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# PATTERNS OF REPTILE DIVERSITY LOSS IN RESPONSE TO DEGRADATION IN THE SPINY FOREST OF SOUTHERN MADAGASCAR

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***Abstract.*—Southern Madagascar, with its semi-arid climate, contains a high number of endemic species. However, the spiny forest is under severe human pressure with a high rate of habitat loss. To understand how reptiles are affected by degradation, we surveyed sites with different levels of habitat degradation in the recently established Ifotaka North Protected Area in the Mandrare Valley. We used species richness, abundance, and microhabitat use of reptiles to examine which species and/or groups of species are most prone to disappear with progressive anthropogenic disturbance. Microhabitat requirements can differ even within closely related species and general patterns for different taxonomic groups (families) were not present. However, combining species with similar microhabitat-use (fossorial, terrestrial, and arboreal), we found patterns in response to degradation. Fossorial species disappeared first, followed by arboreal species. The least sensitive group was the terrestrial lizards, which contains many synanthropic generalists. Anthropogenic effects were generally negative but not in a continuous way. Diversity loss was present even after slight habitat modification as long as some factors (e.g., trees, leaf litter) were unchanged. Even highly degraded areas represented valuable habitats for most species. Although these areas are not inherently suitable as permanent habitats, these areas can be useful as corridors or as stepping stones between fully protected zones.**

*Key Words.*—habitat loss; Ifotaka Nord Protected Area; lizards; microhabitat use; snakes; tortoises

## INTRODUCTION

Habitat loss and degradation are major drivers for species extinction and biodiversity loss (Agarwal et al. 2005). The Malagasy biota with their high rate of endemism is known to suffer from ongoing habitat loss (Scott et al. 2006; Irwin et al. 2010; D'Cruze and Kumar 2011). With a deforestation rate of up to 1.7%/y (Harper et al. 2007), forest clearance in Madagascar remains among the highest in the tropics. As a consequence, the island has been declared one of the world's hottest biodiversity hotspots (Myers et al. 2000). Habitat modification such as degradation and fragmentation affects species richness generally in a negative way (Lehman et al. 2006; Scott et al. 2006; Allnutt et al. 2008). However, because different taxa are affected in different ways, there is a demand for detailed studies on responses of specific taxa to degradation. Knowledge of species ecology and of species sensitivity to anthropogenic disturbance is an important prerequisite for conservation management to create buffer zones and corridors between protected areas (Irwin et al. 2010).

Population declines in different taxa such as lemurs (Ganzhorn et al. 2001) and amphibians (Andreone et al. 2005) are alarming and many species are ranked as vulnerable or endangered because of a shrinking habitat (Irwin et al. 2010). Additionally, the reptile fauna in Madagascar suffers from habitat loss, which is why the IUCN Global Reptile Assessment (Böhm et al. 2013) has designated Madagascar as a centre of threatened species richness. An assessment of the extinction risk of Malagasy reptiles has recently shown that 39% of the data sufficient species are threatened with extinction, although some families contained more threatened species than others (Jenkins et al. 2014). Reptiles are a diverse group in all respects (morphological and ecological), with even closely related species responding differently to degradation (Irwin et al. 2010). Therefore, patterns of species distribution and habitat requirements have to be determined on the genus or species level (D'Cruze and Kumar 2011). Highly specialized forest species (e.g., *Phelsuma antanosy*; Raxworthy and Nussbaum 2000) are not able to survive in modified habitats, whereas their close relatives seem to prefer degraded forests and villages (e.g., *Phelsuma lineata*; Lehtinen et al. 2003). The population decline of the critically endangered Spider Tortoise (*Pyxis arachnoides*) correlates with the vegetation loss but other threats, such as poaching and pet trade, might accelerate the process of local extinction in this species (Walker 2010; Walker et al. 2012). Despite obvious disappearances of forest-specialized species after forest destruction, there is still a lack of understanding of fragmentation and degradation effects on the survival of reptiles (Jenkins et al. 2014).

