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AGONISTIC STRATEGIES AND SPATIAL DISTRIBUTION IN CAPTIVE SOOTY MANGABEYS (*CERCOCEBUS ATYS*)[1, 2]

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Summary.—The aim of this article is to study the relationship between the dominance hierarchy and the spatial distribution of a group of captive sooty mangabeys (*Cercocebus atys*). The analysis of the spatial distribution of individuals in relation to their rank in the dominance hierarchy showed a clear linear hierarchy in which the dominant individual was located in central positions with regard to the rest of the group members. The large open enclosure where the group was living allowed them to adopt a high-risk agonistic strategy in which individuals attacked other individuals whose rank was significantly different from their own. The comparison of the results with a previous study of mangabeys showed that, although the dominance ranks of both groups were similar, the fact that they lived in facilities with different layouts caused different agonistic strategies to emerge and allowed the dominant individual to assume different spatial locations.

Although the social organization of humans has been studied for decades by a variety of social scientists (such as social psychologists, sociologists and politicians), the organization of individuals in social groups is a very common phenomenon in nature. Moreover, the patterns of social structure observed in some species are often as complex as the social patterns observed in humans. Because of the proximity between species, nonhuman primate societies provide a phylogenic point of view that helps highlight some features observed in human societies. Therefore, besides the interest in nonhuman primate societies in and of themselves, studying them may also provide a clearer picture of some features of human societies. For example, the patterns of aggression, dominance hierarchy, and affiliative behaviors observed in

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nonhuman primates can be useful when analyzing the social structure of egalitarian societies and the styles of leadership in small human societies (Younger, 2003, 2010).

The spatial distribution of individuals within a group is a major topic of study in nonhuman primate societies, as it reflects the dominance hierarchies within the group, i.e., the relationships between individuals in which the dominant figures have some privileges over subordinates, such as earlier access to food and females. In a seminal paper, Yamada (1966) used naturalistic observation to study five wild groups of Japanese monkeys (*Macaca fuscata*) on Shodoshima Island (Japan). Three groups were made up of about 150 individuals and two groups had about 50 individuals. In all the groups studied, the dominant male occupied the central position in the group. Although some young males were tolerated in central positions, as a general rule, the more dominant individuals occupied central positions, including dominant females and their offspring, while the more submissive remained in the periphery of the group. In contrast, Altmann (1979) described the spatial position of individuals in the genus *Papio* as random, while a subsequent review of his study (Rhine & Westland, 1981) showed that dominant males were disproportionately observed more often in the periphery and subordinate males were toward the rear. Moreover, a study of a captive group of red-capped mangabeys (*Cercocebus torquatus)* showed random spatial distribution of the dominant individuals (Dolado & Beltran, 2011).

In the current study, a captive group of sooty mangabeys was studied (*Cercocebus atys)*. Sooty mangabeys provide information of human interest in a variety of disciplines, including immunology (Riddick *et al.*, 2010), epidemiology (Santiago *et al.*, 2005) and paleoanthropology (Daegling *et al.*, 2011). The genus *Cercocebus*, which includes mangabeys, belongs to the Cercopithecidae family known as the Old World monkeys. This is the largest family of primates, with 133 species, including baboons (*Papio sp*.) and macaques (*Macaca sp.*). *Cercocebus* inhabits tropical regions of Africa (from Senegal to Kenya) in a broad range of habitats including primary, secondary, flooded, gallery and mangrove forests. The small morphological size of *Cercocebus* (head and body length of about 382–888 mm, tail length of about 434–764 mm and weight of about 3–20 kg; Nowak, 1999) allows them to adapt well to captivity and establish stable groups. Mangabeys are thus an important part of most zoos' primate exhibits (278 subjects were reported; International Species Information System, 2012). Mangabeys are divided into two genera, *Cercocebus* (including the species *galeritus*, *atys* and *torquatus*), *Lophocebus* (including the species *albinega* and *aterrimus*) (Disotell, 1996; Groves, 1978) and a genus recently named *Rungwecebus* (Davenport, *et al.*, 2006). Sooty and red-capped mangabeys (*C. atys* and *C. torquatus*, respectively) are quite similar and both species share a similar morphological size, habitat and diet (Groves, 2001). In fact, the World Association of Zoos and Aquariums (2007) clumps these two species together to establish common criteria for conservation. Despite these similarities, the red cap of *C. torquatus* allows for quick and easy recognition of this species, which contrasts with the gray back and facial whiskers of *C. atys.*

