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ORIGINAL ARTICLE

Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds

Joan B. Silk · Susan C. Alberts · Jeanne Altmann

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Abstract A growing body of evidence suggests that social bonds have adaptive value for animals that live in social groups. Although these findings suggest that natural selection may favor the ability to cultivate and sustain social bonds, we know very little about the factors that influence the quality or stability of social bonds. Here, we draw on data derived from a 16-year study of baboons living in seven different social groups in the Amboseli basin of Kenya to evaluate the quality and stability of social bonds among females. Our results extend previous analyses, which demonstrate that females form the strongest bonds with close maternal and paternal kin, age mates (who may be paternal kin), and females who occupy similar ranks but are not maternal relatives. We show that the same factors influence the quality and strength of social bonds. Moreover, the results demonstrate that the quality of social bonds directly affects their stability.

Keywords Social bonds · Nepotism · Kin selection · Reciprocity · Friendship

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J. B. Silk (✉)
Department of Anthropology, University of California,
Los Angeles, CA, USA
e-mail: jsilk@anthro.ucla.edu

S. C. Alberts
Department of Biology, Duke University,
Durham, NC, USA

S. C. Alberts · J. Altmann
Institute for Primate Research, National Museums of Kenya,
Nairobi, Kenya

J. Altmann
Department of Ecology and Evolutionary Biology,
Princeton University,
Princeton, NJ, USA

J. Altmann
Department of Conservation Biology,
Brookfield Zoo,
Brookfield, IL, USA

Introduction

A growing body of evidence from a range of mammalian species indicates that living in social groups has positive fitness consequences for females [e.g., bushy-tailed wood rats (*Neotoma cinerea*), Moses and Millar 1994; Townsend's voles (*Microtus townsendii*), Lambin and Yoccoz, 1998; house mice (*Mus domesticus*), König 1994; Norway rats (*Rattus norvegicus*), LeFevre and McClintock 1992; gray seals (*Halichoerus grypus*), Pomeroy et al. 2001; bottlenose dolphins (*Tursiops truncatus*), Wells 2003; howler monkeys (*Alouatta palliata*), Pope 2000a,b]. In many of these species, females' reproductive performance is enhanced by association with closely related females. Sociality also enhances the reproductive success of female baboons. In the Amboseli basin of Kenya, female baboons (*Papio cynocephalus*) who spent more time grooming and associating with others were more likely to rear their infants successfully than females who were more socially isolated (Silk et al. 2003). These findings suggest that natural selection may favor the ability to cultivate and sustain social bonds in a range of species, but we know very little about the factors that contribute to variation in the quality or stability of social bonds among females. Here we draw on data derived from a 16-year study in the Amboseli basin of Kenya to address this question. We assessed the influence of maternal kinship, dominance rank, and age proximity (as an assay of paternal kinship) on the quality social bonds, and examined how these factors contributed to variation in the stability of close social bonds.

Cross-sectional analyses demonstrate that female baboons form the strongest bonds with close kin, including their mothers, daughters, maternal sisters, and paternal sisters (Silk et al. 1999, 2004, 2006; Smith et al. 2003). Females also show preferences for unrelated partners who are close to their own age and dominance rank (Silk et al. 1999, 2006). Females seem to compensate for the absence or loss of preferred types of partners by strengthening their relationships with others (Silk et al. 2006, Engh et al. 2006a). Females also experience elevated levels of glucocorticoids when important social bonds are disrupted, social conditions become unstable, or their infants are at risk from potentially infanticidal males (Engh et al. 2006a,b). Close relationships with adult male baboons mitigate the distress of lactating females when potentially infanticidal males are present (Beehner et al. 2005). These data suggest that selection may favor females' ability to maintain close social bonds with preferred partners.

Very little is known about the stability of social bonds among female primates. In one 4-year study of female baboons in South Africa, the top grooming partners of most females changed from year to year (Barrett and Henzi 2002). This led Barrett and Henzi (2002) to conjecture that relationships among female baboons are more like "business partnerships" than "friendships," as females barter commodities that shift in value over time. In contrast, cross-sectional analyses demonstrate strong and consistent biases in favor of particular types of partners such as close kin, females who hold adjacent ranks, and age mates (reviewed by Kapsalis 2003; Silk 2002a, 2005; Silk et al. 2004). These patterns suggest that there might be considerable stability in social relationships among females. Thus, we predicted that females would form the most long-lasting bonds with close kin and with females who are close to them in age and dominance rank.

