

Female Dominance and Female Social Relationships Among Yellow Baboons (*Papio hamadryas cynocephalus*)

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Adult females in a female-bonded, cercopithecine species such as baboons are characterized by hierarchically ranked matriline, i.e., female offspring assume rankings just beneath those of their mothers. In this system of closely ranked matriline, a female should engage in significantly more affiliative interactions with those individuals who are closely ranked to herself than with those individuals who are more distantly ranked. We examine the hypothesis that females in this troop of feral yellow baboons (*Papio hamadryas cynocephalus*) who are closely ranked will also show close social affiliation. We collected focal data on 23 feral, adult female subjects (253 possible dyads) over approximately 1 year at the Tana River National Primate Reserve, Kenya. Following Bramblett's [Behav Brain Sci 4: 435, 1981] method of dominance tabulation and utilizing a modified version of Smuts' [Sex and friendship in baboons, Hawthorne: Aldine Publishing Co., 1985] preferred partner index, we describe and compare the dominance matrix and hierarchy, preferred proximity partner and grooming partner sociograms, and the social networks of these 23 focal females. Over 1,400 interactions were utilized in the dominance tabulations, 41 statistically significant proximity partner preferences were documented, and 100 grooming dyads were recorded. We examine both partners' ranks and the presence of an infant as possible factors influencing proximity and grooming partner preferences. We find that in this population there is no direct correspondence between females' ranks and their affiliation partners. Neither proximity nor grooming preferences are consistently predictable from partners' ranks. While proximity preferences were not significantly influenced by the presence of an infant, grooming partner preferences were. Females with infants had more grooming partners and were more often involved in unidirectional grooming relationships as the recipients than were females without infants. We conclude that females' dominance rankings are not good predictors of either proximity partner or grooming partner preferences and that the presence of an infant does have a significant impact on grooming partner preferences in this population. Am. J. Primatol. 47:321-334, 1999. © 1999 Wiley-Liss, Inc.

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INTRODUCTION

Female cercopithecines are known for their philopatry. In a species where females are philopatric, there is a tendency for the group to be female bonded [Wrangham, 1980], to find ranked matriline, and for affiliative relationships to form primarily along kin lines. In these female-bonded groups, female offspring generally assume dominance ranks just below that of their mothers. These patterns have been documented for many of the cercopithecines [e.g., yellow baboons, Altmann, 1980; gelada baboons, Dunbar, 1979; Japanese macaques, Koyama 1967; vervets, Cheney & Seyfarth, 1990]. Thus, among many of the cercopithecines, females' affiliative relationships should tend to be with other females who are adjacently or closely ranked to themselves.

Yellow baboons (*Papio hamadryas cynocephalus*) are a typical cercopithecine species in that they are characterized by philopatry, female-bonded, and ranked matriline. As long-lived and philopatric individuals, females in this sub-species have many opportunities for social interactions and for forming relationships with their conspecifics. The importance of these relationships cannot be over-emphasized since it is these that are the focal points of a female's life. Acquiring and maintaining the right friends and allies can mean the difference between maintaining and losing one's dominance rank [Chapais, 1992] or keeping or losing one's fetus [Wasser & Starling, 1986], just to give two examples. Thus, given the cercopithecine pattern and the importance of friends and allies, we would expect closely ranked females to also be associated with one another socially.

Here we examine the hypothesis that closely ranked females in this yellow baboon population will show high levels of social affiliation. We undertake this study both to evaluate this hypothesis and to further illuminate the complex social milieu of cercopithecine females. We believe it is important to note the variability within the cercopithecine subfamily as well as within different populations of the same subspecies. Data on this little-studied population will contribute significantly to recognizing and acknowledging that variability.

METHODS

Study Site

The data presented here are based on observations of the Mchelelo yellow baboon (*Papio hamadryas cynocephalus*) troop in the Tana River National Primate Reserve, Kenya [see Bentley-Condit & Smith, 1997, Condit & Smith, 1994, and Marsh, 1976 for detailed site descriptions and maps]. The 23 adult females in this single troop were observed during the period November 1991 through September 1992. Included in these data are over 1,100 hr of observations, 600+ of which were devoted to female focal animal observation [following Altmann, 1974]. All of the focal subjects were well habituated and distinguished by physical characteristics [see Bentley-Condit, 1995 and previously published reports for further details regarding the study and methodology].

