Dominance Hierarchy and Spatial Distribution in Captive Red-Capped Mangabeys (*Cercocebus torquatus torquatus*): Testing Hemelrijk's Agent-Based Model

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Abstract

We empirically tested Hemelrijk's agent-based model (Hemelrijk, 1998), in which dyadic agonistic interaction between primate-group subjects determines their spatial distribution and whether or not the dominant subject has a central position with respect to the other subjects. We studied a group of captive red-capped mangabeys (*Cercocebus torquatus torquatus*) that met the optimal conditions for testing this model (e.g., a linear dominance hierarchy). We analyzed the spatial distribution of the subjects in relation to their rank in the dominance hierarchy and the results confirmed the validity of this model. In accordance with Hemelrijk's model (Hemelrijk, 1998), the group studied showed an ambiguity-reducing strategy that led to non-central spatial positioning on the part of the dominant subject, thus confirming the model indirectly. Nevertheless, for the model to be confirmed directly, the group has to adopt a risk-sensitive strategy so that observers can study whether dominant subjects develop spatial centrality. Our study also demonstrated that agent-based models are a good tool for the study of certain complex behaviors observed in primates because these explanatory models can help formulate suggestive hypotheses for exploring new lines of research in primatology.

Keywords

Dominance-hierarchy rank, spatial distribution, *Cercocebus torquatus*, agent-based models.

Introduction

Inspired by the principles of *Alife* (see Langton, 1988; Farmer & Belin, 1992; Adami, 1998), the adaptive-behavior approach suggests that certain complex global behavioral events are guided by a set of local rules that usually relate to the actions that need to be performed in order to respond to the circumstances of the immediate environment. This set of rules produces an emergent behavior, i.e., an unexpected global phenomenon that arises from the non-linear interaction of many simple elements (see Darley, 1994). The rules that govern the complex global behavior of natural organisms can be studied through agent-based simulation, i.e., by creating a virtual world where the virtual organisms or agents perform actions in dynamic environments (see Maes, 1997; Holland, 1995).

Although it is not currently a common approach, some incipient agent-based simulations have been used in primatology. In a seminal paper, te Boekhorst and Hogeweg (1994) studied sociality in orangutans (*Pongo pygmaeus*). More recently, Sellers, Hill and Logan (2007) developed an agent-based model based on the most important activities of a troop of chacma baboons (*Papio hamadryas ursinus*) that studied how collective decisions can affect the individual fitness of group members. Ramos-Fernández, Boyer and Gómez (2006) also presented an agent-based model based on the complex society of spider monkeys (*Ateles* spp.) and how fission-fusion events emerge from a foraging model.

Hemelrijk (1998) presented an agent-based model based on the social structure of primates. This virtual world (Dom World) consists of a homogeneous space inhabited by artificial entities that form groups and only take part in dominance interactions (i.e., dyadic agonist encounters between two entities) in which the effects of winning and losing are self-reinforcing. Some empirical studies have shown that the dominant subject is spatially located in the center of the group (see Yamada, 1966). Hamilton (1971) hypothesized that the dominant subject is located in the center of the group because it can control all the other subjects in the group from that position and is simultaneously protected from predators.

Hemelrijk (1998) suggests that the dominant subject's centrality may depend on "attack strategies" in dyadic agonistic interactions between the members of the group, i.e., the spatial distribution of the subjects in a group of primates is a self-organized emergent system governed by dyadic agonistic rules of relationships between subjects. Dominance interactions are divided in three attack strategies: a) an "ambiguity-reducing strategy," which is based on the contention that aggression stops once individuals recognize the status of others, and that subjects therefore attack individuals whose rank is similar to their own; b) a "risk-sensitive strategy" that depends on the risks involved, which means that subjects mostly attack individuals whose rank is significantly lower than their own; and c) an "obligate-attack strategy," in which subjects always automatically attack each other. Agent-based simulations show a dominance hierarchy developed in all strategies, which in turn produce different effects on spatial structure. Furthermore, if subjects only attack others when the risk of losing is low (a risk-sensitive strategy), the results show a correlation between subject rank and level of centrality, i.e., dominant subjects are located in the center, close to subjects of similar rank. Otherwise, if subjects attack individuals whose rank is similar to their own (an ambiguity-reducing strategy), they will end up being close to individuals of different ranks, i.e., the dominant subjects will not be located in the center. Certain similarities exist between the ambiguity-reducing and obligate-attack strategies: in both, attacks occur between subjects of similar rank. However, in the obligate-attack strategy, this is due to the emergent proximity of subjects of similar rank, as in the case of the risk-sensitive strategy (Hemelrijk, 1998, 2000).

