

RESEARCH ARTICLES

Familiarity and Dominance Relations Among Female Sooty Mangabeys in the Taï National Park

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Dominance relationships of female sooty mangabeys have thus far been studied exclusively in captive groups. In captivity, adult females form a stable linear hierarchy as would be expected in species exhibiting strong contest competition. However, the same individuals do not exhibit other aspects of behavior that would be expected where contest competition occurs. For example, they show no kin-based alliances leading to hierarchies in which the members of each matriline occupy adjacent ranks. The goal of this study was to provide the first data on dominance relationships of sooty mangabey females in their natural environment in the Taï National Park, Ivory Coast. In our study group, adult females formed a linear dominance hierarchy. Aggression over food increased in food patches, as would be expected for species that experience contest competition. Moreover, females formed highly differentiated social relationships, showing particular affinities with females of adjacent rank. *Am. J. Primatol.* 56:137–153, 2002. © 2002 Wiley-Liss, Inc.

Key words: sooty mangabey; *Cercocebus torquatus atys*; female dominance; foraging efficiency; affiliative relationships; coalition

INTRODUCTION

Following van Schaik [1983] and Dunbar [1988], we assume that terrestrial monkeys, such as the sooty mangabey, live in groups in order to reduce the risk of predation, and that group size is limited by intragroup competition over food. Intragroup competition can vary between two extremes: contest competition, in which an individual's dominance rank largely determines resource intake; and scramble competition, in which foraging skill mainly determines resource intake [van Schaik, 1989; van Hooff & van Schaik, 1992]. Following Trivers [1972] and Wrangham [1979, 1980] we expect that female reproduction is limited by their

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access to food [see also van Schaik, 1996; van Noordwijk & van Schaik, 1987]. Thus, group size and competition are expected to have a strong affect on the reproductive success of females. In addition, the type of competition is thought to determine relationships between females [van Schaik, 1989; Wrangham, 1980].

Contest competition is expected when it is economical to defend resource patches against group members. The economics of resource defense depend on a number of factors: 1) the size and shape of the patch, 2) the value of the patch relative to alternative patches, and 3) the asymmetry in resource holding power (RHP) between the contestants. The latter factor can in turn be influenced by the formation of coalitions. Thus, we predict contest competition when some individuals can systematically exclude others from limited resources, such as fruit, mushrooms, and termites. When the distribution of important elements in the diet is such that contest competition regularly occurs, animals will frequently find themselves faced with the possibility of an escalation of conflicts. This in turn selects for behavior that results in the resolution of conflicts without the costs of overt aggression. The solution often realized in primate groups is priority-of-access based on dominance. Each pair of animals has an established dominance relationship that determines which individual has priority-of-access in each competitive situation. However, other solutions are, in principle, possible—such as the resolution of conflicts on the basis of arbitrary asymmetries [see Pusey & Packer, 1997].

The formation of dominance relationships has a number of repercussions for the social life of females. The most important is that females may try to overcome an unfavorable asymmetry in fighting ability by the formation of alliances. This will only occur if there is a fitness gain from alliance formation for both allies. Important factors are: additional resources gained, sharing of these resources, and time and energy spent on the maintenance of the relationship with the partner. The outcome of the equation is more likely to be positive for closely related partners than for distantly related or unrelated partners [Hamilton, 1964; Dunbar, 1988]. Consequently, if alliance formation is important for females, the females should prefer to remain with their kin, and thus should try to remain in their natal groups. In these groups the cooperative relationships between female kin are characterized by frequent grooming and proximity [van Hooff & van Schaik, 1992]. In vervets (*Cercopithecus aethiops*), baboons (*Papio spp.*), and many macaques (*Macaca spp.*), kin alliances lead to the formation of nepotistic hierarchies in which close kin rank together [see Wrangham, 1980; van Schaik, 1989].

In addition to an indirect causal link from resource distribution to alliance formation, mediated by way of dominance relationships, one can also expect a direct causal effect from patch characteristics to coalition formation: coalitions are most likely formed when the alliance will be able to gain access to a patch that can be easily shared and can feed all allies.

In a system where dominant females can restrict subordinate females' access to food resources, acquisition of food should be positively correlated with dominance rank. As a consequence of uneven food acquisition, the reproductive success of higher-ranking females is higher than the reproductive success of lower-ranking females in several species (*Macaca fuscata* [Saito, 1996; Mori, 1979], *Macaca fascicularis* [van Noordwijk & van Schaik, 1987], *Pan troglodytes schweinfurthii* [Pusey et al, 1997], *Theropithecus gelada* [Dunbar, 1980], and *Papio cynocephalus ursinus* [Busse, 1982]). Other studies, however, have reported no relationship at all (e.g., *Cercopithecus aethiops* [Cheney et al, 1981]).