Dominance Hierarchy

To examine social relationships and the degree to which these affiliative relationships are associated with dominance rank among these females, three data

sets were compared: a) dominance hierarchy data, b) preferred interaction partner data, and c) preferred grooming partner data. Dominance was determined not only by the assertive acts of an individual but also by that individual's submissive acts. Behaviors were classified as either submissive or assertive according to precedents set by other researchers [e.g., Hall & DeVore, 1965; Hausfater, 1975; Sapolsky, 1983] and local observations. Assertive behaviors included "bite," "chase," "displace," "fight," "hold down," "mild aggression," and "threat." Submissive behaviors included "avert head/body," "avoid," "crouch scream," "scream," and "tail up" [see Bentley-Condit, 1995 for operational definitions]. The data were recorded across diverse social situations so that an individual's ranking is not limited to a particular context.

Dominance relationships for the 23 focal females were determined following Bramblett [1981] and were based upon $\approx 1,450$ female-female interactions among 253 unique dyads. Bramblett [1981] presents a simple, straight-forward method for reducing complex dominance relationships to a single score, which addresses problems associated with methods that use ordinal ranking systems and assume stochastic transitivity [see Boyd & Silk, 1983 and Sade, 1992 for discussions of these problems]. Bramblett's [1981] score represents the number of other individuals one individual is likely to dominate. Thus, the hierarchy status of an individual is her net score of dominant relationships less subordinate relationships. A relationship is scored as dominant (+1) if individual "A" wins at least 75% of her interactions with individual "B" (in those interactions that can be scored as wins or losses). In these interactions, "A" is given a score of "+1" and "B" is given a score of "-1". In cases where the 75% criterion is not met or where no interactions occurred between these two individuals, both individuals receive a score of "0." Using this system corrects for frequency of interactions since it is not the absolute number of interactions that is important but the ratio of outcomes. There are several advantages to this system, including its ease of tabulation and interpretation, its reflection of relative status, and its provision of an equal interval scale amenable to analysis by parametric statistical tests [Bramblett 1981; Martin & Bateson 1993].

Preferred Proximity Partners

Data on preferred proximity partners were examined next. The preferred proximity partners (based on z scores, $P \leq 0.05$) were determined using a modified version of Smuts' [1982, 1985] method for assigning composite scores to dyad partners based on proximity, using focal sample behavior durations rather than scan sample behavior frequencies. As shown in the Table I example, the modified method involves calculating:

- 1) total dyadic "all female interactions" time for a given dyad;
- 2) proportion of time at each of the three distance categories;
- 3) multiplying those proportions by the appropriate weighting factor [i.e., the reciprocal of the distance category following Smuts, 1985]; and
- 4) summing the weighted scores to obtain a dyadic composite score.

As Smuts [1985] has shown, this method does not rely on the assumption of equal probability of interactions, corrects for the possibility that two individuals will spend more time together at greater distances, and corrects for both frequency of interactions within a dyad and differences in total focal time for members of the dyad. Composite scores calculated using *only* the

TABLE I. Female-Female Dyad Composite Score Methodology

Distance (m)	Weighting factor	Partner: CO		Partner: DD	
		Score	Score × weighting factor	Score	Score × weighting factor
		Total ♀ Inter. Time: 185,713 (sec)		Total ♀ Inter. Time: 164,491 (sec)	
1	2.0	2.354	4.708	0.732	1.464
3	0.5	2.389	1.195	2.480	1.240
10	0.1538	1.007	0.155	0.757	0.117
Composite proximity score:		AL/CO = 6.058		AL/DD = 2.821	

focal female's total interaction time as the divisor in step 2 above rather than the dyad's combined time did not affect partner preferences. In computing these scores, proximity partner preferences were combined across behavioral contexts (with the exception of the grooming partners discussed below). Combining scores in this manner provides a more robust interpretation of preferences. This methodology is similar to the dominance data methodology as we did not want the rankings or preferences to be limited to particular contexts (e.g., preferred foraging partner, preferred resting partner, etc.).

