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Dominance Style in Female Guerezas (*Colobus guereza* RÜPPELL 1835)

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ABSTRACT. Socioecological models assume that quality and distribution of food ultimately determine female social relationships: a high quality diet and clumped food distribution should result in the establishment of a hierarchy with stable rank relations which is supported by empirical studies on frugivorous cercopithecines. By contrast, folivorous species with their low quality diet and dispersed food distribution should have egalitarian social relationships but empirical data are very rare. This study on female guerezas of a zoo group aimed to test the models in a colobine species and the results largely agreed with the predictions of the models: facial expressions, vocalizations, and gestures were not used for signalling dominance or subordination. Unritualized aggressions occurred frequently but were of low intensity, and interventions by third parties were never observed. Aggressions were exchanged bidirectionally and this was true also for food stealing and retreats. All this indicated the lack of established rank relations. Allogrooming was distributed rather equally and showed no kin bias. All these features characterize egalitarian social relationships and, hence, support the socioecological models.

Key Words: *Colobus guereza*; Colobinae; Female relations; Dominance style; Rank relations; Egalitarian relationships.

INTRODUCTION

Food and security are regarded as key factors for reproductive success in female primates (e.g. VAN SCHAIK, 1989). Although group living increases competition over these resources, most primate females are living in groups. The benefits are assumed either in an easier defence of high-quality feeding sites (WRANGHAM, 1980) or in a better protection against predators (VAN SCHAIK, 1983). Irrespective of the ultimate causes for group living, quality and distribution of food should strongly influence female social relationships (NICHOLSON, 1954; VAN SCHAIK, 1989; VAN HOOFF & VAN SCHAIK, 1992). If food can be monopolized, overt contest competition is expected. Strict rank relations with the establishment of a hierarchy which regulates access to resources are common (ISBELL, 1991). Instead of open and potentially dangerous aggressions, rank relations are formalized i.e. dominance or subordination are signalled by an unidirectional exchange of specific behaviours (facial expressions, gestures, vocalizations: DE WAAL, 1986, 1989). Furthermore, since single food items are comparably valuable, interventions of third parties during conflicts over access to such a resource are common, whereby support of kin is most likely. This ultimately leads to nepotistic hierarchies with related females having adjacent rank positions. Allogrooming and other affiliative behaviours are distributed unevenly and should reinforce or repair social relationships (SEYFARTH, 1977; DUNBAR, 1988, 1991). The potential benefits of a high rank depend also on the amount of competition between groups. Strong competition between groups should favour tolerant and comparably relaxed social relations, since low ranking females are needed as allies during intergroup encounters (DE WAAL & LUTTRELL, 1989; VAN SCHAIK, 1989; VAN HOOFF & VAN SCHAIK, 1992). By contrast, if food quality is low or food items are evenly distributed, competition is by scramble and egalitarian social relationships without strict rank relations are expected. Moreover, female philopatry and comparably strong social bonds among females exist, if competition between groups is high. Based on the amount of competition within and between groups, respectively, STERCK et al. (1997) distinguish four types of female social relationships: resident-nepotistic, resident-nepotistic-tolerant, resident-egalitarian, and dispersal-egalitarian.

The above models were developed with data from cercopithecines which have a largely frugivorous diet and compete by contest. Studies on dominance style and female social relationships in folivorous species focuss on the Asiatic Hanuman langur (*Presbytis entellus*: e.g. SOMMER, 1985; BORRIES, 1993; BORRIES et al., 1991, 1994; KOENIG et al., 1998). Data from African colobines are virtually lacking. We attempted to close this gap by investigating social relationships among female guerezas (*Colobus guereza*). Due to their folivorous diet, food competition should be by scramble, while observations of conflicts between group strongly suggested that females are philopatric (MARLER, 1969; DUNBAR & DUNBAR, 1974; OATES, 1977). Hence, female social relations should be of the resident-egalitarian type, which predicts that: (1) agonistic signals (facial expressions, gestures, body positions, vocalizations) indicating dominance or subordination are absent from the behavioural repertoire; (2) aggressions during conflicts as well as submissions are of low intensity and conflicts rarely escalate; (3) counteraggressions are common, while interventions of third parties and regular coalition formation are absent; (4) aggressions and submissions as well as supplants/retreats are exchanged bidirectionally, with changing directions in different situations; and (5) affiliative behaviours (grooming, huddling) are common, and the distribution of grooming within dyads is balanced. Preferential grooming relations, especially among kin, are absent.