Females are expected to invest most heavily in the relationships that yield the greatest fitness benefits. Although females may enhance their inclusive fitness benefits by directing beneficent behaviors toward relatives, they can also benefit directly from developing relationships with females who provide them with benefits. Here we use the distribution of grooming within dyads to assess the quality of social bonds. We expected closely related adult females to maintain equitable grooming relationships because kin derive inclusive fitness benefits from providing benefits to one another and because kinship facilitates contingent forms of reciprocity (Axelrod and Hamilton 1981). There is little evidence that female baboons exchange grooming for support from unrelated females (Silk et al. 1999, 2004), although they may use grooming to gain access to infants (Barrett and Henzi 2002) or to gain tolerance from higher-ranking females (Barrett et al. 1999). If this is the case, then we might expect the dynamics of short-term and long-term relationships to differ. Short-term relationships might be characterized by less evenly balanced distributions of grooming than long-term relationships.

Although paternal relatedness is known for some pairs of females in the Amboseli population, information about paternal relatedness is not available for enough dyads over long-enough periods to permit us to evaluate the effects of paternal kinship on the quality and stability of social bonds directly. Therefore, we did not include information about paternal relatedness in this analysis (but see Silk et al. 2006 for an analysis of the manner in which paternal kinship affects the strength of social bonds). Instead, we use age proximity as a proxy for paternal relatedness. Age proximity provides a reasonable proxy for paternal kinship because paternal kin tend to be very close in age (Alberts 1999; Smith et al. 2003; Widdig et al. 2001, 2002; Silk et al. 2006). Although it is not yet clear what information monkeys themselves use to assess paternal relatedness, there is a strong association between age proximity and the strength of social bonds among female baboons and macaques (Silk et al. 2006, Smith et al. 2003; Widdig et al. 2001, 2002). We predicted that females would form more stable social bonds with females with whom they are close in age.

Methods

Study population We studied the members of several well-habituated savannah baboon groups that occupied overlapping home ranges in the Amboseli basin at the foot of Mount Kilimanjaro (see Altmann and Alberts 2003 for more details about the study population). The study population is derived from two groups, Alto's Group and Hook's Group, which have been monitored continually since 1971 and 1980, respectively. Between 1980 and 1990, both of the original study groups shifted their home ranges, moving to an area in which suitable sleeping trees and baboon foods were more abundant. Both groups subsequently fissioned. Alto's Group split into three daughter groups between 1989 and 1991. We continued to monitor two of these groups (Nyayo's and Dotty's groups). Hook's Group split into two daughter groups in 1995, and we continued to monitor the two daughter groups (Linda's and Weaver's groups).

Our analyses are based on observations of the 118 adult females that lived in these study groups over a 16-year period from 1984 to 1999, constituting approximately 583 female years. Only some pairs of females were present in the same group at the same time (termed "coresident dyads" hereafter). The sample included a total of 1,430 coresident dyads.

Maternal kinship Information about maternal kin relationships for all of the females in the study groups was derived from genealogical records. Our sample included 63 mother–daughter dyads, 63 pairs of maternal sisters, 4 grandmother–granddaughter pairs, 59 maternal aunt–niece dyads, 21 pairs of maternal cousins, and 4 great-aunt–niece dyads. More distant maternal kin were treated as unrelated through maternal lines. Dyads that were not related through maternal lines, including the subset of females with known paternal kin and females with unknown paternal kin, were included in the category of "not maternal kin" in analyses of the effects of kinship.

Female dominance ranks Monthly dominance ranks for adult females were computed from the outcome of decided dyadic agonistic encounters observed during focal samples and ad libitum. In each case of agonism, observers recorded the identity of individuals involved in the encounter and the outcome of the aggressive encounter. Disputes were considered to be decided if (1) one individual displayed only submissive signals, whereas the other displayed only aggressive signals, or (2) if one individual displayed submissive signals, whereas the other displayed no aggression or submission. All other disputes were considered to be "undecided." Adult females maintained stable, matrilineal dominance hierarchies in which maternal kin occupied adjacent ranks. There were almost no changes in relative rank between adult females over the course of the study period, but normal demographic events (e.g., maturation and deaths) and group fission produced some changes in the ordinal dominance ranks of females.

Behavioral data Behavioral data were derived from approximately 34,000 10-min focal samples (Altmann 1974) on adult females conducted throughout the day from 1984 to 1999. These focal samples represent approximately 5,690 h of observation. At 1-min intervals within each focal sample, observers recorded the focal female's activity (e.g., grooming, being groomed, feeding, resting, and moving) and the identity of the nearest neighbor within 5 m. All adult females in each study group were targets of focal observations. The order of focal subjects was based on a random permutation schedule. Females were added to the observation rota when they reached reproductive maturity, which was defined by the onset of visible perineal swellings.

