THE STRUCTURE OF SOCIAL RELATIONSHIPS AMONG FEMALE SAVANNA BABOONS IN MOREMI RESERVE, BOTSWANA

by

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Summary

Here we examine the effects of maternal kinship, reciprocity, and dominance rank on the social relationships of female baboons (*Papio cynocephalus ursinus*) in a well-habituated, free-ranging group in the Okavango Delta of Botswana. These data are useful for testing comparative hypotheses about the ecological and demographic factors that shape the evolution of social organization in primates and other animals. In this group, adult females had well-differentiated grooming relationships with one another, and limited their grooming to a relatively small subset of available partners. Although there were 19 adult females in the group, the average female groomed only 8 other females, and devoted at least 5% of her grooming to only four other females. Females groomed maternal kin at significantly higher rates and for significantly longer periods than they groomed other females. The bias in favor

of maternal kin was not an artifact of a general attraction toward females of adjacent rank. However, members of high-ranking lineages did devote a relatively greater fraction of grooming to maternal kin than members of low-ranking lineages did. Females most often groomed the females from whom they received the most grooming and grooming was very evenly balanced within the majority of dyads. Female rank had little impact upon grooming patterns and there was no evidence that females competed overtly over access to high-ranking partners.

Introduction

The evolution of sociality among animals reflects a balance between the advantages and disadvantages of living in close proximity to conspecifics (Bertram, 1978; Krebs & Davies, 1993). Animals who live in social groups may be better able to acquire and control resources or less vulnerable to predators, but at the same time they may face more competition over access to food, be more vulnerable to disease, and become more susceptible to cuckoldry, infanticide, and cannibalism. The size and structure of social groups is generally thought to reflect a compromise between the costs and benefits of sociality (Pulliam & Caraco, 1984). The processes that influence the evolution of sociality may have important selective consequences because the size of social groups and the complexity of social interactions within groups may be the primary force driving the evolution of cognitive complexity (Jolly, 1966; Humphrey, 1976, Byrne & Whiten, 1988). Current evidence suggests that social complexity is associated with cognitive complexity among primates (Dunbar, 1992a, 1993, 1995; Whiten & Byrne, 1997), bats (Barton & Dunbar, 1997), carnivores (Barton & Dunbar, 1997), and possibly cetaceans (Connor *et al.*, 1992, 1999).

Comparative analyses provide one method of testing hypotheses about the evolution of sociality. Comparative analyses must take into account phylogenetic relationships among species (Harvey & Pagel, 1991). Detailed data on multiple genera are often unavailable and this inevitably limits the power of comparative analyses. An alternative tactic is to focus on the patterns of variation within a single genus. The species *Papio cynocephalus* provides an appropriate subject for this kind of approach. Savannah baboons occupy a diverse set of habitats, ranging from the temperate mountain regions of South Africa, to the tropical rain forests of Central Africa,

savannah woodlands of East Africa, and the arid deserts of Namibia and Saudi Arabia. Moreover, baboons have been studied for nearly four decades by scores of researchers at a variety of sites providing a wealth of ecological, demographic, and behavioral information (references below). Thus, baboons provide a valuable opportunity to test hypotheses about the selective forces that influence the size and organization of social groups and the nature of interactions within and between groups (Barton *et al.*, 1996).

Many of the hypotheses about the evolution of sociality among primates focus on the behavior of adult females, and generate predictions about the effects of dominance rank and kinship on females' relationships. However, we know very little about the structure of social relationships among adult female baboons because relatively few studies have focused upon their social relationships (Seyfarth, 1976; Saunders, 1988; Barton *et al.*, 1996; Ron *et al.*, 1996; Henzi *et al.*, 1997; Altmann *et al.*, 1998). Moreover, kinship relationships among adult females were known at only one of the sites where females' social relationships have been studied (Saunders, 1988; Altmann *et al.*, 1998). The objective of this paper is, therefore, to describe how kinship, dominance rank, and reciprocity shape the pattern of interactions among adult females in one free ranging group of baboons. We use these data to evaluate predictions derived from several hypotheses of the evolution of primate social organization, and to facilitate comparisons among baboon populations across Africa.

Virtually all of the anthropoid primates live in social groups (Smuts *et al.*, 1987), and there has been considerable discussion of the factors influencing the size and structure of primate groups. Wrangham (1980, 1987) argued that grouping enhances access to resources because groups of females are more successful in intergroup encounters than solitary females. He suggested that permanent alliances among females, particularly related females, would be most effective, and predicted that strong female bonds and female philopatry would be associated with intergroup competition. Wrangham's emphasis on intergroup competition was challenged by van Schaik & van Hooff (van Schaik, 1983, 1989; van Hooff & van Schaik, 1992) who argued that predation played the most important role in the evolution of sociality among primates. They suggested that sociality increased the intensity of resource competition within groups, and led to development of well-differentiated female relationships, strong kin bonds, and kin-based alliances. However, the distribution and abundance of resources influences the relative importance of

alliances and the closeness of female bonds (van Schaik, 1989; Isbell, 1991; van Schaik & van Hooff, 1992).

Although these hypotheses posit different factors favoring the evolution of sociality, they lead to similar predictions about females' responses to competition over resources. When competition over resources favors cooperation among females, females will form close relationships with other females, establish stable kin-based alliances, and remain in their natal groups. The term 'female-bonded kin groups' is commonly used to describe this constellation of features.

