

Habitat preferences and activity patterns of *Furcifer pardalis* (CUVIER, 1829) in the Masoala Rain Forest Hall of the Zurich Zoo

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Abstract. The habitat preferences and activity patterns of panther chameleons, *Furcifer pardalis* (CUVIER, 1829) living in the Masoala Rain Forest Hall of the Zurich Zoo were investigated by means of radiotelemetry. Twelve animals were monitored over periods of up to 32 days. The animals exhibited a significant preference for the upper third, or crown stratum, of the plants. The chameleons were furthermore mostly encountered in the peripheral areas of their trees. Migratory patterns of male specimens in particular followed a largely linear course from the starting point. Distinctions could be made between specimens with a high degree of home range fidelity and more explorative individuals, which differed clearly with regard to the distances they moved away from their respective starting points.

Key words. Reptilia, Chamaeleonidae, *Furcifer pardalis*, habitat preferences, activity patterns, telemetry, zoo.

Introduction

The panther chameleon (*Furcifer pardalis*) is a widely distributed and highly adaptable species of chameleon that is predominantly found in anthropogenically altered and secondary habitats (FERGUSON et al. 2004, ANDREONE et al. 2005, LUTZMANN 2006). This gave rise to a number of studies on the ecology of *F. pardalis* (BOURGAT 1967, 1968, 1970, GRIMM & RUCKSTUHL 1999, RIMMELE 1999, FERGUSON et al. 2004, ANDREONE et al. 2005, LUTZMANN 2006). With a floor space of 11,000 m², the Masoala Rain Forest Hall of the Zurich Zoo presents an opportunity for studying the behaviour of chameleons in a semi-natural environment that about corresponds to the natural habitats most commonly inhabited by *F. pardalis* in Madagascar. The management of husbandry and captive breeding of animals in modern-day "eco-displays", such as the Masoala Rain Forest Hall, necessitates that fundamental behavioural studies be conducted in these artificial environments. These eco-displays replace some of the traditional exhibition of animals in zoological gardens and new

concepts for the captive keeping of animals therefore have to be tested.

Material and methods

The Masoala Rain Forest Hall of the Zurich Zoo

The Masoala Rain Forest Hall of the Zurich Zoo was opened in June of 2003. It measures 120 m in length, 90 m in width, and has a maximum height of 30 m (Fig. 1). Thus providing a floor space of 11,000 m², it is covered with some 17,000 plants, almost all of which are fitted with identification tags that not only give the respective species name, but also a numerical ID number (IDN). These IDNs have been plotted on a scaled map of the hall and were used to exactly pinpoint the locations of individual chameleons.

Radiotelemetry

Radiotelemetric monitoring was effected by means of BD-2 transponders (Holohil Systems Ltd.) that have been tested with success in



Fig. 1. View of the vegetation in the Masoala Rain Forest Hall of Zurich Zoo.

previous studies of chameleons (CUADRADO 2000, 2001). These transponders have a range of about 200 m at a frequency of 148 kHz. A portable R-1000 Telemetry Receiver (Communications Specialists, Inc.) was used in conjunction with both an H- and a rod aerial.

Transponders were fixed with medical Skin Bond Cement, a wound glue manufactured by Bruce Medical Supply. They were attached to the side of the dorsal crest above the hind limbs in all specimens participating in the first trial (Fig. 2), with the aerial being aligned parallel to the tail so that it would not affect movement of either the tail or the hind limbs. The second trial made use of three randomly selected specimens, which were fitted with transponders on the side of the dorsal crest above the front limbs.

Marking of individuals

The participating individuals were marked simply by writing individual numbers with a

felt pen on the front faces of their glued-on telemetry transponders. This enabled us to verify transponder numbers by means of binoculars. Permanent marking of the individuals was achieved by two other means. First, we counted the number of spikes in the individuals' dorsal crests (*crista dorsalis*) from the head backwards and then removed one spike in a certain place. This method is entirely pain-free for the animals and has no effect whatsoever on their behaviour, while it facilitates recognition of individuals beyond doubt and serves as a lasting marker. Even though the scales constituting the dorsal crest grow with the animal, they will not regenerate fully, leaving a cropped tip visible. The second method involved the implantation of a passive integrated transponder (PIT) manufactured by Trovan (ID-100), which can be read by means of a portable scanner.