Analysis methods

The focal samples provided information about grooming and proximity among adult females. Grooming and proximity maintenance are widely considered to provide meaningful measures of social relationships among nonhuman primates (Cords 1997), and they make up the major components of female baboons' social time. Following Silk et al. (2003), we created a sociality index that combined the information about grooming and proximity and that was also indexed relative to other dyads in the same group and year (see Silk et al. 2006 for full details). The sociality index measures the extent to which each dyad deviated from the average dyad of adult females in the same group in the same year. High values of the sociality index represent dyads that had stronger bonds than the average female dyad, and low values of the sociality index represent dyads that had weaker bonds. For dyads that were present in multiple years, some analyses are based on the average value of their sociality index across years.

The quality of social bonds: grooming equality We used information about grooming given and received to measure how evenly grooming was balanced within dyads. We took the absolute difference between the proportion of the pair's grooming that was performed by each partner, a metric that will be 0 for a completely equitable relationship and 1 for a relationship that is maintained completely by one of the partners. We subtracted this value from 1 so that the "grooming index" would be greatest; 1, when the relationship was most equitable; and $1 - \left| \left(\frac{Gi \rightarrow j}{Gi \leftrightarrow j} \right) - \left(\frac{Gj \rightarrow i}{Gi \leftrightarrow j} \right) \right|$ when it was least equitable.

Top partners For each female, we ranked her sociality index scores with all coresident adult females (including kin) each year. We refer to each female's top three partners in the ranking for the year as her "top partners," regardless of the magnitude of the sociality index. This method allowed us to consider the partner preferences of all females, even those who were less sociable than other females in their groups.

The stability of social bonds: persistence over consecutive years To determine how long close social bonds of each female lasted, we adopted the following procedure. For each female, we identified who her top three partners were each year. If female B was among female A's top three partners in 1992–1994, the duration of the close social bond was defined as 3 years. We allowed for a 1-year gap between "consecutive" years. That is, if female B was among female A's top three partners in 1992, 1993, 1995, and 1996, but not in 1994, the duration of the close social bond was scored as 5 years. If a partner recurred among a female's top three partners at intervals greater than 2 years, the bond duration was scored as 1 year. For example, if female C was among female A's top three partners only in 1992 and 1996, the bond duration was scored as 1 year.

Results based on a more conservative measure of bond duration (allowing no gaps between years) are very similar to those reported here.

Females' relationships with their top partners were not always concordant. That is, female A might have been one of female B's top three partners in a given year, but female B might not have been among female A's top three partners in the same year. However, there was considerable congruence in the classification of top partners measured from the perspective of each partner. For 73% of all dyads, the duration of close social bonds measured from the perspective of each partner was exactly the same. For 96% of all dyads, the estimates differed by no more than 1 year. Because these values were so similar, each dyad was treated as a single data point in the statistical analyses. We arbitrarily chose the value associated with the younger member of the dyad for use in our analyses.

Statistical methods

To examine the relationship between the quality and stability of social bonds and continuous variables such as maternal relatedness and age proximity, we used regression methods. Dyads are not independent in our data set, so we used regression models that allowed us to cluster on individuals. We used regression with robust standard errors (Stata 2003) to examine the effects of continuous variables on the strength of social bonds. Regression with robust standard errors produces the same regression coefficients as in ordinary least squares regression, but the estimates of the standard errors accommodate violations of assumptions about normality and homogeneity of variance of residuals. The regression coefficient provides an estimate of the effect of a 1-U change in the independent variable on the value of the dependent variable when the effects of other variables are held constant. Regression coefficients are distorted by the inclusion of outliers. Conventional guidelines suggest that points with studentized residuals less than −3.0 or more than 3 should be excluded from analyses. Dyads that exceeded this criterion were excluded from our analyses of the factors that affect the strength of social bonds among females.

We used Poisson regression to examine the sources of variation in the duration of social bonds. This regression method is appropriate when the dependent variable is a count variable (Stata 2003), and it allowed us to control for variation in coresidence and group size and to cluster on individuals. Goodness of fit tests indicated that the data fit the distribution assumptions for this model. Two-tailed tests of significance were used throughout.

