Behav Ecol Sociobiol (2006) 61:183–195
DOI 10.1007/s00265-006-0249-2

ORIGINAL ARTICLE

Social relationships among adult female baboons (*papio cynocephalus*) I. Variation in the strength of social bonds

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

Received: 21 September 2005 / Revised: 3 July 2006 / Accepted: 5 July 2006 / Published online: 31 August 2006

Abstract Sociality has positive effects on female fitness in many mammalian species. Among female baboons, those who are most socially integrated reproduce most successfully. Here we test a number of predictions derived from kin selection theory about the strength of social bonds among adult female baboons. Our analyses are based on systematic observations of grooming and association patterns among 118 females living in seven different social groups in the Amboseli Basin of Kenya over a 16-year period. Females in these groups formed the strongest bonds with close kin, including their mothers, daughters, and maternal and paternal sisters. Females were also strongly attracted toward females who were close to their own age, perhaps because peers were often paternal sisters. Females' bonds with their maternal sisters were strengthened after their mother's deaths, whereas their relationships with their maternal aunts were weakened after their mother's death. In addition, females formed stronger bonds with their paternal sisters when no close maternal kin were available, and they compensated for the absence of any close kin by forming strong bonds with nonrelatives. Taken together, these data suggest that social bonds play a vital role in females' lives, and the ability to establish and maintain strong social bonds may have important fitness consequences for females.

Keywords Social bonds · Nepotism · Kin selection · Friendship · Dominance · Peer relationships

Communicated by A. Widdig

Joan B. Silk is on sabbatical at Cambridge University from September 2005 to August 2006. Tel.: +44-7929759697; Fax: +44-1223-335460.

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

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

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

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

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

Female philopatry is widespread in mammals (Greenwood 1980; Waser and Jones 1983). A growing body of evidence from a wide range of species suggests that mammalian females gain fitness advantages from remaining in their natal ranges and associating with their relatives (Gerlach and Bartmann 2002; Lambin and Yoccoz, 1998; König 1994; LeFevre and McClintock 1992; Moses and Millar 1994; Pomeroy et al. 2001; Pope 2000a,b; Wells 2003). Association with kin reduces levels of aggression among females (Boonstra and Hogg 1988; Dobson et al. 2000; König 1994; Rusu and Krackow 2004), increases levels of care for dependent young (Arnold 1990; Christal and Whitehead 2001; Dobson et al. 2000; Hackländer et al. 2003; König 1994; McComb et al. 2001), decreases the costs of maternal investment (Gerlach and Bartmann 2002; Hayes and Solomon 2004), and reduces the risk of infanticide (Boonstra and Hogg 1988; Dobson et al. 2000; Lambin and Krebs 1993; Mappes et al. 1995). For female baboons (*Papio cynocephalus*), which are characterized by female philopatry and form groups composed of several matrilines, social integration enhances female fitness (Silk et al. 2003a). In the Amboseli Basin of Kenya, female baboons who groom and associate with other group members relatively more than other females living in the same groups at the same time have higher reproductive success than other females. Here we examine the factors that contribute to variation in the strength of social bonds among pairs of adult females, focusing on a series of predictions derived from kin selection theory. Sources of variation in the quality and stability of social bonds are examined in a companion paper (Silk et al. 2006).

Both evolutionary theory and existing data suggest that female baboons will form strong bonds with close kin. Biases in favor of maternal kin have been reported for a variety of primate species, and these nepotistic biases are especially pronounced in species that live in female-bonded groups as baboons do (Kapsalis 2003; Silk 2005). Although baboons have been studied at multiple sites across Africa, the effects of maternal kinship on the relationships among adult females have been evaluated at only two sites. In the Moremi Reserve of Botswana, adult female baboons preferentially groom and reconcile with maternal kin and also handle the infants of maternal kin at higher rates than others (Silk et al. 1996, 1999, 2003b). In Amboseli, Kenya, female baboons support closely related adult females ($r \geq 0.25$) in agonistic contests at substantially higher rates than they support adult females who are not related through the maternal line, and they show smaller and less consistent biases in favor of more distantly related adult females (Silk et al. 2004). Aged females in Amboseli commonly cede rank to their daughters, but not to unrelated females, and the timing of these rank reversals fits predictions derived from kin selection theory (Combes and Altmann 2001).