Waeber and Hemelrijk (2003) tested the model on a community of wild Alaotran gentle lemurs (*Hapalemur griseus alaotrensis*) in the wetlands of Lac Alaotra, Madagascar. The effect of the dominance hierarchy was examined on aggression, grooming, group behavior and spatial distribution. However, because the females in this species had priority access to food while data were being collected, the anticipated results were not obtained, i.e., that dominant subjects would be located in the center. Moreover, Bryson, Ando and Lehmann (2007) replicated and examined the results of Hemelrijk's study and found that some of Hemelrijk's results relied heavily on aspects of the model that are not well supported by the current primate literature. When the agent-based model results were compared to the behavior of the genus *Macaca*, the essential problems of Dom World were that the rate of change of dominance rankings and the probability of success of subordinate animals in agonistic interactions were exaggerated. Therefore, the main objective of our study was to test Hemelrijk's model on a group of captive red-capped mangabeys.

The dyadic interaction between subjects whose main objective is to attain leadership of the group produces a dominance hierarchy that is characteristic of many primates, especially the Cercopithecidae. Many research papers and reviews have been published on the Cercopithecidae with regard to the mechanism, maintenance and reversal of dominance systems (for the genus *Macaca,* for example, see Singh et al, 2003, 2006*)*. The Cercopithecinae subfamily demonstrates a great variety of social behavior and its social organization has been the subject of numerous research studies (see Yamada, 1966). Similarly, some studies have reported that sooty mangabeys (*Cercocebus torquatus atys*) exhibit a dominance hierarchy that is unrelated to matrilineal kinship except in the first three years of life (Gust & Gordon, 1991, 1994). Unlike the rigid dominance patterns observed in most macaques (Thierry, Singh & Kaumanns, 2004), mangabeys have a relatively dynamic dominance pattern that may be of interest in order to test Hemelrijk's model. In addition, the small morphological constitution of *Cercocebus* allows them to adapt well to captivity, as they are able to establish stable groups. Based on these characteristics of *Cercocebus torquatus torquatus* (relatively dynamic dominance pattern and the formation of stable groups in captivity), we decided that the species could be a suitable candidate for testing Hemelrijk's model and providing more information on this species.

In this study we tested Hemelrijk's model by examining the dominance hierarchy and spatial distribution of a captive group of *Cercocebus torquatus torquatus*. We also identified the group's attack strategy and the spatial distribution of its members. We expected the dominant subject to be located either in the center of the group or not in the center in accordance with Hemelrijk's predictions on attack strategy.

Methods

Subjects

The study of the group of red-capped mangabeys (*Cercocebus torquatus torquatus*) was carried out at Barcelona Zoo. The group studied consisted of 5 subjects: 1 adult male, 2 adult females and 2 infant males. Pascal was an adult male born in 1999 that arrived at Barcelona Zoo in February 2006. Buna and Yambo were sisters that were born in Barcelona Zoo in 2000 and 2002, respectively. Buna spent 5 years at Hanover

Zoo, while Yambo had never left Barcelona Zoo. Yambo gave birth to Mabé in April 2007, and Buna gave birth to Mwana in May 2007. At the time of this study, both infants had begun to acquire independence, but usually stayed in close proximity to their mothers. All the animals were well habituated to human observers and individual recognition was quite easy.

