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Land use in semi-free ranging Tonkean macaques *Macaca tonkeana* depends on environmental conditions: A geographical information system approach

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Abstract Wild animals use their habitat according to ecological pressures such as predation, resource availability or temperature, yet little is known about how individuals use their environment in semi free-ranging conditions. We assessed whether a semi-free ranging group of Tonkean macaques *Macaca tonkeana* used its wooded parkland in a heterogeneous way. GIS and GPS were used to determine whether individuals adjusted their behaviors according to variation in environmental constraints over time of day and the course of a year. We demonstrated that social and resting activities occurred in high altitude areas and areas with a high density of bushes, whereas the group foraged in areas where the density of bushes and grass was low. In general, the animals used areas exposed to the sun that were not on a slope. Semi-free ranging Tonkean macaques seemed to behave like their wild counterparts in terms of activity budget, land use per activity and thermoregulation [*Current Zoology* 57 (1): –, 2011].

Keywords GPS, GIS, Temperature, Topography, Activity budget, Spatial autocorrelation, Primates

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It is commonly accepted that the main factors affecting individual fitness are predation, resource availability, and environmental and meteorological conditions such as temperature or wind (Alexander, 1974; Hill et al., 2004; Wrangham, 1980). Animals are known to selectively use their habitat and change their activity patterns according to the type and strength of ecological pressure in order to maximize their fitness (Boinski and Garber, 2000; Hill, 2006). Apes, for example, choose bed or nesting sites where their preferred food is available (Ancrez et al., 2004; Riley, 2007). Chacma baboons *Papio hamadryas ursinus* and savannah chimpanzees *Pan troglodytes verus* are known to use caves on a thermoregulatory basis, including sleeping in caves because they are more comfortable than sleeping outside (Barrett et al., 2003; Pruetz, 2007). Riley (2007) found that a wild group of Tonkean macaques *Macaca tonkeana* in a more disturbed area (altered by human activity) spent more time foraging and resting, and less time moving, than a group in a less disturbed area. Therefore, wild animals display behaviors adapted to their environmental constraints. The question remains, how do such animals behave when they live in a captive environment?

The majority of studies that have compared wild and captive animals have been carried out on activity budget (Melfi and Feistner, 2002), social behavior (Thierry, 2007) or the emergence of abnormal behaviors (Bashaw et al., 2003; Kerridge, 2005). Few studies have assessed the effect has on the foraging patterns of animals (Dierenfield and McCann, 1999; Jaman and Huffman, 2008; Jaman et al., 2010). Ross and Lukas (2006) reported that captive chimpanzees *Pan troglodytes ssp.* preferred the highest tier of an enclosure, and gorillas *Gorilla gorilla gorilla* preferred the floor level. Other authors suggest that *ad libitum* access to food in captivity decreases foraging time in favor of social activity (Honest and Marin, 2006). Despite free access to commercial primate pellets, semi-free ranging lion-tailed macaques *Macaca silenus* and ring-tailed lemurs *Lemur catta* regularly foraged for plants and seeds (Dierenfield and McCann, 1999). Jaman and Huffman (2008) found similar results: Japanese macaques *Macaca fuscata* living in a vegetated enclosure spent equal amounts of time foraging on natural vegetation and feeding on provisioned food. Thus, like wild animals, captive animals seem to adapt their behavior to their environment, but this assumption needs to be confirmed.

Here, we observed a semi-free ranging group of Tonkean macaques in its 0.32 ha wooded parkland habitat. Given the previously quoted findings and semi-free ranging conditions present, we expected our study group to display shorter foraging and moving time than time spent socializing. In addition, we did not expect to observe homogeneous land use except on the sites where food was available. Following previous results on other captive primates (Ross and Lukas, 2006), we tested our prediction that this group would show preferences for some areas with specific environmental characteristics adequate for foraging or social activities.

1 Material and Methods

1.1 Subjects and environment

The study group was bred under semi-free ranging conditions at the Strasbourg University Centre of Primatology, France. At the time of the study (November 2005–March 2006), the group consisted of ten individuals: one adult male (>5 yr), five adult females (>4 yr) and four juveniles (1–3 yr), which is comparable to the composition of wild groups (Pombo et al., 2004; Riley, 2005, 2007; Supriatna et al., 1992). Wild Tonkean macaques are typically found in the primary and secondary rainforests of Sulawesi (Indonesia) and are mainly frugivorous (Pombo et al., 2004; Supriatna et al., 1992). The Tonkean macaques in our study had complete access to 0.32 ha of wooded parkland in addition to indoor housing within the enclosure. The indoor housing (20 m²) is made of cement and tiles, and animals were able to climb on top of this indoor housing. The enclosure area was made up of various slopes and uneven ground. The distribution of vegetation was also heterogeneous, and we could distinguish three layers (grass, trees and bushes) that were unevenly distributed throughout the enclosure. Commercial primate pellets and water were available *ad libitum* in the indoor housing. Fresh fruit and vegetables were provided once a week, and were always given at the same location one hour after the end of the observation session. Thus, behavior of the animals was most likely not affected by this feeding event. Animals were habituated to the presence of humans in their enclosure.

