0.37 ^{ns}	-0.04 ^{ns}	-0.03^{ns}	-0.80	0.05^{ns}	-0.58	-0.14 ^{ns}	-0.81	-0.50	
Orchard	0.69	0.28^{ns}	-0.18 ^{ns}	0.17^{ns}	-0.82	-0.01 ^{ns}	-0.44	0.35^{ns}	-0.50	-0.50

shrubs, termitarias, forest areas, or clear cut areas (Table 2).

The multiple regression model that included habitat parameters provided the best model (model-2; AIC = -20.12; Table 4) as compared to the model without habitat parameters (model-1; AIC = -8.31; Table 4). This emphasizes the important influence of habitat types, in addition to habitat characteristics, on the abundance of *P. m. grandis*. The best model explained 57% of the variation in *P. m. grandis* abundance (model-2; Table 4). Orchard habitat type was one of the best predictors of abundance of *P. m. grandis* (partial $r^2 = 0.483$; model-2; Table 4), which suggests that orchards provide a critical habitat for *P. m. grandis*.

DISCUSSION

With 14 gecko species living sympatrically in the study area, Montagne des Français appears to have one of the most diverse gecko communities in Madagascar. The apparent dominance of P. m. grandis may reflect biases of the VES method. This species is large, brightly colored, diurnal, and is known to be active irrespective of the season (D'Cruze et al. 2007); so we detected it easily. The other species encountered during this study have one or more of the following characteristics that limit their detection with VES. They are (1) small; (2) more cryptic; (3) predominantly nocturnal; and (4) predominantly terrestrial (Table 1). We acknowledge that additional survey techniques and further studies are required in order to draw conclusions about what affects gecko community structure and ecological divergence at our study site.

We found that the number of *P. m. grandis* is not evenly distributed among the three habitats. Structural characteristics of each habitat appeared to influence our observation rates of this gecko species. The results of

TABLE 3. Comparison of habitat types by measured habitat characteristics (Kruskal-Wallis test statistic = H). Reject/accept = reject or accept the hypothesis of equal population means.

Comparison of			Probability	
habitat types by	Н	df	(P)	Conclusion
Specimens (N)	36.49	2	< 0.0001	Reject
H structure	7.54	2	0.023	Reject
Shrubs	11.20	2	0.004	Reject
Foliar cover (%)	56.75	2	< 0.0001	Reject
Litter (cm)	63.16	2	< 0.0001	Reject
Logs	33.95	2	< 0.0001	Reject
Termitarias	26.57	2	< 0.0001	Reject
Trees (N)	39.60	2	< 0.0001	Reject

this study are consistent with natural history observations reported elsewhere for this species (Henkel and Schmidt 2000; Bauer 2003; Ikeuchi et al. 2005; Glaw and Vences 2007). For example, *P. m. grandis* is known to occur in various plantations and orchards (Glaw and Vences 2007; Bauer 2003). Interestingly, in our study we found that this species was most abundant in orchard habitat type and that this habitat type was the most important factor influencing the abundance of *P. m. grandis*. The orchard sites contain a large number of a few cultivated fruit tree species. Local farmers regularly maintain and clear these areas to access the fruiting trees. As a result, orchards have a relatively low number of ground level shrubs and shallow litter depth.

Our study suggests that abundance of *P. m. grandis* is positively correlated with foliar cover and the number of trees. We hypothesize that this might be because diurnal arboreal lizards select and utilize perch microhabitats based on a number of factors including thermoregulatory value (Ramírez-Bautista and Benabib 2001), density of prey items (Reagan 1986), interspecific competition (Evans and Evans 1980), intraspecific competition (D'Cruze and Stafford 2006), and the effects of

TABLE 4. The best regression models linking patterns of *Phelsuma madagascariensis grandis* gecko abundance (n = 75) with measures of habitat characteristics without and with habitat types included. Variables were transformed where appropriate. AIC is Akaike's Information Criterion. The independent (or predictor) variables in the models are arranged in order of their decreasing influence on the abundance of *P. m. grandis*.

ndependent variable	Parameter	Et D	Partial r ²	Model	
	estimate	Factor P	Partial r	Adj. r^2 , F , P	AIC
Model1: Only habitat characteristi	cs				
Litter	- 0.244	< 0.0001	0.283	$r^2 = 0.49$,	-8.31
Trees (N)	0.188	< 0.0001	0.189	$F_{4,70} = 18.51,$	
Shrubs	- 0.076	0.0540	0.025	P < 0.0001	
Anthropogenic structure	0.364	< 0.1280	0.017		
Model2: Habitat characteristics pl	us habitat types				
Orchard habitat	0.212	0.0143	0.483	$r^2 = 0.57$,	-20.12
Foliar cover (%)	0.190	0.0105	0.041	$F_{5,69} = 20.33,$	
Number of logs	0.152	0.0114	0.033	P < 0.0001	
Forest habitat	- 0.347	0.0020	0.021		
	- 0.085	0.0279	0.019		

morphology (Losos and Sinervo 1989). This species may be more abundant in orchard sites because, although mainly insectivorous, members of this genus are able to consume nectar, pollen, and fruit (Murphy and Myers 1996; Fölling et al. 2001; Hansen et al. 2007). Alternatively the fruit may attract higher numbers of arthropod prey that support larger populations. In addition, this large and robust gecko may reduce the abundance of the closely related *Phelsuma abotti*. Unlike *P. m. grandis*, this smaller *Phelsuma* species (TL 130 – 150 mm; Glaw and Vences 2007) occurred mainly in the forest habitats.

The orchard areas occur at the edge of human habitation and associated human structures. We presume that these areas may also favor this species by proving additional perch sites (Glaw and Vences 2007; Bauer 2003) and cover from predators such as birds, snakes, primates, and other mammals (Meier 1977; Bauer and Russell 1992).

Conservation implications.—In view of the measured habitat parameters, the orchard sites supporting P. m. grandis have a more moderate level of structural diversity than the clear cut or the forested sites. Therefore, unlike many other gecko species endemic to Madagascar that are solely restricted to forest habitat, e.g., members of other genera such as *Uroplatus* or even more closely related species from the same genus such as Phelsuma antanosy, (Glaw and Vences 2007; Bauer 2003), high structural diversity is less important for the survival of this species. Therefore, we conclude that unlike these other species, P. m. grandis populations may be less vulnerable to extinction because of continued habitat destruction. However, this species was not abundant in all of the different types of anthropogenically altered habitats present in this region (e.g., clear cut areas). Furthermore, members of this particular genus have additional pressures from collection for the international pet trade. Consequently, we strongly recommend a detailed taxonomic, ecological, and conservation focused review of this species and the entire *Phelsuma* genus in Madagascar.

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APPENDIX

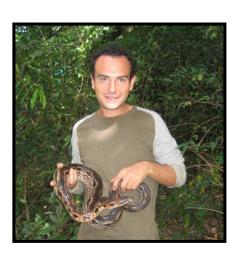
Voucher specimens from Montagne des Français.

- 1. Between "Kings Lodge" and French Fort: Blaesodactylus boivini (ZSM 534/2000, 999/2003, 263/2004); Geckolepis maculata (ZSM 523/2000, 998/2003); Lygodactylus heterurus trilineigularis (ZSM 915/2003); Paroedura stumpffi (ZSM 635/2000); Phelsuma abbotti chekei (ZSM 528/2000); Phelsuma madagascariensis grandis (ZSM 524/2000); Uroplatus sp. (ZSM 525/2000, 526/2000, 1000/2003.
- 2. Andavakoera: Lygodactylus heterurus trilineigularis (ZSM 308/2004).

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