Recent work demonstrates that female baboons and macaques can also distinguish paternal sisters from nonkin, although the strength of their preferences for paternal sisters seems to vary across sites. Although female baboons in Amboseli had similar preferences for maternal and paternal sisters (Smith et al. 2003), female macaques on Cayo Santiago formed substantially stronger relationships with maternal sisters than with paternal sisters (Widdig et al. 2001, 2002). Smith et al. (2003) hypothesized that the discrepancy between these studies might reflect a contingent response to differences in the size and composition of kin networks. In the provisioned groups of macaques on Cayo Santiago, matrilines are large, and close maternal kin are numerous. In contrast, female matrilines are considerably smaller in wild baboon groups, and close maternal kin are consequently less numerous. If there is a greater chance of misidentifying paternal than maternal kin, females may prefer maternal sisters more than paternal sisters when maternal sisters are available. In contrast, when maternal sisters are not available, females may form stronger bonds with paternal sisters. The observed differences in the strength of social bonds among maternal and paternal sisters in Amboseli and Cayo Santiago are consistent with this hypothesis, but there are many other differences between these populations that might influence the strength of social bonds. Here we make use of a larger sample of paternal kin than was available to Smith et al. (2003) to examine the magnitude of the effects of paternal kinship on the strength of social bonds. We then test the prediction that variation in the strength of paternal sibling bonds is related to the availability of close maternal kin in a single population.

Most researchers assume that maternal kin biases in behavior are the direct product of kin selection. If this is the case, then altruistic behavior among kin is expected to be deployed according to Hamilton' rule, $br>c$ (Hamilton 1964). However, Chapais and his colleagues have noted that the deployment of high- and low-cost forms of altruistic behavior (e.g., agonistic support and grooming) follow very similar patterns in macaque groups (Chapais 2001, 2005; Chapais and Bélisle 2004). This leads them to suggest that high rates of interaction among some categories of maternal kin might be maintained by reciprocal altruism or mutualism rather than kin selection (Chapais 2001, 2005; Chapais and Bélisle 2004). That is, they may arise as a by-product of associations with other relatives and may persist not because they confer inclusive fitness benefits but because they confer direct benefits. For example, strong ties between mothers and daughters would automatically generate high levels of association between sisters even if sisters were not strongly attracted to one another; sisters would then be the most likely pairs (after mother–daughter pairs) to develop mutualistic or reciprocally altruistic relationships. Of course, if females gain inclusive fitness benefits through their interactions with relatives, then kin selection will influence the evolution of these relationships. However, kin-biased relationships may not always satisfy the conditions of Hamilton's rule, leading to a situation in which kin-biased behaviors are not kin-selected behaviors. How might one differentiate kin-selected from simply kin-biased behaviors? If kin-biased behaviors occur as a by-product of associations with other relatives but do not confer inclusive fitness benefits, then they might be less persistent than kin-selected relationships. For example, they might depend more on the presence of "connecting" females so that when a female dies, her sister and her daughter, previously closely connected through her, would tend to lose their bond. To test this, we compared the strength of social bonds among maternal sisters, and among maternal aunts and nieces, in the presence and absence of connecting females.

Strong bonds among maternal kin might also be a by-product of an attraction to females of similar rank. Seyfarth (1977, 1983) hypothesized that grooming is exchanged for other commodities, including support in alliances (Seyfarth 1977, 1983; Schino 2001), tolerance at feeding sites (Fairbanks 1980; Silk 1982; Barrett et al. 1999), or access to infants (Henzi and Barrett 2002). Because high-ranking females are more valuable allies in agonistic alliances than low-ranking females, females will prefer high-ranking partners and attempt to groom them. However, competition will restrict females' access to high-ranking partners, and females will be forced to settle for females who are close to their own rank. A number of studies have documented strong ties among females who hold adjacent ranks (reviewed by Kapsalis 2003). If this process was solely responsible for the formation of social bonds among females, then we would expect to find no difference between kin and nonkin who hold adjacent ranks. If this process complements kin selection, then we would expect females to prefer maternal kin over nonkin who hold adjacent ranks, and for females to form stronger social bonds with unrelated females who occupy adjacent ranks than unrelated females who occupy more disparate ranks.

If kin selection is the primary factor influencing the strength of social bonds, and females prefer to interact with close kin, then the size of females' social networks is expected to be related to the number of preferred partners present. The number and type of preferred partners available may change systematically as females mature. Moreover, because high-ranking females reproduce more successfully than low-ranking females in this population (Altmann and Alberts 2003; Silk et al. 2003a), dominance rank may also influence the availability of close kin. Here we examine how age and dominance rank influence the availability of preferred partners, and we assess the relationship between the size of females' social networks and the availability of preferred types of partners.