The Cercopithecidae family is characterized by a clear pattern of agonistic behavior and a well-known dominance hierarchy (Thierry, Singh, & Kaumanns, 2004). Many research papers and reviews have been published on Cercopithecidae with regard to the formation, maintenance and reversal of dominance ranks (see Singh, Singh, Sharma, & Krishna, 2003; Singh, Krishna, & Singh, 2006). Like the other members of this family, the genus *Cercocebus* develops dominance hierarchies based on dyadic interactions between different individuals in the group. Some studies have reported that both *C. torquatus* and *C. atys* exhibit a dominance hierarchy that is related to matrilineal kinship for the first three years of offspring development (Gust & Gordon, 1994).

Hemelrijk (1996, 1998, 2000) suggested that the dominant individual's centrality may depend on agonistic strategies in dyadic agonistic interactions between the members of the group. Hemelrijk tested her model by including two agonistic strategies using an agent-based simulation program: (a) a risk-sensitive strategy in which attack depended on the risks involved, i.e., individuals attacked other individuals whose rank was significantly different from their own. In this strategy, the outcomes of interactions were clear; the lower-ranked individuals were being repeatedly defeated and consequently moved further from the others, thus generating a spatial structure where dominant individuals were located in central positions; and (b) an ambiguity-reducing strategy, based on the contention that aggression stopped once the ranks were well differentiated among the individuals, meaning that individuals attacked others whose rank was similar to their own. In this strategy, the outcomes were uncertain and dominant individuals increasingly tolerated other individuals more distant in rank. Thus, the spatial structure with the dominant individuals in the central position did not develop.

Aggression is not the only variable that has been studied to define spatial structure among group members. Stahl and Kaumanns (2003) studied the foraging behavior of two captive groups of sooty mangabeys. The study showed an increase in competition among group members when food was clumped (placed in a box). The dominant individual was generally located in a central position and monopolized the food. But when the food was dispersed throughout the entire enclosure, the individuals also dispersed throughout the enclosure. Moreover, in captivity, other variables such as weather conditions and enrichment elements located inside the enclosure can modify the spatial structure of group members.

Dolado and Beltran (2011) empirically tested Hemelrijk's agent-based model in a group of captive red-capped mangabeys. The group was made up of five individuals, three males and two females, specifically, one adult male, two adult females and the offspring of both females (two juvenile males). The individuals had been housed together for three years before the study. The group lived in a box-shaped enclosure with an area of 23.25 m^2 and walls that were 4.86 m high. The enclosure also had a glass front through which the animals could be observed. This enclosure was enriched with items such as ropes, nets and pieces of wood. The enclosure was outdoors but had a covered area that protected the group from bad weather (see Fig. 1a). The dominance rank was established based on the dyadic agonistic interactions observed between all the members of the group and their spatial distribution was determined. The results showed an ambiguity-reducing strategy that led to the non-central spatial positioning of the dominant individual.

In the current study, the agonistic strategy and spatial distribution of a group of captive sooty mangabeys was observed (*C. atys*). The tested group lived in a different enclosure than the group studied by Dolado and Beltran (2011). The spatial configuration of an enclosure determines the locations of the individuals and where they can move. Therefore, the probability of one particular individual meeting another particular individual and, therefore, the probability of a particular pair of individuals being involved in an agonistic encounter varies depending on the features of the enclosure, and the agonistic strategy could also change accordingly. The objective of this study was to show that, under conditions of captivity, a specific agonistic strategy was adopted depending on the characteristics of the enclosure.

A group of sooty mangabeys living in an open enclosure, rather than a cage, was chosen. The group was made up of seven members, in contrast to the five studied in Dolado and Beltran's (2011) group, but both groups shared a similar social structure (one adult male, two females and their offspring). The red-capped and sooty species (*C. torquatus* and *C. atys,* respectively) are so similar that, until recently, they were classified as subspecies (*C. toquatus lunulatus* and *C. torquatus atys*, respectively) (Oates, 1996; Kingdon, 1997). Their behavioral patterns are so similar that the World Association of Zoos and Aquariums applies the same criteria to both species to guarantee their conservation and welfare, as explained above.