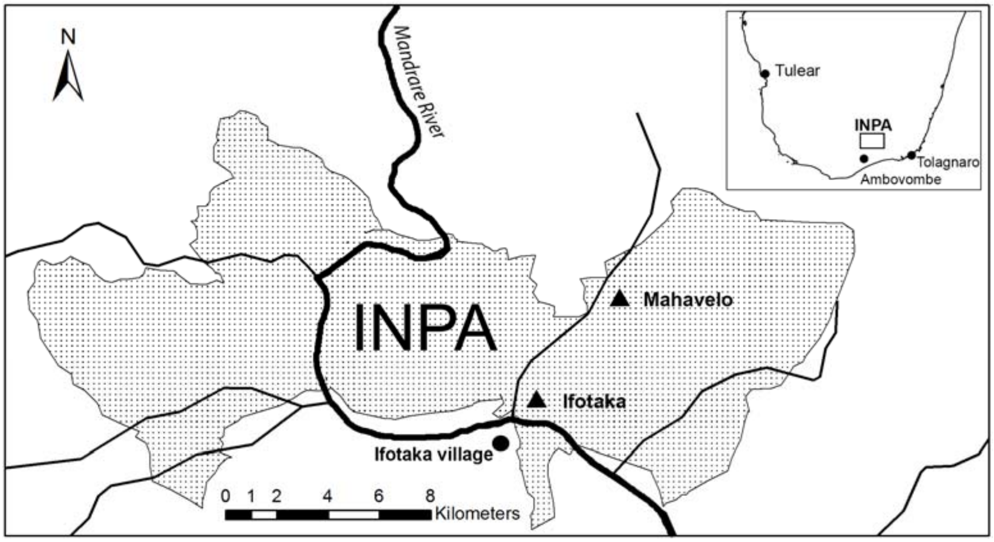


**FIGURE 1.** Map of the Ifotaka North Protected Area (stippled) in southeast Madagascar. Black circle: Ifotaka village; Black triangles: study areas with survey sites (map adapted and modified from: IUCN and UNEP-WCMC (2014), The World Database on Protected Areas (WDPA) [On-line]. Cambridge, UK: UNEP-WCMC. (Available at www.protectedplanet.net [Accessed 17 July 2014]).

The spiny forest in southern Madagascar provides habitat for a variety of endemic reptile species, but these species are under severe human pressure (Scott et al. 2006). Because southern Madagascar is a semi-arid region, possibilities for agriculture are limited. Selective logging for the production of timber and charcoal, cattle grazing, and unsustainable slash and burn agriculture are major threats for the flora and fauna (World Wildlife Foundation, unpubl. report).

To counter the ongoing habitat loss, the establishment of new protected areas has been promoted since 2003 (Borrini-Feyerabend and Dudley 2005). These include the Ifotaka Nord Protected Area (INPA), which is located in the Mandrare Valley about 40 km north of Ambovombe. This protected area is designed to integrate local people into management and conservation. It includes intact spiny forest (core zone) as well as restoration zones, pasture land, and villages (World Wildlife Foundation, unpubl. report). We began a comprehensive flora and fauna conservation monitoring program in 2011, during which we investigated reptile assemblages in different zones of the INPA with differently degraded habitats.

The aim of our study was to find out whether species reactions are apparent from incipient degradation or if they tolerate certain anthropogenic disturbances.

## MATERIALS AND METHODS

***Study site.***—This study was conducted in the spiny forest of the INPA in Southern Madagascar (24°41'–24°50' S; 46°14'–45°57' E) between June and August 2011 (Appendix 1). The semi-arid climate is seasonal with a cool dry season (May-November) and a hot rainy season (December-April). Almost the entire precipitation of 400 mm p.a. occurs during the austral summer months. The INPA comprises an area of 22,256 ha, which is divided into a priority conservation zone (36%), traditionally protected sacred forest (3%), zones with usage rights (31%), and buffer and restoration zones (30%). The largest portion of the INPA consists of spiny forest with trees of six to eight meters height and spiny shrub (Raselimanana 2008). Only a few patches of gallery forest can be found along the Mandrare River and its temporary contributories (World Wildlife Foundation, unpubl. report).

We investigated differently degraded sites in two zones of the INPA during this survey (Fig. 1). The sites of Ifotaka consist of more or less degraded spiny forest because of its proximity to the village of Ifotaka. Only a small portion of the forest is traditionally protected due to the presence of tombs. The soil consists of clay and sand without larger rock accumulations. The sites of Mahavelo (approximately 5 km northeast of Ifotaka Village) lie within the priority conservation zone of the INPA, surrounded by degraded spiny forest. This conservation zone is under full protection and consists of intact forest fragments and also some overgrown hatsake (slash and burn agriculture). The soil is rockier in Mahavelo with high limestone cliffs at the northern and western border of the INPA.

We assigned sites to five different degrees of degradation in this area: (1) undisturbed forest with no obvious human impact, including a lot of dead wood and leaf litter; (2) slightly disturbed forest with some traces of grazing zebus or goats and former selective logging;

(3) moderately disturbed forest with regular cattle grazing and recent traces of selective logging; (4) highly disturbed forest with regular cattle grazing, intensive logging, few remaining trees (mainly *Alluaudia* and *Euphorbia*), shrub, a high number of sisal plants and *Opuntia* and little deadwood; and (5) cleared area with no deadwood, almost no trees, no leaf litter and *Opuntia* and sisal as the dominant plant species. We only used data from the spiny forest and excluded the gallery forest because reptile diversity is generally higher in riparian habitats (D'Cruze et al. 2009) and the species composition differs markedly.