1.2 Scoring of variables

Observations occurred from 18 November 2005–23 March 2006, for four hours each day between 09:00–13:00 h or between 13:00–17:00 h, with an equal number of morning and afternoon sessions across the study period.

In order to assess our predictions, we used a geographical information system (GIS) for data analysis and global positioning system (GPS) for data collection. The topography of the ground (coordinates and altitude) was recorded using GPS at the beginning of the study. We only retained points with precision inferior to one meter. A total of 225 points were used to create a Digital Elevation Model (DEM, resolution: 100 cm²) using ArcView (Li et al., 2005; Ormsby et al., 2004). In order to verify the precision of our DEM, we compared it to satellite and aerial pictures (provided by Image et Villes laboratory). No correction was necessary.

Direct *in situ* observations were also used to map the vegetation in the enclosure. We used a 9 m² quadrants visual method (Bonham, 1989; Foster et al., 1991; Meese and Tornich, 1992) to estimate the cover percentage of different vegetal strataes (grass, bushes, and trees). This estimation was carried out every 15 days during the study. Four observers evaluated the cover percentage of each striate. Each observer estimated the cover percentage for an

individual quadrant, which was calculated as a mean. In each quadrant, we estimated the mean cover percentage for each vegetal strata. We used this estimation with topographic measurements to divide the enclosure into 22 areas with differing vegetation types and topography. These different areas were included in ArcView. Table 1 summarizes the cover percentage for each area. Area 0 was the indoor housing and area above it.

We also recorded the temperature for each hour of observation using a handheld weather station (± 3 m from subjects). The temperature ranged from -5.2 – 14.5°C , with an average value of $4.11 \pm 0.22^{\circ}\text{C}$ ($n=96$).

Every 10 minutes, one observer noted the position of each animal in the enclosure on a map (scale: 1/550; precision: one meter) along with its activity using the instantaneous sampling method (Altmann, 1974). The map contained 77 landmarks measured before the study allowing the 1 m level of precision. The activity and position of each individual were then recorded in Arc View 9.0.1. (Environmental Systems Research Institute Inc., Redlands, CA) (Li et al., 2005; Ormsby et al., 2004). The activities we were interested in (listed below) were defined according to the same criteria used by Riley (2007) and Pombo et al. (2004) for Tonkean macaques and by other authors for different species (Melfi and Feistner, 2002; O'Brien and Kinnaird, 1997):

- **Moving** locomotion including walking, running, climbing and jumping;
- **Foraging** reaching for, picking, manipulating, masticating, or placing food in mouth, as well as manipulating the contents of a cheek pouch (if an individual walked while masticating, the activity was classified as moving);
- **Resting** body stationary, usually sitting or lying down;
- **Social** playing, grooming, sexual and aggressive behavior.

We only retained scans where the position and the activity of all individuals could be noted. At the end of the study, we obtained 24 days of observation, 558 scans and 5580 recordings of individual positions in the enclosure.

1.3 Data analysis

1.3.1 Parameters First, we studied whether the group was cohesive by analyzing the distance between group members. In this study we defined the group as cohesive if the distance separating individuals was less than the theoretical distance under the independence hypothesis (where individuals are independent). For each scan, we calculated the distance separating two individuals, which was 45 distances per scan. We then calculated the mean distance among individuals ($n=45$ by 558 scans =25110). We calculated the theoretical mean distance under the hypothesis that individuals are independent by generating a random matrix in Ucinet 6.0 (Borgatti et al., 2002), with 0 meter as minimum distance and 40 meters (park length divided per two) as maximum distance.

We estimated the activity budget of each individual by determining the percentage of time spent on each activity (number of scans spent on an activity divided by the total number of scans).

The same calculation was used for the percentage of time animals spent in trees.

Animals want to be in trees during the leafing period so they can eat buds and young leaves. The beginning of the leafing period was set at 15 February, according to the leafing period of the principal tree species in the enclosure (*Acer pseudo-Platanus L.*, *Fraxinus excelsior L.*, *Robinia pseudacacia L.*; herbierfrance.free.fr/, www.tela-botanica.org/). This condition was approved by field observations.

The time spent in each square meter area for individual activities and in total was calculated in order to determine whether the animals carried out a specific activity in certain areas. Our main dependent variables were total duration of all activities and duration of each individual activity expressed in minutes per square meter. For analyses and graphs, values were truncated to two decimal places.