MATERIALS AND METHODS

The study was conducted at the multi-male guereza group of the Zoo Münster, Germany. During the 3-month study period (May – July 1998) the group consisted of two adult males (6 and 11 yr), two adolescent males (4 yr), four adult females (7 – 20 yr), one adolescent female (3 yr), and five immatures. The five females were chosen as focal subjects. They represented two lineages: *E* with her daughters *A* and *M*, and *S* with her daughter *J*. *E* and *S* had lived together since foundation of the group in 1985.

The group was kept in an enclosure consisting of an indoor cage of 20 m^2 floor space (height: 3.10 m) and an outdoor cage of a ground area of 70 m^2. Both cages were equipped with several shelves, ropes, and wooden climbing devices and connected with a 3-m runway. Except for a short period each day when the cage was cleaned, the animals had continuous access to all parts of their enclosure. Animals were usually fed indoors. Different sorts of vegetables (carrots, salads, cauliflower, leek, potatoes) were offered twice daily in two large food dishes. A third feeding consisted of foliated twigs and small branches of willow, maple, or oak. In addition, different seeds were distributed on the floor hidden in straw. This rather clumped distribution of high quality food deviated from natural conditions, since it favoured monopolization and contest competition. However, we regarded this as a quasi-experimental situation that would reveal any tendencies to form dominance relations.

Data were collected with continuous recording with focal sessions lasting 15 min and a total observation time of 300 hr (60 hr/female). As potential indicators of formalized dominance relations we analyzed five facial expressions: *mouth opening, teeth baring, grimace, yawning,* and *staring*; four vocalizations: *snarling, grunting, shrieking,* and *tongue clicking* (for a description, see MARLER, 1969; OATES, 1977); and three gestures/body positions: *mounting, embracing,* and *presenting.* Unritualized aggressions analyzed were *biting, punching* hitting or pushing another animal with the hand, and *dragging* forcefully grabbing the fur or part of the face of an animal and pulling it towards oneself. In addition, *food stealing* forcefully grabbing and taking of a food item out of the hands of another animal, *retreat* leaving a location when being merely approached by another animal, and *allogrooming* were analyzed for the present study. The majority of allogrooming episodes were short (< 30 sec), and, hence, the absolute number of episodes were considered during analysis.

Binomial test was used for testing the statistical significance of a bias in directionality. Due to multiple entrances of the same individuals into the tests, Bonferroni correction was applied to the test results (LEHNER, 1996, p. 353). Due to this, results were regarded as significant only, if $p \leq 0.005$.

RESULTS

Teeth baring and *grimace* occurred among the males (ad lib observations), but were never observed among the females. *Yawning* was recorded 64 times (2 – 26/female) but was never directed towards a specific group member. Table 1 shows that *mouth opening, staring, grunting,* and *shrieking* were very rare, while *snarling* occurred more frequently and also in the context of aggression. The majority of this vocalization (17/23) occurred in the two dyads that had a bidirectional interaction pattern (*A-M*: 7 : 5; *A-J*: 3 : 2), however, without a significant bias in directionality. *Tongue clicking* was a very frequent vocalization which occurred in all dyads (Table 2). Simultaneous vocalization was recorded a total of 16 times in 6 different dyads. *Tongue clicking* was exchanged bidirectionally in all dyads, with a significant bias in directionality in only four dyads. In addition to these directed vocalizations, all females showed *tongue clicking* without orientation towards a specific group member (n = 38; 3 – 14/female).

Table 1. Frequency and directionality of facial expressions (f), vocalizations (v), and gestures/body positions (g).