***Survey methods.—***We established 12 transects within the two different areas (Ifotaka and Mahavelo) of the INPA. Each transect was 250 m long and 10 m wide (2,500 $m^2$) and was searched three times: twice in the morning (between 0900 and 1200) and once again in the afternoon (between 1300 and 1500) by six investigators. We spent a similar amount of time for each search (1h/transect). We conducted active searching with refugia examination under rocks, in leaf litter, on trees, in crevices, under bark, in tree holes, and in leaf axils. We recorded the number of individuals for each species found during the different transect searches. All species were identified directly in the field according to Glaw and Vences (2007).

For a better comparison of the transect results, we conducted the survey only on days with similar weather conditions (no wind, sunny, with no clouds) to avoid biased results caused by different activity patterns of the reptiles (Sun et al. 2001). It should be noted that in contrast to other herpetological studies in Madagascar (e.g., Raxworthy and Nussbaum 1996; Andreone et al. 2001), we investigated the reptile assemblages during the dry season where the overall activity is reduced. Our intention was not to receive the highest individual and species numbers in this region but to have constant and comparable weather conditions for a firm analysis, which is given during the dry season. Pitfall trapping (Ribeiro et al. 2008) and artificial ground and the use of tree cover objects (Joppa et al. 2009) did not lead to results that could be analyzed. For this reason, we excluded these methods from our analysis and compiled the results together with *ad libitum* findings in a comprehensive species list for the INAP (Appendix 1).

***Data analysis.—***For a comparison of species richness (number of species) in each transect and degradation category respectively, we used a presence-absence-matrix. To analyze species diversity, we used the Shannon Index (Spellerberg and Fedor 2003) and Shannon Evenness (Greig-Smith 1983). We divided the reptile assemblages into three groups with similar microhabitat use (arboreal, terrestrial, and fossorial) to analyze degradation effects on species with different habitat requirements. We calculated the Spearman correlation using IBM SPSS Statistics (Version 20.0, Armonk, New York, USA) to investigate relationships between the degree of degradation, species richness, and species diversity. Our analysis was based on the relative abundance of species, calculated with maximum numbers of individuals per transect for each species.

## RESULTS

We recorded 26 reptile species during the standardized transects in the spiny forest. These represent 70% of the overall species richness of 37 species (Appendix 2) from the INPA. In total, we found 654 individuals of 26 reptile species comprising two fossorial, 16 terrestrial, and eight arboreal species (Table 1). The average abundance was 54.5 individuals of 10.6 species per transect. However, there was a high variance in species richness from three up to 16 species, depending on the habitat condition. The accumulated species richness for the intact forest (cat. 1) was 22 species (85%), whereas the cleared area (cat. 5) only comprised seven species (27%). The most dominant species was the terrestrial lizard *Trachylepis elegans*, which accounted for up to 80% of all individuals. Most recorded species were restricted to the dry western and south-western portion of the island, respectively. Only four were generalists (*Dromicodryas bernieri*, *Hemidactylus mercatorius*, *Trachylepis elegans*, and *Trachylepis gravenhorstii*) occurring all over the island, even in rain forest habitats (Glaw and Vences 2007).

The overall species richness was negatively correlated with an increasing degree of degradation (Fig. 2). However, the decline in species richness ($r_s$ = -0.68; $P <$ 0.05; n = 12), Shannon diversity index ($r_s$ = -0.62; $P <$ 0.05; n = 12) and Shannon Evenness ($r_s$ = -0.49; $P$ = 0.11; n = 12) was not continuous. First, we observed a steep decrease in species richness and diversity from intact forest to slightly disturbed forest. Then, species numbers and species diversity increased again; however, the variance between the different transects increased as well. Eventually, the cleared area (degradation degree 5) had the lowest species numbers with a high dominance of *Trachylepis elegans*. We found the highest species richness and diversity in the conservation zone (core area) in Mahavelo and the lowest in the restoration zone in Ifotaka.

Comparing the mean species numbers for each degradation category, there was decreasing species richness in all taxa from intact to disturbed forest (Fig. 3). After a peak with high species numbers in the moderately degraded forest (cat. 3), the species richness declined to a only six species in cleared areas. Individual numbers also decreased with increasing degradation. The decline was most pronounced in geckos, where species richness was significantly

**TABLE 1.** Reptile species list of the Ifotaka North Protected Area recorded with standardized transects. The Spearman rho shows whether the species response is positive (increasing abundance of individuals) or negative (decreasing abundance of individuals) to increasing degradation (from 1: "undisturbed forest" to 5: "cleared area"). RE: regionally endemic; E: endemic to Madagascar; NE: non endemic; a: arboreal; f: fossorial; t: terrestrial; D: diurnal; N: nocturnal; n.s.: not significant.