Using the DEM, we calculated topographic variables such as altitude, slope and exposure. We used the cover percentage of grassland, bushes and trees and the number of bushes as independent variables for vegetation.

We checked if high altitude gave the animals better visibility of their surroundings. For the group under investigation, the most crucial area of the enclosure was the entrance, as negative enforcement (vets and keepers) and positive ones (food) arrived from this location. The areas from which animals could see this entrance were determined using a viewshed analysis in ArcView.

Sun exposure was evaluated by scoring the cardinal direction of the slope (south facing slopes are exposed to the sun, north facing slopes are not exposed) and the cover percentage of bushes and trees. We obtained sunlight exposure values from 0 (northern exposure, cover 100%) to 881 (southern exposure, cover 0%). This index was calculated using Zonal Statistics in ArcView.

1.3.2 Spatial autocorrelation When studying biogeographic patterns such as the duration of land use by animals, it is important to check for spatial autocorrelation (Fortin and Dale, 2005; Legendre et al., 2002). Spatial autocorrelation is the probability that neighboring spatial units (adjacent areas) are more likely to have similar patterns, than by chance alone. This probability may lead to false-positive results in correlations (Fortin and Dale, 2005; Legendre et al., 2002). In our study we analyzed patterns for the duration of activity. Spatial autocorrelation was therefore checked using a Dietz R-test that tested correlation between two matrices. The first matrix was the distance in meters between the cores of each pair of areas. The second matrix was the differences of activity duration between each area. We computed one matrix for the duration of socializing activity, and another for the duration of foraging activity. We then carried out matrix correlations using Socprog 2.3 (Whitehead, 1997), setting the number of permutations at 10 000 for each matrix correlation test (Whitehead, 1997). Results showed that there was no evidence of spatial autocorrelation, neither for the duration of socializing activity ($n=22$, $r=-0.08$,

$P=0.779$) nor for the duration of foraging activity ($n =22$, $r=-0.10$, $P=0.829$), making controls for spatial autocorrelation unnecessary.

We also tested for collinearity of topographic and vegetation variables. No two variables were collinear in our study (collinearity diagnostics, $VIF \leq 2.957$); we could therefore consider all topographic and vegetation variables as independent (Pallant, 2007).

1.3.3 Statistics We compared the observed mean distance between individuals and the theoretical distance using a Mann-Whitney test.

The possible influence of leaves/buds on trees on the number of observations where animals were present in trees per day was assessed using Spearman rank correlation test. A Mann-Whitney test was then carried out to assess if the mean number of scans in trees was different between the non-leaving period ($n=11$ days) and leaving period ($n=13$ days).

We tested total duration differences between areas using the Kruskal-Wallis test with the Monte Carlo option using comparisons with 10 000 random tables. A Kruskal-Wallis test followed by a Dunn's multiple comparisons test established which area differed from the others in term of land use. The duration of land use was expressed in min/m^2 (see above) in order to compare areas of different size. Duration of land use is represented in Fig.1. Maps were obtained using ArcView. Each area was then compared using a Spearman rank correlation test to establish if they were used in the same way for both socializing and foraging. Path analysis was used to assess the influence of independent variables (topography and vegetation) on the duration of foraging and socializing activity of different locations. This analysis was made using AMOS 5 software (AMOS Development Corporation, Spring House, PA, USA.) with maximum likelihood estimations (for non-parametrical analyses).

Sun exposure for each individual's position was correlated to temperatures using the Spearman rank correlation test.

Except for matrix correlations, analyses were performed using SPSS 10 (SPSS Inc., Chicago, USA). Tests were significant for $\alpha=0.05$. Means are $\pm SE$ (standard error).

2 Results

2.1 Activity budget

The mean observed distance between individuals was 4.17 ± 0.05 m. The mean theoretical distance was 29.47 ± 1.69 m. These results showed that individuals were seven times closer to each other than under the independent hypothesis (Mann-Whitney, $n=45$, $U=1469$, $P<0.00001$), and were therefore cohesive. Indeed, 54%

of the total data (25110 calculated distances) involved individuals in contact with or close to another individual (≤ 1 m).

The group spent most time resting (36.7%), followed by socializing (28%), moving (19.8%) and foraging (15.5%).