Behaviour	Total number of interactions	Dyads with interactions	Bidirectional dyads	Dyads with significant bias in directionality*	Remarks
Mouth opening (f)	6	3	2	0	Much more frequent among males (ad lib observations)
Staring (f)	3	3	0	–	
Snarling (v)	23	5	2	0	10/23 snarls during aggressive interactions emitted by the aggressor
Grunting (v)	4	4	0	–	
Shrieking (v)	4	3	0	–	Shown only by the adolescent female when receiving aggressions
Mounting (g)	39	10(all)	6	0	Unidirectional only in dyads in which <3 interactions were observed
Embracing (g)	27	8	5	0	Unidirectional only in dyads in which <3 interactions were observed
Presenting (g)	10	6	2	0	Unidirectional only in dyads in which only a single interaction was observed

* Binomial test: $p<0.005$.

Table 2. Frequency and direction of *tongue clicking*.

	E	*S*	*A*	*M*	*J*	Σ
E	–	**17**	**35**	20	7	79
S	**2**	–	22	**7**	3	34
A	**14**	16	–	**11**	6	47
M	27	**39**	**61**	–	2	129
J	3	6	5	8	–	22
Σ	46	78	123	46	18	311

Females are ordered from oldest to youngest. Rows represent actors, columns recipients. Members of the '*S*'-matriline are underlined. Significant biases ($p \leq 0.005$) in directionality are shown in bold type ($Z_{E\text{-}S} = 3.21$, $p<0.002$; $Z_{E\text{-}A} = 2.86$, $p<0.005$; $Z_{S\text{-}M} = 4.57$, $p<10^{-5}$; $Z_{A\text{-}M} = 5.77$, $p<10^{-8}$).

Table 3. Frequency and direction of *biting, punching, and dragging*.*

	E	*S*	*A*	*M*	*J*	Σ
E	–		5	4		9
S	1	–	6	7	12	26
A		4	–	**7**	13	24
M	6	12	**35**	–	8	61
J	4	2	8	2	–	16
Σ	11	18	54	20	33	136

* $Z_{A\text{-}M} = 4.17$, $p<10^{-4}$. Further details see Table 2.

Mounting occurred in all possible female dyads and was exchanged bidirectionally in all dyads in which at least three interactions were recorded (Table 1). Half of all mountings were observed in a single dyad (*A-E*: 6 : 14), but neither this nor any other dyad showed a significant bias in directionality. *Embracing* was not significantly biased either (Table 1). It occurred in all but two of the possible dyads and was again exchanged bidirectionally in all dyads in which at least three interactions occurred. *Presenting* was rare, also exchanged bidirectionally without a significant bias in directionality (Table 1). In sum, the analyzed facial expressions, vocalizations, and gestures/body positions were either extremely rare or the interaction pattern was bidirectional. Hence, none of these behaviours could serve as a signal for dominance or subordination.

Aggressions that resulted in injuries never occurred during the study period, while less severe aggressions were quite frequent (Table 3). Aggressions were bidirectional in almost all dyads and except of one dyad (*M-A*) without a significant bias in directionality. Counteraggressions were common occurring after 12% of all aggressions. Females never chased other females and other animals never intervened during their conflicts. Half of all aggressions could not be related to specific contexts, while the others were preceded by touching, food stealing, mounting attempts or embraces, whereby the recipient of these behaviours was almost always the aggressor. This suggested that aggressions were often used to repulse social initiatives of other group members.

Food stealing which might not be expected among adult individuals was, in fact, not rare. It was performed by all females a total of 47 times (1 – 16/female). It was observed in nine of the ten possible female dyads and occurred bidirectionally in six of these dyads. More than half of all *food stealing* was observed in two dyads (*A-M*: 5 : 6; *M-J*: 6 : 7). No significant bias in directionality existed in any dyad.