| Species | Geographical range | Microhabitat use | Total no. of individuals | Degradation category/ mean no. of individuals per transect ($2,500 m^2$) | | | | | Spearman rho ($r_s$) | Significance |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | | |
| TESTUDINIDAE | | | | | | | | | | |
| *Astrochelys radiata* | RE | t/D | 1 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | -0.178 | n.s. |
| PSEUDOXYRHOPHIIDAE | | | | | | | | | | |
| *Dromicodryas bernieri* | E | t/D | 2 | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 0.066 | n.s. |
| *Lycodryas pseudogranuliceps* | E | a/N | 2 | 0.3 | 0.0 | 0.0 | 0.5 | 0.0 | -0.099 | n.s. |
| PSAMMOPHIIDAE | | | | | | | | | | |
| *Mimophis mahfalensis* | E | t/D | 6 | 0.3 | 0.5 | 0.7 | 1.0 | 0.0 | -0.051 | n.s. |
| OPLURIDAE | | | | | | | | | | |
| *Oplurus cyclurus* | E | a/D | 23 | 3.0 | 3.5 | 0.7 | 2.5 | 0.0 | -0.639 | < 0.05 |
| *Oplurus quadrimaculatus* | E | t/D | 5 | 0.7 | 0.0 | 0.3 | 1.0 | 0.0 | -0.068 | n.s. |
| *Oplurus saxicola* | E | t/D | 11 | 2.3 | 0.0 | 0.7 | 1.0 | 0.0 | -0.529 | n.s. |
| CHAMAELEONIDAE | | | | | | | | | | |
| *Furcifer verrucosus* | E | a/D | 1 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.045 | n.s. |
| GERRHOSAURIDAE | | | | | | | | | | |
| *Tracheloptychus madagascariensis* | E | t/D | 72 | 7.0 | 8.0 | 5.7 | 7.5 | 1.5 | -0.438 | n.s. |
| *Zonosaurus laticaudatus* | E | t/D | 2 | 0.3 | 0.0 | 0.0 | 0.5 | 0.0 | -0.099 | n.s. |
| SCINCIDAE | | | | | | | | | | |
| *Madascincus igneocaudatus* | E | f/D | 1 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | -0.401 | n.s. |
| *Trachylepis aureopunctata* | E | t/D | 16 | 0.3 | 2.0 | 1.3 | 1.0 | 2.5 | 0.582 | < 0.05 |
| *Trachylepis dumasi* | RE | t/D | 17 | 2.0 | 2.0 | 1.7 | 1.0 | 0.0 | -0.492 | n.s. |
| *Trachylepis elegans* | E | t/D | 380 | 28.7 | 40.0 | 36.7 | 26.0 | 26.0 | -0.050 | n.s. |
| *Trachylepis gravenhorstii* | E | t/D | 2 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.267 | n.s. |
| *Trachylepis vato* | E | t/D | 51 | 10.3 | 1.0 | 2.7 | 3.5 | 1.5 | -0.291 | n.s. |
| *Voeltzkowia lineata* | E | f/D | 1 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | -0.401 | n.s. |
| GEKKONIDAE | | | | | | | | | | |
| *Geckolepis typica* | E | a/N | 18 | 2.3 | 1.5 | 1.7 | 1.0 | 0.5 | -0.526 | n.s. |
| *Hemidactylus mercatorius* | NE | a/N | 14 | 1.0 | 2.5 | 1.0 | 1.0 | 0.5 | -0.205 | n.s. |
| *Lygodactylus decaryi* | RE | a/D | 5 | 1.3 | 0.0 | 0.3 | 0.0 | 0.0 | -0.502 | n.s. |
| *Lygodactylus tuberosus* | E | a/D | 3 | 0.3 | 1.0 | 0.0 | 0.0 | 0.0 | -0.483 | n.s. |
| *Lygodactylus verticillatus* | E | a/D | 7 | 2.0 | 0.0 | 0.3 | 0.0 | 0.0 | -0.526 | n.s. |
| *Paroedura androyensis* | RE | t/N | 2 | 0.3 | 0.0 | 0.3 | 0.0 | 0.0 | -0.264 | n.s. |
| *Paroedura bastardi* | E | t/N | 1 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | -0.401 | n.s. |
| *Paroedura picta* | E | t/N | 2 | 0.3 | 0.0 | 0.3 | 0.0 | 0.0 | -0.264 | n.s. |
| *Phelsuma mutabilis* | E | a/D | 9 | 0.7 | 1.0 | 0.3 | 1.5 | 0.5 | 0.030 | n.s. |
| Total | | | 654 | 66 | 64 | 56 | 50 | 33 | -0.620 | < 0.05 |

correlated with degradation ($r_s$ = -0.88; $P < 0.01$; n = 12). This pattern was similar in all taxonomic groups but in contrast to species numbers, individual numbers decreased continuously.