The mode of competition is expected to be rather different when economically defensible patches play no crucial role in a species' diet [van Hooff & van Schaik, 1992; van Schaik, 1989; Sterck et al., 1997]. Scramble competition is likely to

prevail when patches are very large and can feed multiple individuals simultaneously, or are very small and spread out. Thus, primates that forage on foliage or cryptic insects are expected to experience mainly scramble competition. Scramble competition does not lead to direct conflict, and thus will not lead to selection for conflict resolution mechanisms, such as consistent subordinate behavior towards certain individuals. Coalitions bring no advantage in scramble competition, and thus the suite of related phenomena listed above is not expected. In other words, where scramble competition over resources prevails, we don't expect pronounced dominance relationships, unless conflicts regularly arise in other contexts.

To date, the social system of the sooty mangabey (*Cercocebus torquatus atys*) has been studied only in captivity [Bernstein, 1971; Ehardt, 1988a, b; Gust & Gordon, 1991, 1994; Gust, 1995; Stahl, 1998]. These authors found no particular bonds between related females [Ehardt, 1988a], and no signs of nepotism, such as support for kin or kin occupying adjacent ranks in the hierarchy [Gust & Gordon, 1994].

Bernstein [1976] found a stable dominance rank order over several years. Gust & Gordon [1994] noted that the relative ranks of 11 females remained stable over a period of 12 years. Furthermore, Gust and Gordon [1991] observed severe aggression when two females challenged the alpha female in a newly formed group. Both authors, however, indicated that juvenile animals of both sexes move up the hierarchy at the approximate age of 3 years with little or no resistance from higher-ranking animals. Since the social organization of sooty mangabeys in captivity, while stable, is not matrilineal, inherited rank cannot be the explanation for the ease with which juveniles increase their rank in the dominance hierarchy. If the social system described for captive sooty mangabeys is the same as for sooty mangabeys in their natural environment, it would be inconsistent with the theoretical framework outlined above and differ from the social systems of other primate species.

The crucial links among social organization, resource distribution, and migration cannot be elucidated well in captivity. We therefore started observations on a semihabituated group of sooty mangabeys in the Taï National Park in 1997. The species spends approximately 80% of daytime on the ground and lives in large multimale/multifemale groups (Bergmüller et al., unpublished results). Little is known about natural migration patterns.

In this study we address the following issues: First, can sooty mangabey females be ranked in a linear dominance hierarchy? Second, does rank correlate with foraging success? Furthermore, we examine the structure of social relationships among adult female sooty mangabeys by analyzing association patterns, grooming relationships, and coalition formation.

METHODS

Study Site and Subjects

The sooty mangabey is found in the high forest throughout West Africa. This study was conducted in the Taï National Park in southwestern Ivory Coast (6°20'N to 5°10'N and 4°20'W to 6°50'W). The park is the last remaining major block of primary forest in West Africa and covers approximately 454,000 ha. With a mean annual temperature of 24°C, a mean annual rainfall of 1,875 mm (average of 1991–1999; data: Taï Monkey Project), and a distinct dry season in December–January, the forest can be classified as “tropical moist forest” according to Whitmore [1990]. The study area of about 7 km² is situated near the western border of the park, approximately 20 km southeast of the town of Taï.

The study group's home range contains the 2-km² core area of the Tai Monkey Project, where multiple primate groups have been studied continuously since 1991. Due to repeated exposure to people within their range and an 8-month study on their feeding ecology (Bergmüller et al., unpublished results), the group became well habituated to human observers prior to the start of this study. The study group was followed from dawn to dusk over a period of 73 days from December 1997 to April 1998, and for 66 days from April 2000 to July 2000.

During the first study period, 1997–1998, the group consisted of six to 10 adult males, 26 adult females, approximately 42 juveniles and subadults, and four to 22 infants. During the second study period, in 2000, seven to 13 males and 24 females were observed in the group. One adult female vanished in July 2000. Unless otherwise indicated, all data refer to the second study period.

Data Collection

Data on each of the 24 adult female members of the group were collected opportunistically by focal animal sampling [Altmann, 1974]. Because the mangabeys were often dispersed in dense undergrowth over considerable distances, it was difficult to collect data on a predetermined schedule. On most observation days each focal animal was sampled once. Focal samples were 15 min long, with at least 60 min between consecutive samples of the same individual. Between 810 and 897 min were collected per individual. All data were collected by the same observer (F.R.).

Each minute the activity and the nearest adult female within 5 m of the focal animal were recorded by means of instantaneous sampling [Altmann, 1974]. Social interactions were recorded continuously. For definitions of the behavioral categories see Table I. The data are taken from focal sampling, if not otherwise indicated.

Two types of food patches were recognized: 1) areas of up to 10 m in diameter on the forest floor with either mushrooms or termites (*Macrotermes spec.*), and 2) larger circular patches of seeds or fruits on the forest floor around the trunks of food trees (radius up to 10 m). If animals were inside the boundaries of a food patch, they were considered to be inside a food patch; if they were outside the boundaries of a food patch, they were recorded as being outside of a food patch. We noted whether or not an activity took place in or outside a food patch.