Recently, Barton and his colleagues evaluated predictions derived from these hypotheses with data from baboons in Kenya and South Africa (Barton *et al.*, 1992, 1996; Barton & Whiten, 1993). They found that in Laikipia, Kenya, where within-group competition for food was high and predation pressures were high, groups tended to be large, females formed strong bonds with one another, and females rarely transferred from their natal groups. In the Drakensburg Mountains of South Africa, food was more evenly distributed and predation pressure was relaxed. There, groups were typically smaller, bonds among females were weaker, female dispersal was more common, and bonds between females and males were strengthened (Barton *et al.*, 1992). Thus, they concluded that data from these two baboons populations conformed to predicted relationships between food distribution and social organization (Barton *et al.*, 1996). However, there are also baboon populations in which predation pressure is low, but female bonds are strong (Seyfarth, 1976).

Cheney (1992) hypothesized that the nature of participation in intergroup encounters will also influence the distribution of grooming within primate groups. Grooming is considered an essential element of female relationships because it sustains alliances and maintains social bonds (Seyfarth, 1977; Dunbar & Sharman, 1984). Thus, Cheney predicted that when groups participate actively in aggressive encounters with members of other groups, grooming will be spread widely among group members, as this behavior provides a means to sustain cooperative alliances across the group. When groups do not participate in aggressive intergroup encounters, grooming is expected to focus on a relatively small subset of available partners. She also predicted that the degree of nepotism in grooming would be associated with the extent of competition between groups — when competition between groups is high, females should be less nepotistic in their grooming.

Cheney tested these predictions with comparative data from a variety of primate species. Her findings generally indicated that grooming was distributed more widely among group members in female-bonded species than in non-female-bonded species. However, she could not demonstrate that the distribution of grooming among females was actually associated with their role in intergroup encounters; in species in which females participated in resource defense, grooming was no more evenly distributed than in species in which females did not participate in resource defense. Moreover, the extent of nepotism in grooming was not associated with the intensity of competition between groups.

Other researchers have considered how demographic and ecological factors influence the quantity and quality of affiliative interactions among females. In these formulations, grooming is the principal mechanism for maintaining social bonds (Seyfarth, 1977; McKenna, 1978; Dunbar & Sharman, 1984; Dunbar, 1991, 1992a). When groups are small, females can easily groom all of the other females in the group, but as groups grow larger this becomes more difficult. As group size increases, females may increase the total amount of time that they spend grooming and/or alter the distribution of grooming (Dunbar, 1991, 1992b). Comparative data indicate that the amount of time spent grooming in catarrhine species generally increases as a direct function of group size (Dunbar, 1991), although it is not clear how the distribution of grooming changes as groups become larger. Ultimately, ecological factors may limit the amount of time that females have to socialize. The proportion of time devoted to grooming does not exceed 20% in any of the groups that Dunbar (1991) surveyed. This suggests that when groups become too large, females are unable to groom their partners adequately. Consequently, social bonds fray, relationships deteriorate, social networks become fragmented, and groups eventually fission. In short, group size is limited by females' ability to maintain social bonds with other group members.

While Dunbar (1991) was unable to determine whether group size influenced the distribution of grooming within groups, recent evidence suggests that this may be the case. Henzi et al. (1997) evaluated the distribution of grooming among female baboons in four groups, containing 2 to 12 females, in the Drakensburg Mts. The number of grooming partners rose as the number of females increased from 2 to 9, but declined slightly in the group which contained 12 females. When groups exceeded 23 members (and 9 females),

they often divided. Further evidence that there may be limits to the size of grooming networks comes from two studies of baboons in Laikipia, Kenya. In one group of 40 individuals, females groomed on average 9 other adult and subadult females, while in a group of 80 individuals, females groomed on average 11 adult and subadult females (Sambrook *et al.*, 1995; numbers of adult females in group not available). Over a 10-month period at the same site, adult females groomed, on average, 6.3 of the 16 other adult females in one group (range = 1-9; computed from data provided by D. Castles). In Amboseli, females groomed on average 12.5 (range 7-14) of the 18 other adult females in the group (computed from Appendix 5.1 in Saunders, 1988).

Finally, there have been efforts to how competition within groups structures the patterning of grooming among females. Seyfarth (1976, 1983) considered how grooming is expected to be distributed within primate groups in which dominance relationships are clearly established and alliances play an important role. He assumed that grooming is exchanged for other beneficial behaviors, such as support in alliances. Since high ranking females are more effective alliance partners than low ranking females, females are attracted to high ranking grooming partners and attempt to groom them. However, overt competition and competitive exclusion restrict some females' access to high ranking partners, and as a result females spend much of their time grooming females who occupy adjacent ranks. In species that form matrilineal hierarchies, both a preference for interacting with kin and competition for access to high ranking females will contribute to high rates of grooming among females who occupy adjacent ranks (Seyfarth, 1983).

Predictions derived from Seyfarth's model have been tested in a variety of Old World primate species, with mixed results. There is a tendency to direct grooming up the hierarchy in some groups (Stammbach, 1978; Fairbanks, 1980; Seyfarth, 1980; Silk, 1982; Chapais, 1983; Sambrook *et al.*, 1995; Dufty & Silk, in prep.), but not in others (Altmann *et al.*, 1998; Sinha, unpubl. ms). There is also a tendency for the highest ranking lineages to be most closely bonded (Cheney, 1977; Berman, 1980). However, there is less consistent evidence that females compete for access to high ranking females (competition observed: Stammbach, 1978; Fairbanks, 1980; Seyfarth, 1980; no competition: Silk, 1982; Chapais, 1983; de Waal & Luttrell, 1986) or that females selectively support the females that groom them most often (support exchanged for aid: Seyfarth, 1980, Seyfarth & Cheney, 1984; not exchanged: Fairbanks, 1980; Silk, 1982).