The group of *Cercocebus torquatus torquatus* at Barcelona Zoo lived in a facility with an area of approximately 23.25 m^2 that was over 4.86 m high. Their environment was enriched with items such as ropes, nets and pieces of wood. The facility was located outdoors but had a covered area that protected the group from bad weather. It also had a glass front through which the animals could be observed. The food consisted of a varied diet of fruits and vegetables enriched with nuts and fodder that was provided at least twice a day.

Materials

The animals were filmed using a Sony DCR-SR72 video camera placed outside the facility in front of the glass. To ensure good image quality and avoid reflection produced by the sun on the glass, we set up large sheets of black plastic around the camera to block the sun. This equipment was set up each morning when the animals were not present and taken down at the end of each filming session.

Procedures

Data were collected from November 2007 to March 2008. From November 2007 to January 2008 we carried out *ad libitum* and focal samplings of the animals (we observed each adult at random for 15 minutes and each infant for 10 minutes) from 9 a.m. to noon in order to establish a complete ethogram, from which we obtained the frequencies of individual and social activity. From February 2008 to March 2008 we filmed 15 hours (900 minutes) of footage on the video camera over the course of 17 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. The filmed observations were used to analyze the frequency of social behaviors (agonistic interaction, grooming, etc.) and the spatial distribution of the subjects. The analysis was done using version XT 6.0.16 of the OBSERVER computer program. This software allows the footage to be viewed and notes to be added on the same screen. Data can also be analyzed using the program. We then used OBSERVER XT 6.0.16 to observe the behaviors filmed. The frequencies of social behaviors for each subject were recorded based on the agonistic behavior (see Table 1: Social Behavior, Agonistic).

OBSERVER XT 6.0.16 was also used to record the positions of the five subjects every 30 seconds during the 17 filmed observation sessions, and the centrality of each subject was calculated at each time unit.

Results

The frequencies of all the behaviors mentioned in the complete ethogram (see Table 1) showed a clear dominance of individual activity (75.97%) over social activity (23.67%). Only 16.48% of social activity took the form of agonistic behaviors (see Table 1: Social Behavior, Agonistic). The inter-investigator reliability between the 2 investigators (two doctoral students in our research group who were familiar with the group of *Cercocebus torquatus torquatus* at Barcelona Zoo) was 99% for the complete ethogram and 90% for agonistic behaviors.

Dominance hierarchy

The dominance hierarchy was established based on the dyadic agonistic interactions between all the members of the group, based on data obtained from the 17 filmed sessions. The hierarchy index was calculated following the modifications of the Landau (1951) and Appleby (1983) index proposed by Singh et al (2003). We established the following dominance ranks ordered from highest to lowest: Pascal (adult male, rank 5), Yambo (adult female, rank 4), Mabé (infant male, Yambo's son, rank 3), Buna (adult female, rank 2) and Mwana (infant male, Buna's son, rank 1). This result indicates a linear organization based on a matrilineal hierarchy in which an infant acquires its mother's rank. However, in accordance with Gordon and Gust (1991, 1994), this feature is only temporary and will disappear when infants become adolescents.

Centrality

The subjects' centrality was calculated in accordance with Mardia (1972), i.e., for each subject i, a unit vector towards every other subject j was calculated every 30 seconds, $\vec{w_{IJ}} = (t_{ij}, u_{ij} v_{ij},)$, with coordinates $t_{ij} = (x_j - x_i) / d_{ij}$, $u_{ij} = (y_j - y_i) / d_{ij}$ and $v_{ij} = (z_j - z_i) / d_{ij}$, where (x_i, y_i, z_i) and (x_j, y_j, z_j) are subject i's and j's coordinates every 30 seconds, respectively, and d_{ij} is the distance between them. The centrality of subject i is then the module of the sum of its unit vectors towards all the other subjects. Subjects with smaller modules are more central than other subjects. The method used to test the spatial centrality of the subjects is the same used by Hemelrijk (1998). This ensures that the differences found between the Hemelrijk's agent-based model and the empirical study cannot be due to differences in the method for calculating the spatial centrality.