Table 4. Frequency and direction of *retreat.**

	E	*S*	*A*	*M*	*J*	Σ
E	–	13	17	15	14	59
S	6	–	25	25	26	82
A	15	32	–	**71**	**150**	268
M	10	18	**36**	–	41	105
J	20	23	**59**	56	–	158
Σ	51	86	137	167	231	672

* $Z_{A\text{-}M} = 3.29, p<0.002$; $Z_{A\text{-}J} = 6.23, p<10^{-9}$. Further details see Table 2.

Table 5. Frequency and direction of *allogrooming.**

	E	*S*	*A*	*M*	*J*	Σ
E	–	**2**	9	**1**	9	21
S	**26**	–	18	56	4	104
A	20	40	–	19	12	91
M	**38**	45	35	–	**38**	156
J	1	2	2	**4**	–	9
Σ	85	89	64	80	63	381

*$Z_{E\text{-}S} = 4.35, p<2\bullet10^{-5}$; $Z_{E\text{-}M} = 5.76, p<10^{-8}$; $Z_{M\text{-}J} = 5.09, p<10^{-6}$. Further details see Table 2.

Retreats when being approached occurred very often but had a bidirectional interaction pattern in all dyads (Table 4). Two dyads showed a significant bias in directionality. In the dyad *J*-*A* this was at least partly due to a stereotype locomotion pattern of *A*. This female circled along the fence of the outdoor enclosure during certain times of each day making short stops at specific locations. She was sometimes followed by *J*, and although it did not appear that *A* left her position as a reaction to *J*'s approaches, technically she retreated to her.

The females differed largely in their *allogrooming* activiy, whereby the youngest and the oldest female were the least active groomers (Table 5). However, all females distributed their grooming rather evenly among their female group mates. Grooming was bidirectional in all dyads, and only three dyads showed a significant bias in directionality. Preferences among kin or other demographic classes did not exist.

DISCUSSION

The present study agrees with the predictions of the hypothesis that primate females with a diet of low quality and dispersed distribution have an egalitarian dominance style without formalized rank relations. Facial expressions, vocalizations, and gestures/body positions of the folivorous guerezas were either very rare or exchanged bidirectionally and could therefore not serve as signals of dominance or subordination. Physical aggressions were not rare but never harmful, and the frequent counteraggressions never resulted in dangerous escalations of a conflict. The tolerant attitude towards food stealing further emphasized the general friendly and relaxed relationships. In contrast to Hanuman langurs (Borries, 1993; Koenig et al., 1998), female guerezas did not even establish a hierarchy based on retreats. Only two females, *A* and *M*, had a significant bias in the direction of aggressions and retreats indicating that *M* was dominant over *A*. Such individualistic dominance relations are also expected in egalitarian species and, hence, do not contradict the notion that a rank system is absent.

Coalition formation is regarded as important for the acquisition and stabilisation of rank positions of female cercopithecines (SEYFARTH, 1977). Consequently, coalitions should be absent in egalitarian species. In fact, coalitions among the females were never observed during the present study. Notably, clearcut rank relations and complex interactions patterns during conflicts are not completely absent from the behavioural repertoire of the species. The retreat pattern among the two adult males was strict and completely unidirectional, and a mutual support pattern existed between the dominant adult male and one adolescent male against the second adult male (GRUNAU, 1999).

Preferential allogrooming among kin in cercopithecinae is regarded as a mechanism to reinforce social bonds and facilitate coalitions. Hence, if coalitions during within-group conflicts are absent in egalitarian species, reinforcing social bonds via kin biased grooming is not expected either. In fact, grooming among the study females showed no consistent pattern with respect to age or kin but appeared to be based on individual preferences. The grooming frequency was rather high as expected in a resident-egalitarian species in which affiliative behaviours function as cohesive forces for uniting the whole group during between-group conflicts. All findings agree with the hypothesis that scramble competition, due to a folivorous diet, results in relaxed social relationships. Even under the restricted living conditions of the study group which favoured contest competition and gave few possibilities to avoid conflicts, females maintained their egalitarian dominance style. The present results combined with findings on between-group encounters and female philopatry from field studies support the model of STERCK et al. (1997) that guerezas have a resident-egalitarian social structure.

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