Between focal samples, we recorded all observed agonistic interactions between identified individuals ("ad libitum" sampling [Altmann, 1974]). The reproductive state of females (sexual swelling or lactating), and births, immigrations, and disappearances were noted on a daily basis.

Data Analysis

Dominance relationships and competition. Dominance rank was defined according to the direction of submissive behavior (avoid, yield, and supplant). We used one interaction to establish directionality in any dyad (left of the diagonal: 905 total entries/38 empty cells). To determine the degree of unidirectionality of the dominance relationships among the focal females [van Hooff & Wensing, 1987] and the degree of linearity of their rank order [de Vries, 1995], we pooled focal animal and ad libitum data. When a relationship between two females was unclear, the average rank was assigned to both.

Competition rates were estimated on the basis of the following two parameters: 1) the supplant rate is the number of approaches resulting in nonaggressive

TABLE I. Ethogram

Activity	Definition
Maintenance activities	
Feeding	Animal sits or stands at one place and puts objects in its mouth continuously, moving its jaws, emptying its cheek pouches or the animal sits at one place and opens a food-containing object with its teeth, hands and feet.
Searching	Animal moves slowly forward while visually scanning the forest floor, occasionally putting objects in its mouth.
Traveling	Animal walks steadily forward without visually scanning the forest floor.
Resting	Combines behavior like grooming, playing, sitting or sleeping.
Behavior	Definition
Social behavior	
Yield	The actor jumps or walks away from an approaching individual.
Avoid	The actor leans aside or shifts body position in response to another individual that approaches or walks by.
Crouch	The belly is close to the ground. The crouch may occur during a severe physical attack, signaling complete submission [Bernstein, 1976].
Stare	The actor raises the eyebrows and forehead while staring directly at a target animal; the head can be rapidly lowered and raised while exhibiting the stare.
Stare and lunge	After the stare the actor darts rapidly towards the recipient, but stops before reaching the recipient at which time the actor lowers its shoulders as in preparation to jump forward.
Fighting	Any hard aggressive contact: biting, hitting, gripping and fighting.
Taking place	The actor takes the place of the recipient after the recipient is threatened or pushed away.
Non-agonistic supplant	The actor approaches another individual who is occupying a resource and replaces that individual <i>without overt</i> aggression.
Grooming	The actor cleans the fur of the recipient with the mouth and/or hands [Altmann, 1962].
Invite groom	The actor can use various behaviours to illicit grooming from another individual: the actor presents and/or exposes a part of his body to reactor while standing or sitting stiffly [Hinde & Rowell, 1962].
Ventral-hug	The actor approaches a seated animal and lifts its leg onto the shoulder of the seated reactor. It moves its head towards the genital area of the seated reactor.
Hugging	The actor places the arm on the recipient's shoulder. One or both animals may rise onto two legs or remain seated and place both arms around the other's ventrum.
Touch	The actor lightly places one of its hands on the reactor.
Approach	The actor moves into the reactor's space ($r < 2m$).
Agonistic support	An intervention of a third individual in an agonistic dyad on behalf of one individual, directed against its opponent.
Coalition	The combined agonistic interaction of two animals against one opponent.

supplants over food per hour; and 2) the aggression rate is the number of aggressive behaviors (stare, stare and lunge, fighting, grip, taking place) per hour [see Sterck, 1995]. We used the Wilcoxon matched-pair test to determine whether or not aggression rates were dependent on location (inside patch or outside). Even though the aggression rates of members of the same group are only partially independent of each other, we felt that this was the best statistical method for these data.

We predicted that high-ranking individuals would be less disturbed than low-ranking individuals during foraging once dominance relationships were established. We quantified the degree of disturbance for each individual with the “foraging efficiency coefficient,” defined as the ratio feeding time/searching time (for definitions see Table I). Feeding and searching times for each female were defined as the percentages of instantaneous samples during focal animal observation the focal spent feeding or searching, respectively.

Nearest neighbor analysis. Association indices were calculated using the ratio of the number of minutes two individuals were nearest neighbors, divided by the sum of the number of minutes each was observed without the other and the number of minutes they were neighbors (simple ratio association index [Cairns & Schwager, 1987]). Association indices could vary from 1 (nearest neighbor all the time) to 0 (never nearest neighbor). To test whether adult females associated significantly more with certain companions than would have been expected if each individual associated with others by chance alone, we used a permutation test in the SOCPROG software. The tests are based on the Monte Carlo procedure, modified by Whitehead and Dufault [1999] (software is available at <http://www.dal.ca/~hwhitehe/social.htm>). The test compares observed association indices with the results obtained from a random set of data generated by 20,000 permutations of the original data set. To generate the permutations, the total numbers of observations for each individual and the total number of association partners per individual are drawn from the matrix of actual observations. The 20,000 permutations are used as the null-hypothesis against which the observed values are tested. We used the mean, the standard deviation (SD), and a *P*-value to compare the two matrices with each other. Samples including grooming interactions were excluded from this analysis and analyzed separately to see if differences between close associates and grooming partners existed.

