



Relatedness and Social Behaviors in *Cercopithecus solatus*

Marie J. E. Charpentier · Delphine Deubel ·
Patricia Peignot

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Abstract Inclusive fitness and kin selection theories predict that organisms will evolve biased behavior toward kin when the inclusive fitness benefits outweigh the costs of such behaviors. Researchers have long observed that primates bias their behavior toward relatives, particularly maternal kin. We examined the effect of kinship on social behaviors in a semifree-ranging colony of *Cercopithecus solatus*, a poorly studied forest guenon species. We used microsatellite loci and paternity analyses to determine the degree of relatedness between individuals, as well as kinship. Individuals biased some of their behavior according to relatedness. Specifically, related individuals are more spatially associated and less aggressive toward each other. When we replaced the relatedness coefficients with defined kin categories, *Cercopithecus solatus* seemed to behave preferentially toward maternal kin versus paternal kin. Even though the setting of the colony and the small sample size limit our conclusions, we discuss the potential implications of our finding for the study of the impact of kin selection in primate social relationships.

Keywords kin selection · kinship · semifree-ranging group · social behaviors · sun-tailed monkey

Introduction

Inclusive fitness (Hamilton 1964) and kin selection theories (Maynard Smith 1964) predict the evolution of biased behavior toward kin whenever the inclusive fitness benefits—direct fitness via an individual's own reproduction and indirect fitness via

M. J. E. Charpentier (✉)
Department of Biology, Duke University, Science Drive, Durham, NC 27708, USA
e-mail: mariecharp@yahoo.fr

M. J. E. Charpentier
CEFE-CNRS UMR 5175, 34293 Montpellier Cedex 5, France

M. J. E. Charpentier · D. Deubel · P. Peignot
UGENET, CIRMF, BP 769, Franceville, Gabon

the reproduction of relatives— outweigh the costs of such behaviors (Hamilton 1963, 1964; West-Eberhard 1975). Female philopatry and male dispersal characterize most of the Old World Monkeys in multimale-multifemale groups (Pusey and Packer 1987). Consequently, females may live in the same social group throughout their lives and may interact with the same female partners for a long period of time. In matrilineal societies, mother-infant bonds often endure for many years; consequently, younger siblings will be in proximity to older maternal siblings and possibly other maternal relatives. Researchers have long observed primate females living in such matrilineal societies to bias their behavior toward relatives, particularly maternal kin. Maternally-related females are more affiliative than unrelated females in a number of ways: they spend much of their time in close association, sitting together while resting and feeding, grooming, and handling their infants (Gouzoules and Gouzoules 1987, Silk 2002). By contrast, researchers know less about how paternal relatedness shapes social relationships in primates, and have reported conflicting results on whether or not primates are able to discriminate and bias their behaviors toward paternal kin (Silk 2002; Widdig 2007).

Sun-tailed monkeys (*Cercopithecus solatus*: Harrison 1988) are a poorly studied forest guenon species, endemic to a single forest in Gabon (Brugière *et al.* 1998; Brugière and Gautier 1999; Gautier *et al.* 1986; Harrison 1988). Owing to their very secretive and cryptic nature and the difficult terrain of their home range, few eco-ethological studies have focused on the species. As in most other forest guenons (Cords 1988, 2000), the social organization of *Cercopithecus solatus* is a one-male unit, comprising 1 adult male and several adult females with their young (Gautier *et al.* 1986). On average, social groups contain 16 adult females (Brugière *et al.* 2002; Gautier 1998). Females are philopatric while males disperse away from their natal group (Gautier 1998). Researchers have acquired much of the information on the ecology and social organization of *Cercopithecus solatus* from observations on the only captive group of the species, maintained at CIRMF (Centre International de Recherches Médicales de Franceville, Gabon). In the group, one-male organization occurs with prolonged male tenure (Peignot *et al.* 1999, 2002). Their reproductive system is a harem type, with only the α -males reproducing (Charpentier *et al.* 2005).