A number of the predictions about the structure of female social relationships described above can be tested with data we collected on female baboons (*Papio cyncocephalus*) in the Okavango Delta, Botswana. Our analyses are based upon behavioral observations conducted during a one-year study of a well-habituated group of baboons in the Moremi Reserve. In this population, groups are relatively large, predation pressure is relatively high, females are philopatric, home ranges of neighboring groups overlap extensively, and males are the principal protagonists in intergroup encounters (Hamilton *et al.*, 1975; Bulger & Hamilton, 1987). Ecological conditions in Moremi are expected to produce well-differentiated grooming, dominance, and coalitionary relationships and well-established dominance hierarchies among females (Barton *et al.*, 1996). Moreover, since alliances are often based upon kinship, close relationships among related females are expected to be formed. Since females do not play an active role in intergroup encounters and time available for grooming is limited, females are expected to limit their grooming to a relatively small number of partners (Cheney, 1992; Dunbar, 1992a, 1993). These conditions might generate competition over grooming partners, and produce the grooming patterns described in Seyfarth's model (1977, 1983).

Methods

Study group and subjects

The study was conducted from July 1992 to July 1993 in the Moremi Reserve which is located in the Okavango Delta of Botswana. One group of baboons at this site has been observed continuously since 1977 by William J. Hamilton III and his colleagues (*e.g.* Bulger & Hamilton, 1987; Hamilton & Bulger, 1992). The animals were fully habituated to humans on foot and could be identified individually. The 19 adult (> 6 years) female members of the group were the subjects of this analysis.

The ages of all females born in the group since 1977 were known. The ages of females who were present in the group when demographic monitoring began in 1977 were estimated based upon the assumption that they were at least 6 years old when their first known infant was born. In 1992, subjects ranged in age from 6 years to at least 21 years of age.

Here, we use the term 'maternal kin' to refer to animals who are known to belong to the same matriline. The mothers of all individuals born in the group since demographic monitoring began in 1977 are known, allowing us to construct geneaologies from that point forward in time. However, we do not know the maternal kinship relationships of females who were born before demographic monitoring began, and our knowledge of maternal kinship is therefore incomplete. This is unlikely to generate systematic bias in our results because incorrectly categorizing some maternal kin as "nonkin" will tend to obscure differences between maternal kin and nonkin. No information about paternal kinship is available.

Data collection and analysis

A. Behavioral sampling

We conducted 10-minute focal observations on each of the 19 adult female members of the group. Observations spanned an 11-month period from August 1992 through June 1993, and 182 to 191 (mean = 186) focal samples were collected on each of the subjects. All focal observations were collected between 0600 and 1400 hrs. Since the group was often dispersed over considerable distances and much of their habitat was bushy or wooded, it was not practical to follow a fixed sampling schedule. Instead, we sampled focal animals opportunistically, working our way through the list of subjects once before beginning again. We deliberately avoided sampling females who were interacting with the previous focal subject.

At the beginning of each focal observation, we recorded the focal subject's activity and the identities of all other baboons within a two-meter radius. During focal observations, we recorded all approaches, social interactions, and vocalizations involving the focal animal and adult partners. We also noted whether the focal individual or her partner performed the behavior.

The analysis that follows focuses mainly upon the pattern of grooming, but includes data on the rate of approaches, grunts, and other forms of nonaggressive contact. For each grooming bout, we recorded which individual performed the grooming, when grooming began, and when grooming ended. If the female being groomed began grooming her partner, a new grooming bout was scored. No information about the quality of grooming was recorded.

We recorded an approach when one individual moved to within two meters of the focal animal or the focal female moved to within two meters of another adult. We recorded all approaches that we observed, regardless of how long the two animals remained in proximity or whether the two animals subsequently interacted. Sometimes focal females approached or were approached by several other individuals at the same time. In these cases, we recorded an approach to (or by) each partner separately.

Grunts were low amplitude calls that appeared to be addressed to a particular individual based on the direction of gaze, proximity, and behavioral interactions. During focal observations, there was generally little ambiguity about who gave a grunt, but it was not always clear to whom a particular grunt was directed. This was often the case when several individuals were clustered together or no one was in close proximity to the focal female. When we were uncertain about to whom a grunt was directed, we did not assign the call to a specific partner. 13% of all grunts which occurred during focal observations of adult females were excluded from analysis because we could not determine who the intended recipient was.

A number of types of nonaggressive interactions occurred at low frequency among females. These included embraces, presents, and touching. Since the function of these interactions is not well-established, we will refer to them collectively as 'nonaggressive contact'. Embraces were scored when one female put her arm(s) around the body of another individual. Presents were scored when one female stood in close proximity to another individual and presented her rump or side. Touching included any form of gentle, nonaggressive contact.

Although the relationship between grooming and coalition formation is of theoretical and empirical interest, virtually no alliances among adult females were observed over the course of our study.