Results

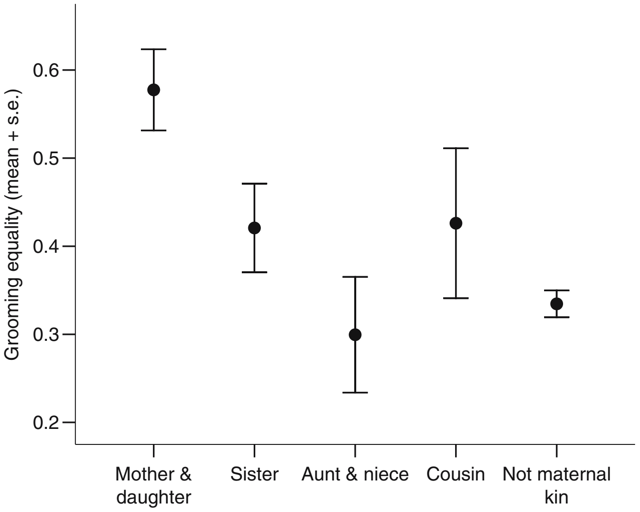
Sources of variation in the quality of social bonds

We were able to measure the degree of grooming equality for 735 dyads that groomed during focal samples. Pairs of close maternal kin groomed more equitably than less closely related females (regression with robust standard errors relatedness; relatedness: $b=0.4457\pm0.0901$, $t=4.94$, $p<0.001$ $R^2=0.0281$, $n=735$ dyads; Fig. 1a). Among females who were not related through maternal lines, those who were close in age and dominance rank also groomed more equitably than females who were more disparate in age and dominance rank (age proximity: $b=-0.0112\pm0.0041$, $t=-2.78$, $p=0.006$; rank similarity: $b=-0.0138\pm0.0035$, $t=-0.395$, $p<0.001$, $R^2=0.0326$, $n=595$ dyads; Fig. 1b,c). Thus, females formed the most equitable grooming relationships with females to whom they were closely related through maternal lines, close in age, or close in dominance rank.

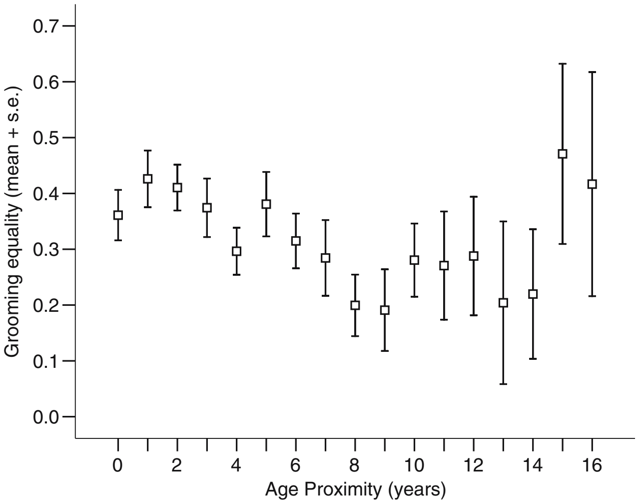
Dyads with strong social bonds also groomed more equitably than dyads with weaker social bonds. The value of the sociality index was positively associated with the degree of grooming equality ($b=0.0830\pm0.0103$, $t=8.05$, $p<0.001$, $R^2=0.0828$; $n=721$ dyads; 14 outliers excluded; Fig. 2). This result could be an artifact of maternal kinship or age proximity because close maternal kin and age mates tended to groom equitably and also had strong social bonds. However, the strength of social bonds remained a significant predictor of grooming equality even when maternal kin were excluded from the analysis and when we controlled for the effects of age proximity and dominance rank differences in the regression (Table 1). Together, these three variables explained about 10% of the variation in the extent of grooming equality among females who were not related through maternal lines ($R^2=0.1033$, $n=591$ dyads; four outliers excluded).

The relationship between grooming equality and the value of the sociality index might be influenced by the fact that dyads that groomed often had higher sociality index scores than dyads that groomed less often. Therefore, we repeated the analysis, holding the total amount of grooming within dyads constant. The relationship between grooming equality and the strength of social bonds remained highly significant (sociality index: $b=0.0435\pm0.0105$, $t=4.14$, $p<0.001$; grooming total: $b=0.0039\pm0.0006$, $t=7.05$, $p<0.001$; $R^2=0.1740$; $N=721$ dyads; 14 outliers excluded). We obtained very similar results when we excluded maternal kin from the analyses (sociality index: $b=0.0790\pm0.0165$, $t=4.79$, $p<0.001$; grooming total: $b=0.0047\pm0.0010$, $t=4.94$, $p<0.001$; $R^2=0.1894$; $N=591$ dyads; four outliers excluded).

