SALAMANDRA	45	3	147-153	Rheinbach, 20 August 2009	ISSN 0036-3375

Movement patterns and habitat selection of the giant day gecko (*Phelsuma madagascariensis grandis*) in the Masoala rainforest exhibit, Zurich Zoo

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Abstract. In 2003, Zurich Zoo opened the Masoala exhibit to help preserving the endemic flora and fauna of Madagascar and to raise public awareness of the threats to this biodiversity hotspot. The enclosure houses more than 45 animal taxa and over 35000 individual plants on almost 11 000 m². After three years of establishment of food webs and demographic changes in the community, there is an urgent demand for animal population monitoring. Therefore, this paper aims (i) to determine how increasing gecko density affects gecko movement patterns in the exhibit and (ii) to assess habitat selection in 12 heterogeneous areas within the exhibit, differing in various environmental parameters (e.g., plant species, sun hours, and food sources). In contrast to an earlier study on this gecko population, our results on gecko movement patterns show that moved distances are evenly distributed amongst distances between 0 to 70 m. Moreover, geckos showed strong habitat preferences for certain areas; plants like *Ravenala madagascariensis* and *Pandanus* spp. as well as ventilation tubes and cages were most frequently used as perch sites. When discussed in the framework of the ideal free distribution theory, our results suggest that gecko movement patterns are strongly affected by increasing gecko density.

Key words. artificial ecosystem, gecko, movement pattern, habitat selection, ideal free distribution theory.

Introduction

Due to its high number of endemic species, Madagascar is one of the biodiversity hotspots in the world (Myers et al. 2000). Anthropogenic land use has caused substantial deforestation, therefore, putting an enormous pressure on the native flora and fauna (Green & Sussman 1990). During the last decade, research has intensified to document human impact on a variety of taxonomic groups such as amphibians, reptiles, birds, and small mammals, their habitats, and community structures (Ganzhorn et al. 2003, Lehtinen et al. 2003, Andreone et al. 2005, Watson et al. 2005, Scott et al. 2006).

Zoological gardens are involved in preserving the diverse flora and fauna of Madagascar, and thereby creating awareness amongst the public for its highly endangered ecosystems. In 2003, Zurich Zoo opened the Masoala rainforest exhibit, a dome-shaped ecosystem hall covering an area of 10 856 m² and measuring 35m in height. Surface structures, plant composition and water bodies are heterogeneously distributed to imitate a natural rainforest in north-eastern Madagascar. The enclosure houses more than 45 different animal taxa, such as 6 mammal species, 22 birds, 7 reptiles, 2 amphibians and 3 species of fish, and over 35 000 individual plants representing more than 450 species (S.C. Furrer, pers. obs., Zurich Zoo 2005). Over the last three years, food webs have become established and the community in the exhibit now appears to be subject to natural demographic processes, which has resulted in a demand to conduct intensive monitoring of the animal collection. This work has already led to successful improvement of the captive environment of the primates in the exhibit (Sommerfeld et al. 2006, Traber & Muller 2006). However, monitoring of smaller vertebrates has so far been limited to two reptile species, the panther chameleon (*Fucifer pardalis*; Lutzmann 2006, Gehring et al. 2008, T. Zellweger, unpubl. data) and the giant day gecko (*Phelsuma madagascariensis grandis*), which was subject to an intensive survey shortly after the exhibit was opened. Sixty geckos (in this paper "gecko" refers to day geckos if not explicitly stated otherwise) were released into the ecosystem hall, and data was gathered on habitat selection and spatial distribution by monitoring 18 radio-tracked individuals (Furrer et al. 2006). As the population size has increased substantially over the last three years (112 animals; Wanger et al. 2009), the present study targets the effects of increasing population size on movement patterns and habitat selection of these geckos. We interpret our results in the framework of the ideal free distribution theory (Fretwell & Lucas 1970) that relates changes in animal movement patterns to changes in population densities based on resource distributions and habitat selection.