We calculated the Kendall rank correlation between the subjects' dominance rank and spatial distribution (centrality vectors of each subject every 30 seconds). According to Hemelrijk (1998), a negative Kendall rank correlation indicates a high dominance-rank value and low centrality vectors that correspond to the centrality of the dominant subject of the group. Moreover, a Kendall rank correlation of around zero indicates that subjects of different rank are randomly distributed in the group, because a correlation between the dominance rank and the centrality of the dominant subject cannot be established. The Kendall rank correlation between the dominance rank and the spatial distribution of the subjects obtained in our study was 0.05. We cannot therefore confirm the existence of a correlation between the dominance rank or hierarchy and the centrality of the dominant subject.

An analysis of the frequencies of space occupation suggested that the dominant subject occupied non-central positions in the facility 46.19% of the time, thus confirming the results obtained with the Kendall rank correlation. However, this analysis also showed that the dominant subject occupied central positions in the facility 26.14% of the time, corresponding to feeding time (the food was mainly located in the center of the cage). Therefore, the dominant subject may have occupied a central position with regard to the rest of the group members during feeding time. In order to determine whether or not this was the case, we carried out a Kendall rank correlation using only the footage that showed feeding time (335 minutes of footage). The Kendall rank correlation between the dominance rank and the spatial distribution of the subjects during feeding time was -0.03. Therefore, the dominant subject did not occupy a central position with regard to the rest of the group during feeding time.

Attack strategy

Finally, we determined the attack strategy developed by the subjects in the group. Note taking during the 17 filmed sessions confirmed the lack of aggression between Pascal (the highest-ranked subject) and Mwana (the lowest-ranked subject). However, aggression between the medium-ranked subjects was common. In accordance with Hemelrijk's model, the kind of aggression shown by the group subjects fit in with the ambiguity-reducing strategy, in which subjects of different rank do not attack each other.

According to Hemelrijk's model, if similarly ranked subjects attack each other, they will often be located close to others of very different rank. Therefore, the dominant subject will not occupy a central position (Hemelrijk, 1998). This was empirically confirmed in this study, as the subjects developed an ambiguity-reducing agonistic strategy and the Kendall rank correlation between hierarchical rank and spatial position indicated that the dominant subject occupied a random distribution in the group.

Discussion

Hemelrijk's model (1998) predicts that the kind of dyadic agonistic interactions that take place between the members of a group of primates determines the spatial distribution. The present study supports this hypothesis. The spatial distribution showed by *Cercocebus torquatus torquatus* at Barcelona Zoo is consistent with the agonistic strategy they adopted. The analysis of agonistic behavior showed that an ambiguity-reducing strategy of dyadic agonistic interactions existed between the group members. The results also showed a clear linear hierarchy within the group. In accordance with Hemelrijk's model (Hemelrijk, 1998), the dominant subject did not have to occupy a central position with regard to the rest of the group members. The correlations between hierarchical rank and spatial position, as well as the study of spatial location, confirmed that the dominant subject remained in non-central zones.

However, our results cannot be considered general because of the low-N. Moreover, although studying subjects in captivity makes it possible to completely determine their spatial location, the fact that the subjects are captive could be a determining factor in their spatial distribution. For example, in this study, the dominant subject's position in the peripheral zones of the facility enabled it to easily observe all the members of the group. If the facility were larger or had a different layout, it might have been necessary for the dominant subject to occupy a different position to ensure the same level of observation.