Grooming Partners

The preferred grooming partner data are based upon the proportion of the total interaction time that a dyad spent grooming. Preferred grooming partners (based on z scores, $P \leq 0.05$) were calculated in the following manner. Because many dyads were never observed to groom one another, only the subset of females with whom a focal female was observed to groom were considered in the analyses. A total of 100 grooming dyads (of 253 possible) were recorded and included. Thus, these data represent those grooming partners with whom a female spent a significantly larger proportion of dyad interaction time when compared to her other grooming partners. These preferences are therefore a more stringent interpretation of grooming partner preferences than would be achieved if all of the female's possible dyads were considered.

We conducted an additional analysis of the grooming data by using the ANTHROPAC - 4.0 [Borgatti, 1992a] software to evaluate Johnson's hierarchical clusterings. This program groups data according to shared similarities using the "average method," which forms clusters by assuming the "proximity between two clusters to be the average proximity between members of the two clusters" [Borgatti 1992b:26]. In this case, those shared similarities were shared grooming partners. Again, the proportion of a dyad's time represented were the data analyzed. However, the data were normalized using a scale of 0-5 (i.e., 0=0-1.9%; 1=2-5.9%; 3=11-15.9%; 4=17-28.4%; 5=36-62%) so that the clusters would not be disproportionately skewed by extremes. For the cluster analysis, all dyads and data were included so that any grouping patterns would become apparent.

RESULTS

The dominance hierarchy presented in Table II reveals that there are numerous ties within the Mchelelo females' rankings. The scores represent the number of dyads where a female was clearly dominant less the number where she was subordinate. Thus, the highest ranking possible was a +22 (if a female was dominant over all of the other focal females and thus had a +1 score for each dyad) and the lowest a -22 (if a female was subordinate to all of the others and thus had a -1 score for each of her dyads). As can be seen, there are six ranks that are shared by two or three females (i.e., +18, +5, -3, -8, -9, and -17). However, despite the fact that these females share overall rankings with at least one other female, in only two of the ten dyads represented are the relationships ambivalent (CO/PA and CO/MH). For each of the other eight shared-rank dyads, there is a clear dominant/subordinate ranking within the dyad.

Dyadic composite scores were calculated following Smuts [1982, 1985] for all of the Mchelelo focal female dyads ($n=253$). All females had one to three preferred proximity partners whose composite scores were significantly higher (z scores, $P \leq 0.05$) than that female's other dyads. Where the dyad ranks for the focal female will vary based on her other dyad scores. Given the method of calculation, it is possible for female "A" to have "B" as a preferred partner even though "B" may not prefer "A." Consequently, some dyads reflect *unidirectional* while others reflect *bidirectional* preferences. In unidirectional dyads, the initiation and maintenance of proximity is more one-sided than in bidirectional dyads. The sociogram (Fig. 1), constructed from statistically significant scores, reflects preferences and their directionality ($n=28$ unique dyads representing 41 statistically significant proximity partner preferences). Directionality is indicated by the presence or absence of an arrow. This preferred proximity partner sociogram readily sorts itself into four subgroups. These subgroups are arranged parsimoniously so as to maintain linked bidirectional preferences. In doing so, there are only three individuals (DD, KN, and LS) who could easily be considered members of a group other than the one to which they have been assigned and it is these individuals who are either the actor or the recipient of four of the six unidirectional preferences between subgroups.

Grooming partner preferences are presented in Figure 2 and represented by the arrows. The directionality of the arrows indicate which member of the dyad was the recipient of grooming (i.e., the gromee) in more ($\geq 60\%$) of the bouts.