B. Dominance hierarchy

Female dominance rank was determined from the pattern of supplants observed during focal observations and *ad libitum*. Supplants were recorded when one female moved to within two meters of another female who then moved away. Matrices based upon supplants generated precisely the same rank order as matrices based upon more overt forms of aggression and formal submission. Supplants were more common than more overt forms of aggression and submission and were therefore more useful in assessing dominance relationships.

All females were placed in a square matrix and ordered so as to minimize the number of entries (reversals) below the diagonal. Initially, separate matrices were constructed for each month of the study. However, the rank ordering among adult females did not change from one month to the next, so we combined the monthly matrices into a single matrix. The outcome of supplants could be predicted with a great degree of certainty, with only 15 reversals in 2,351 interactions (0.6%).

As in many other Old World monkeys groups (Gouzoules & Gouzoules, 1986), the females formed a linear, matrilineal dominance hierarchy. Female maternal kin almost always occupied contiguous ranks, mothers outranked their daughters, and females generally outranked their older sisters.

C. Analysis

Hourly rates of interactions were computed for each dyad (A, B) by summing the total number of interactions between A and B, and then dividing by the sum of the total number of hours that A was observed and the total number of hours that B was observed. Rates of interactions initiated and received were computed separately for each dyad. Since we recorded the onset and termination of grooming bouts, we were also able to compute the amount of time that each dyad spent grooming. These figures are expressed as the average number of seconds spent grooming per hour of observation.

To assess the effects of rank and maternal kinship on rates of interaction, we computed the mean rate of interaction for each female with all of her partners. This procedure eliminates problems that might arise from the nonindependence of dyads, but is less powerful than the matrix correlation methods described by Hemelrijk (1990a, 1990b) and de Vries (1993). Therefore, parallel analyses using matrix correlation methods were conducted to verify the results reported here. For all analyses, we obtained consistent results using the two methods of analysis. We have elected to present the results based upon individuals because they are more readily interpreted and can be illustrated graphically.

Following Cheney (1992) and Henzi *et al.* (1997a), we used the Shannon-Weaver diversity index to quantify how evenly females' interactions are spread out among potential partners. The diversity index, *H*, for a group of *N* females is calculated as:

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

where p_i is equal to the relative proportion of grooming directed toward the ith female. *H* is maximized when females interact with all possible partners with equal frequency, and minimized when females focus all of their interactions on one partner. To standardize the measure for comparison with values obtained in studies of other groups, we computed ratios between the observed diversity index, *H*, and the maximum possible value of the diversity index for a group of this size, $H_{\max} = -\ln(N - 1)$.

We used two different methods to assess reciprocity. Matrix correlation methods were used to determine whether grooming was reciprocated within the group. A rowwise correlation test (Kr test) was used to determine whether actor and recipient matrices were correlated, and the partial rowwise correlation test was used to determine whether dominance rank or maternal kinship influenced these relationships (Hemelrijk, 1990a, 1990b; de Vries, 1993). The MatMan software package (de Vries *et al.*, 1993) was used for these computations.

The matrix correlation methods provide information about the patterning of interactions among females, but not about the extent of reciprocity *within* particular dyads. To assess how well balanced interactions are within dyads, de Waal & Lutrell (1988) and Silk (1992) computed the fraction of interactions initiated by one member of the dyad, $A \rightarrow B/(A \leftrightarrow B)$. When both partners contribute equally, the index equals 0.5. These kinds of indexes are problematic because skews in small samples are likely to occur by chance. Since some behaviors of interest occur at relatively low frequency and some pairs of individuals interact infrequently, small sample effects could significantly distort results. Although we might reduce this problem by limiting the analysis to pairs of animals that interact more often than a threshold value as de Waal & Luttrell (1988) did, it is not clear where this threshold should be set.

Thus, to assess the extent of reciprocity within dyads, we adopted the following method (Boyd & Silk, in prep.). Consider a dyad composed of two individuals, D and S. D initiates interactions toward S d times, while S initiates interactions toward D s times. The total number of events, N, is equal to $s + d$. We compute the cumulative Binomial probability of the smaller of the two values in a sample of N events. This value gives the likelihood of obtaining the observed values of s and d, if interactions were actually evenly balanced within the dyad.

The reciprocity index, RI, is computed as the ratio between the cumulative Binomial probability of the smaller of the two values and the cumulative Binomial probability of the larger of the two values. When these values are equal, the probabilities are the same, and the ratio is thus equal to 1. The reciprocity index ranges from 0 when interactions are highly skewed to 1 when interactions are perfectly balanced within dyads.

The reciprocity index is rescaled to provide information about the direction of the skew. If $d > s$, the scaled, signed index, RI_{adj}, equals $1 - (0.5 \times RI)$. If $d \leqslant s$, $RI_{adj} = 0.5 \times RI$. RI_{adj} approaches 1 when D is responsible for the majority of interactions and approaches 0 when S is responsible for the majority of interactions. Here, D represents the dominant member of the pair and S represents the subordinate member of the dyad. Thus, when RI_{adj} approaches 1, interactions are mainly directed down the hierarchy, and when RI_{adj} approaches 0, interactions are mainly directed up the hierarchy.

Following Cheney (1992), we also computed the ratio between the observed and expected proportion of interactions directed toward maternal kin. If females distributed interactions at random with respect to maternal kinship then the expected proportion of interactions directed toward maternal kin would equal $k/(N - 1)$, where k equals the number of adult female maternal kin in the group and N equals the total number of adult females in the group. If the ratio exceeds 1.0, then females interacted with maternal kin more often than expected by chance. These ratios are useful because they make it possible to compare the magnitude of maternal kin biases among females who have different numbers of relatives.