Materials and methods

Study species and site

The distribution of the giant day gecko (*Phelsuma madagascariensis grandis,* Gekkonidae) is confined to the northern part of Madagascar (Glaw & Vences 1994). This diurnal and arboreal gecko species may reach a total length of up to 30 cm. The dorsal colour patterns, being highly polymorphic and variable between individuals, consist of red stripes and dots on a shiny green background (Henkel & Schmidt 1991). Photographing each lizard in the enclosure allowed us to identify every individual, and, thus, to avoid invasive marking techniques. As none of the lizards were captured and male and female geckos are only slightly dimorphic (males being slightly larger and having wider heads than females; Hallmann et al. 1997), individuals could not be sexed. However, when an individual was less than one third of the total length of an adult (i.e., 10 cm), we classified it as a juvenile. During the reproductive season in the wild, ranging from the end of November until May, most females lay clutches of two eggs, which they deposit into phytotelms or other plant cavities (Hallmann et al. 1997). We monitored the Masoala exhibit population during four weeks, from mid-March to mid-April, within the reproductive season in their natural habitat.

Recently, the subspecies *Phelsuma madagascariensis grandis* was elevated to species rank *Phelsuma grandis* (Raxworthy et al. 2007). However, the applied methodology – niche modeling – seems not yet a fully accepted tool in systematic research and hybrids between *Phelsuma madagascariensis* subspecies exist. We, therefore, decided to use the old species name *Phelsuma madagascariensis grandis* in this paper.

Movement patterns and habitat selection

To record movement distances, we marked every gecko sighting on a map and estimated the distances covered to the nearest 0.1 m using the measuring function in the program AUTODESK. We obtained movement distances recorded in a previous study either directly from the original dataset or from Fig. 2 in Furrer et al. (2006). This gecko species has been shown to move according to a stop-and-go fashion, that is, some individuals remain stationary for weeks in their territory, whereas others keep moving between habitat patches within days (Furrer et al. 2006), thus, allowing us to record movement patterns rather than just position points of an individual. To the best of our knowledge, there is no data on movement patterns available from natural populations neither of this nor of another subspecies.

The habitats in the exhibit were divided into 12 sections based on differences in plant species, sun hours (northern, central, and southern part), food sources, and artificial structures such as ventilation tubes, ani-

Tab. 1. Habitat characteristics of the 12 areas in the rainforest exhibit. Abbreviations for the areas are as follows: NA, CA, SA = Northern, Central, and Southern Area, respectively. Abbreviations for the plant species most important to the day geckos (numbers given indicate the number of individuals of this plant species): Rm = *Ravenala madagascariensis*; Fa = *Ficus altissima*; Pd = *Pandanus* spp.; B = *Bismarckia* spp.; Dn = *Daibergia nigrescens*; M = *Musa* spp.; Dr = *Dracaena marginata*. Numbers of ventilation tubes, cages, houses and food areas indicate their numbers in the areas. Sun hours were measured from 9.30 h until 18 h. All areas [m^2] added together with water bodies (1356 m^2) give the total area of the Masoala rainforest exhibit (10 856 m^2).

	Areas											
	NA1	NA2	NA3	NA4	CA1	CA2	CA3	CA4	SA1	SA2	SA3	SA4
Rm	0	3	0	0	13	0	0	0	1	1	1	0
Fa	2	0	0	0	8	0	0	2	0	3	0	2
Pd	17	20	17	4	43	2	3	18	2	4	11	15
B	0	0	1	0	1	0	0	0	0	1	1	0
Dn	0	0	0	0	4	0	0	1	0	0	0	0
M	0	7	0	0	0	0	0	0	40	0	1	0
Dr	0	0	0	0	3	0	0	0	1	1	1	1
Ventilation tubes	4	2	2	2	0	0	0	0	3	3	1	3
Cages	1	1	0	0	0	0	0	0	0	1	0	1
Houses	0	0	0	0	1	0	0	0	2	0	1	0
Food areas	8	5	2	0	15	0	0	0	1	8	1	9
Sun hours	6	6	3	3	8.5	3	8.5	5.5	8.5	8.5	5.5	5.5
Area [m^2]	704	932	628	396	2217	264	280	1100	872	1020	484	603