Cluster analysis shows the preferred grooming partner sociogram to sort itself into subgroups. The clusters (enclosed by dashed lines) in Figure 2 represent the fewest clusters in which all 23 focal females were included as a member of a grooming subgroup. These six clusters thus represent the "lowest common denominator" of clusters for the troop. Each of these clusters, through individual members, has one to six links with the other clusters indicated. The 31 unique dyads represented in this sociogram were each determined to be preferred grooming partners following the methods described earlier. The partners within these 31 grooming dyads are separated in the hierarchy by zero to 22 ranks ($\bar{x}=10$). The directionality distribution of the 31 grooming dyads (i.e., unidirectional, bidirectional, higher \gg lower, etc.) is presented in Table III. Twenty of the thirty-one dyads represent unidirectional preferences; in 14 of those 20 dyads (70%), the partner indicated as the groomer was responsible for 100% of the grooming.

A comparison of the pairings expected based on the dominance hierarchy matrix in Table I, the preferred proximity partner sociogram represented in Figure 1, and the preferred grooming partner sociogram and clusters in Figure 2

TABLE II. Mcheleo Adult Female Dominance Matrix

Winner	Loser																Score									
	PO	NQ	KM	KN	PS	SK	HQ	ST	WK	LL	NY	PA	MH	CO	RS	AL		ML	PT	DD	PH	LS	MM	LY		
PO	-	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+18	
NQ	-1	-	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+18	
KM	-1	-1	-	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+17	
KN	-1	-1	-1	-	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+14	
PS	-1	-1	-1	-1	-	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+9	
SK	0	-1	-1	-1	0	-	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	0	0	+8	
HQ	-1	-1	-1	-1	-1	0	-	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+7	
ST	-1	-1	-1	-1	-1	0	-	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+6	
WK	0	0	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	0	0	+5	
LL	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+5	
PA	0	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+3	
NY	0	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	0	0	-1	-3
MA	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-3
MH	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-3
CO	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-3
RS	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-5
AL	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-8
ML	-1	0	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-8
PT	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-9
DD	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-9
PH	0	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-11
LS	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-17
MM	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-17
LY	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-17