Affiliative relationships. We calculated hourly rates of interaction for each female-female dyad by dividing the number of total interactions between A and B by the sum of the total observation time (h) that A and B were observed. The duration of grooming bouts was recorded to the nearest minute during focal sampling. The total amount of time spent grooming was estimated for each dyad as the proportion of all sample intervals during which grooming occurred. Minutes per hour were calculated for each female dyad.

The Shannon-Weaver diversity index was used to quantify how evenly females’ interactions are spread out among potential partners. Because this measurement has been widely used [Cheney, 1992; Henzi & Weingrill, 1997; Silk et al., 1999], a direct comparison with other studies is possible.

The diversity index, *H*, for a group of *n* females is calculated as:

$$H = - \sum_{i=1}^N p_i * \log p_i$$

where p_i is equal to the relative proportion of interaction directed toward the i^{th} female. *H* reaches its highest value when females interact equally with all possible partners, and is lowest when females focus all their interactions on one partner. To standardize the measure for comparison between species, ratios between the observed diversity index, *H*, and the maximum possible value of the diversity index for a group of a particular size, $H_{\text{max}} = \ln(N - 1)$ were computed (range for H_{max} : 0–1).

To test whether the distribution of grooming among female sooty mangabeys differed from the expected distribution, we used the permutation test in the SOCPROG software (see above).

Furthermore, we tested whether rank distance affected affiliative behavior among sooty mangabeys. Rank distance was defined as the number of adult individuals ranking between the two individuals concerned plus 1 (i.e., adjacently ranking individuals have a rank distance of 1). This measure was based on the constructed dominance hierarchy. The second variable was proximity, defined as the percentage of instantaneous samples during focal animal observation spent as nearest neighbor excluding grooming. The third variable was duration of grooming, defined as the percentage of instantaneous samples during focal animal observation spent grooming. Dyadic matrixes, one for each variable, were created for female–female relations. All matrixes were symmetrical; that is, one value applied to both directions per dyad.

The probability of a correlation was tested by comparing the Pearson correlation coefficient and Kendall rank correlation between two matrices with the empirical distribution of this statistic estimated on the basis of random permutations of the same matrices [Hemelrijk, 1990; de Waal, 1991]. We used a rowwise matrix correlation procedure to correct for individual differences in behavior [Hemelrijk & Ek, 1991; Hemelrijk, 1990; de Vries, 1993] based on 20,000 permutations. The Bonferroni technique (carrying out each individual test at a critical probability of $\alpha' = \alpha/k$, where k is the number of intended tests) was used to correct for multiple tests.

Statistics. Statistical analyses were performed with the SPSS (Version 7.5.1.) statistical program for Windows 2000, SOCPROG (Version 1.3) and MATMAN (Version 1.0, Noldus Technologies). Spearman's test of correlation between ranks was used to test for a correlation between foraging efficiency and the rank order. This test was one-tailed, as the prediction was directional. The results were considered significant when $P < 0.05$. (Alpha was set at 0.05 unless we corrected for multiple tests with the same data set).

RESULTS

Dominance Hierarchy

On the basis of a total of 921 agonistic interactions, we could determine the dominance relationships in 220 of the 276 possible adult female dyads (79.71%). The focal females could be arranged in a linear rank order with one circular triadic relationship (Va-Ti-Bi) (Fig. 1). Two female dyads (Co-Vi, Po-Va) were assigned equal rank in this rank order, because no interactions were observed between them. Another pair (Ka-Gi) was assigned equal rank since both showed an equal number (1) of submissive interactions to each other. The linear rank order was constructed based on the assumption that one observed dominance interaction is sufficient to determine directionality between any given dyad. In support of the assumption, only one rank reversal occurred when the matrix was constructed after omitting all single dominance interactions.

The degree of unidirectionality of the dominance relationships among the focal females was calculated as $DC = 0.965$. The probability that the observed linearity ($h' = 0.71$) resulted from a random process was $P < 0.001$. The dominance relationships of the highest-ranking females in the group ($n = 7$) did not change between the first study (1998) and second study (2000). For the lower ranking females, data from the first study were not sufficient to construct a well-defined dominance hierarchy that would allow a comparison between the relative ranks of low-ranking females for the two study periods.