Number of monitored specimens and monitoring

The studied group comprised a total of twelve specimens, representing eleven males and one female. All animals were either just approaching sexual maturity or had recently reached this state. Table 1 shows the grouping of the individuals used.

The chameleons were released into the hall in two groups. The first group (Group 1) of five specimens was released on 24.01.2005, with the second, comprising seven individuals, following in two sub-groups (Groups 2/1 and 2/2) on 28.02.2005. The two groups were released in different spots. While Group 1 was released in the western section of the hall, near the public entrance, Group 2/1 was set free in the southern sector, which is an area not accessible to the public and has the highest degree of sun-exposure. Group 2/2 was released in the northern sector, which is likewise not open to the public, but is marked by less sun-exposure and higher vegetation. The variety of release points was chosen to investigate the possible influences of environmental factors on the behaviour of the animals.

The animals were telemetry-located four times every day during the course of the study period, at intervals of one to two hours during the day. The times at which they were traced were varied so that a record would be available for every specimen for every hour within a time span of at maximum five days. Data collection was limited to the time between sunrise and sunset. With chameleons being diurnal, they were not expected to relocate at night.

Recorded data

Once a chameleon had been located, the time and the exact location were recorded. The IDN of the respective tree or shrub was noted. The animal's position in the plant was evaluated according to standard categories, i.e., whether it was on the ground, or perched on the trunk, a branch, or a leaf. A tree was stratified into lower third, midriff, and crown. Peripheral perch sites were recorded as such. The height of the perch above the ground was estimated in metres, more readily accessible perches were measured in centimetres.

Data analysis

The data gathered thus were analysed using the software Statistika. The tests were limited

Tab. 1. Distribution of specimens and their sexes in three groups.

Group	Specimen No.	Sex
1	A1	1,0
1	A2	1,0
1	A3	1,0
1	A4	1,0
1	A5	0,1
2/1	B1	1,0
2/1	B2	1,0
2/1	B3	1,0
2/1	B4	1,0
2/2	C1	1,0
2/2	C2	1,0
2/2	C3	1,0



Fig. 2. Male *Furcifer pardalis* carrying a glued-on BD-2 transponder.

to a level of significance of $\alpha = 0.05$ at maximum. Horizontal migrations were calculated by means of the GIS software ArcView 3.2. The individual points of sightings were plotted from the individual points of release to the last sighting, graphically connected by straight lines, and these were then measured and totalled. The distances between two points were identified by measuring them on a scaled map of the hall.

Perch heights (h_1 / h_2) were calculated on the basis of the Pythagorean theorem, with the horizontal distance between two perches forming the first short side of a rectangular triangle (d) and the difference between the two perch heights ($h_1 - h_2$) the second. The long side (hypotenuse) of the resultant rectangular triangle thus equals the calculated distance of relocation of the animal:

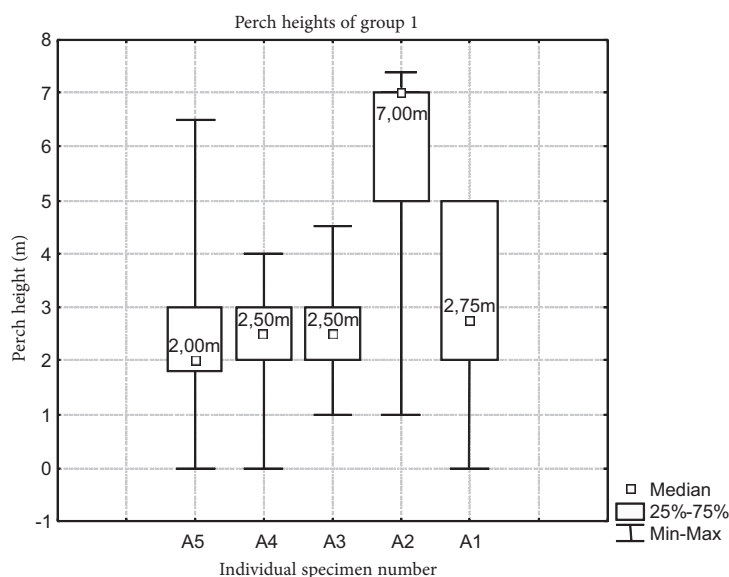


Fig. 3. Perch heights of the specimens in group 1. Box and whisker plots: The box comprises percentages 25-75% of the observations, while the open squares indicate means. The whiskers delimit minima and maxima. The Y-axis shows perch heights in metres, while the X-axis shows the individual specimens. Observations: A5 n=78; A4 n=120; A3 n=35; A2 n=15; A1 n=63. Standard deviations: A5 - 1.34 m; A4 - 1.02 m; A3 - 0.83 m; A2 - 1.87 m; A1 - 1.66 m.

$$a = \sqrt{d^2 + (h_1 - h_2)^2}$$

Because it may be supposed that the animals migrated from one tree to another via neighbouring branches rather than crossing over on the ground, especially in densely vegetated areas, this method of calculation appears to be fairly realistic.

Within a tree, the vertical migration (a_v) was calculated as the difference ($a_v = h_1 - h_2$) between two perch heights.

The extent of activity was always evaluated for the last eight days of the study period of the respective specimen.

Results

Habitat utilization

Our observations did not suggest to animals to have any particular predilection for certain

species of plants or trees present in the hall. Quite to the contrary, they even made use of plants (e.g., *Pandanus baptiste*, *Bismarckia nobilis*, *Ravenala madagascariensis*) and structures (e.g., hot air pipes and ventilation grilles) that would appear rather unsuited for chameleons. Water surfaces were crossed via the lush vegetation of aquatic plants (*Pistia stratiotes*).

A total of 505 perch heights were recorded during the monitoring period. Figure 3 illustrates the perch heights recorded for the animals in Group 1. The mean value for the perch heights of the five participating individuals amounts to 3.29 m (n = 311; SD = 1.34 m; min. = 0 m, max. = 7 m). The mean of perch heights recorded for the individual animals lies between min. = 2,00 m and max. = 7,00 m. Half of all observations involved animals that were perched at heights above two metres. The three groups differed substantially with regard to the distribution of their perch heights. Figure 4 illustrates the distribution of

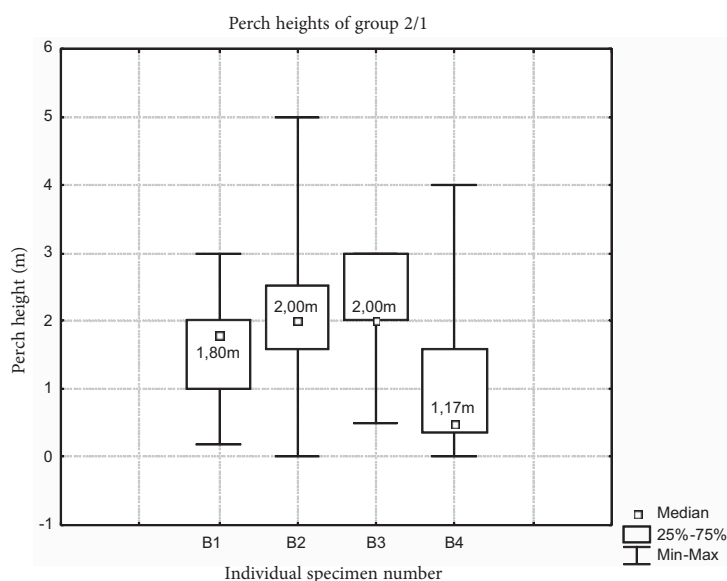


Fig. 4. Perch heights of the specimens in group 2/1. Box and whisker plots: The box comprises percentages 25-75% of the observations, while the open squares indicate means. The whiskers delimit minima and maxima. The Y-axis shows perch heights in metres, while the X-axis shows the individual specimens. Observations: B1 n=30; B2 n=46; B3 n=10; B4 n=11. Standard deviations: B1 - 0.64 m; B2 - 1.02 m; B3 - 0.50 m; B4 - 0.50 m.