Hypothesis 1. The group studied was expected to show a different agonistic strategy than the one observed in the Dolado and Beltran (2011) group, based on the different features of the enclosures where they lived.

Method

Participants

The group of mangabeys studied at Barcelona Zoo was made up of seven individuals, three males and four females. The offspring of the adult male (François, 14 years old) and an adult female (Yani, 12 years old) consisted of a young female (Clara, 4 years old) and a juvenile male (Machito, 2 years old). The adult male also had offspring with another adult female (Kasi, 9 years old): a young male (Fosc, 4 years old) and a juvenile female (Mini, 1 year old). The individuals had been housed together for five years before the study. All the individuals were well habituated to human observers and individual recognition was quite easy.

Measures

The group lived in an open outdoor enclosure with an irregular area of 73.41 m^2 and no covered areas. However, the individuals had access to a dorm area in case of bad weather[3]. The enclosure was enriched with items such as ropes, nets and pieces of wood (see Fig. 1b), which were kept in the same place during the study to avoid disruptions in the spatial distribution of group members. To record the individuals' spatial distribution, the enclosure was divided into different subareas. Previous observations allowed us to identify the zones and elements most used by the individuals and to define 22 subareas of different shapes and sizes depending on the substratum (Fig. 2). Each subarea was defined by a point with three coordinates (x, y and z) located in the center of the subarea. Observer XT 6.0.16, an event logging software for the collection, analysis and presentation of observational data, was used to record the positions of the seven individuals every 30 seconds during all filmed

[3]During rainy days, individuals remained in the dorm areas, where recording their activity was impossible.

observation sessions. These positions were then used to calculate the centrality of the individuals at each time unit for every group.

Procedures

Previous *ad libitum* observations of the animals' behavior were carried out to establish an ethogram of agonistic behaviors (see Table 1). *Ad libitum* observations, i.e., the free notes taken by the researcher on what is happening during a pre-established period of time, make it possible to become familiar with the behavior of the individuals and to prepare the ethogram (Altmann, 1974). After the *ad libitum* observation sessions, the group was filmed with a mini DV JVC GR-DX77E video camera Sony Tokio, Japan. All observations were filmed from a fixed angle that allowed for maximum visibility and eliminated unobservable areas. The equipment was set up while the animals were inside the enclosure.

The animals were filmed for 22.5 hours (1,350 minutes) over the course of 30 observation sessions. Data were collected early each morning (8 a.m. to 10 a.m.) from Monday to Friday when no members of the public were present. As per the investigators' request, the enclosure components (e.g., platforms, wood, plants, etc.) were not changed while data were recorded.

Analysis

The filmed observations were used to describe the dyadic agonistic interactions and spatial distribution of the individuals. The analysis was done using version XT 6.0.16 of the Observer (2005) computer program.

The dominance hierarchy was established based on the dyadic agonistic interactions following the modifications of the Landau (1951) and Appleby (1983) index proposed by Singh *et al*. (2003). Following the procedure proposed by Singh *et al*. (2003), after generating a win/loss matrix, the hierarchy index was found that included modifications for the individuals that had no encounters with other individuals. The scores were also standardized (*z*) to construct an interval scale for individual rank. Then, based on the methodology proposed by Hemelrijk (1998), the individuals were ranked depending on the score (*z*) obtained to establish the dominance hierarchy.

Individual centrality was calculated in accordance with Hemelrijk (1998), as based on Mardia (1972). For each individual *i*, a unit vector toward every other individual was calculated every 30 seconds. The module of this unit vector provided the distance between individual *i* and the rest of the individuals of the group. The centrality of individual *i* was thus the module of the sum of its unit vectors toward all the other individuals. We calculated one module per individual and time unit group to assess the spatial distribution of the individuals at each time unit. If the module value (or distance) is high, the individual occupies a peripheral position. If the module value is low, the individual occupies a central position with respect to the other individuals (Fig. 3).