Hemelrijk's model contends that if subjects follow rules to improve their rank (a risk-sensitive strategy), dominant subjects develop spatial centrality, while spatial centrality is not developed if subjects follow rules to diminish aggression (an ambiguity-reducing strategy). In this case, subjects ended up being positioned close to others whose rank was very different form their own, without the development of spatial centrality on the part of dominant subjects (Hemelrijk, 2000). Obviously, for the model to be confirmed directly, the group has to adopt a risk-sensitive strategy so that observers can study whether dominant subjects develop spatial centrality. An ambiguity-reducing strategy (i.e., the group of *Cercocebus torquatus torquatus* we studied at Barcelona Zoo) confirms the model indirectly, as it only predicts that the dominant subjects will not take a center position. In summary, it definitely would have been desirable to have a larger sample, but the results show that this species may exhibit dynamics similar to Hemelrijk's model and this may be a consequence of a more dynamic dominance pattern in *Cercocebus* (lack of matrilineal kinship except for the first three years of life). We recommend extending these studies with larger groups in different types of facilities (if captive groups are studied) and using more groups of Cercopithecidae or other primates that adopt risk-sensitive strategies.

Finally, this study also demonstrated the utility of Cercopithecidae as a biological model for testing and extending Hemelrijk's agent-based model. It also demonstrated that agent-based models are a good tool for studying certain complex behaviors observed in primates, owing to their ability to establish explanatory models and formulate suggestive hypotheses for exploring new lines of research.

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Table 1. Complete ethogram obtained from the group of *Cercocebus torquatus torquatus* at Barcelona Zoo.

Individual Behavior	**Behavioral unit**	**Definition and description**
Postural	Lying down	Subject rests in any position, without any limb support, with its eyes open.
	Sitting	Subject stands upright by supporting itself on both hind limbs with buttocks on the ground or substrate.
	On all fours	Subject stands on all fours on the ground or substrate without performing any action and with its tail parallel to the substrate.
	Bipedal	Subject stands by supporting itself on the ground using only two feet, without performing any action.
	Sleeping	Subject rests without any limb support, with its eyes closed.
Movement	Walking	Subject moves slowly along a substrate using three or four legs.
	Running	Subject moves quickly on a substrate on all fours.
	Climbing	Subject moves vertically along a substrate.
	Jumping	Subject jumps up on a substrate on two or four legs without any intention of displacement and falls back in the same place it started from. This behavior does not include acrobatic jumps with rotations in the air, which the subject may perform in the behavior "playing without object."
Feeding	Drinking	Subject drinks water by putting it into its mouth and swallowing, either by using its hands or bending over to slurp it up. The position can be supported on 3 or 4 legs with its head down; the tail must be relaxed at ground level.
	Eating	Subject ingests any food by putting it into its mouth and swallowing it, either by using its hands or bending over to pick it up in its mouth. It may be in a sitting position or standing on 3 legs; the tail must be relaxed at ground level.
	Foraging	Subject turns over the substrate in search of food. This includes sniffing for food in the substrate or in its hand, but not putting the food in its mouth. It may be in a sitting position or standing on 3 legs; the tail must be relaxed at ground level.
Playing	Playing without object	Subject performs actions such as acrobatics, jumps on the walls without a sense of displacement, without using any object and without any other subject.
	Playing with object	Subject performs actions with an object such as a stick or a piece of food without using it for its natural purpose (i.e., not using a piece of food to eat, but to throw it from one side to the other inside the facility). This action should not involve other subjects.
Sexual	Masturbating	Subject self-stimulates its genitals with one or both hands, while sitting on the substrate with its legs slightly apart.
Grooming	Self-grooming	Subject performs inspection of any part of its body with its hands, mouth or tongue. It moves the hair from one side to another and removes impurities by hand. The subject can either be sitting or on all fours when performing this action, with its tail relaxed and parallel to the substrate.