2.2 Locomotion substrate

We investigated whether the studied animals spent more time in trees or on the ground. From the total of all observations, we found that they spent 11.5% of their time in trees. Given the distribution of trees in the park, if the stratum use is random then animals should have theoretically only spent 3.3% of their time in trees. The observed duration was approximately 3.5 times longer than expected, showing that animals seemed to appreciate being in trees. Time spent in trees significantly varied over time (Spearman rank correlation, $r=0.534$, $n=24$, $P=0.007$). Animals spent more time in trees when they were covered with leaves and buds than when they were not (Mann-Whitney, $U=26.5$, $n_{\text{leafing}}=13$, $n_{\text{non-leafing}}=11$, $P=0.008$, $m_{\text{leafing}}=15.2\pm 2.5\%$, $m_{\text{non-leafing}}=6.8\pm 3.4\%$). Moreover, animals spend more time foraging outside when there was an increase in leaves and buds on trees (Spearman rank correlation, $r_s=0.41$, $n=24$, $P=0.046$).

2.3 Use of parkland

The analysis of overall group activity on the ground showed that the group used the enclosure in a heterogeneous way (Kruskall-Wallis test, $H=533.108$, $df=508$, $n=509$, based on the number of 1 m² squares, $P<0.00001$, Fig. 1a). Two zones were found to be the core areas for all activities. The first area was inside and just above the indoor housing (180–960 min/m², area 0) and its vicinity (40–160 min/m², areas 3, 6, 15, 16, 17). The second was located in the southwestern part of the enclosure, where the group stayed between 10 to 40 minutes per square meter (areas 8 and 10). The land use of area 0 was significantly different to the of all other areas (Kruskall-Wallis test: $H=400.377$, $df=20$, $n=21$, $P<0.0001$; Dunn's multiple comparisons test: $P<0.0001$ for all comparisons). Land use did not significantly differ between areas 3, 6, 8, 10, 15, 16, and 17 (Dunn's multiple comparisons test: $P>0.05$ for all comparisons) but it did however differ from all other areas (Dunn's multiple comparisons test: $P<0.05$ for all comparisons). Thus, we can regroup adjacent areas into two different zones. We mapped the entire enclosure for land use duration for resting and socializing (Fig. 1b) and for foraging (Fig. 1c), and consequently found that the areas used for resting or socializing were not the same as those used for foraging (Spearman rank correlation, $r=0.282$, $n=17$, $P=0.272$). Figure 1 shows that resting and socializing activities (Fig. 1b) were located in the same core zones previously determined for general land use (Fig. 1a). In contrast, the

foraging areas were more widespread throughout the enclosure. The animals spent 36.3% of foraging time finding seeds and leaves and 66.7% foraging within the indoor housing.

2.4 Characteristics of used areas

We wanted to assess whether preferentially used areas had any specific topographical or vegetative characteristics. The results showed that only altitude and sun exposure significantly influenced the dependent variable (Path analysis: $df=3$; $R^2_{\text{altitude}}=0.50$, $P<0.0001$; $R^2_{\text{exposure}}=0.36$, $P<0.0001$; Fig. 2a and Fig. 2b). For foraging activity, slope and sun exposure significantly influenced activity duration ($df=3$; $R^2_{\text{slope}}=0.61$, $P < 0.0001$; $R^2_{\text{exposure}}=0.09$, $P=0.005$, Fig. 2c and Fig. 2d). As far as the influence of the vegetation on resting and social activities is concerned, only the cover percentage of bushes and trees significantly influenced the duration of socializing activity ($df=6$; $R^2_{\text{bushes}}=0.28$, $P<0.0001$; $R^2_{\text{trees}}=0.07$, $P=0.022$; Fig. 2e and Fig. 2f). However, the analysis of foraging activity showed that only the number of bushes and the cover percentage of grass significantly influenced the dependent variable ($df=6$; $R^2_{\text{grass}}=0.08$, $P=0.001$; $R^2_{\text{bushes}}=0.92$, $P<0.0001$; Fig. 2g and Fig. 2h).

2.5 Altitude and viewshed analysis

The resulting map (Fig. 3) clearly showed that higher altitude areas (areas 0, 3, 5 and 8) were the only ones from which the entrance could be seen by Tonkean macaques (Spearman rank correlation, $r=0.587$, $n=18$, $P=0.010$).

2.6 Influence of temperature on enclosure use

A Spearman rank correlation test showed that temperatures were correlated with the exposure to sunlight ($r=-0.248$, $n=5580$, $P<0.0001$). Animals seemed to choose their areas according to the temperature: exposed areas with sunlight when temperature was lowest, non-exposed areas when temperature was highest (in the temperature range observed during observations).

3 Discussion

By comparing observed distances between individuals to the theoretical distances under the hypothesis that animals are independent, we showed that the study group of Tonkean macaques seemed to be cohesive by their proximities. They spent more than half their time in body contact or very close proximity. Previous results showed that they are also cohesive in their coordination (Sueur and Petit, 2008; Sueur et al., 2009). Tonkean macaques also used their land in a heterogeneous way according to the type of activity, temperature and topographic

variables. Social and resting activities occurred in the highest altitude areas with high density of bushes. On the other hand, the group foraged in areas where the density of bushes and grass were low. In general, the areas animals used most were exposed to the sun and not sloped. Our results could not have been obtained so accurately without the use of GIS methodology.