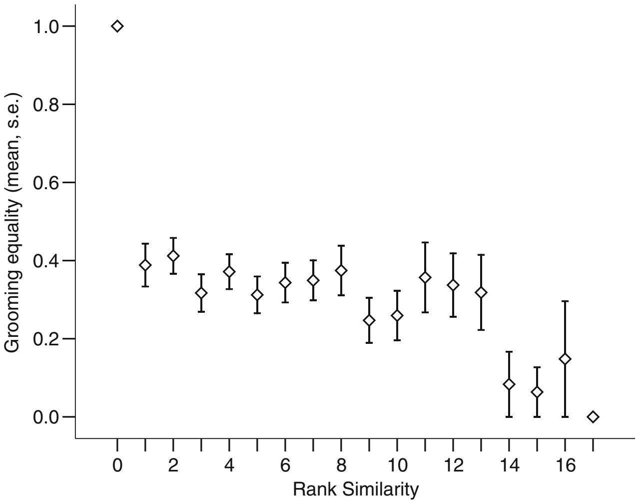
a. Maternal kinship



b. Age proximity



c. Rank similarity



◀ **Fig. 1** Sources of variation in grooming equality. Grooming equality measures the distribution of grooming within dyads. When grooming is perfectly balanced within dyads, the value of the grooming equality index is 1, and when one female does all of the grooming, the grooming equality index equals 0. The effects of maternal relatedness (*n*=735 dyads) (**a**), age proximity (*n*=595) (**b**), and rank similarity (*n*=595) (**c**) on the degree of grooming equality among females are shown. The sample is restricted to dyads that were not related through maternal lines (**b** and **c**). Values of age proximity and similar rank are rounded to the nearest integer. See text for statistical tests

Stability of close social bonds

Here we focused on females' relationships with their top three partners in each year. For each female, we tabulated how many consecutive years each of the other females was among her top partners and used these values to estimate the duration of close social bonds.

Analyses of the duration of social bonds were complicated by the fact that not all dyads were coresident for the same length of time. Some females coresided for only 1 year, whereas a few coresided for up to 14 years. The mean period of coresidence was 3.47±0.0594 years. About one quarter of all pairs of females lived in the group together for at least 5 years.

We computed the probability that social bonds would endure for various lengths of time. To obtain these values, we divided the number of dyads that maintained close social bonds for a given length of time by the number of dyads that coresided for the same number of years. Figure 3 shows that 90% of all mother–daughter dyads and 70% of all pairs of maternal sisters established close social bonds that lasted at least 1 year. Among females who were not related through maternal lines, approximately half of all peer dyads formed close social bonds that lasted at least 1 year, whereas only about one third of nonpeer dyads formed close social bonds that lasted 1 year. Figure 3 also shows that close maternal kin were likely to maintain close social bonds for longer periods of time than other pairs of females were.

We examined the effects of maternal kinship, age proximity, and rank similarity on the stability of close social bonds. In these analyses, we controlled for variation in the number of years of coresidence. Females formed significantly longer-lasting relationships with close maternal kin than with other females (maternal relatedness: Poisson regression, b=3.1523±0.1597, z=19.74, p<0.001; N=1,430 dyads). Among females who were not related through maternal lines, those who were close in age and dominance rank also formed more long-lasting social bonds than females who were further apart in age or rank (age proximity: b=−0.0364±0.0114, z=−3.19, p=0.001; rank

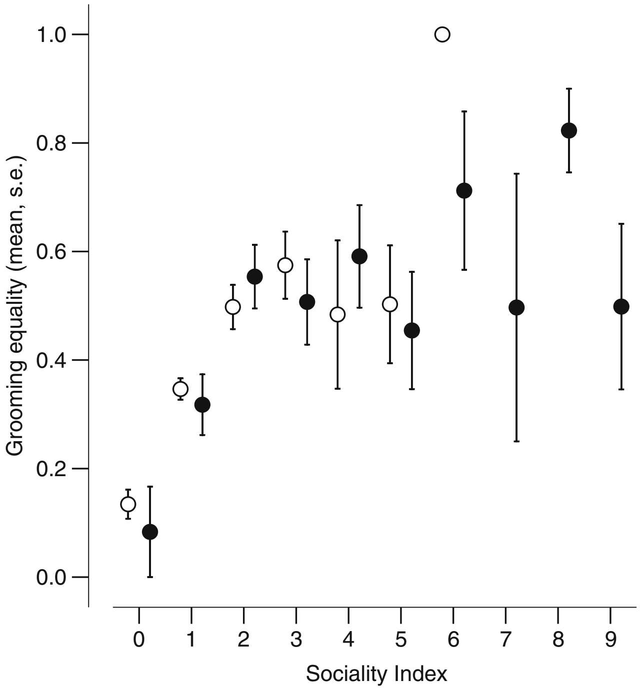


Fig. 2 The relationship between sociality index and grooming equality. *Closed circles* represent maternal kin (n=130 dyads), and *open circles* represent dyads that are not related through maternal lines (n=591). Outliers were excluded (see "Methods"). Sociality index values were rounded to the nearest integer

similarity: b=−0.0831±0.0130, z=−6.39, p<0.001, n=1,216 dyads). Thus, females formed the most enduring social bonds with those to whom they were closely related and those with whom they were close in age and dominance rank.