mal cages, and huts (original houses of local people for decoration; (see Table 1 for habitat characteristics). To determine gecko habitat preferences, the area of all 12 habitats was determined and compared to the percentage of geckos recorded in each area. Maps of the exhibit in AUTODESK provided exact numbers of each individual plant species and locations. We sampled all habitats following transect lines in random order twice a day (10-12 h and 15-17 h) and we conducted surveys from a moveable maintenance ramp underneath the roofing foil. Ground and ramp sampling was inter-changed daily between morning and afternoon sessions. However, due to safety reasons, and a rare breeding occasion of a cuckoo (*Coua cristata*), we sampled only 33% of the total exhibit from the ramp. When determining gecko plant utilization, all observations of a single individual on a different plant species were included. We recorded sun hours for each area 10 times from 9.30 h until 18.00 h once per hour. Additionally, food sources and artificial structures per area were also taken into account when analyzing gecko habitat use.

Statistical analysis

Not all the data obtained could be transformed to normality, and, hence, non-parametric tests were used in all analyses.

Results

Gecko movement

We recorded movement data for 52 adults and 18 juveniles. Distances moved were not correlated with the number of times a gecko was observed (Spearman rank correlation; $r_s = 0.116$, $P = 0.691$, $n = 14$, Fig. 1). Thus, the number of observations did not affect move-

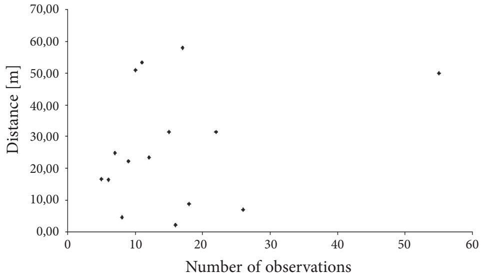

Fig. 1. Relationship between the number of individual gecko observations and their moved distances.

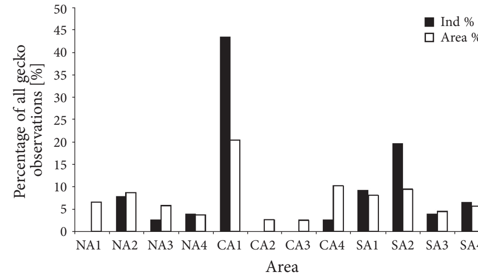

Fig. 3. Habitat preference of observed geckos. The percentage of all gecko observations per area (black bars) was compared to the percentage per area of the whole exhibit (white bars). As both distributions are significantly different (see text), there is a distinct habitat preference in these animals. Areas are shown on the x-axis (NA = northern exhibit area; CA = central exhibit area; SA = southern exhibit area; numbers resemble specific areas).

ment distances recorded. However, in spite of this, the subsequent analyses are based on lizards observed on more than 5 occasions. We did not observe any difference in movement distances between adults and juvenile geckos (Mann Witney *U*-test, $U = 133.0$, $P = 0.93$, mean distance 22.9 ± 23.1 m (SD) and 17.3 ± 14.4 m for adults and juveniles, respectively).

The distribution of movement distances recorded in the present study were significantly different compared to distances observed in the study conducted shortly after the lizards were released into the exhibit by Furrer et al. (2006; Chi Square Test, $\chi^2 = 25.82$, $df = 9$, $P = 0.002$, Fig.2). Movement distances recorded in the former study showed a distinct peak at short distances from 1 to 10 m, whereas distances moved recorded in the present study were evenly distributed between 0 and 70 meters (Fig. 2).

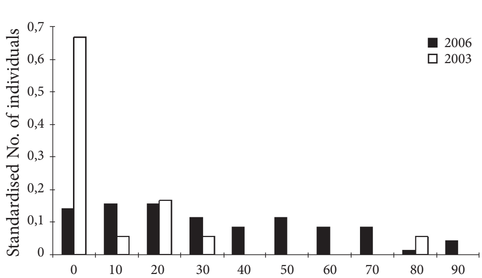

Fig. 2. Comparison of movement distances recorded during the present study and the earlier study by Furrer et al. (2006). For comparison, individual numbers where divided by the sample sizes of each study for standardization. 2006: $n = 70$; 2003: $n = 18$.