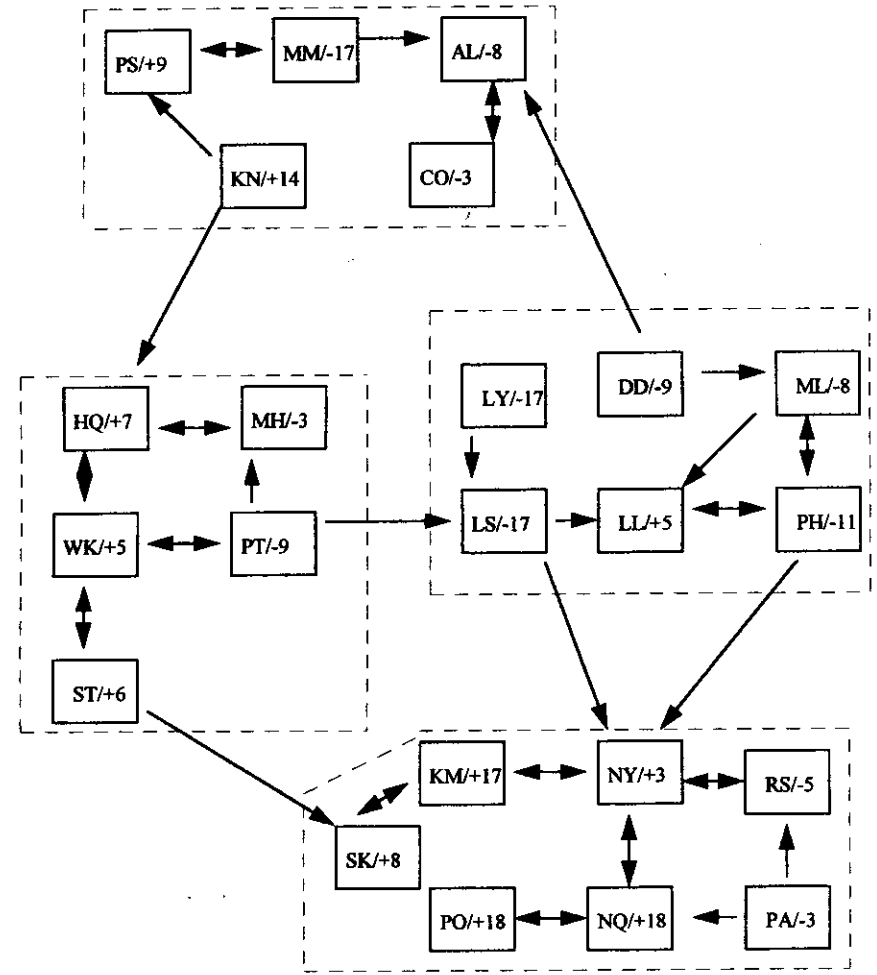


Fig. 1. Mcheleo females and their statistically significant preferred proximity partners. Females and their ranks are indicated in each box. →, unidirectional preferences. ↔, bidirectional preferences. Subgroups are enclosed in dashed lines.

reveals that neither proximity nor grooming preferences are consistently predictable from rank in this population. Table IV presents the correspondences and lack of correspondences between the expected and observed pairings. Rather than following a traditional "priority of access" model [Seyfarth 1977] with higher ranking females receiving more grooming/relationships and most grooming/relationships occurring between adjacent pairs, both of the sociograms offer evidence of affiliation between disparately ranked Mcheleo females. While there are subsets of correspondence across all four classifiers in Table IV (e.g., the two highest ranking and two of the lowest ranked females are linked in all four, some same or adjacently ranked females are in the same grooming clusters or social sub-