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).

Study animals and determination of kinship The sample of individuals for this study consisted of 118 females that resided in study groups as adults between 1984 and 1999. These females comprised 1,430 dyads that resided in the same group at the same time ("coresident dyads" hereafter). Information about maternal kin relationships for all of these females was derived from genealogical records. Paternity was established for a subset of these adult females (N=54), allowing us to identify some pairs of paternal kin. Our methods for genetic analysis and identification of paternal kin are described in detail elsewhere (Alberts et al. 2006; Buchan et al. 2003, 2005; Smith et al. 2003). Briefly, we obtained DNA for 404 individuals (337 from fecal samples, 67 from blood) that resided in the study population between 1989 and 2001. We genotyped these animals at 12 tetranucleotide and 2 dinucleotide loci amplified with human primers. We used the multitubes approach (Navidi et al. 1992; Taberlet et al. 1996), and we used quantitative polymerase chain reaction (PCR) to measure DNA concentrations in baboon fecal extracts before genotyping began, as recommended by Morin et al. (2001). We assigned paternity to 286 offspring (including 54 females that had reached adulthood during the current study) using both simple exclusion and the program CERVUS 2.0 (Marshall et al. 1998). Our loci exhibited very good power for detecting paternity, and in every case, our exclusion-based assignments agreed with assignments at 95% confidence by CERVUS (see details in Alberts et al. 2006; Buchan et al. 2003).

In addition to the paternal kin that we identified through traditional paternity analysis, Smith et al. (2003) identified nine pairs of paternal sisters based on analysis of X-chromosome microsatellite loci. For these adult females, we were unable to obtain samples from potential fathers (because the females were adult when we began collecting samples for DNA extraction, and most of their potential fathers were long gone from the study population). X-chromosome loci are particularly powerful for identifying paternal sisters because all paternal sisters inherit a single identical (nonrecombined) X-chromosome from their father. We accepted the identification of these nine pairs of females as paternal sisters and included them in our analysis (see Smith et al. 2003 for details).

Types of dyads in the data set Our sample of animals related only through the maternal line comprised 209 dyads (Table 1), including 63 mother–daughter dyads, 62 pairs of maternal half-sisters ("maternal sisters" hereafter), 4 grandmother–granddaughter dyads, 58 maternal aunt–niece dyads, 18 pairs of maternal cousins, and 4 great aunt–niece

Table 1 Composition of samples used in analysis

	Number of dyads	Number of dyads excluded as outliers
Dyads of known maternal and paternal relatedness	504	10
Related only through maternal lines	209	10
Related only through paternal lines	54	0
Related through maternal and paternal lines	5	0
True nonkin	236	0
Dyads not related through maternal lines	1,216	4
Related only through paternal lines	54	0
Unrelated through maternal lines, paternal relatedness unknown	926	4
True nonkin	236	0

dyads. More distantly related maternal kin were treated as unrelated through maternal lines. Our sample also included 41 pairs of paternal half-sisters ("paternal sisters" hereafter) and 13 known paternal aunt–niece dyads for a total of 54 dyads related only through paternal lines (Table 1). We also had one pair of full sisters, one pair of paternal half-sisters that were also maternal aunt and niece, and three pairs of paternal half-sisters that were also maternal cousins for a total of five dyads related through both maternal and paternal kin. Two hundred thirty-six dyads were known to be unrelated through maternal lines or paternal lines, and for 926 coresident dyads, we were able to establish relatedness through maternal lines but not through paternal lines (Table 1).

Maternal relatedness was known for all dyads, whereas both maternal and paternal relatednesses were known for 504 of these dyads. Although some of these pairs could have been related through paternal lines, 1,216 dyads were known to be unrelated through maternal lines. We used different subsamples of the data for particular analyses. For example, comparisons of the effects of paternal relatedness are limited to dyads for which both maternal and paternal relatedness were known; the five dyads related through both maternal and paternal lines were excluded from these analyses. Comparisons of the effects of age proximity and rank distance are based on dyads that are not related through maternal lines.

Behavioral data collection Behavioral data were derived from approximately 34,000 10-min focal samples (Altmann 1974) on adult females conducted throughout the day between 1984 and 1999. These focal samples represent approximately 5,690 h of observation over the course of 583 female years. At 1-min intervals within each focal sample, observers recorded the focal female's activity 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.