The observation that *Cercopithecus solatus* form a matrilineal society wherein social relationships are supposed to be biased between maternal kin, motivated our study. Moreover, the harem-reproductive system in the colony has generated cohorts of paternal half-sibs. Behavioral biases between related individuals are therefore possible. The conditions invite the examination of the effects of relatedness on shaping social behaviors.

Methods

Subjects

CIRMF established the sun-tailed monkey colony between 1986 and 1989, when they acquired 4 individuals (2 males and 2 females, age 1–2 yr) and housed them in a large outdoor cage. In 1995, CIRMF transferred 11 individuals (3 remaining founders and their offspring) into a 0.5-ha rain forested enclosure (Peignot *et al.*

1999). Between 1989 and 2002, 17 infants (10 males, 5 females, 2 of unknown sex) were born into the colony. In 2002, DNA samples from 11 offspring and 3 founders that reproduced were available for analysis (Charpentier *et al.* 2005). From August to October 2000, the group numbered 4 females (including 1 juvenile) and 6 males (including 1 juvenile). Subjects ate locally available fruit and monkey chow, supplemented by natural foraging, twice a day; water was available *ad libitum*.

Pedigree Generation and Relatedness

We assigned maternity via observations of maternal behavior during the first months of life until the infants were weaned, and we usually captured infants with their mothers and tattooed them during the first months. We determined paternities for 11 past and present individuals via Cervus version 2.0 (Charpentier *et al.* 2005; Marshall *et al.* 1998). We constructed a partial pedigree allowing calculations of relatedness (R) between individuals (Fig. 1 in Charpentier *et al.* 2005). For 9 of the 10 subjects, we knew the pedigree accurately. For the remaining nongenotyped individual, 2 potential sires were present at his conception. Therefore, we performed the analyses twice, using relatedness coefficients obtained as if the individual were the offspring of each one of the potential fathers. The results remained the same, so we provide only the ones obtained when this nongenotyped offspring was the son of the α -male because α -males of the colony monopolize all reproductions (Charpentier *et al.* 2005). In the semifree-ranging colony, in which males are unable to migrate, mean relatedness between individuals from which we recorded behaviors was quite high (mean \pm SEM: 0.35 \pm 0.02). Different kin classes occurred: mother-offspring, maternal and paternal half-siblings, full-siblings and more distant kin classes, e.g., uncle-nephew and aunt-nephew. We grouped the latter into the same kin category because of the limited sample size.

Behavioral Measures

We routinely monitored male and female hierarchies via the outcome of agonistic behavior and approach-avoidance interactions (Peignot *et al.* 2002). To study the

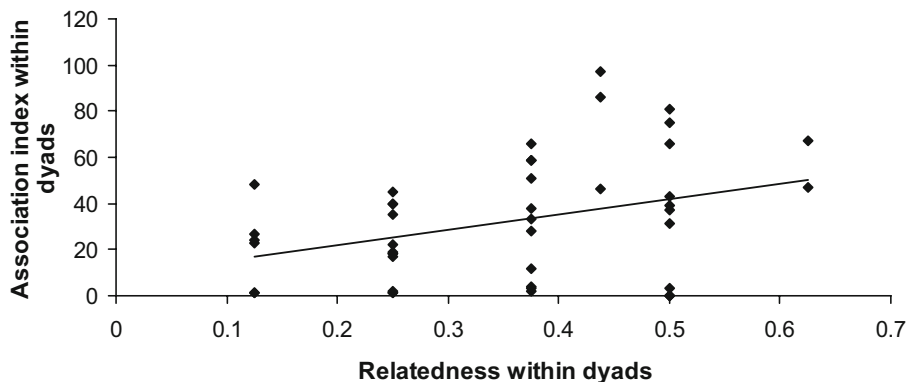


Fig. 1 Association index and relatedness within dyads ($N=45$).