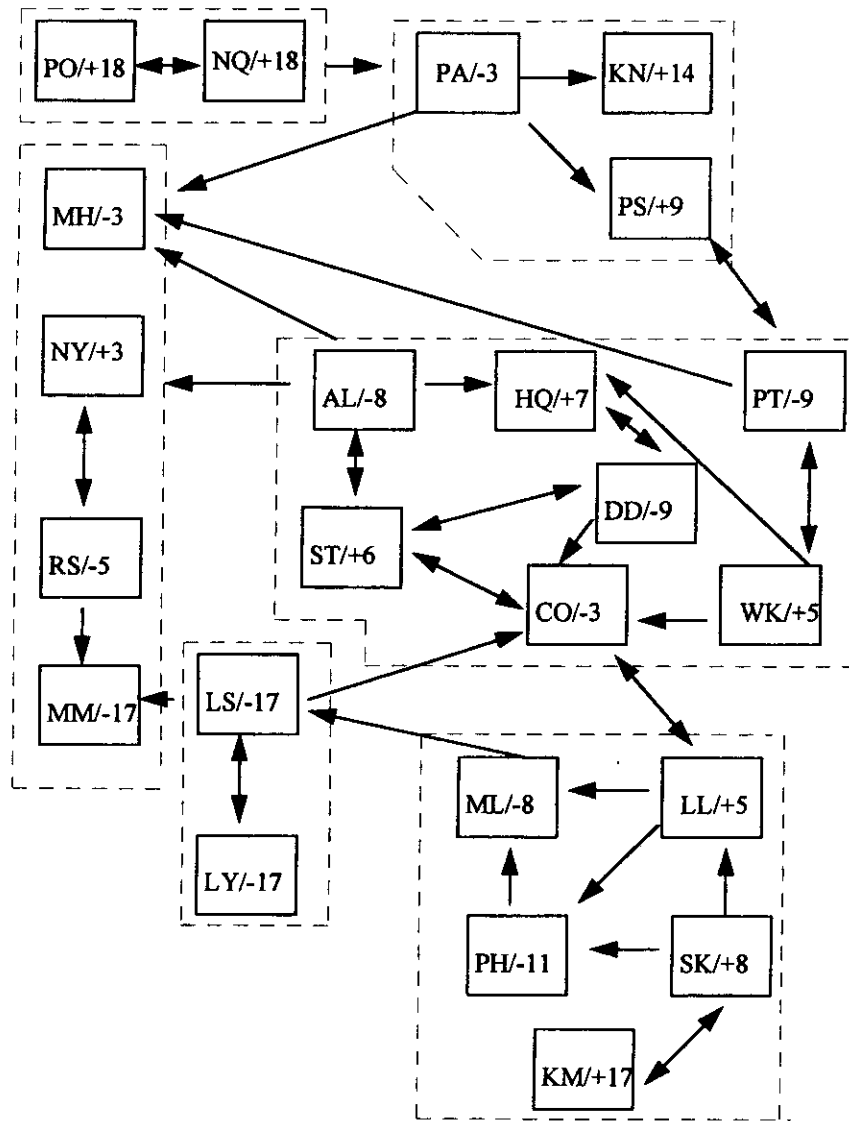


Fig. 2. Mchelelo females and their statistically significant preferred grooming partners. Females and their ranks are indicated in each box. →, unidirectional preferences. ↔, bidirectional preferences. Cluster analysis subgroups are enclosed in dashed lines.

groups), there is no overall correspondence. There are, in fact, individuals from various ranks included in each of the preferred grooming partner clusters (with the exception of the two isolate dyads) and the preferred proximity partner subgroups (see Figs. 1, 2).

TABLE III. Distribution of Grooming Dyads

	Unidirectional	Bidirectional
Higher>>Lower	8	
Lower>>Higher	10	
Same>>Same	2	2
Totals	20	11

In examining why the Mchelelo females seek females disparately ranked from themselves as proximity or grooming partners, we have to consider what it is that makes these preferred individuals attractive. High rank or the presence of a newborn infant are reported to affect the extent to which, and by whom, a female is sought as an interaction partner [e.g., Cheney & Seyfarth 1990; Seyfarth 1976]. With regard to grooming partners (Fig. 2, Table III), while only 10 (50%) of the 20 unidirectional dyads were directed toward higher ranking females, 18 (90%) were directed towards females with infants. Similarly, in 7 of the 11 (63.6%) bidirectional grooming dyads, at least one of the females had an infant. However, given that eleven of the 23 focal females had infants, the total number of grooming dyads including females with infants ($n=25/31$, 80.6%) is not over-represented as chance could account for up to 73.9% of these dyads [based upon the proportion of total female-female dyads (187/253) that could include a female with an infant.] A chi-squared test indicated no significant difference between observed and expected ($\chi^2_{1df} = 0.738$, $P > 0.5$).

When one focuses on the number of grooming preferences ($n=42$) rather than the number of dyads, a different picture emerges. None of the four highest ranked females were preferred by more than one grooming partner while three of the four most popular (i.e., preferred by three or more females) had infants. First, a chi-squared test shows a significant difference in the distribution with regard to number of partners ($\chi^2_{1DF}=10.145$, $P < 0.05$). Where 10 of 11 females with infants had more than one partner, only 3 of 12 females without infants had more than one partner. Additionally, there is a significant difference in the distribution of directionality of those preferences ($\chi^2_{1DF}=12.780$, $P < 0.05$). Females with infants ($n=11$) were the recipients of 18 of 20 unidirectional preferences and partners in 8 of 22 bidirectional preferences. Females without infants ($n=12$), on the other hand, were the recipients of 2 of 20 unidirectional preferences and partners in 14 of 22 bidirectional preferences. Thus, there appears to be a difference between females with infants and females without infants with regard to whether they reciprocate grooming. The presence of an infant seems to influence a female's popularity as a preferred grooming partner and females with infants are more likely than females without infants to be the recipient of unidirectional grooming.

Infants' effect proximity partner preferences scores differently than grooming partner preferences. Figure 1 shows most females (18/23) have either two or three dyadic partners. The modal number of partners by whom a female is preferred is two ($n=9$; range = 0-4). All of the females who were not preferred by others as proximity partners ($n=4$) were females without infants. Of the 28 unique dyads represented, 21 (75%) include at least 1 female with an infant. This distribution does not differ significantly from chance ($\chi^2_{1DF}=0.048$, $P > 0.05$). As well, of the 41 statistically significant preferences represented in the Figure 1 sociogram, only 25 (61%) indicate preferences for a female with an infant. Again, this distribution is not statistically significant ($\chi^2_{1DF}=0.322$, $P > 0.05$). Neither preferences for females with infants nor unique dyads including females with infants occur more frequently in this proximity distribution. Thus, infants or some feature of a mother-infant pair