	Sa	Lo	Hi	Fu	Di	Ri	Em	Lu	Ma	Bi	Ti	Va	Po	Ol	Si	Cl	St	Fa	Ka	Gi	So	Ro	Vi	Co
Sa																								
Lo	11			1																				
Hi	9+1	10																						
Fu	9	13	14+2	1																				
Di	8	8	5	8																				
Ri	10	9	14+2	15	8																			
Em	6	6	7	5	6	12+1											1							
Lu	4	4	3	4	4	3+1	5																	
Ma	1		4	2		3		3																
Bi	4	11	1	2	1	3	2	6	12		1	2												
Ti		4	4	3	4	2	3	1+1	1	3														
Va	2	5	1	3	5	1	3	3	2	1	5				1							1		
Po	4		5	2		3		5	3	4	1													
Ol	1	1	2	3	1+1		5	3		1	2	3	8		1						1	1		
Si	1		1	1		1	3		1	4+1	2	3	6	3								1		
Cl		1	1	1	1	2		1	3			1	3	2	3				1					1
St	2	5		1	5		3		5	2	7	4			5	8								
Fa		4	2		4	6	4	2	1	1	3	1	4	2	5	10	1		1					
Ka	3	1	3	1	1	3	2	3			1	3	5+1	4	10	6	3	4		1		1		
Gi	5	1	5		1		1		5	3	1	3+1	15	2	1	3	5	2	1		1			
So	3		2				1	3		4	5	1	4	5	4	3	4		3	4				
Ro	2		2	3		1	3	1	2	1	4	4+1	3	2	1	5+1		3	6	2+2	1			
Vi	3	1	1		1	2	1	7	5	3	2	1	4	6	12	6	3	6	1	6	13	5		
Co	1	4	2	3	4	9	5	2	2	7	2	3	4	6	1	2	1	2+1	2	3	1	3		

Fig. 1. Matrix based on interactions among adult females involving submissive behaviors (avoid and yield) recorded during both focal animal and ad libitum sampling (342 hr). Individuals are noted by two-letter codes, and the order is chosen by minimizing the circular triads. Ad libitum data are noted as bold numbers.

Contest Intensity

The members of the study group spent on average 24.48% (STD 6.41) of the observation time in food patches. They allocated the largest proportion of feeding time to eating the seeds of *Sacoglottis gabonensis* (32.94%), which occurs in large patches (up to 706.5 m² (Bergmüller et al., unpublished results)). If contest competition is typical for sooty mangabeys, we would expect aggression to occur at higher rates inside than outside food patches. We therefore calculated the rates (per hour) of aggression and supplants inside and outside food patches for all adult females. The aggression rate was significantly higher inside food patches (0.59) than outside food patches (0.39) (Wilcoxon matched pairs test, $n = 24$ females, $z = -1.999$, $P < 0.05$). The difference was even greater for the supplant rate, which increased from 0.36 outside food patches to 0.91 inside food patches (Wilcoxon matched pairs test, $n = 24$ females, $z = -2.590$, $P < 0.01$). The observed effect of increased rates of aggression and supplants within food patches was not due to one or two females, because even after removal of the two females with the highest supplant and aggression rates, results were still significant at the 5% level.

Foraging Efficiency

Focal females were observed feeding on average 28.79% (STD = 4.07%) of the observation time, and searching 45.18% (STD = 4.74%) of the observation time. Altogether more than 74% of the observation time was spent on activities related to foraging. The rest of the time (other activity) was spent resting and travelling. The foraging efficiency coefficient (ratio feeding/searching) was correlated with rank (Spearman rank correlation: $r_s = -0.634$, $n = 24$, $P = 0.01$). The highest-ranking females had the highest scores for foraging efficiency (Fig. 2).

Nearest Neighbor Analysis

To test whether the association patterns represented in Fig. 3 differ significantly from what would be expected if each individual associated with other individuals at random, a random data set was generated as described above and compared with the observed association matrix. The mean association indices for dyads differed significantly between the observed matrix and the generated matrix (0.079 vs. 0.081, $P < 0.01$), suggesting that dyads associated less than expected. Moreover, the SD for dyads was significantly higher for the observed matrix than for the random matrix (0.056 vs. 0.035; $P < 0.001$), indicating that the pattern of association indices deviated significantly from an equal distribution. This result can be expected if animals are more diversified in their associations than expected, avoiding certain animals and actively associating with others. The female dyads with the highest association indices are represented in a sociogram (Fig. 3).

Affiliative Relationships

Adult females did not distribute their grooming evenly among the other adult females in the group (grooming bouts, $n = 191$). On average, each female groomed four of the other 23 females at least once (range = 0–13) (Figs. 4 and 5). Moreover, females tended to restrict most of their grooming to very few partners: 11 females concentrated 50% or more of their grooming on a single partner. If the