Females with the most equitable grooming relationships also had the most enduring social bonds (b=0.7387±0.1035, z=7.14, p<0.001, n=735 dyads). Again, this relationship might be an artifact of kinship, age proximity, or rank similarity because these variables are related to the stability of social bonds. However, the same pattern held when we restricted the sample to pairs of females who were not related through maternal lines and controlled for age and rank differences among females (b=0.5720±0.1162, z=4.92, p<0.001, n=595 dyads). Thus, females tended to form the most enduring bonds with those that they groomed most equitably, and this pattern was characteristic of both maternal kin and others (Fig. 4).

Discussion

These analyses demonstrate that females formed the most equitable and most enduring relationships with close maternal kin and with females who were close to their own age and dominance rank. Thus, the same factors that influenced the strength of social bonds among females (Silk et al. 2006) also influenced the quality and stability of social bonds.

The most enduring social bonds were formed by close kin. In our sample, there were 14 dyads who maintained close social bonds for at least 5 years. These 14 dyads included five mother–daughter dyads and five pairs of maternal sisters. Among the other four dyads, three pairs were identified as paternal kin through genetic analyses (see Silk et al. 2006 for more detailed analysis on the subset of dyads for whom we knew paternal relatedness). The fourth pair consisted of two females who were born only 94 days apart, making them likely to be paternal sisters as well, although we lacked genetic data to confirm this. Although close kin and age mates formed the most enduring social bonds, not all enduring bonds involved relatives. Our sample included 13 pairs of true nonkin (confirmed through genetic analyses) who maintained social bonds for at least 3 years.

Females' preferences for particular partners are apparently influenced by the quality of their interactions. Females who groomed most equitably had the strongest and most enduring social bonds. We do not know if females came to groom more equitably as their relationships matured or if females continued to associate and interact often with those who groomed them most equitably. Longitudinal analyses of the development of social relationships among females are needed address this question.

Demographic factors influenced the composition and stability of females' social networks. We found that females formed stronger ties with their sisters when closer kin (mothers and daughters) were unavailable (Silk et al. 2006); but even in the absence of close maternal kin, most females formed strong social bonds with at least one partner. Female baboons in Moremi experienced considerable distress after the sudden loss of preferred partners (Engh et al. 2006a), and subsequently increased the amount of time they spent grooming and the number of females that they groom. In Amboseli, females may face such situations with some regularity because the average period of coresidence for pairs of adult females was only 3.5 years, much less than the average females' adult life span. Although adult females may lose preferred partners to predation, illness, old age, and, occasionally, group fission, they may also gain new partners as younger sisters or their own daughters mature. Females' ability to adjust to changes

Table 1 Predictors of grooming equality among females not related through maternal lines

Predictor variable	b	Robust SE	t	p
Sociality index	0.1108	0.0165	6.70	<0.001
Age proximity	−0.0080	0.0039	−2.03	0.045
Rank similarity	−0.0113	0.0037	−3.07	0.003

in the availability of preferred types of partners may have important consequences.

Our data confirm that female baboons invest in long-term relationships and in more ephemeral social bonds. Short-term relationships are less equitable than long-term relationships, and the dynamics of short-term relationships may be shaped by the kind of market forces Barrett and her colleagues have emphasized (Barrett et al. 1999; Barrett and Henzi 2002). However, some of the long-lasting relationships that we have documented may be better characterized as strong family ties, and some may be appropriately characterized as "friendships."

Silk (2002b) suggested that we reserve the term friendship for relationships among nonkin that are "characterized by frequent participation in affiliative interactions (often, but not necessarily, including grooming); involvement in coalitionary aggression, particularly in defense of the partner; high rates of association; mutual responsibility for maintaining proximity; high degrees of reciprocity in directional, nonaggressive activities such as grooming and food sharing; continuity across time and context; high degrees of tolerance (cofeeding), loyalty, and compatibility; and low degrees of stress when together." The theoretical rationale for excluding close ties among kin from the category of friendship was that kin selection may shape close family ties, whereas reciprocal altruism or mutualism is expected to shape close relationships among nonkin. Although this distinction may be relevant to the evolution of social bonds, it may not necessarily be a meaningful distinction when we assess the structure of social relationships among females.