TABLE IV. Mchelelo Females' Comparison

(1) Expected pairings based on rank	(2) Pairings based on pref. prox. partners	(3) Preferred grooming partners	(4) Pairings based on cluster analysis
PO/NQ	PO/NQ	PO/NQ	NP/NQ
NQ/KM	NQ/PO	NQ/PO NQ/PA	NQ/PO
KM/KN	KM/SK KM/NY		
KN/PS	KN/PS	KN/PA	KN/PA
PS/SK	PS/MM	PS/PT	
SK/HQ	SK/KM	SK/LL SK/PH SK/KM	SK/LL
HQ/ST	HQ/WK HQ/MK	HQ/WK HQ/AL HQ/DD	HQ/AL
ST/WK	ST/WK ST/SK	ST/AL ST/DD	ST/DD
WK/LL	WK/PT WK/ST WK/HQ	WK/PT WK/ST WK/HQ	WK/PT
LL/NY	LL/PH	LL/PH LL/CO LL/LS LL/ML LL/SK	LL/SK
NY/PA or NY/MH	NY/RS NY/NQ	NY/RS NY/AL	NY/RS
PA/MH	PA/NQ PA/RS	PA/MH PA/NQ PA/KN PA/PS	PA/KN
MH/CO	MH/HQ	MH/AL MH/PA MH/PT	MH/MM
CO/RS	CO/AL	CO/DD CO/LL CO/LS CO/ST CO/WK	
RS/AL	RS/NY	RS/NY RS/MM	RS/NY
AL/MM	AL/CO	AL/HQ AL/MH AL/ST AL/NY	AL/HQ

(continued)

TABLE IV. Mchelelo Females' Comparison (continued)

(1) Expected pairings based on rank	(2) Pairings based on pref. prox. partners	(3) Preferred grooming partners	(4) Pairings based on cluster analysis
ML/PT	ML/LL ML/PH	ML/LL ML/PH	
PT/DD	PT/LS PT/MH PT/MH	PT/MH PT/WK	PT/WK
DD/PH	DD/AL DD/ML	DD/ST DD/HQ	DD/ST
PH/LS	PH/ML PH/NY PH/LL	PH/ML PH/SK PH/LL	
LS/MM	LS/LL LS/NY	LS/LY	LS/LY
MM/LY	MM/AL MM/PS	MM/LS MM/RS	MM/MH
LY/MM or LY/LS	LY/LS	LY/LS	LY/LS

seem to play a larger role in determining attractiveness in Mchelelo adult female grooming dyads than in the adult female preferred proximity partner dyads. The attractiveness of infants could have been masked in the proximity partner data (since these data include individuals up to 10 m in proximity). However, the proximity data were normalized (i.e., multiplied by a weighting factor: see Methods) prior to analysis so that closer proximity actually received more weight. Thus, it is unlikely that being attracted to females with infants would be masked by the larger distance data. As well, the distribution of the 41 (Fig. 1) unidirectional and bidirectional preferences by preference for a higher ranked, lower ranked, or same ranked female does not differ significantly from what would be expected by chance ($\chi^2_{2DF}=1.685$, $P>0.05$). Again, it appears that neither rank nor the presence of an infant are sufficient to explain these proximity partner preferences.

DISCUSSION

Still, the question remains, why do the Mchelelo females seek to be in the proximity of females disparately ranked from themselves. In both sociograms, rank does not appear to be the deciding feature. The presence of an infant, on the other hand, is more of a factor in grooming than in proximity relationships. These data suggest that although dominance rank plays an important role in a female baboon's life, it is not the determinant factor of social relationships. Neither is the presence of an infant. The difference in importance of infants between the two sociograms likely represents differences in the quality of the social relationships. The grooming data are, to some extent, more easily influenced by the presence of an infant. It is well documented that baboon females seek to be near and touch the infants of other females [e.g., Altmann, 1980] and that females with infants are popular grooming partners [e.g., Rose, 1977]. A female's best chance of getting to touch or hold another female's infant is by grooming the mother to gain proximity to the infant. Thus, physical contact with the mother

greatly increases the opportunities for access to her infant. The proximity data, based upon 1, 3, and 10 m distances, cannot as easily reflect this attraction since grooming occupies such a small proportion of the total time dyad partners spent at the 1 m proximity category.