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.

Analysis

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. For each pair of adult females in each calendar year, we computed (a) the number of point samples in which they were in proximity and (b) the number of point samples in which they were grooming. These values represent the raw frequency of interaction for each dyad in each year.

Not all pairs of females were present in the same study group for the same amounts of sampling time, and some pairs of females therefore had more opportunities to interact than others. We corrected for variation in the availability of partners in the following way. For each point sample on each adult female in each year, we determined whether each of the other adult females in the study population was present (had reached menarche and was living in the same social group) or absent (had not reached menarche, had died, or was living in a different social group; some pairs were coresident in some years and not others if they joined different groups during permanent group fissions). We summed the coresidence values for each dyad in each calendar year. For each dyad each year, we divided the frequency of proximity and the frequency of grooming by the appropriate coresidence value to obtain the adjusted frequency of proximity and the adjusted frequency of grooming, (i.e., an estimate of the probability that a pair would groom or be in proximity given that they were both in the same group).

We used the frequency of grooming and proximity to compute a composite index of sociality for each dyad in each year. The sociality index was computed as follows:

$$\frac{\left(\frac{Gij}{Gxy}+\frac{Pij}{Pxy}\right)}{2}$$

The first term in the numerator is the adjusted frequency of grooming for dyad *i,j* divided by the mean adjusted frequency of grooming for all dyads in group *x* in year *y*. The second term in the numerator is the adjusted frequency of proximity for dyad *i,j* divided by the mean adjusted frequency of proximity for all dyads in group *x* in year *y*.

The sociality index measures the extent to which each dyad deviated from other dyads 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. We used the sociality index to identify dyads that established very strong bonds.

Statistical analyses

To examine the relationship between the sociality index and continuous variables such as maternal and paternal relatedness, 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 relatedness, age differences, and dominance rank differences 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 influence the strength of social bonds.

We used Poisson regression to examine the sources of variation in size of females' social networks. 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.

We used both parametric and nonparametric methods to examine differences between categories of dyads. We conducted *t* tests to examine the differences between means. The *t* test is more powerful than nonparametric tests and is relatively insensitive to violations of distributional assumptions. For each comparison, we tested the equality of the variances using Levene's equality of variance test. When the variances were significantly different, we report the test statistic and probability levels computed under the assumption of unequal variances. We conducted power analyses to determine the likelihood of detecting significant differences between two samples. This information is particularly useful for interpreting nonsignificant results. Thus, for *t* tests that generated nonsignificant differences between categories, we report the power of the two-sample comparison of means.

We used the nonparametric Mann–Whitney test to evaluate the difference in the strength of social bonds between different categories of kin and between peers and others. We used the Wilcoxon matched-pairs signed-rank test to examine the effect of the presence or absence of kin on the strength of social bonds within dyads. Two-tailed tests of significance were used throughout.

Results

Magnitude of variation in bond strength

We computed the sociality index for the full sample of coresident dyads (N=1,430 dyads). The distribution of theses scores provides a measure of how evenly females' social contacts are distributed across potential partners. As Fig. 1 shows, the distribution of sociality scores was strongly skewed to the left. Although the mean was, by definition, 1, the median value was 0.5, and the sociality index exceeded 2.0 for only 10% of all dyads. That is,