Reliability analysis was performed on intra-observer and inter-observer variability and concordance using 10% of the footage. The reliability index was calculated by carrying out concordance analysis (Cohen's kappa) and showed intra-observer concordance of 0.99 and inter-observer concordance of 0.97.

Results

The dominance hierarchy based on the dyadic agonistic interactions index (Singh *et al*., 2003) established the following dominance ranks in the group: Yani (rank 1), François (rank 2), Kasi (rank 3), Fosc (rank 4), Machito (rank 5), Clara (rank 6) and Mini (rank 7). The results indicate a strong linear organization in the group (h = 0.79) (Table 2).

We calculated the Kendall rank correlation between each individual's dominance rank and spatial distribution (centrality vectors of each individual every 30 seconds). A negative Kendall rank correlation indicated centrality of the dominant individual in the group and a Kendall rank correlation near zero indicated that the dominant individual was not positioned in central areas. The Kendall rank correlation between dominance rank and the spatial distribution obtained was –.23 (p < .001, 95%CI = –.24, –.21), which confirmed the existence of a relationship between dominance rank or hierarchy and the centrality of a dominant individual in the group. The individuals therefore used a risk-sensitive agonistic strategy and the dominant individual occupied a central position.

To identify the agonistic strategy used by the individuals, the Kendall correlation was computed between the rank of the individuals that showed aggression and the rank of the individuals that received aggression. When the individuals were arranged by rank, a positive correlation indicated that one individual showed more aggression toward an individual of close rank (ambiguity-reduction strategy), while a negative correlation indicated that one individual showed aggression toward an individual of a distant rank (risk-sensitive strategy). The results showed a negative correlation ($r_{kendall}$ = –.21, p < .001, 95%CI = –.34, –.10), which indicated that aggression occurred between individuals of very different ranks (i.e., a risk-sensitive strategy).

Discussion

According to Hemelrijk (1998), the kind of dyadic agonistic interactions that take place between the members of a group of primates determines spatial distribution; specifically, spatial centrality is be found when a group displays a risk-sensitive strategy. The sooty mangabey group displayed a risk-sensitive strategy and the correlation between dominant hierarchical rank and spatial position confirmed that the dominant individual remained in central areas. The results therefore agree with Hemelrijk's proposal and Hypothesis 1 was supported.

The use of a risk-based agonistic strategy meant that individuals attacked other individuals whose rank was quite different from their own. These dyadic agonistic interactions can cause significant changes in the dominance ranks of the group; if a lower-ranked individual wins several agonistic encounters against a higher-ranked individual, the dominance relationships can change and thus affect group stability. Because of the structure of the enclosure where the group lived, the losing individual (higher or lower ranked) had enough room in the enclosure to flee and avoid undesired agonistic encounters. However, the red-capped mangabey group studied by Dolado and Beltran (2011) displayed the ambiguity-reducing strategy, in which the dominant individual did not stay in central areas. This group was living in a small habitat where there were no remote places to hide after losing an agonistic encounter. In such a situation, continuous fighting between individuals of significantly different rank could have meant that a losing individual would be excluded from the group. Given the fact that both groups showed a similar social structure, consisting of one adult male and two females and their offspring, and that the behavioral patterns of both species are quite similar, a probable explanation for the difference between the agonistic strategy shown by each group was the kind of enclosure (while the sooty mangabey group lived in an open area of 73.41 m^2, the red-capped mangabey group lived in a box-shaped cage with an area of 23.25 m^2).

The ambiguity-reducing strategy is a conservative agonistic strategy in which dyadic agonistic interactions do not cause significant changes in the hierarchical structure of the group and help maintain group stability in reduced spaces. The emergence of a conservative agonistic strategy where agonistic interactions between individuals of different ranks are avoided deserves special attention. By using this strategy, the group tries to maintain the current dominance structure. But if the number of individuals increases and the social structure of the group is changed, it seems reasonable to assume that stressful scenarios will start to arise. In this case, changes will be necessary, such as enlarging the cage or moving the animals to an outdoor enclosure like the one used by the sooty group, to provide the individuals with escape routes after they lose a dominance interaction, i.e., a fight (Caws, Wehnelt, & Aureli, 2008).