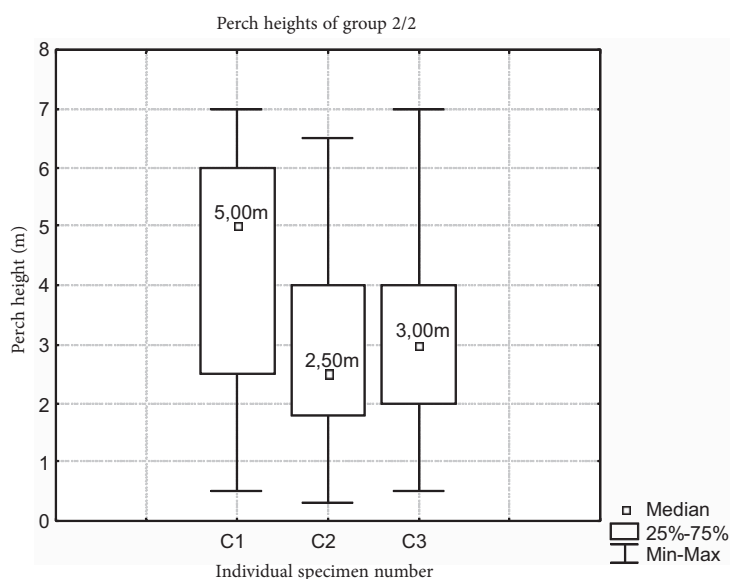


Fig. 5. Perch heights of the specimens in group 2/2. Box and whisker plots: The box comprises percentages 25-75% of the observations, while the open squares indicate means. The whiskers delimit minima and maxima. The Y-axis shows perch heights in metres, while the X-axis shows the individual specimens. Observations: C1 n=21; C2 n=41; C3 n=35. Standard deviations: C1 - 2.03 m; C2 - 1.60 m; C3 - 1.52 m.

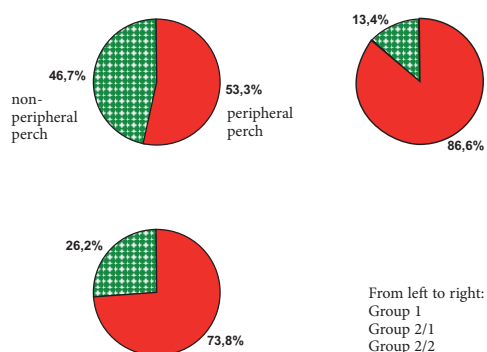


Fig. 6. Illustration of the distribution of peripheral and non-peripheral perches within the utilized plants for the individual groups. The peripheral proportions are shown as red solid areas and the non-peripheral proportions in green dotted areas.

perch heights noted for Group 2/1. This group produced a mean perch height of 1.88 m ($n = 97$; $SD = 0.89$ m; min.: 0 m, max.: 5 m). More than 50% of the observations involved animals perched at heights between one and three metres. The perch heights recorded for Group 2/2 are higher than those for Group 2/1. The mean value for the perch heights recorded for Group 2/2 lies at 3.54 m ($n = 97$; $SD = 1.71$ m; min.: 0.30 m, max.: 7.00 m). Figure 5 is a graphic illustration of the distribution of perch heights of the individual animals of Group 2/2.