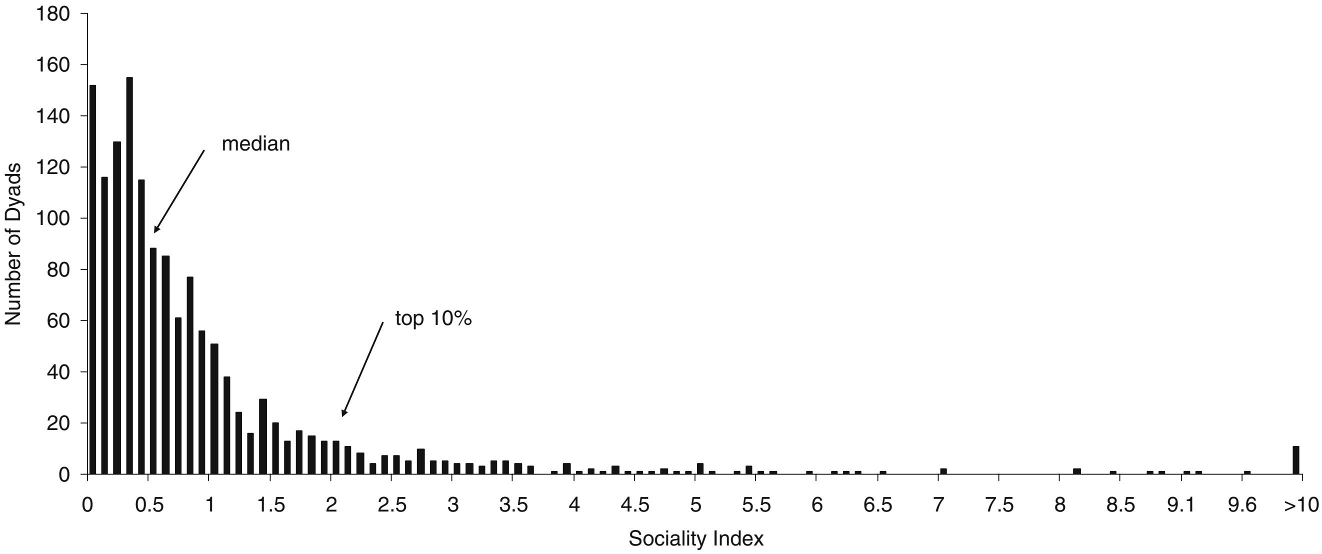


Fig. 1 Distribution of sociality index values. The value of the sociality index is plotted on the *x axis*, and number of dyads is plotted on the *y axis*. Each *bar* indicates the number of dyads that had sociality index values that were of the magnitude indicated on the *x axis*. The median value of the sociality index was 0.5, and the sociality index exceeded 2.0 for only 10% of all dyads (N=1,430 dyads). See text for additional details

many dyads had very weak social bonds, whereas very few had strong bonds.

Effects of maternal relatedness on the strength of social bonds

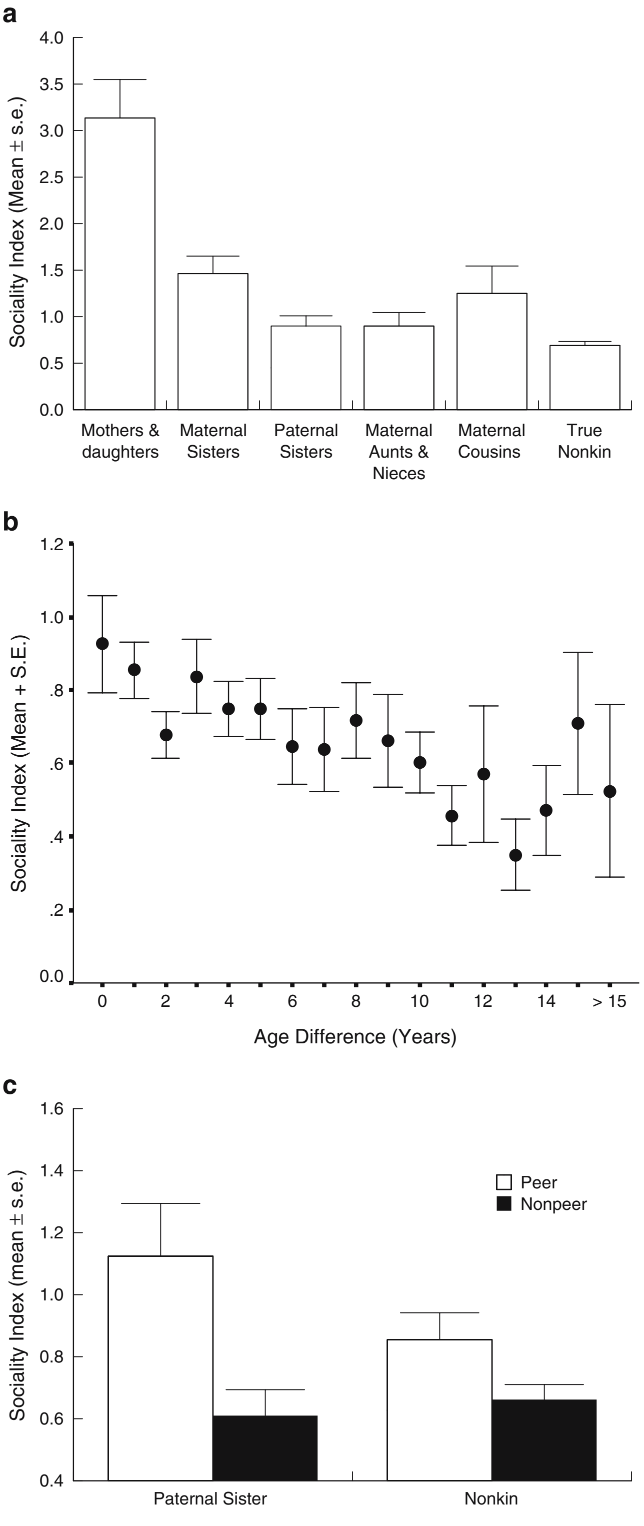
As expected, maternal relatedness had a strong effect on the strength of social bonds (Fig. 2a). Close maternal kin had significantly stronger social bonds than less closely related females, and maternal relatedness accounted for a substantial fraction of the total variation in the strength of social bonds (regression with robust standard errors: b=4.6557± 0.4780, t=9.74, p<0.001, R^2=0.2213, N=1,416 dyads; 14 dyads excluded as outliers). An even stronger pattern emerged when we limited the sample to dyads of known relatedness through maternal and paternal lines (b=4.7619± 0.5524, t=8.62, p<0.001, R^2=0.3110, N=489; five dyads related through maternal and paternal lines and ten outliers excluded; see Table 1 for composition of sample). Thus, the degree of maternal relatedness explained between 22 and 31% of the total variation in the strength of social bonds among females.