The group exhibited a shorter foraging time than time spent socializing or resting as predicted. There seemed to be greater difference between the activity budget for two wild groups of Tonkean macaques studied by Pombo et al. (2004) than between our study group and these wild groups. Similarly, Melfi and Feistner (2002) found through direct comparison that there were greater differences between two captive groups and between two wild groups of crested black macaques *Macaca nigra* than for comparisons between captive and wild groups. In support of other studies on wild Tonkean macaques (Riley, 2007, 2008), we suggest that resting is the most prominent activity both in the wild and captivity, whilst foraging is not. The most striking differences between wild and captive groups are in socializing and moving activities. Social activity is a good substitute for boredom in captivity, and when monkeys are allowed to express this activity properly their suffering is reduced.

Despite *ad libitum* access to commercial primate pellets, the group still foraged for leaves and seeds in the enclosure. Similar results were found by Jaman and Huffman (2008) and Jaman et al. (2010) in a group of Japanese macaques living in a vegetated enclosure. According to Dierenfeld and McCann (1999) and Jaman et al. (2010), this natural foraging could be due to a high level of fibers and proteins in these plants. Analysis of the nutrient composition of the selected plants species is necessary to validate this hypothesis.

The study group appeared to spend more time on the ground than in trees, even though they spent more time in trees than expected. Previous reports stated that Tonkean macaques spent most of their time in trees (Pombo et al., 2004; Riley, 2007, 2008). We showed that animals tended to spend more time in trees during the leafing season (spring) and were therefore sensitive to seasonal changes. Similarly, wild Tonkean macaques spend more time in trees with fruit availability (Riley, 2008). Animals seem to adapt their behavior according to leafing or fruiting periods, because buds and fruits are rich in proteins. These results showed that natural vegetation in enclosures benefits animals as they can enhance their foraging activities and consequently their welfare.

In our study the Tonkean macaque group used its enclosure in a heterogeneous way with a preference for certain areas. The group foraged in areas where the density of bushes and grass was low. This allowed individuals to have easy access to plants, seeds and leaves, and also to the ground where seeds and invertebrates are buried. Tonkean macaques are mainly frugivorous, but invertebrates also seem to be an important part of their diet (Pombo et al., 2004; Supriatna et al., 1992). Social activities occurred in different areas, but most often in areas

with high altitude and high density of bushes. These results may be explained in terms of vigilance and visibility (Boinski and Garber, 2000; Stanford, 2002). These areas allowed the animals to monitor the enclosure entrance where vet staff and keepers enter. We showed that animals did not use sloping areas, where walking seems to be more difficult. In the same way, African savannah elephants *Loxodonta Africana* seemed to avoid costly mountaineering (Wall et al., 2006). The temperature measured in the park was very different from temperatures in the natural environment of Tonkean macaques (Pombo et al., 2004; Riley, 2007; Supriatna et al., 1992). This difference may explain why captive animals spend a lot of time in area 0, which was inside or close to their indoor housing. Animals seemed to choose areas on a thermoregulatory basis, as shown in other species (Boinski and Garber, 2000; Hill et al., 2004; Pruettz, 2007). They exposed themselves to sunlight when the temperature was low, and avoided exposed areas when the temperature was high. This behavior may also show the animals' adaptation to a non-natural environment. A park with heterogeneous vegetation and hilly landscape seems to lead to a greater variety and prevalence of animal activities. Specifically, some areas with higher altitude in our study seemed to allow Tonkean macaques to better observe their environments and enhance their well-being.

To conclude, the GIS methodology allowed us to note, visualize and analyze several parameters that would have been difficult to measure with classical methodology. The behavior of the primates seemed to be constrained by factors similar to those affecting wild populations (Hill, 2006; Iwata and Ando, 2007; Pruettz, 2007; Riley, 2007; Ross and Lukas, 2006). A heterogeneous environment in terms of vegetation, topography and meteorological variations appeared to affect group activity, and the captive animals seemed to behave in the same way as their wild counterparts, as found in previous studies: they are cohesive and their movements are coordinated, and they adapted their behavior to their environment (Jaman and Huffman, 2008; Ross and Lukas, 2006; Sueur et al., 2009). What is usually missing in captivity is the variability between time and space (too much time and limited space). Animals need space which gives them chances to properly manage social interactions, mainly sexual and agonistic. Nevertheless, this appears to not have been a problem for our study group. This type of study is crucial to attain a better understanding of captive animal behavior, and to assess whether they behave like their wild counterparts. Following on from our study, we could proceed to an accurate survey that would assure their welfare (Jaman and Huffman, 2008; Ross and Lukas, 2006). Our results could be used to design appropriate enclosures for primates bred in zoological parks.