Given the fact that changes in the wellbeing of a group of primates can be observed through behavioral patterns (Estep & Baker, 1991; Neveu & Deputte, 1996), the results suggest that it would be desirable to extend the study to other types of enclosures. This study could include other factors such as the presence of other primate groups in neighboring enclosures, the presence of metal bars around the enclosure and the proximity of zoo visitors (Mallapur, Waran, & Sinha, 2005), as well as external factors imposed by the specific location of zoo enclosures that might affect the adoption of agonistic strategies. Although studying individuals in captivity makes it possible to accurately record the spatial locations of the individuals, the group studied here was small and had a very simple social structure. It would be desirable to extend the study to larger groups comprising several males and females, like those that occur in the wild. Moreover, studies should be extended to more groups of Cercopithecidae and other captive primates to see if the same phenomena are observed in other species. Finally, this study also showed that agent-based models are a good tool for studying certain behaviors observed in captive primates because of they can help establish explanatory models and formulate parsimonious hypotheses.

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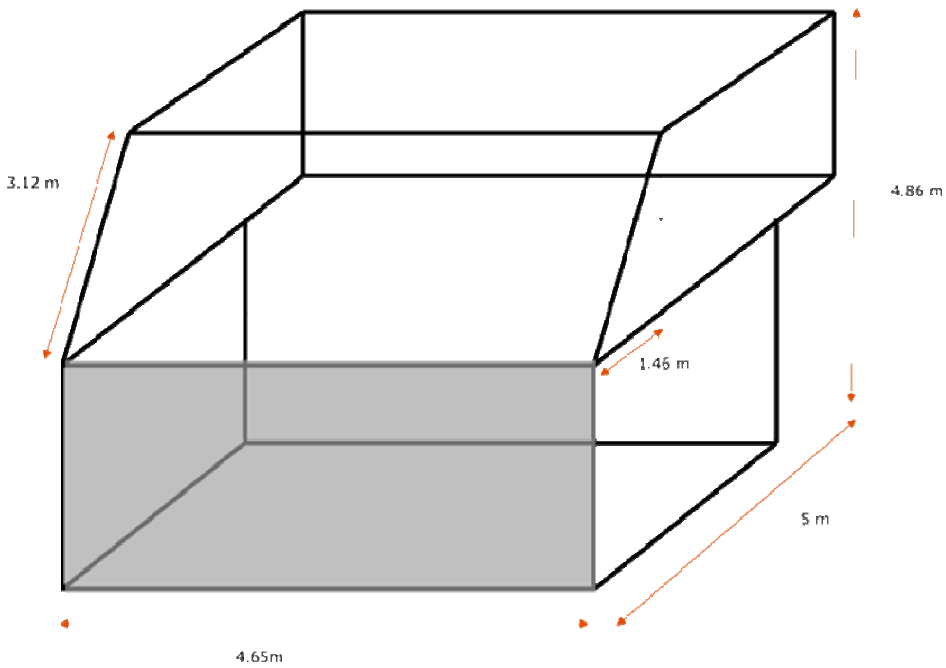
Table 1
Agonistic ethogram obtained from the sooty mangabey group (Cercocebus atys) at Barcelona Zoo