A number of pairs of females in our study groups formed relationships that fulfill most of the defining criteria for friendship. Although most of the dyads with strong and enduring relationships were close kin or age mates who might have been paternal relatives, some unrelated females also maintained close and enduring bonds (Fig. 4). In Amboseli, females tend to feed and rest with the same females that they groom most often (Smith et al. 2003), so we may infer that close social bonds are also associated with high levels of social tolerance. Furthermore, females in Moremi experience elevated cortisol levels when preferred partners abruptly disappear (Engh et al. 2006a), suggesting that close social partners play a role in mitigating the stresses of social life for female baboons. Thus, female baboons seem to form some relationships that meet most of the defining criteria for friendship. The capacity to form and maintain strong, equitable, and enduring family ties and friendships, as well as more opportunistic relationships, may provide long-term benefits for female baboons.

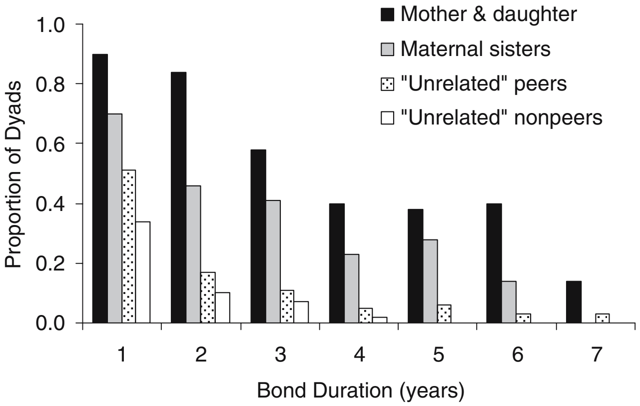


Fig. 3 Stability of close social bonds. The duration of close social bonds for dyads composed of mothers and daughters (*black bars*, *N*=63 dyads), maternal sisters (*gray bars*, *N*=63), peers who are not related through maternal lines (*stippled bars*, *N*=164), and nonpeers who are not related through maternal lines (*white bars*, *N*=1,052) is shown here. For each type of dyad, the proportion of dyads that maintained close social bonds for a given number of years is plotted on the *y axis*. The values were obtained by dividing the number of dyads that maintained a close social bond for at least *x* years by the total number of dyads that were coresident for *x* or more years. For example, 57 of the 63 mother–daughter dyads (90%) who were coresident for at least 1 year maintained close social bonds for at least 1 year

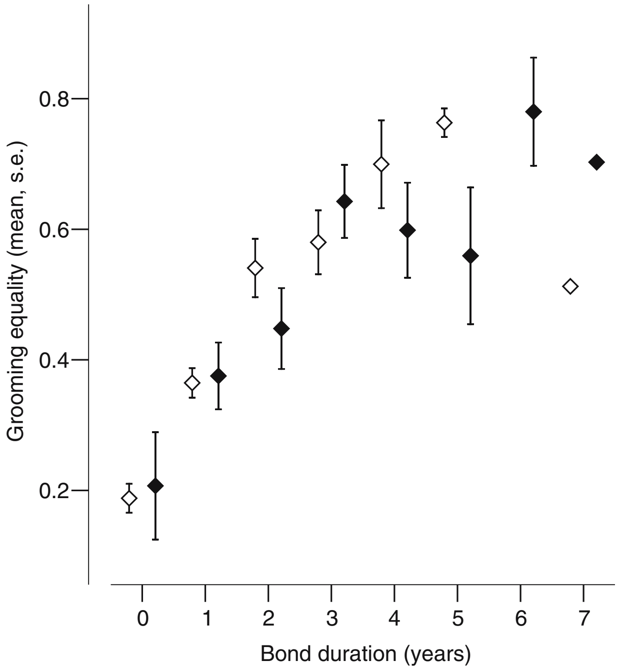


Fig. 4 The relationship between grooming equality and bond stability. Bond stability is the number of consecutive years in which the same female was among a given female's top three partners. Each point represents the mean (and standard error) of the grooming equality index for dyads with bonds of different length. *Open diamonds* represent dyads that are not related through maternal lines (*n*=595 dyads), and *solid diamonds* represent maternal kin (maternal relatedness≥0.0625, *n*=140)

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References

Alberts SC (1999) Paternal kin discrimination in wild baboons. Proc R Soc Lond B Biol Sci 266:1501–1506