A comparison of the utilized tree strata showed that the perches recorded from within a tree highly significantly deviated from a balanced utilization of all strata available within a tree (χ^2 -Test; $p < 0.01$). All observations of all animals instead revealed a significant predilection for the upper third, respectively the crown stratum (H-Test; $p < 0.01$; mean: 3.0) of plants. The three groups showed differences, however. Both Groups 1 and 2/1 had a significant predilection for the top third respectively the crown stratum (H-Test; $p < 0.01$; mean: 3.0). Group 2/2 instead exhibited a significant predilection for the middle third (H-Test; $p < 0.01$; mean 2.0). Figure 6 illustrates that the animals of all three groups were relatively more often spotted in peripheral regions of their trees. These

values likewise refer only to the last twenty observations.

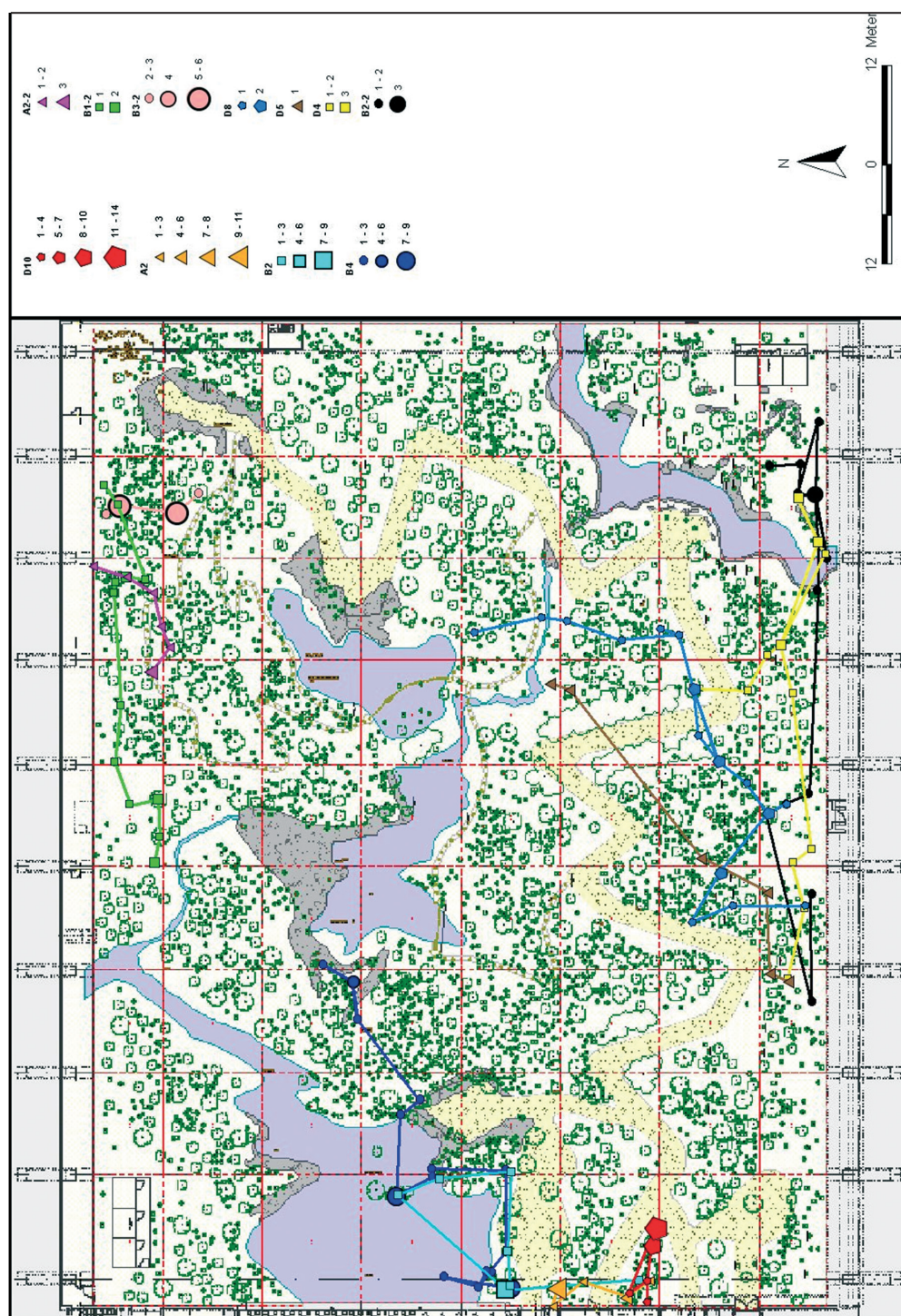
Activity patterns and spatial utilization