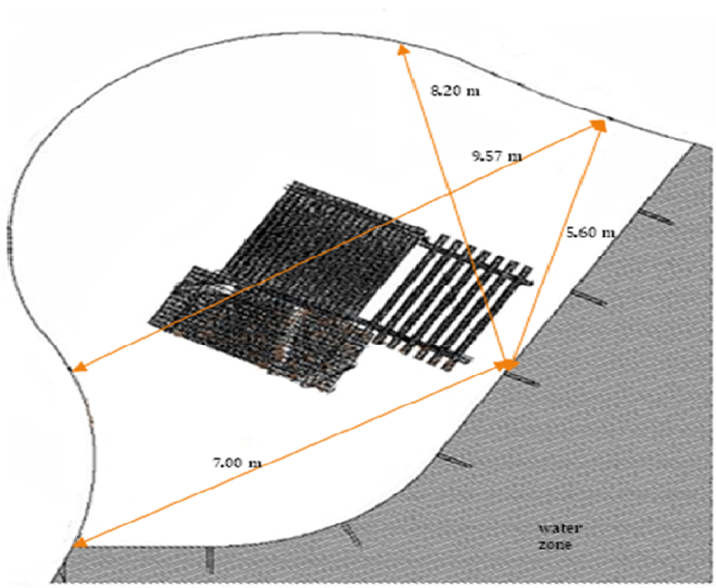
Behavioral Unit	Definition and Description
Chasing	Following another individual through different substrates. Signs of aggression nay be observed, such as short breaks in which the individuals observe each other while baring their teeth, and tension among the other group individuals.
Hitting	One individual quickly approaches another and strikes a blow with the hand or an object, usually to the head. The other individual may be in any position, though sitting is most common if there is no fight before the blow, and a quadruped stance is most common if the fight is already occurring when the blow is struck.
Yawning	Opening the mouth and breathing in and out slowly with the lips drawn back to expose the teeth.
Grabbing	Violently taking hold of any part of another individual’s body (including coat) using one or both hands.
Biting	Gripping someone or something with the teeth. May be accompanied by raised hair on the back of the neck and/or flattening of the ears against the skull.
Hair on end	Alarm status, quadruped stance with hair on end and back curved upward, associated with an individual’s reaction to an aggression or the presentation of teeth by another individual. The individual remains in this position while it waits for the behavior of the aggressor. It is unlike yawning in that the individual who performs the action does not have its mouth open.
Supplanting	An individual’s spatial position is taken over by another that enters the facility. The supplanting individual can either run or walk toward the one it will supplant.
Mounting	Genital contact between individuals in the copulation position. This occurs between individuals of the same sex (males or females) and also includes the face-to-face form of mounting, where one individual mounts on the head of another.
Crouching	One individual bends its limbs (the front ones or all four) to be at ground level over another.
Escaping	One individual runs away from another that is pursuing it. The body posture is rigid, the back is curved up and the tail is vertical.
Reacting to a bite	An individual is bitten during the yawning behavior and remains still for a few seconds until the other reacts.

Table 2
Hierarchy ranks in the sooty mangabey group (*Cercocebus atys*) at Barcelona Zoo according to the Singh, *et al*. (2003) index.

Individual	*z*	Rank
Yani	1.31	1
François	1.12	2
Kasi	0.52	3
Fosc	-0.27	4
Machito	-0.56	5
Clara	-0.80	6
Mini	-1.31	7



A



B

Fig. 1. Sketch of the enclosures. (A) The shaped-box enclosure of the red-capped mangabeys (*Cercocebus torquatus*) at Barcelona Zoo studied by Dolado and Beltran (2011). The front glass is light gray. (B) The enclosure of the sooty mangabeys (*Cercocebus atys*) in the current study. In the sooty mangabey enclosure, the elevated platform area is shaded dark gray and the water area is shaded light gray.