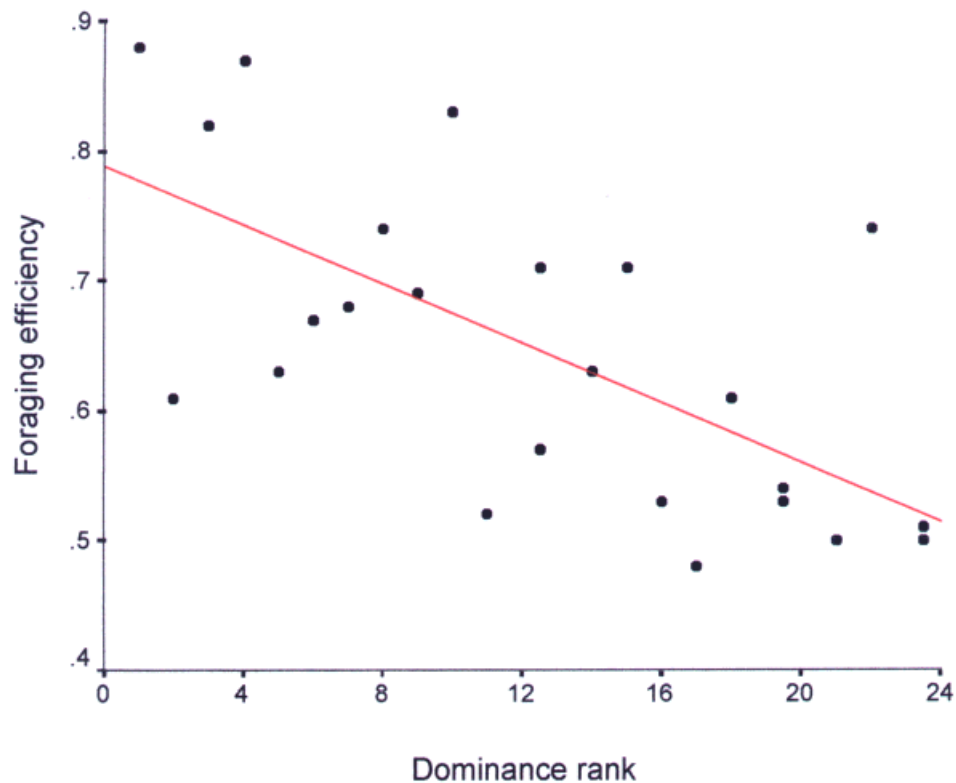


Fig. 2. The relationship between the foraging efficiency coefficient (time feeding/time searching) and dominance rank of adult females. Spearman's rank coefficient: $r_s = -0.634$, $P < 0.01$.

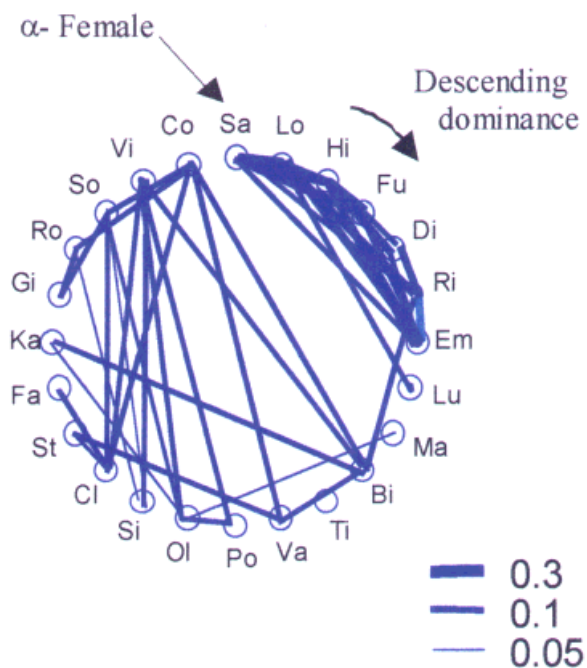


Fig. 3. Association among adult females in the subject group. The simple ratio association index was used to calculate associations between two females (A and B) using frequencies of the total observation time of A and B that A and B were nearest neighbors. Association indices could vary from 1 (nearest neighbor all the time) to 0 (never nearest neighbor). Only association indices, which are higher than 0.05, are represented. Ranks decline in clockwise direction (Sa has the highest rank).