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Table 1 Mean cover percentage for three strates (grass, trees, bushes) and topography (mean altitude, mean slope, mean exposure) for the different areas in the enclosure of the Tonkean macaques group

Zone	Cover percentage: grass (%)	Cover percentage: trees (%)	Cover percentage: bushes (%)	Number of bushes	Mean altitude (m)	Mean slope (°)	Mean exposure (°)
1	10.00	5.00	5.00	26	183.82	21.50	148.31
2	8.75	5.00	5.00	26	186.22	25.06	149.74
3	5.00	5.00	5.00	18	190.76	22.20	190.15
4	10.00	0.00	10.00	28	188.69	29.86	161.05
5	7.50	5.00	5.00	35	193.91	39.74	134.28
6	5.00	5.00	5.00	26	189.94	9.29	216.91
7	10.00	5.00	5.00	89	185.65	30.11	294.95
8	5.00	0.00	5.00	61	191.39	24.32	156.16
9	10.00	5.00	5.00	36	190.63	19.18	149.03
10	11.25	5.00	5.00	47	191.14	9.10	272.87
11	100.00	0.00	0.00	0	189.43	12.06	98.50
12	98.75	0.00	0.00	0	183.05	11.14	171.33
13	10.00	5.00	0.00	0	185.06	15.25	121.20
14	10.00	5.00	0.00	0	187.45	7.50	178.34
15	20.00	5.00	0.00	0	188.68	20.78	159.69
16	90.00	0.00	0.00	0	187.87	11.31	163.40
17	10.00	5.00	0.00	0	189.49	15.56	175.23
18	0.00	5.00	0.00	0	186.33	35.50	335.21
19	11.25	0.00	0.00	0	185.16	41.64	307.73
20	10.00	0.00	0.00	0	177.72	2.74	165.97
21	0.00	5.00	0.00	0	184.36	37.36	285.94

Area 0 is not indicated because it corresponds to indoor housing.