All significance levels cited in the text are two-tailed.

Results

A. *Differentiation in female relationships*

Females did not distribute their grooming evenly among all the females in the group. Each female groomed on average 7.6 of the other 18 adult females in the group at least once (range = 5-11 partners). Females devoted most of their grooming time to an even more restricted set of grooming partners. Females devoted at least 5% of their grooming to only 3.8 other females on average (range = 1-7). Nine of the 19 females devoted more than 50% of their grooming to a single partner (Fig. 1).

Values of the diversity index for grooming were low, reflecting the fact that females focused their grooming on a relatively small number of other females. The fifteen females who had adult maternal kin in the group had significantly lower diversity indexes for grooming than the four females who did not have adult female maternal kin in the group (grooming bouts: Mann-Whitney $U = 10.00$, $p = 0.0049$; grooming duration: $U = 8.00$, $p = 0.027$). Diversity indexes for grooming were considerably lower than values of the diversity index for approaches, grunts, and nonaggressive contact (Table 1).

B. *Maternal kinship*

Fifteen of the 19 focal subjects had known adult female maternal kin in the group. For these 15 females, the number of maternal kin ranged from 1 to
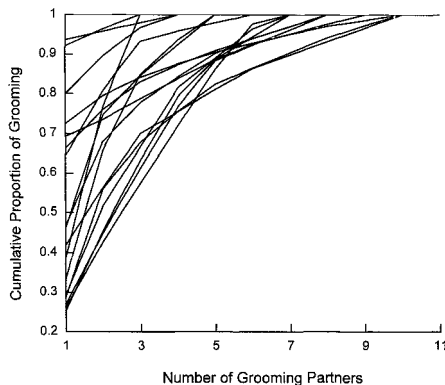

Fig. 1.   The cumulative proportion of all grooming bouts directed to each adult female in the group is shown. Most females concentrated the great majority of their grooming on a small number of partners.

TABLE 1. *Value of diversity indexes for different interactions and vocalizations*

Form of interaction	Diversity index (H)		Diversity ratio (H/H_{max})		Sample size
	Mean	SE	Mean	SE	
Approach	2.7185	0.012	0.9405	0.004	19
Grunt	2.3842	0.035	0.8249	0.012	19
Groom (bout)	1.3947	0.132	0.4825	0.046	19
Groom (duration)	1.2748	0.147	0.4411	0.051	19
Nonaggressive contact	1.8731	0.091	0.6480	0.032	19

4 (mean = 2.3). For these females, we compared the rate and duration of grooming with maternal kin and other females. Females groomed maternal kin at higher rates and for longer periods on average than they groomed other females (rate: Wilcoxon signed ranks test, $z = -3.351$, $p = 0.001$, 0 ties; duration: $z = -3.294$, $p = 0.001$, 0 ties; Fig. 2). Overall, females devoted approximately 60% of their grooming toward maternal kin. Grooming was more strongly biased toward maternal kin than other kinds of interactions were (Table 2).

The bias in favor of interacting with maternal kin might be the result of a general attraction among females of adjacent rank (Seyfarth, 1977, 1983). In order to control for this possibility, we repeated the analysis, limiting the sample to dyads composed of females who held adjacent ranks (rank difference ± 1). Some of the females included in the previous analysis had to be dropped from this analysis because they were related to both of the females who occupied adjacent ranks. Among females who held adjacent ranks, maternal kin groomed each other at higher rates than did other females (rate: $z = -2.429$, $p = 0.015$, 0 ties; duration: $z = -2.429$, 0 ties; $N = 9$; Fig. 2). Thus, the bias in favor of interacting with maternal kin was apparently not the result of a general attraction among females of adjacent rank.

Females' attraction toward maternal kin is partially a function of their dominance rank. The members of high ranking lineages devoted a greater fraction of their grooming to maternal kin than members of lower ranking lineages did (bouts: Spearman $r = -0.821$, $p < 0.002$; duration: $r = -0.821$, $p < 0.001$; $N = 15$; Fig. 3). It is possible that high ranking females devoted a greater fraction of grooming to maternal kin than members of low
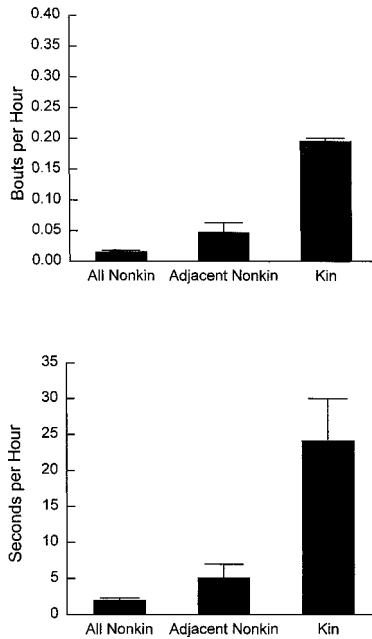
Fig. 2. In the upper figure, the rates of grooming (bouts per hour) directed toward all related females, all unrelated females, and unrelated females who held adjacent ranks (± 1 position) are shown. Means and standard errors are shown. In the lower figure, the duration of grooming (seconds per hour) of grooming directed toward all related females, all unrelated females, and unrelated females who held adjacent ranks (± 1 position) are shown. Means and standard errors are shown.