Arboreal species were more prone to disappear with increasing degradation (arboreal: $r_s$ = -0.77; $P < 0.01$; n = 12; terrestrial: $r_s$ = -0.54; $P$ = 0.07; n = 12; fossorial: $r_s$ = -0.40; $P$ = 0.20; n = 12). Most skinks belong to the terrestrial species, whereas geckos represent the majority of arboreal species (Table 1). The two fossorial species were only present in the intact forest and completely absent in disturbed areas (Fig. 4). Degradation did not affect terrestrial lizards as much as arboreal and fossorial species, respectively. Species numbers remained high until the area was completely cleared. Arboreal reptiles were influenced in a more continuous way.

## DISCUSSION

The species assemblages in the INPA were typical for spiny forest in this region with high numbers of terrestrial skinks (*Trachylepis*) and only a single *Phelsuma* species. With this comprehensive survey, we were able to add 12 reptile species to the known species list. The total number of 37 species was higher than expected but not extraordinary for the spiny forest (Raselimanana 2008).

As expected, reptile species richness and diversity decreased with increasing degradation. This is a general pattern and can be observed in several taxa and all functional groups (Gardner et al. 2007; Irwin et al. 2010). However, neither species richness nor species diversity decline continuously. Habitat requirements differ among species (Glaw and Vences 2007), as does the sensitivity to habitat modification (D'Cruze and Kumar 2011). After an initial decline in species richness, ongoing degradation seemed to have positive effects on lizard diversity. Intact forest contained high numbers of forest specialists and fewer generalists. Vitt et al. (1998) showed that selective logging leads to a decrease in canopy cover and higher insolation, which has a strong effect on the microclimate in these forest gaps. In our case, synanthrophic species such as *Trachylepis elegans, T. aureopunctata,* and *Tracheloptychus madagascariensis* benefited from degradation, seen as an increase in abundance. Similar to this edge effect, this supported forest-avoiding species but still provided suitable habitat for some of the forest specialists (Lehtinen et al. 2003), especially arboreal species. Studies have shown that vegetation structure complexity has a strong effect on lizard communities (Read 2002; James 2003) and selective logging can support this complexity up to a certain degree. However, high habitat complexity did not equate to high ecological significance in our study. Threatened species like *Astrochelys radiata*, *Paroedura androyensis,* and *Trachylepis dumasi* disappeared after initial habitat modification and we observed an increase in abundant synanthropic species with low habitat requirements. Hence, species richness at intermediate degradation increased at the expense of forest specialists but favoured generalist species.

We found terrestrial reptiles to be the group least affected by degradation. *Trachylepis elegans* is one of the most common lizards in Madagascar, especially in degraded and cleared habitats (Scott et al. 2006; D'Cruze and Kumar 2011). This lizard, other species of the genus *Trachylepis* (e.g. *T. gravenhorstii, T. aureopunctata*), and *Tracheloptychus madagascariensis* dominated areas with human impacts and their abundance increased with degradation. Similar to other synanthropic lizard communities from mainland Africa (Wasiolka and Blaum 2011), their ecological flexibility and lack of interspecific competition allows them to inhabit areas with adverse environmental conditions (e.g., higher insolation, limited resource availability, and higher predation risk). In this context, the thermal environment could be a key factor for the distribution of

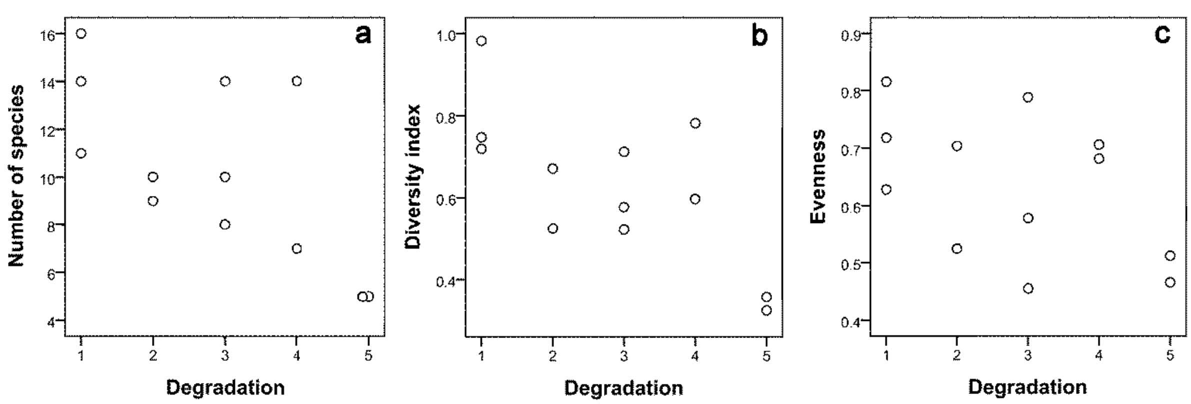


**FIGURE 2.** Correlation between habitat degradation (from 1: "undisturbed forest" to 5: "cleared area") and a) species richness, b) Shannon Diversity index, and c) Shannon Evenness of the reptiles in the Ifotaka North Protected Area in southeast Madagascar.