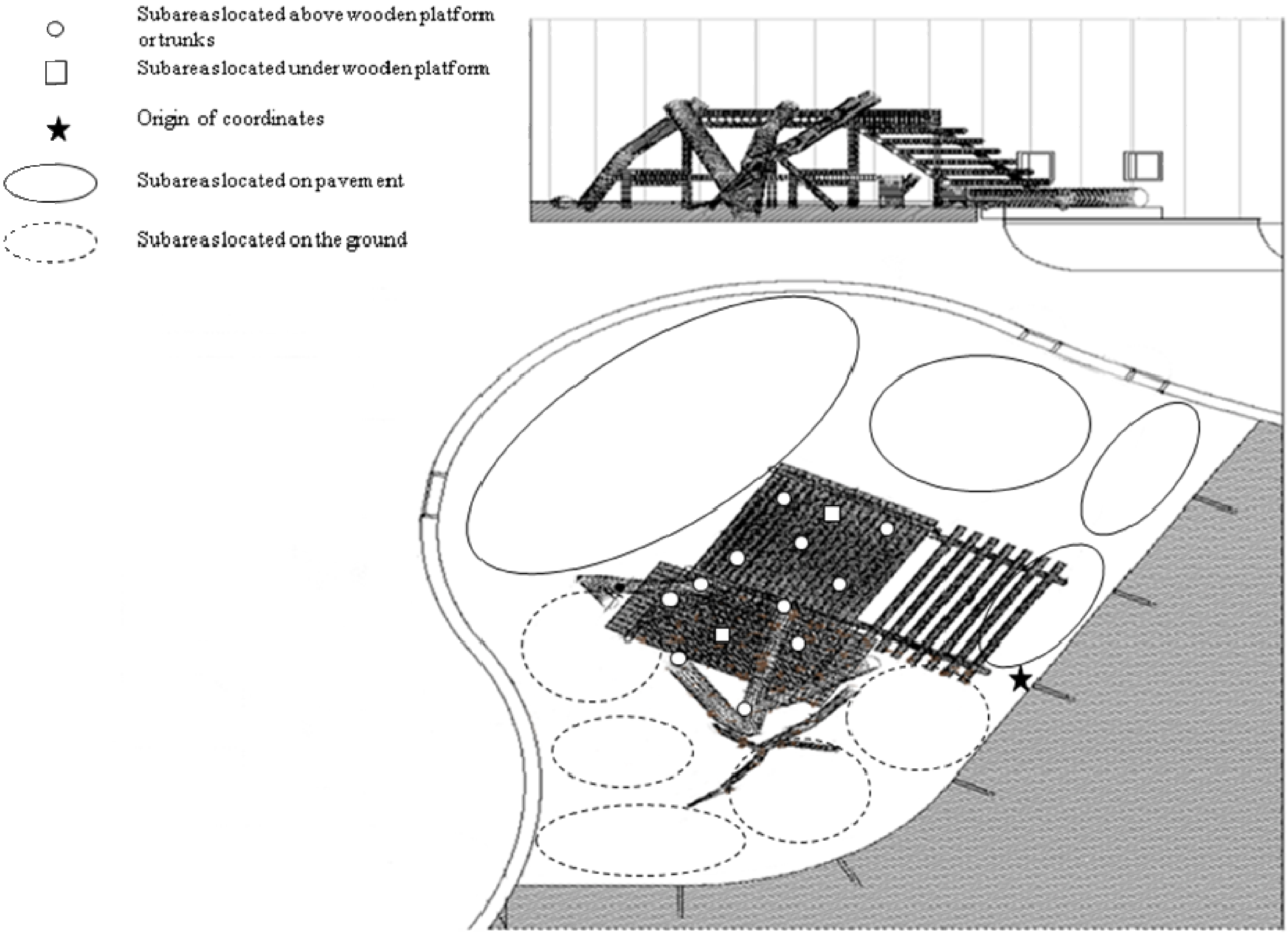
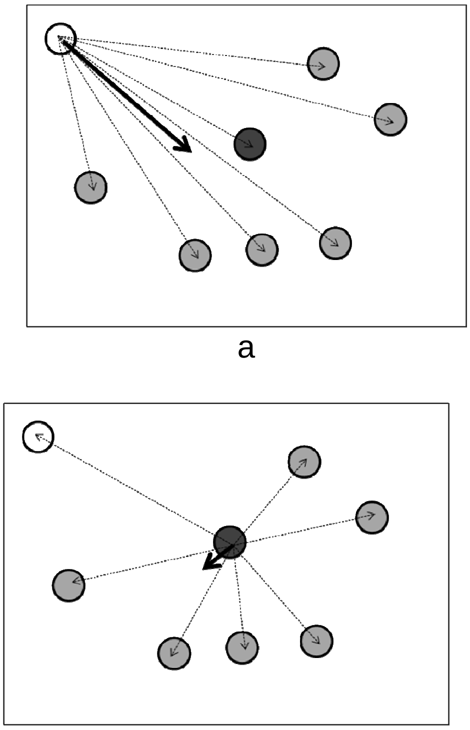


Fig. 2. Sketch of the 22 subareas in which the enclosure was divided to establish the spatial distribution of the members of the group.



a

b

Fig. 3. Measurement of centrality according to Mardia (1972). The figures show two examples of seven dots distributed on a flat surface. The gray arrows show the module of the vectors (equal to the distance) between the target dot and the rest of the dots. The black arrows show the sum of the unit vectors from the target dot toward all the other dots. (a) The value of the white dot's centrality. (b) The centrality of the black dot. The shorter black arrows indicate greater centrality of the black dot over the white dot.