What we are witnessing with the Mchelelo females' social relationships may be attributable to at least two, not necessarily mutually exclusive, factors. First, there is the possibility that these relationships are influenced by kinship. We may be seeing matrilineal where some of the younger females are still in the process of fully establishing their rank. This could partially account for the disparity of ranking within the subgroups of Figure 1 as each of these groups contained from one to three younger (i.e., nulliparous or primiparous) and lower-ranking females. Unfortunately, we are unable to address this issue since we do not have genealogical data on these females.

Second, the distribution of social relationships across dominance rankings may be related to the very nature of living in a large troop. Sambrook et al. [1995], in their comparison of two olive baboon troops, one with 40 members and one with 80 members, remarked that relationships between females necessarily become weaker as troop size increases. The Mchelelo troop averaged 75 members during our study period. The bidirectional and unidirectional preferences illustrated in Figure 1 appear to represent two levels of investment by the participants. Bidirectional relationships indicate that both partners are involved in the maintenance and/or seeking of proximity and are the stronger of the two types. Unidirectional relationships are characterized by only one partner investing in maintaining and/or seeking proximity to the other. It is notable that in all six cases of proximity partner preferences outside the Figure 1 subgroups, the preferences are unidirectional. These unidirectional relationships both between and within subgroups may represent "weak ties" instrumental in contributing to social group cohesion [Granovetter 1973; de Waal & Luttrell 1989]. These ties may be particularly important to a female in female-bonded groups such as baboons as they not only provide her with access to other subgroups or matrilineal but, as well, provide the social glue which binds the troop into a cohesive unit.

It has also been suggested that grooming is used to maintain social relationships [e.g., Stammbach & Kummer, 1982] and that females attempt to groom all other female troop members while employing longer bouts of reciprocal grooming to maintain closer relationships with a few females [Henzi et al., 1997]. A "cap" or upper limit is thus put on cluster/subgroup size by the ability (time) to reciprocate. Among the Mchelelo females, that upper limit would appear to be seven females. Henzi et al. [1997] found 7.4 to be the upper limit on "cliques" among troops of chacma baboons (*Papio hamadryas ursinus*). Seven may represent the maximum number of individuals who are able to maintain close ties with one another given the time and environmental constraints with which females are faced.

Any combination of the above three aspects (i.e., kinship, weak ties, and upper limit) could have an impact on a female's social network. We leave their exploration to future research. We realize that we have posed more questions than we have answered but we have shown that within this particular study population, females associate with other females who are disparately ranked from themselves. We have shown that neither rank nor the presence of an infant appear to be the prime determinant of proximity partner preferences. We have shown that the presence of an infant may affect both the number of grooming partners of a given female and the nature of those partnerships and that infants seem to be more attractive than rank. We have suggested that kinship may be a con-

founding factor and that the number of potential partners may be constrained by time and energy. We conclude that rank is a poor predictor of both proximity and grooming partners in the study troop and that the presence of an infant is a better predictor of grooming than proximity partners. We are still left with many questions regarding the Mchelelo females and their social relationships. At best, we have provided only a few of the puzzle pieces while showing again the variability present within the cercopithecines.

CONCLUSIONS

1. Among this troop of yellow baboons, the females' dominance rankings are not good predictors of either proximity partner or grooming partner preferences.
2. Unidirectional and bidirectional preferences represent differences in relationship investment.
3. The presence of an infant appears to have a stronger affect on grooming preferences than on proximity preferences.
4. Females with infants have more grooming partners than females without infants regardless of rank.
5. Females with infants are more likely than females without infants to be involved in a unidirectional grooming relationship as the recipient.
6. Seven individuals appears to represent the upper limit for a female's grooming or proximity partner subgroup/cluster in this population.

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