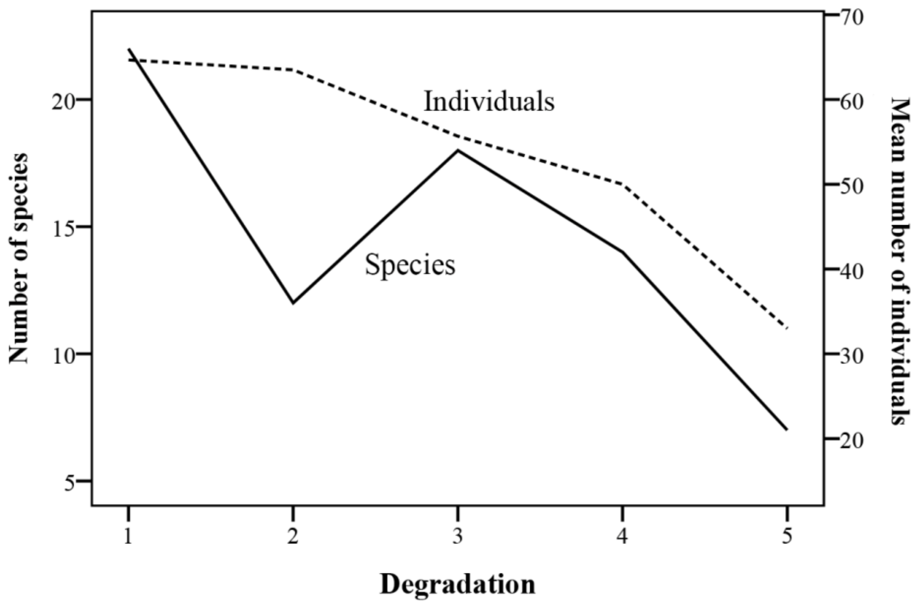


**FIGURE 3**. Number of reptile species and individuals at different habitat degradation categories (from 1: "undisturbed forest" to 5: "cleared area") in the Ifotaka North Protected Area in southeast Madagascar.

ectothermic species (Kearney et al. 2009; Sinervo et al. 2010) and specific microhabitat use can increase or decrease the chance of survival. Studies on the impact of tree harvesting have shown that man-made forest gaps lead to more intense insolation and higher temperatures. Consequently, heliothermic lizards use gaps to achieve their preferred body temperature for optimal foraging success, whereas thigmothermic lizards, which often have lower preferred body temperatures, avoid these gaps (Vitt et al. 1998). A further issue for species distribution in the INPA is microhabitat structure and soil consistency. Some of the terrestrial lizards are obligatorily saxicolous (e.g., *Oplurus saxicola, O. quadrimaculatus*, and *T. vato*), which means that these species are absent if there are no larger rock accumulations with accessible crevices, even though the forest is undisturbed.

Fossorial lizards were significantly affected by degradation: in the INPA survey sites, they occurred in very low densities. The few specimens captured were only found in forest with degradation category 1. Even though these numbers are too low for general conclusions, our results are consistent with a study from Gregory (1980). This group often requires an intact habitat with soft soil, leaf litter, and accessible refugia. Since most fossorial lizards are obligatory thigmotherms, a well buffered thermal environment is essential. Higher ambient temperature amplitude and higher maximum daily temperatures in degraded areas can lead to thermoregulatory constraints. Hence, fossorial lizards must avoid open and degraded areas (Gregory 1980). However, very little is known about the environmental thermal requirements of this group because behavioural observations are difficult. In addition, fossorial lizards often occur in very low densities and show patchy distributions (Maritz and Alexander 2009). Survey methods need to be improved for fossorial species, otherwise the abundance and species richness is underestimated as it was probably the case in our study. Arboreal reptiles such as geckos and snakes also showed a relatively clear negative response to degradation. This is, in all probability, related to the number, quality, and size of available trees, which declined with increasing degradation. Trees and dead wood provide refugia and food (insects, larvae, millipedes etc.) for lizards. Exposed trees that remain after selective logging cannot provide protection from potential predators (birds of prey or small mammals), leading to a decline in species and individual numbers. Furthermore, as the canopy decreases and the gaps grow larger, the remaining trees are presumably not able to buffer thermal oscillations, which can be challenging for species that prefer lower environmental temperatures.