TABLE 2. *Proportion of interactions directed toward maternal kin*

Behavior	Mean	SE	*N*
Approach	0.21	0.029	15
Grunt	0.22	0.052	15
Groom (frequency)	0.61	0.076	15
Groom (duration)	0.62	0.082	15
Nonaggressive contact	0.43	0.054	15

ranking lineages did simply because they had more relatives in the group. In this group, the relationship between dominance rank and the number of adult female maternal kin was weakly positive ($r = 0.381$, $p = 0.107$, $N = 19$). To determine whether members of high ranking lineages interacted at higher rates than expected given their size, we repeated the analyses using
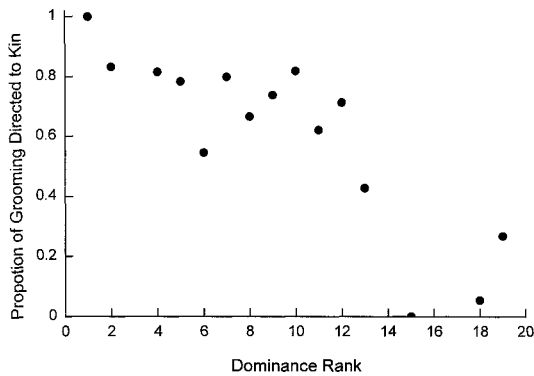
Fig. 3.   The proportion of grooming directed toward maternal kin is negatively related to female dominance rank as high ranking females devote a greater fraction of their grooming to maternal kin than low ranking females do.

partial correlations to control for the effects of the number of adult female maternal kin. The effects of female rank on the fraction of grooming devoted to maternal kin were independent of lineage size (bouts: partial correlation $r = -0.827, p < 0.001$; duration: partial $r = -0.762, p = 0.002$; df = 12).

C. Reciprocity

Overall, females most often groomed the females who most often groomed them (Kr = 1167, $p < 0.001$). This pattern characterized all of the females in the group, as all of the rowwise correlations were positive (Table 3).

An overall association between the amount of grooming given and received does not necessarily mean that grooming was evenly balanced within dyads. Grooming was observed among 90 of the 171 possible pairs of females. For these 90 dyads, observed values of RI ranged from 0 to 1.0, but were clustered around the middle of this range (Fig. 4). There were only six dyads (6%) in which one member of the pair was responsible for performing significantly more than half of the grooming bouts (Binomial probability $\leqslant 0.05$).

Thus, in the vast majority of dyads we could not reject the hypothesis that grooming was evenly balanced between partners. However, in the six dyads in which grooming was not evenly balanced between partners, the lower ranking female groomed her partner more than she was groomed. This suggests that females' dominance rank may have some effect upon grooming behavior.

TABLE 3. *Results of rowwise matrix correlation test for grooming bouts*

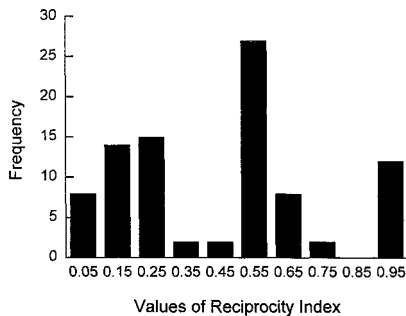| Female	Kendall's tau	Weight	Contribution
ST	0.42	40.82	17
SY	0.80	66.27	53
BT	0.62	103.61	64
SD	0.90	85.98	77
HL	0.46	114.37	53
HN	0.52	98.21	51
SH	0.28	93.28	26
SS	0.78	116.57	91
WR	0.63	84.41	53
JL	0.69	93.20	64
LE	0.60	102.69	62
NI	0.67	102.47	69
NN	0.58	84.48	49
NT	0.51	114.82	58
MR	0.74	99.35	74
AL	0.80	83.46	67
OL	0.90	96.50	87
JN	0.64	110.5	71
CD	0.75	108.41	81

Fig. 4. The distribution of the values of the reciprocity index are shown for grooming bouts. Values near 0 indicate that grooming was very highly skewed within dyads, while values near 1 indicate that grooming was evenly balanced.

D. Dominance rank

Females' rank did not influence the number of adult females who groomed them ($r = 0.115$, $p = 0.640$, $N = 19$). It is possible, however, that high ranking females had more *unrelated* grooming partners than low ranking

females did. The number of adult female maternal kin varied (range 0-4), so we computed the proportion of unrelated females that each female was groomed by. Dominance rank was unrelated to the proportion of unrelated females that females were groomed by ($r = 0.166, p = 0.496, N = 19$).

The high degree of reciprocity largely precluded the possibility that grooming was biased toward higher ranking females. Overall, 54% (421/776) of all grooming bouts were directed toward higher ranking females. However, in the six dyads in which grooming was not evenly balanced between partners, the lower ranking female groomed her partner more than she was groomed. In order to determine whether females consistently biased grooming toward higher ranking females, we compared the average rates of grooming directed toward higher and lower ranking females. For this analysis, the highest ranking and lowest ranking females had to be excluded because they could not direct grooming to higher and lower ranking females, respectively. Ten females groomed higher ranking females at higher rates on average than they groomed lower ranking females, while seven females groomed lower ranking females at higher rates on average than they groomed higher ranking females ($z = -0.047, p = 0.962$, 0 ties). When related dyads were removed from the sample, the results remained the same.