During the observation period, the individual animals relocated over varying distances from the original point of release. Table 2 summarizes these relocations of the individual animals. This is based merely on a supposed two-dimensional distance between the point of release and the location of the last recording, however (see 2.6).

Displacing itself by a total of 129.50 m within 12 days, a male from Group 2/1 (B₁) travelled the greatest distance. A male from Group 2/2 (C₃), on the other hand, covered only a distance of 12.40 m within a similar period of time (14 days). In general, it is obvious that the animals in Group 2/1 walked substantially larger distances during the observation period. Every animal in this group covered a distance of about 100 m within 14 days, whereas these distances averaged only about 40 m (Group 1) and 20 m (Group 2/2) within 14 days, respectively. In order to create a nearly three-dimensional impression of the distances really covered by the animals, their activity ranges (a) were calculated in addition to the individually recorded perch heights (h) (see 2.6). Furthermore, all vertical relocations (a_v) within a tree that were not included in the activity range were worked out. The activity ranges were evaluated for the last eight days of the observation period for each animal. The results are presented in Table 3.

The graphic illustration of the distances covered by the chameleons (Fig. 7) reveals two migratory patterns, which are distributed unevenly between the three groups. Group 1 and 2/2 both comprised animals with relative-

right page: Fig. 7. Illustration of distances covered by the individual specimens. The recorded perch sites are marked with symbols whose sizes are correlated to the numbers of days on which the animals were found in these spots.



Tab. 2. Overview of distances travelled by individual specimens and their groups from the original point of release to the last sighting. Distances are given in metres and refer only to the assumed two-dimensional displacement. The observation period is given in days.

	A1	A3	A4	A5	B1	B2	B3	B4	C1	C2	C3
Group	1	1	1	1	2/1	2/1	2/1	2/1	2/2	2/2	2/2
Distance in m	21.30	61.80	80.30	25.60	129.50	94.10	49.20	108.90	18.50	55.10	12.40
Period in days	15	14	29	31	12	15	8	14	15	15	14

ly high degrees of site fidelity and those that were more explorative. In Group 1, the animals A1 and A5 presented themselves as rather stationary, and in Group 2/2, animal C3 was notable for displacing itself only by a small distance from the start-off point. The members of Group 2/1 all covered larger distances from their point of release. The activity patterns show a distinctly linear course, especially as far as Group 2/1 is concerned.

Durability of transponder attachment

The period of time throughout which the animals carried their transponders, and the durability of the attachment (glue) in particular, differed substantially between the three groups. The animals of the first group carried their transponders for an average of 18 days and could each be observed for another four days on average after they had lost their transponders.

In the second group, transponders remained affixed for only 6.5 days on average, which equals half of the average total observation period of 13 days. Some specimens could be regularly traced even after they had lost their transponders also here. Female A5 was the animal observed longest, i.e., for a total of 31 days. Specimens A1 carried its transponder for the longest period of time, i.e., for 32 days.

The two different points of attachment (above the front limbs vs. above the hind limbs) proved to be varyingly well suited, with all three animals on which the transponder had been affixed above the shoulder losing their equipment within the first three days after release.

Regular shedding enabled all animals to rid themselves of remains of the glue, not leaving any residue or causing skin irritation.