Winter conditions in the spiny forest are cool and dry and food and water availability is scarce, forcing lizards to save energy. Assuming that some spiny forest species show reduced activity, and thus lower detectability, we would expect higher species abundance and species richness in the rainy season. Also, seasonality of certain chameleon species, overwintering as eggs, is known to happen in the dry parts of Madagascar (Karsten et al. 2008) and brumation of some species might restrict their active period to the rainy season (Ultsch 2006). However, our aim was not to detect a maximum number of species but to characterize reptile assemblages in differently degraded habitats. Weather conditions during

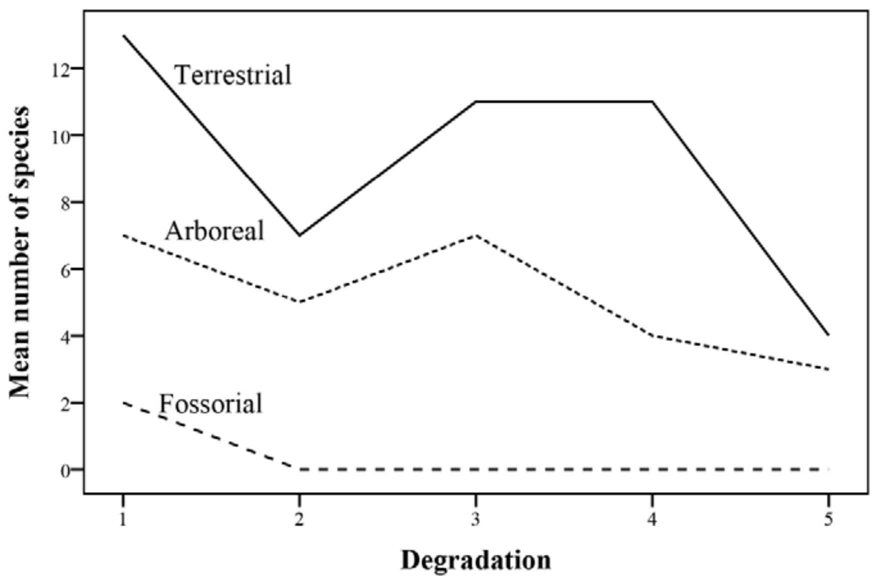


**FIGURE 4**. Mean number of reptile species divided into three groups with different microhabitat use in different habitat degradation categories (from 1: "undisturbed forest" to 5: "cleared area") in the Ifotaka North Protected Area in southeast Madagascar.

the rainy season are variable, causing strong differences in the activity of reptiles among or even within days (Sun et al., 2001). This makes a comparison between different survey days difficult. The dry season conditions were rather constant with only small changes in weather, which was necessary to achieve our project objectives.

For our comparison analysis, we used only day transect searches. This may have biased estimations of species diversity and species richness. The INPA species richness for the standardized transects was probably underestimated, especially for cryptic or nocturnal species. For this reason, we conducted 20 h of night searches in addition to day transects but the success was too low. One reason for the low individual and species numbers might be the low ambient night temperature that did not allow the reptiles to reach the minimum body temperature for activity. We had the lowest success rate with artificial tree (for arboreal species) and ground cover objects (for terrestrial and fossorial species) installed in two one-hectare grids. These were designed to provide shelter against predators or for thermoregulatory purposes. Apart from a few individual *Hemidactylus mercatorius* caught under tree cover and *T. elegans* under ground cover, we did not detect other species. Similar to the night searches, the temperature was probably too low and there was no need for the lizards to hide in the shade. As shown by Joppa et al. (2009), the highest trap success is at higher temperature, which correlates with activity patterns of animals. Finally, we also installed pitfall lines at only four different sites. This was not possible at all survey sites because of rocky soil. Again, the success was low, did not contribute to the results of the day searches and we did not trap as many species and individuals as expected in comparison with other surveys (Nussbaum et al. 1999; Enge 2001). To maximise the number of trapped species we recommend repeating this survey during the austral summer when temperature, and therefore reptile activity, is higher. However, the duration of the survey also plays an important role in its success. Although Raselimanana (2008) conducted his survey in the INPA in April (i.e., the end of the rainy season) he caught fewer species, probably owing to the short trapping duration of only five days.

In conclusion, degradation affected almost all reptiles studied in a negative way. While the reptile assemblage of the intact forest consisted of 14 species, the degraded forest was dominated by only five species. Relatively few lizards benefit from anthropogenic habitat modification and these are synanthropic, flexible generalists with broad habitat requirements. Even if species richness and diversity do not decline in a continuous way, the most sensitive species will disappear first and more resistant lizards will remain. In the spiny forest fossorial lizards are the most negatively affected by degradation, arboreal species are threatened by refuge destruction and terrestrial reptiles are the least affected. Considering that intact forest contains almost all the reptile fauna of the INPA, the highly degraded and cleared areas do not contribute to the species richness of the area. However, areas with moderate habitat modification acting as corridors between intact zones may also preserve sensitive Malagasy reptile species from local extinction.