sociospatial occupation of semifree-ranging sun-tailed monkeys, we observed the behavior of 10 focal individuals from August to October 2000, from 0600 h to 1800 h, excluding the feeding time. We collected data via the focal method for the 10 focal individuals (Altmann 1974); we observed subjects in a randomized sequence. We recorded social behaviors during a 5-min period. We considered within each dyad: 1) the total number of grooming bouts, i.e., 1 bout corresponded to a behavior, here grooming, when the beginning and the end of the behavior were clearly defined and separated from one another and 2) the total number of aggressive and submissive behaviors. For aggressive and submissive behaviors, data were available for only 7 of 10 individuals. The 3 other individuals were too young to show such behaviors. Finally, 3) we also computed an association index (Martin and Bateson, 1993), calculated as follows:

$$IAab = \left(\frac{Nab}{Na + Nb + Nab} \right) \times 100$$

wherein Nab represents the number of times we saw a and b together (≤ 5 m); Na is the number of times when we saw a without b ; and Nb is the number of times when we saw b without a . $IAab$ varies from 0 (no association) to 100 (total association).

In total, we recorded 121 periods of 5-min focal individual samples for 7–10 subjects (*ca.* 100 h of observations), belonging to $N=45$ dyads (association, grooming) or $N=21$ dyads (aggression, submission).

Statistical Analyses

Because we worked on dyads, each individual appeared several times in the data set, which could have led to pseudoreplication of the data. We therefore computed partial Mantel tests with 2000 data randomizations (Fstat version 2.9.3.2; Goudet 2001) to analyze the relationship between the following response variables: association index, number of grooming, aggressive and submissive behaviors within a dyad, and predictor variables. First, we considered the absolute value of the difference in ages between the 2 interacting individuals. Second, we considered whether the 2 interacting individuals were from different (coded 0) or equivalent (coded 1) social ranks. We considered 3 classes of individuals: high-, mid- and low-ranking. We also considered whether 2 interacting individuals were from different (coded 0) or same (coded 1) sex. The dyads comprised 2 females (code 1), 2 males (code 1), or 1 male and 1 female (code 0). Finally, we considered the relatedness R within each dyad, calculated from the pedigree. Then, we replaced the quantitative value with the kin classes. Because partial Mantel tests do not allow testing qualitative explanatory variables such as the kin classes, we used pairwise comparisons, with the 2 kin classes compared coded 0 and 1.

Results

First, the sex of the dyad significantly influenced the association index (Table 1), i.e., same-sex dyads were more associated (mean \pm SEM: 40.3 \pm 5.5, $N=25$) than female-male dyads (22.4 \pm 4.8, $N=20$). The association index also correlates positively with

Table 1 Effects of different predictors on behaviors within each dyad

	Number of dyads	Sex (0/1)		Social ranks (0/1)		Difference in age		Relatedness		
Association	45	$r=$ 0.34	$p=$ 0.02	$r=$ 0.06	$p=$ 0.69	$r=$ 0.09	$p=$ 0.55	$r=$ 0.36	$p=$ 0.02	More related dyads are more spatially associated
Grooming	45	$r=$ 0.17	$p=$ 0.25	$r=$ 0.07	$p=$ 0.65	$r=$ -0.15	$p=$ 0.34	$r=$ -0.08	$p=$ 0.42	
Aggression	21	$r=$ 0.35	$p=$ 0.16	$r=$ 0.04	$p=$ 0.85	$r=$ 0.15	$p=$ 0.53	$r=$ -0.41	$p=$ 0.07	More related dyads are less aggressive
Submission	21	$r=$ 0.28	$p=$ 0.28	$r=$ 0.06	$p=$ 0.79	$r=$ -0.02	$p=$ 0.94	$r=$ -0.31	$p=$ 0.16	

Partial Mantel tests (Goudet, 2001). The r -values represent the partial correlation of each explanatory variable with the dependent variables. p -values for the coefficient associated with each variable are given.

the dyad’s relatedness (Table 1; Fig. 1). The dyad’s relatedness also marginally influenced the occurrence of aggressive behaviors within dyads (Table 1): the more the dyads were related, the less aggression occurred (Fig. 2). None of the variables influenced submissive and grooming behaviors within each dyad (Table 1).