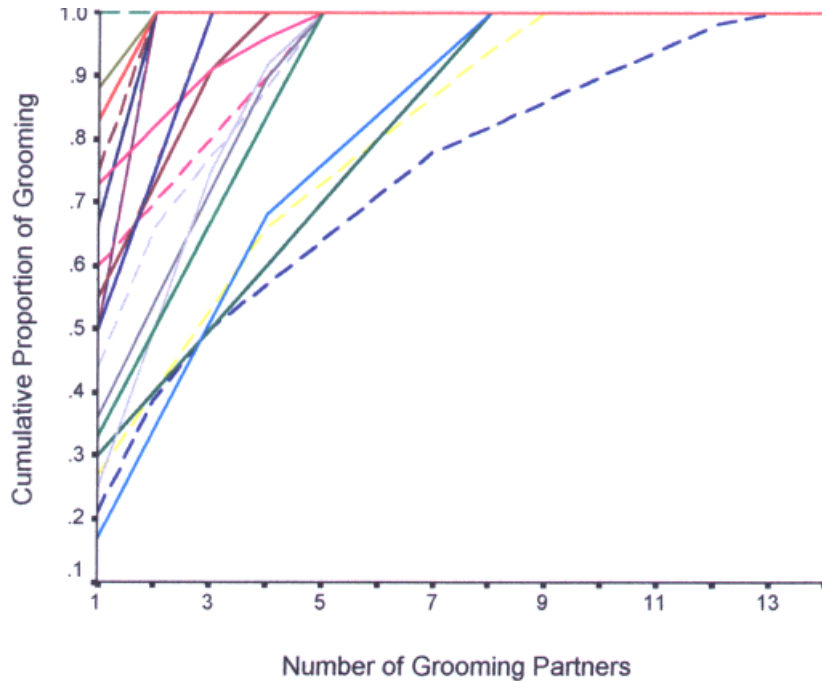


Fig. 4. The cumulative proportion of all grooming bouts directed to each adult female in the group.

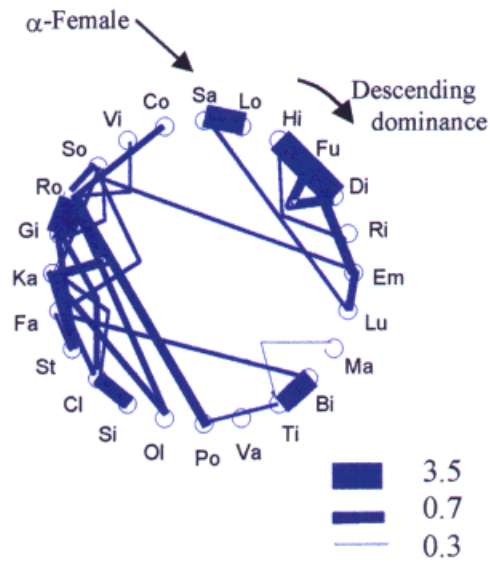


Fig. 5. Grooming network among adult female sooty mangabeys based on grooming duration (rates per hour). Bars only give examples for duration. Females are shown in decreasing rank order reading clockwise from the top.

TABLE II. Shannon-Weaver Indices for Different Interactions Among Adult Females

Form of interaction	Diversity index (H)		Diversity ratio (H/H _{Max})		Sample size
	Mean	SD	Mean	SD	
Approach	2.67	0.17	0.85	0.05	24
Groom (bout)	1.11	0.61	0.36	0.20	24
Groom (duration)	1.02	0.55	0.33	0.17	24
Nonaggressive contact	1.02	0.59	0.32	0.19	24

duration of grooming is taken into account, 14 females devoted more than 50% of their grooming to a single partner.

The very low Shannon-Weaver diversity indices indicate that adult females were very restrictive in their choice of grooming partners (Table II). In particular, the diversity indices for grooming and nonaggressive contact are considerably lower than the index calculated for approaches.

The sociogram shows how individual females distributed grooming (Fig. 5). To test whether the grooming patterns differ significantly from what would be expected if each individual groomed another individual at random, a random data set was generated as described above and compared with the observed grooming matrix. The mean as well as the variance for dyads differed significantly between the observed and the generated matrix (mean = 0.024, STD = 0.083 vs. mean = 0.23, STD = 0.043; $P < 0.01$) indicating that the pattern of grooming indices was not what would have been expected if grooming had been equally distributed. Grooming within dyads occurred less than expected (lower mean in observed matrix), but females had preferred grooming partners (higher SD in observed matrix than in the generated matrix).

Table III shows the correlation between rank-distance, association, and grooming. Correlations between rank-distance and proximity/grooming were negative, which means that relatively high levels of these behaviors were observed among individuals close in rank. The distribution of grooming and of association among the females was positively correlated ($r = 0.38$); however, the effect was partially due to rank-distance (after control for rank-distance: $pr = 0.25$, $P < 0.0001$).

Coalitions

Thirty coalitions between adult females were observed using ad libitum and focal animal data. Nineteen coalitions occurred between the eight highest-ranking females, and 11 coalitions were observed among middle- and low-ranking

TABLE III. Correlations Among Three Variables

Correlation	r	pr	$P_{r }$ - values	τ_{rw}	τ_{rwXYZ}	$P_{r }$ - values
Rank-distance–proximity	-0.56		$P_1 = 0.00005$	-0.42		$P_1 = 0.00005$
Rank-distance–grooming	-0.32		$P_1 = 0.00005$	-0.33		$P_1 = 0.00005$
Proximity–Grooming (Partial for rank-distance)	0.38	0.25	$P_r = 0.00075$	0.29	0.18	$P_r = 0.00075$

The table presents row-wise Pearson correlations (r) and Kendall rank correlations (τ_{rw}) between matrices, and row-wise partial correlations (pr and τ_{rwXYZ}) after adjustment of the data for the effect of rank-distance. P_r = one-tailed probability value in the right tail of the permutation distribution. P_1 = one-tailed probability value in the left tail of the permutation distribution. (P -levels refer to partial correlations whenever applicable). P corrected for Bonferroni = 0.02. All probabilities are estimated based on 20000 permutations.