Discussion

Choice of habitat

The panther chameleons living in the Masoala Rain Forest Hall exhibited a significant predilection for the upper third of the plants utilized. Living mainly in an area with numerous large trees (> 4 m), the animals of Group 1 were particularly commonly found in the top third or crown stratum. All groups exhibited a predilection for the middle and top thirds of their plants. The animals were encountered in the bottom third of their plants rather rarely and usually only when they were on the move. Furthermore, the panther chameleons apparently spent more time in the peripheral areas of their plants than elsewhere. These results suggest that panther chameleons will tend to select perches at greater heights in an environment that offers tall trees and there preferably utilize the peripheral areas. This confirms the observations made by GLAW & VENCES (1994) and RAXWORTHY (1988). Because the availability of microclimates that can facilitate thermoregulation is one of the most important determinants for the choice of habitat in reptiles (e.g., ZUG et al. 2001), higher ambient temperatures and the availability of basking spots could offer an explanation for a predilection for the crown stratum. Research on the distribution of microclimates in rain forests has shown that temperatures rise higher during the day in the upper storeys of trees than on the forest floor (comp., e.g., TERBORGH 1993).

Panther chameleons inhabit within their distribution range a wide variety of vegetation types and landscapes, rendering descriptions of natural habitats partly highly contradictory. They mention in common, though, a presence of trees, bushes and shrubs in open landscapes and cultivated areas with low secondary vegetation, including human settlements (e.g., ANDREONE et al. 2005, FERGUSON et al. 2004, GLAW & VENCES 1994, HENKEL & HEINECKE 1993, HENKEL & SCHMIDT 1995, MÜLLER et al. 2004, NECAS 2004, SCHMIDT et al. 1996, own obs.). However, descriptions of primary rain forest habitats in which *F. pardalis* occurs differ substantially: while some authors explicitly exclude dense forests (HENKEL & HEINECKE 1993, HENKEL & SCHMIDT 1995, SCHMIDT et al. 1996, SCHMIDT & LIEBEL 2004), others have published records of *F. pardalis* from rain forest regions (ANDREONE et al. 2000, 2005, GLAW & VENCES 1994, KLINGELHÖFER 1957, LUTZMANN 2006, MÜLLER et al. 2004, RAMANANTSOA 1974, RAXWORTHY 1988, RIMMELE 1999, own obs.). It is notable, though, that population densities of *F. pardalis*, as derived from transect studies, are much lower in rain forest regions than in areas with secondary vegetation, even when the respective authors tried to also search the crowns of trees from the ground (ANDREONE et al. 2005). RAXWORTHY (1988), GLAW & VENCES (1994), and LUTZMANN (2006) presumed that *F. pardalis* would be exclusive to the crown stratum in primary rain forests because only this region would permit sufficient insolation to satisfy the thermal requirements of these distinctly heliophilic chameleons. This is also indicated

by studies of the top storey of the Masoala rain forest by means of an airship, which produced records of only one species of chameleon, i.e., *F. pardalis* (ANDREONE et al. 2005), even though it remained unclear whether this undertaking was in search of chameleons or how they were traced. However, further studies in the canopy of malagasy rainforests need to be carried out, to clarify the occurrence and the densities of *F. pardalis* in the forest overstory. *F. pardalis* was most commonly encountered in secondary vegetation or anthropogenously altered habitats. In forested areas, *F. pardalis* was mostly found along rivers or in clearings, even though LUTZMANN (2006) observed females laying their eggs in closed forest areas. ANDREONE et al. (2005) presumed that *F. pardalis* preferred these open areas because unimpeded insolation would create optimum conditions for basking and visual communication.

According to this, the panther chameleon appears to have been a "forest edge species" originally, which lived in open spaces and marginal zones of the once-expansive rain forests. As the destruction of the forests progressed, more and more open areas and cultivated land with low secondary vegetation emerged, which appear to offer panther chameleons optimum conditions. Consequently, high population densities are found in exactly these areas (ANDREONE et al. 2005, LUTZMANN 2006).

The preferred utilization of the peripheral areas of trees could also be a function of the more intense insolation in these parts of the trees. Also imaginable would be an anti-predator strategy, as potential, larger predators would be unable to follow the chamele-

Tab. 3. Overview of individual activity ranges (a) and vertical displacement (a_v) of the individual chameleons during the last eight days of observation. * = Specimens for which no continuous data were available for the last eight days (A1: 5 days; A3: 4 days; B1: 6 days).