	Scratching	Subject repeatedly and rapidly moves the palms of its hands against any part of its body, creating friction.
Excretion	Urinating	Subject eliminates urine from its body on all fours or sitting.
	Defecating	Subject eliminates feces from its body on all fours.
	Examining feces	Subject smells or uses its hands to inspect its own feces or those of other subjects.
Other	Inspecting environment	Subject looks at its environment in search of food or other objects. This behavior is different from "locating" in that its head is not pointed towards any other subject. It may be in a sitting position or on all fours, with its head slightly forward in relation to its torso if it is sitting, and looking down while making head movements if it is on all fours.
	Inspecting object	Subject inspects a non-edible object it holds in both hands. It can also inspect it with its mouth by inserting the object in its mouth and biting, usually with the rear part of the jaw.
Social Behavior		
	Approaching	Subject walks towards another subject while on all fours or sitting a short distance away. The other subject does not change positions during this process. This differs from the behavior "Walking" in that the subject moves in the direction of the other subject.
	Following another	Subject walks behind another subject while following the same path. This process includes changes in substrate, jumping and stopping.
Sexual	Showing genitals	Subject stands still on all fours with its genitals pointed in the direction of another subject. This can include touching its own genitals with its tail over its head.
	Rubbing face	Subject sniffs the genitals of another subject while on all fours. The receiver is also on all fours or lying down. The performing subject does not use its hands to stimulate the female.
	Squeezing	Subject sniffs the genitals of a female while in a bipedal standing position with hands resting on the other’s back and tail up, prior to mating. During this behavior, touching with one or both hands can occur.
	Inspecting	Subject touches another subject's genitals with one hand while the receiver is presenting itself on all fours or lying down. The subject performing the action has one hand resting on the ground.
	Copulating	Bipedal subject inserts its penis into another's genitals as the other stands on all fours. The upper extremities of the subject who performs the action are supported on the back of the other and its tail is pointed upwards.
Agonistic	Hitting	Moving the arm violently so that it comes into contact with another subject or an object.
	Grabbing	Violently taking hold of any part of another subject’s body (usually an extremity or the tail) 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.
	Threatening	Staring at another subject in order to make it go away and taking its place.
	Supplanting	Subject changes its position in the facility after receiving a threat.
	Chasing	Following another subject through the different substrates. Signs of aggression may be observed, such as short breaks in which the subjects observe each other while baring their teeth, and tension among the other group subjects.

	Mounting	Genital contact between subjects in the copulation position. This occurs between subjects of the same sex (males and females) and also includes the face-to-face form of mounting, where one subject mounts on the head of another.
	Yawning	Opening the mouth and breathing in and out slowly with the lips drawn back to expose the teeth.
Allogrooming	Grooming	Subject touches or inspects the skin of another subject with its hands or mouth. Both subjects may be on all fours, sitting or lying down, with their tails resting on the ground. If they are on all fours, their tails are parallel to the ground.
	Being groomed	Subject's skin is touched or inspected by another subject. Both subjects may be on all fours, sitting or lying down, with their tails resting on the ground. If they are on all fours, their tails are parallel to the ground.
Social Feeding	Asking for food	Subject approaches another that is eating and stretches out one or two hands, so that the subject receiving the action "gives food."
	Giving food	Subject puts a piece of food into the mouth or hands of another subject. The position of both subjects is relaxed, on all fours, sitting or lying down.
	Receiving food	Subject receives any food item. Position is relaxed, on all fours, sitting or lying down.
	Stealing food	Subject approaches another subject while walking or running and performs a quick movement to take the portion of food the other is eating.
Other	Locating	Subject watches one or more other subjects change spatial position. The locating subject may be in any position, but not in motion.
	Playing	Non-sexual and non-aggressive interaction of two subjects moving along the substrate, usually accompanied by both subjects jumping to meet each other in the air, flipping and spinning on their own axes or subjects chasing and being chased while jumping to land on each other. It can be clearly distinguished from aggression, because the other subjects in the group remain calm and do not usually take sides.
Interspecies		
Displaying	To visitors	Subject makes vocalizations or gestures directed at the public and the zookeepers at the facility. Includes subject vocalizing or remaining upright while listening to another species, usually the vocalizations of another primate species.
	To zookeepers	Subject makes vocalizations or gestures directed at the zookeepers at the facility.
	To other species	Subject vocalizes or remains upright while listening to another species, usually the vocalizations of another primate species.