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the predominant food resource was the seeds of *Sacoglottis gabonensis*, which are usually found in large circular patches around trees. These patches are too large to be defended by an individual or a small group of individuals; however, it is unlikely that all individuals of the groups (~90 animals) can feed simultaneously, which supposedly would invoke contest competition. The latter is supported by higher supplant rates, as well as higher aggression rates inside food patches than outside food patches. There are several possible explanations that could account for the observed pattern. First, increased aggression and supplant rates could solely arise due to increased crowdedness inside food patches (decreased interindividual distances). Second, since not all individuals fit into the food patch, high-ranking animals could exclude the lowest-ranking animals. Finally, the observed effect of increased aggression could function to regulate spatial positions within a feeding group rather than to monopolize a food patch. As a result, one could expect that dominant animals are in preferred positions with respect to both food and safety, while lower-ranking animals would be expected at the periphery. Furthermore, individual positioning could affect foraging success, since females in center positions would not lose as much feeding time on scanning the environment for predators as individuals in the periphery. However, these hypotheses have to be tested in the field before any firm conclusions can be drawn.

Foraging efficiency was also positively correlated with rank—a further indication that female sooty mangabeys experience contest competition. If sooty mangabeys mainly experience scramble competition, no effect of rank on foraging success should have been observed [see van Schaik, 1989]. A study recently conducted on rank-related food benefits among female sooty mangabeys in captivity [Stahl, 1998] did not find an increase in agonistic interactions among females feeding on clumped compared to dispersed food conditions. However, there was a rank-related increase in foraging success when clumped food distributions were provided, as was found in our field study. This discrepancy in agonistic interactions observed in the two studies is difficult to assess since it could solely arise due to the unnatural setting of the experiment in captivity: a food box with very limited space at the food source, a situation rarely observed in Tai, and the absence of predation risk. Further research may help to answer questions about the nature of feeding competition in sooty mangabeys.

Affiliative Relationships

In theory, social relationships among females should be highly differentiated when contest competition over access to resources is frequent. In Tai, adult female sooty mangabeys had well-differentiated social relationships. Females were observed to associate with a limited number of female partners. Grooming was even less equally distributed among potential female partners, and reflected preferred associations. Nine females restricted their grooming to only one or two other females. The study also demonstrates that adult females with positions close in rank tend to associate and groom each other more frequently than females far apart in the rank order. The observed correlations resemble the correlations obtained for three different rhesus macaque groups in captivity [de Waal, 1991]. However, based on the present data it is not possible to derive the underlying mechanism that drives the observed pattern. Females could be attracted to high-ranking females [Seyfarth, 1977], or they could be attracted to similar ranks [de Waal & Luttrell, 1986]. Both hypotheses predict the observed pattern of social interactions among female sooty mangabeys with or without underlying nepotistic mechanisms.

The amount of differentiation in female relationships among sooty mangabeys is similar to that observed for several baboon groups at different study sites [Silk et al., 1999]. Though diversity is even lower in sooty mangabeys than in baboon groups, this could be explained by the larger group size of sooty mangabeys [Silk et al., 1999]. Silk and colleagues [1999] presented some evidence for this hypothesis, and the results on sooty mangabeys easily fit the predicted correlation between group size and diversity. Moreover, as in female baboons, coalitions between adult female sooty mangabeys occurred infrequently. Only one dyad (Sa-Lo: α and β females) was observed to support each other several times in 2000, as well as in 1998.

Migration Patterns

Several observations suggest that female sooty mangabeys are philopatric, although migration events are difficult to observe. First, two juvenile females that were recognized in 1998 remained and started to reproduce in their natal group. Second, unknown sooty mangabeys males have been observed to join the group ($n = 4$), whereas known, young adult males have vanished from the group several times ($n = 3$). This has not been observed for females. Moreover, we have frequently observed lone males, but not females, in the home range of the study group. Third, female sooty mangabeys have been observed to aggressively attack individuals of neighboring groups in intergroup encounters, while males were not observed to participate in such conflicts.

This first study on female sooty mangabeys in their natural environment supports the general dominance pattern observed in captive studies. However, the presented data suggest that female sooty mangabeys experience contest competition and that dominance rank has an influence on food intake, which could influence reproductive success. In the light of these data, the observed pattern that juveniles move up the hierarchy without facing aggression from higher-ranking females in captivity is perplexing. Moreover, the affiliation and migration patterns observed resemble social relationships observed in female baboons, suggesting the possibility of a matrilineally-based social system. However, no firm conclusions can be drawn before a DNA analysis has been conducted in order to establish genetic relationships. If such a DNA analysis reveals that sooty mangabeys do not fit the predictions of the current socioecological theories, finer-grained studies of the social behavior of sooty mangabeys would have to be conducted to help us understand the discrepancies, and to redefine the current socioecological theories.

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