To extend the analysis of relatedness, we replaced R values with the kin class of each dyad, for the study of association index and aggressive behaviors. We distinguished the following kin categories: full-sibs ($N=6$ and $N=2$ for association and aggression, respectively), maternal ($N=6$ and $N=4$ for association and aggression, respectively), and paternal half-sibs ($N=16$ and $N=9$ for association and aggression, respectively), and dyads of less closely related individuals (such as aunt-nephew or cousins; $N=16$ and $N=6$ for association and aggression, respectively). We excluded 1 mother-offspring dyad from the analysis. Pairwise comparisons showed that 1) the association index among maternal half-sibs tended to be higher than among less related dyads (Table 2) and 2) aggressive behaviors are more numerous among paternal half-sibs than among full-sibs (Table 2). The 2 effects are marginally significant, certainly owing to the small sample size of the kin classes

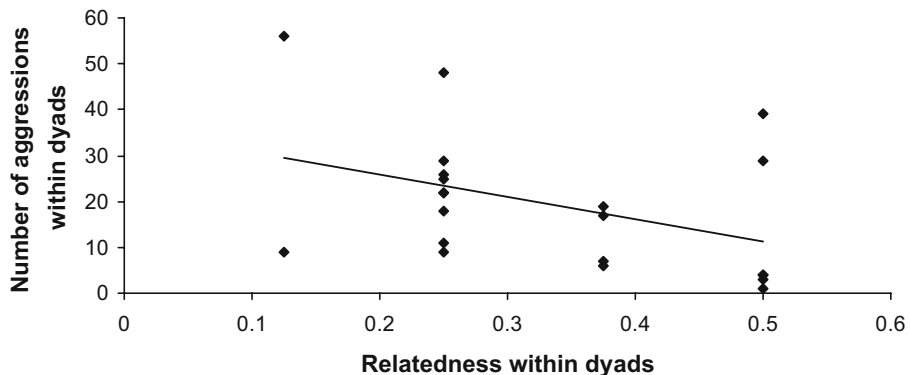


Fig. 2 Aggression and relatedness within dyads ($N=21$).

Table 2 Pairwise comparisons between each kin class defined

	Full-sibs	Maternal half-sibs	Paternal half-sibs	Less related dyads
Full-sibs	—	$r=0.50$ $p=0.10$	$r=-0.15$ $p=0.57$	$r=0.22$ $p=0.33$
Maternal half-sibs	$r=0.12$ $p=0.67$	—	$r=-0.27$ $P=0.22$	$r=-0.37$ $p=0.08$
Paternal half-sibs	$r=0.56$ $p=0.06$	$r=0.43$ $p=0.14$	—	$r=-0.02$ $p=0.89$
Less related dyads	$r=0.58$ $p=0.15$	$r=0.46$ $p=0.17$	$r=0.07$ $p=0.82$	—

Results for the association index are in the upper left corner; results for aggression in the bottom right corner. The r -values represent the partial correlation of the kin class with the dependent variables. The sign of the r -values displayed depends on the coding. p -values for the coefficient associated with each variable are given.

compared. However, a general trend appeared: maternal sibs (full-sibs and maternal half-sibs) tend to be more associated and less aggressive toward each other than dyads comprising paternal half-sibs and less related individuals are (Fig. 3).

Discussion

Researchers have recently demonstrated that female primates gain fitness advantages from associating with their relatives. For example, female red howlers (*Alouatta seniculus*) that form coalitions with relatives increase their reproductive success versus females that form coalitions with unrelated partners (Pope 2000). *Cercopithecus solatus* biased some of their behavior according to relatedness. First, closely related individuals are more often closely associated with each other than less related individuals are. A greater spatial proximity between relatives also occurs in various Old World monkeys: kin generally travel, feed, and sleep together