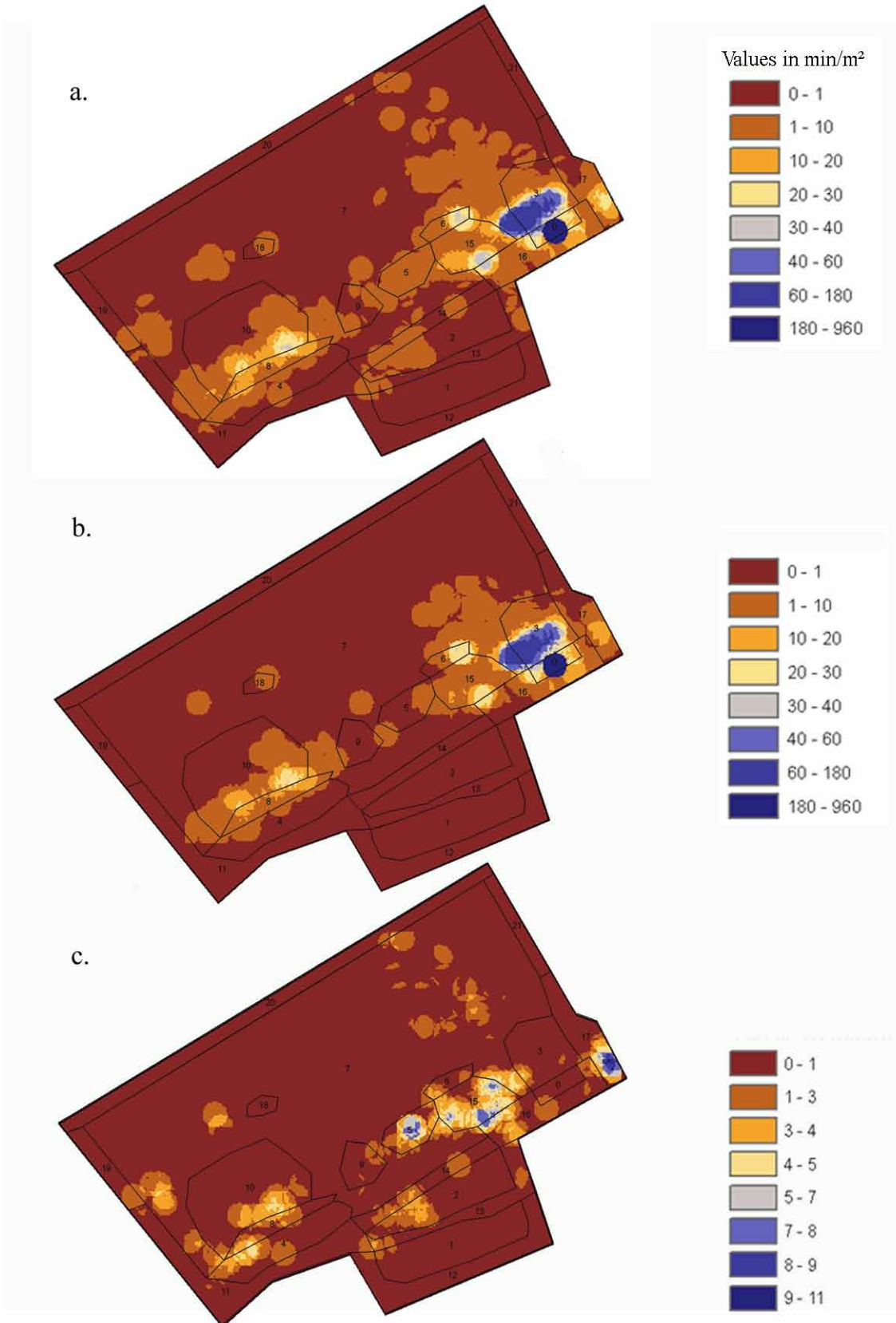


Fig. 1 Maps of land use duration in the enclosure (in minutes per square meter, for the total number of observations) for (a) all activities, (b) resting and socializing, (c) foraging

Numbers on the maps indicate the different areas, from 0 to 21.