High ranking females tended to be groomed at higher rates ($r = -0.442, p = 0.058, N = 19$) than were lower ranking females. However, this result was an artifact of high rates of grooming between certain pairs of high ranking relatives. When related dyads were removed from the sample, the relationship between female dominance rank and the rate of grooming received disappeared ($r = 0.229, p = 0.326, N = 19$). Dominance rank did not consistently affect the duration of grooming ($r = -0.407, p = 0.084, N = 19$; maternal kin removed: $r = 0.405, p = 0.085, N = 19$).

Since maternal kin occupied adjacent ranks and generally interacted at high rates, it was not surprising to find that the rates and duration of grooming were elevated among females who held adjacent ranks (rate: $z = -3.662, p < 0.001$, 0 ties; duration: $z = -3.702, p < 0.001$, 0 ties). Again, however, these differences disappeared when maternal kin were excluded from the analysis. There were no consistent differences in grooming given to unrelated females who held adjacent and nonadjacent ranks (rate: $z = -1.293, p = 0.196$, 0 ties; duration: $z = -0.943, p = 0.345$, 0 ties).

In order to determine whether the extent of reciprocity in grooming differed among females who occupied adjacent ranks and those who were

more distantly ranked, we compared the values of RI_{adj}. There were no significant differences in the values of RI_{adj} between females who occupied adjacent and nonadjacent ranks ($z = -0.454$, $p = 0.650$, 0 ties). Since maternal kin constituted a substantial fraction of the females who held adjacent ranks, we repeated the analysis for unrelated dyads. Again, we found no evidence that the extent of reciprocity was greater among females who occupied adjacent ranks than among females who were more distantly ranked ($z = -0.676$, $p = 0.499$, 0 ties).

There was no direct evidence that females competed over access to high ranking grooming partners. We examined the sequence of events during all grooming bouts ($N = 600$) that were observed from beginning to end. Approximately 8% of all grooming bouts (46/600) ended when one of the participants was supplanted or harassed by an adult or immature female. When females actively interrupted ongoing grooming bouts, the intruder usually outranked both grooming partners (34/46 = 74%), and the intruder therefore did not gain access to a female who was higher ranking than herself. After females interrupted grooming bouts involving higher ranking females, they were unlikely to begin grooming them (2/12 = 17%).

Although overt competition for grooming partners was rare, we cannot rule out the possibility that the grooming opportunities of low-ranking females were more constrained than those of high-ranking females as a result of competitive exclusion. Grooming bouts were invariably dyadic, and a female could neither disrupt nor join any grooming bout involving two females who outranked her.

Discussion

The baboons in Moremi were expected to exemplify "the supposedly 'classic' savanna baboon multi-male female-bonded groups" (Barton *et al.*, 1996, p. 327) because they live in large groups, face relatively high levels of predation, and rely on clumped resources. In such groups, females are assumed to form close and well-differentiated bonds with one another, establish stable matrilineal dominance hierarchies, and rarely disperse from their natal groups. Our data suggest that Moremi females largely conformed to this picture of baboon society. The female dominance hierarchy was linear and stable, and related females occupied adjacent ranks. Moreover, females developed highly-differentiated social relationships, showing particular affinities for maternal kin and reciprocating partners.

TABLE 4. *Grooming diversity in free-ranging groups of Old World monkeys*

Site	Number of adult females	Mean grooming diversity ratio (H/H_{max})	Source
Moremi Reserve, Botswana	19	0.48	this study
Laikipia, Kenya	17	0.57	Castles, pers. comm.
Amboseli National Park, Kenya	18	0.71	Cheney, 1992[1]
Mt. Zebra National Park, South Africa	8	0.86	Cheney, 1992
Drakensburg Mts., South Africa	6	0.76	Henzi, pers. comm.
	9	0.58	Henzi, pers. comm.
	12	0.64	Henzi, pers. comm.

[1] Computed from data presented in Saunders (1988).

Grooming was less evenly distributed among females in Moremi than it was among female baboons observed at other sites (see Table 5 in Cheney, 1992; Table 4). There are a number of possible reasons that Moremi females may have differed from females at these sites. Cheney (1992) predicted that grooming should be most evenly distributed when females collectively defend resources or territories. Grooming was less evenly distributed among female babons in Moremi than among female macaques and vervets, species in which females generally do participate actively in hostile intergroup encounters (Cheney, 1992). However, grooming diversity was lower among Moremi baboons than in other baboon populations, even though females do not participate in intergroup encounters at any of these sites (Cheney, 1987; Barton *et al.*, 1996).

The extent of differentiation in female relationships in Moremi might be a function of the intensity of intragroup competition over resources. Van Schaik and his colleagues (van Schaik, 1989; van Hooff & van Schaik, 1992; Sterck *et al.*, 1997) have argued that well-differentiated relationships among females will be established when competition over access to resources within groups is intense. We do not know whether intragroup competition played a more important role in Moremi than in other baboon populations. However, if competition was more intense in Moremi than at other sites, then it is surprising that alliances among adult females were so rarely observed there.
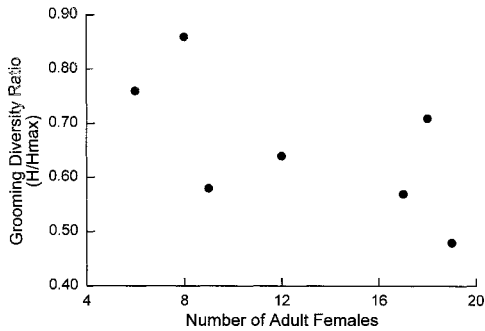
Fig. 5. Grooming diversity ratios are plotted against group size for several baboon groups. Data are taken from Table 4. Grooming diversity ratios tend to decline as the number of females in the group increases ($r = -0.714$, two-tailed $p = 0.071$, $N = 7$).