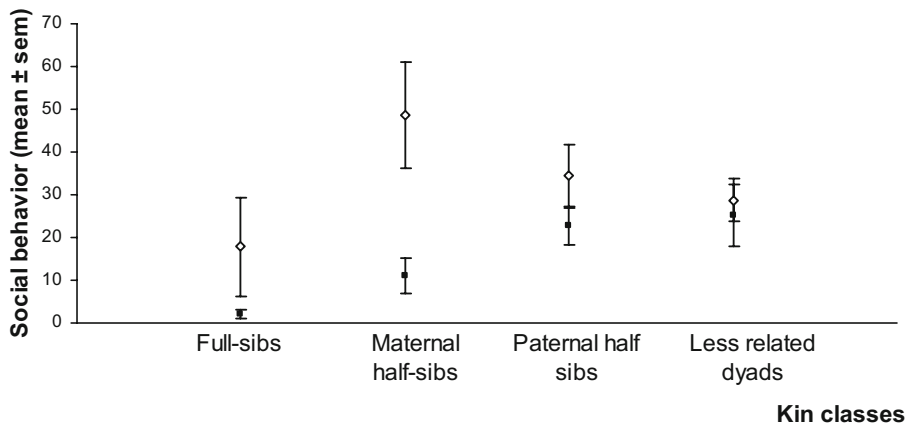


Fig. 3 Social behaviors and kinship within kin classes. Mean (\pm SEM) association index (open diamonds) and aggressive behaviors (filled squares) within kin classes are represented.

(Gouzoules and Gouzoules 1987). However, kinship provides little protection against aggression because rates of aggression are as high or even higher among relatives than among non-relatives (Silk 2002; Widdig 2002). Researchers generally consider a higher rate of aggression among relatives to be the result of increased proximity. However, we found instead that related individuals tend to be less aggressive toward each other.

Our analyses on kin classes did not reveal clear patterns; however, in general, maternal kin appeared to bias their behaviors preferentially toward each other. We noted no evidence for behavioral biases between paternal relatives. Biases in favor of maternal kin occur in a variety of primate species, and the nepotistic behaviors are especially pronounced in species, e.g., *Cercopithecus solatus*, that live in female-bonded groups (Kapsalis 2003). Maternal bonds often endure for many years in matrilineal societies in which females remain in their natal groups throughout life (Bernstein 1991; Gouzoules 1984; Gouzoules and Gouzoules 1987; Walters 1987; Walters and Seyfarth 1987). Researchers have therefore cited kin discrimination produced by familiarity because of prior association or spatial location as the most feasible mechanism for discrimination of maternally related individuals (Bernstein 1991; Gouzoules 1984; Walters 1987). However, whether primates are able to discriminate relatives with which they are not raised, such as paternal kin, still remains largely debated and there are conflicting results in the current primate literature (Silk 2002; Widdig 2007). We noted no evidence that paternal relatives biased their behaviors. However, the limited sample size, due to the setting of the colony, could have reduced statistical power of detection. We could not conduct a power analysis because we did not have a hypothesis *a priori* about the strength of the potential effect of paternal kinship in shaping behavior. Further analyses on a greater sample size are therefore needed to conclude whether *Cercopithecus solatus* might discriminate paternal relatives.

Researchers know relatively little about how nepotism varies with degree of relatedness. In general, the frequencies of agonistic support in conflicts dropped significantly beyond $R=0.25$ (e.g., half-siblings: Chapais *et al.* 1997). By contrast, affiliative behaviors generally decreased with kinship well past $R=0.125$ (Berman 1982; Kurland 1977). One potential bias of our study is that all dyads were related at least at $R=0.125$. The absence of completely unrelated individuals does not allow us to assess accurately whether nepotism in *Cercopithecus solatus* increases linearly with R or whether a threshold occurs, and if the latter is true, where it is situated. We performed an additional test for a quadratic effect of R by adding a squared term of R in the partial Mantel tests. A quadratic effect would suggest that the relationship between R and behavior is not linear. We detected no quadratic effect either for spatial association or aggression (data not shown). However, even if we have no access to unrelated dyads, we can conclude that *Cercopithecus solatus* do not interact with relatives according to a relatedness threshold at $R=0.25$, as demonstrated in Japanese macaques (*Macaca fuscata*: Chapais *et al.* 1997).

To conclude, we shed new light on kin discrimination in a poorly studied species, for which no datum on social behaviors are available in the wild, and few even in captivity (*cf.* Peignot *et al.* 1999, 2002). Though our sample size was limited, sun-tailed monkeys show kin biases in the form of higher spatial association and decreased aggression, especially among maternal relatives.

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