	A1	A3	A4	A5	B1	B2	B3	B4	C1	C2	C3
Group	1	1	1	1	2/1	2/1	2/1	2/1	2/2	2/2	2/2
a (m)	14.00*	14.40*	33.50	15.00	50.60*	51.30	46.50	57.30	19.83	33.10	11.20
a_v (m)	3.50	14.50	5.40	2.10	12.00	6.80	1.00	29.00	8.50	15.70	15.00
Σ_a (m)	17.50	28.90	38.90	17.10	62.60	58.10	47.50	86.30	28.33	48.80	26.20

ons out onto the thinner peripheral branches, or would at least announce their presence through vibrations (“perch release”, PARCHER 1974). As a result of the highly biased sex ratio in our study groups, no statistical evaluation of a possibly sex-dependent choice of habitat could be performed. ANDREONE et al. (2005) noted a significant difference at least with regard to perch heights between male and female *F. pardalis* living on Nosy Be, which was explained by a higher perch providing males with a better overview of their territories. LUTZMANN (2006) did not find differences in perch heights between males and females in Maroantsetra, but could also not detect indications of male territoriality.

Activity patterns and spatial utilization

As Figure 7 illustrates, it showed that there were two types of activity patterns present: the more resident type and the more explorative type. Both types were notable for their typically linear movements from a start-off point, i.e. both rarely visited the same area more than once. Specimens A5, A1 and C3 presented themselves as rather stationary and this was particularly evident in the female A5. While this animal stayed within a certain range throughout the entire observation period, the males A1 and C3 showed a linear type of relocation. Even though not as expressed as in other specimens, female A5 moved about continually within a certain perimeter and visited certain spots repeatedly. She also relocated between various perches during the course of a day. During phases of sexual inactivity, which in the wild coincides with the dry season (MÜLLER et al. 2004, ANDREONE et al. 2005), inter-male competition is not particularly expressed. This must surely be viewed as an avoidance of energy-intensive squabbles at a time when resources are limited. In the Hall, males were repeatedly seen right next to each other without showing any gestures of aggression. This peaceful coexistence was also described by MÜLLER et al. (2004), and FERGUSON

et al. (2004) even noted it in some males during the mating season.

The activity patterns displayed by males (Fig. 5) followed a highly linear course. The young males of Group 2 covered particularly long distances. This might suggest that *F. pardalis* males do not establish permanent “territories”, but rather roam their environment in search of food, or, during the mating season, in a quest to locate a female. If the environmental conditions turn unfavourable (temperatures, weather or others), they will stay in an area for some time without displaying territorial behaviour towards other males. The observations made in the Hall, as well as during studies of *Chamaeleo chamaeleon* (CUADRADO 2001), suggest that females maintain fixed home ranges instead. If a male happens to come upon a female, he will stay in her vicinity for some days and mate with her. In an attempt to secure his own reproductive success, he will remain in the female’s immediate vicinity and defend her with a great degree of aggression against potential competitors. Whether he will copulate more than once with this particular female during this period of time is as yet unknown. “Female-guarding” was also noted by LUTZMANN (2002) in the case of *Chamaeleo africanus* in Egypt. “Partner-bonding” in *F. pardalis* during the mating season was reported about by BOURGAT (1970) and found confirmation in observations made following a successful mating observed in the Masoala Rain Forest Hall during the present study. Whether the males will resume their meandering after a while in order to find and mate with other females has not been proven, but it appears likely. Mated females exhibit very strong defensive responses toward other males. A polygynic mating system of this kind has also been noted in the case of *C. chamaeleon* (CUADRADO 2001). The males would guard their females for a number of days after copulation, until the latter clearly showed by means of their colour pattern that they would not be receptive to a male any longer. The guarding behaviour of the males culminates in a strongly

territorial display within the home range of the female in that it is defended against potential competitors. Females, on the other hand, do not exhibit competitive behaviour towards other females.

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