Our data provide a better fit for the hypothesis that group size influences the distribution of grooming. Dunbar (1991) predicted that females who live in larger groups will spend more time grooming and/or focus grooming on a smaller number of partners. Data from several baboon groups indicates that grooming diversity generally declines as group size increases (Fig. 5). Females in Moremi behaved much like females in other large baboons groups do. Thus, the low diversity of grooming among Moremi females may simply reflect the fact that they lived in a relatively large group.

While these data support the notion that females focus their grooming on a relatively small number of partners, we found no evidence that this selectivity inevitably leads to the disintegration of social groups (Dunbar, 1991, Henzi et al., 1997). The Moremi group remained a cohesive social unit for at least six years after these data were collected. While the small size of females' social networks and the strong bonds among maternal kin might seem to predispose groups to splinter along matrilineal lines, the reciprocal links forged between females from different lineages might tie groups together. Perhaps this is what lends long-term stability to groups which are actually composed of "subgroups allied in a loose confederation" (Cheney, 1992, p. 344).

Moremi females seem to devote a greater fraction of grooming to their relatives than females in other populations do. Cheney (1992) computed ratios between the observed and expected proportions of grooming directed to adult female maternal kin (mothers, sisters, daughters, grandmothers, and granddaughters) for seven species of primates. The mean values of the

grooming ratio ranged from 1.2 in vervet monkeys in Amboseli to 2.6 among rhesus monkeys on Cayo Santiago. In Moremi, the average ratio equaled 7.7. This value is considerably higher than the average ratio for baboons in Amboseli (1.7; computed by Cheney, 1992 from Saunders, 1988). It is not clear why the bias in favor of maternal kin was more pronounced in Moremi than in other primate groups.

Female baboons in Moremi did not conform to most of the predictions derived from Seyfarth's (1977, 1983) model. They did not compete overtly over access to grooming partners, and they did not seem to be strongly attracted to high ranking females. However, high-ranking matrilines were more cohesive than low-ranking matrilines, as would be predicted if attraction to maternal kin coexisted with attraction to high ranking individuals.

The Moremi females do not seem to be particularly unusual in this respect. Data compiled from Saunders' (1988) study of female baboons in Amboseli indicate that approximately 37% of all grooming bouts were directed toward higher ranking females, while Altmann *et al.* (1998) found that in two-thirds of all dyads females groomed lower ranking partners more often than they were groomed in return. In Laikipia, approximately 49% of all grooming bouts among adult females were directed toward higher ranking females (computed from data provided by D. Castles; see also Sambrook *et al.*, 1995). Female baboons may have little incentive to groom higher ranking females because they do not often obtain support from other adult females. Alliances among adult females are uncommon in Moremi and most other sites (Seyfarth, 1976; Lee & Oliver, 1979; Walters, 1980; Johnson, 1987; Samuels *et al.*, 1987; Byrne *et al.*, 1990; Ron *et al.*, 1996; but see Barton *et al.*, 1996).

The rarity of alliances among adult female baboons is surprising because well-differentiated relationships, strong ties among maternal kin, linear matrilineal dominance hierarchies, and female philopatry are generally associated with the formation of alliances among females (*e.g.* Wrangham 1980, 1987; van Schaik 1989; Isbell, 1991; van Hooff & van Schaik 1992; Sterck *et al.*, 1997). Moreover, alliances are thought to contribute to the stability of dominance relationships among Cercopithecine primate females (Chapais, 1992). These features are apparently decoupled in baboons. Female philopatry characterizes nearly all baboon populations (Pusey & Packer, 1987), although female dispersal may sometimes occur among baboons living in the

mountains of South Africa (Anderson, 1981). Baboon females form matrilineal dominance hierarchies (Seyfarth, 1976; Moore, 1978; Lee & Oliver, 1979; Hausfater *et al.*, 1982; Johnson, 1989; this study). Female dominance hierarchies in these populations are typically stable over time (*e.g.* Hausfater *et al.*, 1982; Smuts, 1985; Samuels *et al.*, 1987) and highly linear (Hausfater, 1975; Barton & Whiten, 1993). Female baboons also establish strong ties with their adult female maternal kin (Saunders, 1988; this study). Coalitions play an important role in the acquisition and maintenance of dominance rank by juvenile baboons (Cheney, 1977; Lee & Oliver, 1979; Walters, 1980; Pereira 1988, 1989, 1992, 1995; Lee & Johnson, 1992), much as they do among vervets (Horrocks & Hunte, 1983; Lee, 1983) and macaques (reviewed by Chapais, 1992). However, alliances among adult females are uncommon at most sites. It is possible that coalition are uncommon, but play a critical role when the status quo is disrupted (*e.g.* Samuels *et al.*, 1987). However, present data seem to suggest that alliances play a less important role in the lives of adult female baboons than they do in other species that maintain stable and linear matrilineal dominance hiearchies. Future research may reveal the processes that underly such stability across species.

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