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**Ole Theisinger's** main research interests are the diversity, ecology, and physiology of reptiles. During his studies of the herpetofaunal diversity of the Andohahela National Park in Madagascar for his MSc degree, he was fascinated by the different ecological and microclimatic demands of the reptiles in this area. Following this, Ole now investigates the thermal adaptation and energy budgets of reptiles with respect to habitat modification and conservation management for his PhD at the department of animal ecology and conservation at the University of Hamburg. (Photographed by Wiebke Berg).

**MARCEL CHRISTIAN RATIANARIVO** graduated from the Centre Ecologique de Libanona, Madagascar, with a degree in Environmental Management and Development in 2012. For his undergraduate thesis, he followed his deep interest in herpetology and investigated the impact of humans on the reptile communities in the forests of Mahavelo. Christian is currently studying for his M.Sc. degree in Natural Resource Management at the ISSEDD in Tamatave, where he continues to expand his knowledge about Madagascar's rich herpetofaunal diversity. (Photographed by Hubert Tokiarisoa Mahamaro).

**APPENDIX 1.** Coordinates and altitude of standardized reptile survey transects with different degrees of habitat degradation (from 1: "undisturbed forest" to 5: "cleared area") in the Ifotaka North Protected Area in southeast Madagascar.

| Transect number | Transect location | Degradation | Coordinates | Elevation (m a.s.l.) |
|---|---|---|---|---|
| 1 | Ifotaka | 3 | S24° 46.952'S 46° 09.409'E | 111 |
| 2 | Ifotaka | 5 | S24° 47.154'S 46° 09.280'E | 127 |
| 3 | Ifotaka | 5 | S24° 47.546'S 46° 08.635'E | 83 |
| 4 | Mahavelo | 3 | S24° 45.709'S 46° 09.407'E | 138 |
| 5 | Mahavelo | 4 | S24° 45.607'S 46° 10.112'E | 188 |
| 6 | Mahavelo | 1 | S24° 45.492'S 46° 09.821'E | 164 |
| 7 | Mahavelo | 2 | S24° 45.734'S 46° 09.823'E | 208 |
| 8 | Mahavelo | 3 | S24° 45.331'S 46° 09.329'E | 180 |
| 9 | Mahavelo | 1 | S24° 45.479'S 46° 10.002'E | 184 |
| 10 | Mahavelo | 4 | S24° 46.219'S 46° 09.070'E | 139 |
| 11 | Mahavelo | 2 | S24° 46.305'S 46° 08.720'E | 132 |
| 12 | Mahavelo | 1 | S24° 45.439'S 46° 09.495'E | 156 |

**APPENDIX 2.** Total reptile species list and their IUCN conservation status of the Ifotaka North Protected Area in southeast Madagascar including ad libitum findings and literature data. Asterisk: species known to occur in the Ifotaka North Protected Area (Raselimanana 2008) but not found during our survey; NE: not evaluated; DD: data deficient; LC: least concern; VU: Vulnerable; CR: critically endangered.

| Family / Species | IUCN status | Family / Species | IUCN status |
|---|---|---|---|
| BOIDAE | | GERRHOSAURIDAE | |
| *Acrantophis dumerili* | LC | *Tracheloptychus madagascariensis* | LC |
| TESTUDINIDAE | | *Zonosaurus laticaudatus* | LC |
| *Astrochelys radiata* | CR | SCINCIDAE | |
| PELOMEDUSIDAE | | *Madascincus igneocaudatus* | LC |
| *Pelomedusa subrufa** | LC | *Trachylepis aureopunctata* | LC |
| PSEUDOXYRHOPHIIDAE | | *Trachylepis dumasi* | VU |
| *Dromicodryas bernieri* | LC | *Trachylepis elegans* | LC |
| *Ithycyphus oursi* | LC | *Trachylepis gravenhorstii* | LC |
| *Leioheterodon madagascariensis* | LC | *Trachylepis vato* | LC |
| *Leioheterodon modestus* | LC | *Voeltzkowia lineata* | LC |
| *Lycodryas pseudogranuliceps* | NE | GEKKONIDAE | |
| *Madagascarophis meridionalis* | LC | *Blaesodactylus sakalava* | LC |
| PSAMMOPHIIDAE | | *Geckolepis typica* | LC |
| *Mimophis mahfalensis* | LC | *Hemidactylus mercatorius* | LC |
| IGUANIDAE | | *Lygodactylus decaryi* | DD |
| *Chalarodon madagascariensis* | LC | *Lygodactylus tolampyae** | LC |
| *Oplurus cyclurus* | LC | *Lygodactylus tuberosus* | LC |
| *Oplurus quadrimaculatus* | LC | *Lygodactylus verticillatus* | LC |
| *Oplurus saxicola* | LC | *Paroedura bastardi* | LC |
| CHAMAELEONIDAE | | *Paroedura androyensis* | VU |
| *Furcifer major* | LC | *Paroedura picta* | LC |
| *Furcifer oustaleti* | LC | *Phelsuma mutabilis* | LC |
| *Furcifer verrucosus* | LC | | |