In the present study, we observed seven copulations each time followed by mate guarding, head bobbing, and several occasions of territorial defensive behaviours.

Habitat selection

We observed a significant difference between habitat area and gecko observations per area ($\chi^2 = 36.13$, $df = 11$, $P < 0.001$, Fig. 3), suggesting that geckos showed preferences for certain areas compared to others.

Pandanus spp. and *Ravenala madagascariensis* were the most frequently visited plant species whereas ventilation tubes followed by cages were the most utilized artificial structures (Fig. 4).

Discussion

Our results showed a remarkable uniform distribution of movement distances compared to the highly skewed distances record-

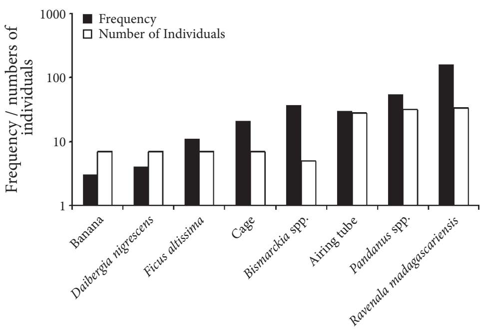

Fig. 4. Frequency of visited plant species and artificial structures and number of visits of individuals. Note that the y-axis is on a logarithmic scale.

ed by Furrer et al. (2006). We suggest that the dramatic difference in gecko spatial biology between the two studies is caused by the increase in population size, from 60 to 112 lizards (Wanger et al. 2009), and corresponds to what could be expected from the ideal free distribution theory (Fretwell & Lucas 1970). That is; at low population density in a patchy environment where resources are unequally distributed, all individuals will be able to occupy an optimal habitat, which, in turn, may result in a restricted movement pattern. At higher population densities, however, all or most of the optimal habitats are occupied, and hence a large proportion of individuals are forced to move into suboptimal habitats, resulting in larger areas covered to obtain sufficient resources. The latter are often referred to as "floaters" (Sarre et al. 1996, Gruber & Henle 2004).

When the giant day gecko population was founded in 2003, gecko numbers and, hence, density was low, and numerous high quality habitats were available and could be occupied without intraspecific competition. Accordingly, most geckos in the earlier study only had to cover short distances to locate optimal habitats, and the few individuals moving long distances were either released near release sites of conspecifics or in unsuitable habitat (Fig. 2 in Furrer et al. 2006). However, as gecko density increased over the last three years (Wanger et al. 2009) only the most competitive (presumably larger) adults were able to occupy high quality habitats, whereas the less competitive (presumably smaller) adults were forced to become floaters. Furthermore, as we did not observe any difference in movement distances of juveniles and adults this suggests that juvenile geckos also adopted a floating strategy, and hence were forced out of optimal habitats. The assumptions that increased density will lead to territorial and reproductive behavioral displays (Furrer et al. 2006) were confirmed by numerous observations of open-mouth threat displays, tail weaving and body flattening.

In the present study, geckos showed strong habitat preferences for specific areas in the exhibit, frequently visited plant species and artificial structures being a major determinant. The most frequently visited plant species like *Ravenala madagascariensis, Pandanus* spp., *Bismarckia* spp., and *Musa* spp. offer good hiding spaces in their leaf axils and possibilities for egg deposition (e.g., Furrer et al. 2006, Lehtinen 2002, T. C. Wanger & I. Motzke pers. obs.). Artificial structures such as ventilation tubes provided opportunities for thermoregulation being beneficial at temperatures below 0°C in the exterior environment (T.C. Wanger & I. Motzke, pers. obs.). Cages were presumably preferred as perch sites because additional food was provided inside for the primates. In the previous study, Furrer et al. (2006) found plant species like *Dracaena marginata* and *Dypsis* spp. and huts also frequently used. However, in our study these plant species and structure were of minor importance.

Acknowledgements

We thank Zurich Zoo for the permission to work in the Masoala exhibit and for logistic support. M. Bauert, T. Zellweger and his animal keeper team provided us with all the essential details of the exhibit. The first author would especially like to thank T. Madsen for helpful discussions and his improving comments.

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Manuscript received: 17 November 2007

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