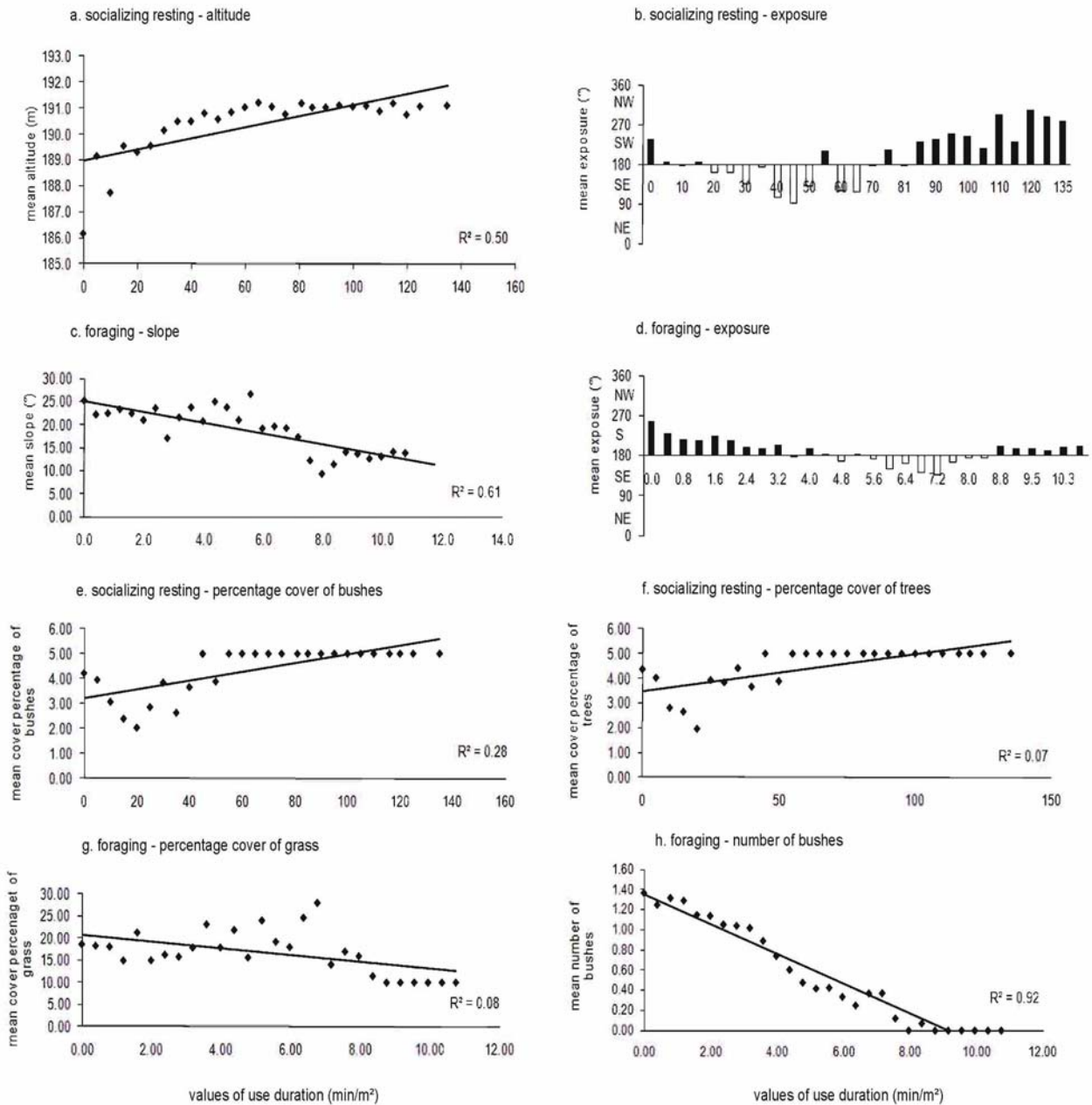


Fig. 2 Influence of topography and vegetation on land use duration for socializing-resting and for foraging activities

a. Influence of altitude on land use duration for socializing-resting activities. **b.** Influence of sunlight exposure on land use duration for socializing-resting activities. **c.** Influence of slope intensity on land use duration for foraging activity. **d.** Influence of sunlight exposure on land use duration for foraging activity. **e.** Influence of bush cover percentage on land use duration for socializing-resting activities. **f.** Influence of tree cover percentage on land use duration for socializing-resting activities. **g.** Influence of grass cover percentage on land use duration for foraging activity. **h.** Influence of number of bushes per square meter on land-use duration for foraging activity.

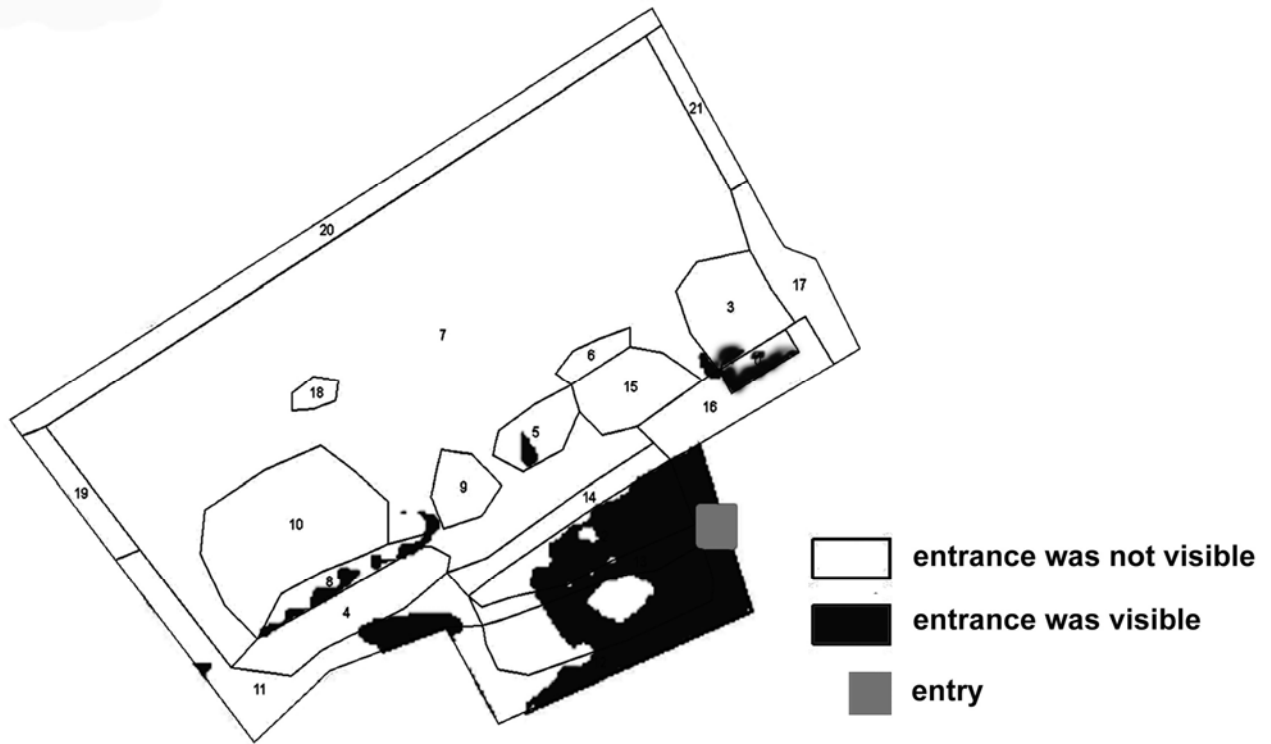


Fig. 3 Map of the enclosure with zones where the entrance is visible (grey) or not visible (white)

This map was obtained using a surface analysis in ArcView. Entry in grey and entrance visible in black.