Altmann J, Alberts SC (2003) Intraspecific variability in fertility and offspring survival in a nonhuman primate: behavioral control of ecological and social sources. In: Wachter KW, Bulatao RA (eds) Offspring: the biodemography of fertility and family behavior. National Academy, Washington, DC, pp 140–169

Axelrod R, Hamilton W (1981) The evolution of cooperation. Science 211:1390–1396

Barrett L, Henzi SP, Weingrill T, Lycett JE, Hill RA (1999) Market forces predict grooming reciprocity in female baboons. Proc R Soc Lond B 266:665–670

Barrett L, Henzi SP (2002) Constraints of relationship formation among female primates. Behaviour 139:263–289

Beehner JC, Bergman TJ, Cheney DL, Seyfarth RM, Whitten PL (2005) The effect of new alpha males on female stress in free-ranging baboons. Anim Behav 69:1211–1221

Cords M (1997) Friendship, alliances, reciprocity and repair. In: Whiten A, Byrne RW (eds) Machiavellian intelligence II. Cambridge University Press, Cambridge, pp 24–49

Engh AL, Beehner JC, Bergmann TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2006a) Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). Proc R Soc Lond B Biol Sci 273:707–712

Engh AL, Beehner JC, Berman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2006b) Female hierarchy instability, male immigration, and infanticide increase glucocorticoid levels in female chacma baboons. Anim Behav 71:1227–1237

Henzi SP, Barrett L (1999) The value of grooming to female primates. Primates 40:47–59

Kapsalis E (2003) Matrilineal kinship and primate behavior. In: Chapais B, Berman C (eds) Kinship and behavior in primates. Oxford University Press, Oxford, pp 153–176

Henzi SP, Barrett L (2002) Infants as a commodity in a baboon market. Anim Behav 63:915–921

König B (1994) Components of lifetime reproductive success in communally and solitarily nursing house mice—a laboratory study. Behav Ecol Sociobiol 34:275–283

Lambin X, Yoccoz NG (1998) The impact of population kin-structure on nestling survival in Townsend's voles, *Microtus townsendii*. J Anim Ecol 67:1–16

LeFevre JA, McClintock MK (1992) Social modulation of behavioral reproductive senescence in female rats. Physiol Behav 52:603–608

Moses RA, Millar JS (1994) Philopatry and mother–daughter associations in bushy-tailed woodrats—space use and reproductive success. Biomed Environ Sci 35:131–140

Pomeroy PP, Wilmar JW, Amos W, Twiss SD (2001) Reproductive performance links to fine-scale spatial patterns of female grey seal relatedness. Proc R Soc Lond B Biol Sci 265:711–717

Pope TR (2000a) Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). Biomed Environ Sci 48:253–267

Pope TR (2000b) The evolution of male philopatry in neotropical monkeys. In: Kappeler PM (ed) Primate males. Cambridge University Press, Cambridge, pp 219–235

Silk JB, Cheney DL, Seyfarth RM (1999) The structure of social relationships among female savannah baboons in Moremi Reserve, Botswana. Behaviour 136:679–703

Silk JB (2002a) Kin selection in primate groups. Intl J Primatol 23:849–875

Silk JB (2002b) Using the 'F' word in primatology. Behaviour 139:421–446

Silk JB, Alberts SC, Altmann (2003) Social bonds of female baboons enhance infant survival. Science 302:1331–1334

Silk JB, Alberts SC, Altmann J (2004) Patterns of coalition formation by adult female baboons in Amboseli, Kenya. Anim Behav 67:573–582

Silk JB (2005) Practicing Hamilton's rule: Kin selection in primate groups. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans: mechanisms and evolution. Cambridge University Press, Cambridge, pp 25–46

Silk JB, Altmann J, Alberts SC (2006) Social relationships among adult female baboons (*Papio cynocephalus*) I. Sources of variation in the strength of social bonds. Behav Ecol Sociobiol (in press) DOI 10.1007/s00265-006-0249-2

Smith K, Alberts SC, Altmann J (2003) Wild female baboons bias their social behaviour towards paternal half-sisters. Proc R Soc Lond B Biol Sci 270:503–510

Stata (2003) Base reference manual. Stata, College Station

Wells RS (2003) Dolphin social complexity: lessons from long-term study and life history. In: de Waal FBM, Tyack PL (eds) Animal social complexity. Harvard University Press, Cambridge, pp 32–56

Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB (2001) Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. Proc Natl Acad Sci 98:13769–13773

Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB (2002) Affiliation and aggression among adult female rhesus macaques: a genetic analysis of paternal cohorts. Behaviour 139:371–391