We also conducted pairwise comparisons between categories of maternal kin to assess the range of maternal kin biases. Females formed significantly stronger bonds with their mothers and daughters than with their maternal sisters ($t_{58,59}$=5.183, p<0.001; Mann–Whitney U=748, Z=−5.250, p<0.001; eight dyads excluded as outliers), and clearly preferred both mothers and daughters and maternal sisters more than true nonkin (mothers and daughters vs nonkin: $t_{58,236}$=8.553, p<0.001, U=1,630, Z=−8.989, p<0.001; five dyads excluded; sisters vs nonkin: $t_{59,236}$=3.992, p<0.001, U=4,145, Z=−4.807, p<0.001; three dyads excluded). Females also formed significantly stronger bonds with their maternal sisters than with their maternal aunts or nieces ($t_{59,56}$=2.351, p=0.020, U=1,121, Z=−2.972, p=0.003; five dyads excluded). Females did not differentiate between their maternal aunts and nieces and their maternal cousins ($t_{56,18}$=−0.739, p=0.462, U=428, Z=−0.958, p=0.338; power=0.1054; two dyads excluded), although the small number of pairs of maternal cousins greatly limits the power of this comparison. In addition, females did not consistently distinguish between their maternal aunts and nieces and true nonkin ($t_{56,236}$=1.391, p=0.169, U=6,478, Z=−0.229, p=0.819; power=0.2851; two dyads excluded), or between maternal cousins and true nonkin ($t_{18,236}$=1.460, p=0.162, U=1,726, Z=−1.325, p=0.185; power=0.3090). Again, the power of these analyses is quite low. Thus, females' preferences were ordered approximately as follows: mothers and daughters> maternal sisters>maternal aunts and nieces≈maternal cousins≈true nonkin.

Effects of paternal relatedness on the strength of social bonds

Females also seemed to prefer paternal sisters over nonkin. If we compare paternal sisters with true nonkin, the difference was not quite significant with a two-tailed test ($t_{41,236}$=1.844, p=0.066; U=3,928, Z=1.922, p=0.055; power=0.4298; Fig. 2a). However, the power analysis indicates that we had relatively little power to detect a

Fig. 2 Sources of variation in the strength of social bonds. **a** Genetic relatedness. The category of genetic relatedness is plotted on the *x axis*, and the value of the sociality index is plotted on the *y axis*. Each *bar* represents the mean (and standard error) of the sociality index for a given category of kin (mothers and daughters, N=58, five dyads excluded as outliers; maternal sisters, N=59, three dyads excluded; paternal sisters, N=41; maternal aunts and nieces, N=56, two dyads excluded; maternal cousins, N=18; true nonkin, N=236). **b** Age differences. The age difference between pairs of females who are not related through maternal lines is plotted on the *x axis*, and the value of the sociality index is plotted on the *y axis*. Each *point* represents the mean (and standard error) of the sociality index for a given age difference category (N=1,212, four dyads excluded as outliers). **c** Paternal kinship and age proximity. The sociality index for paternal sister peers (N=23), true nonkin peers (N=34), paternal sister nonpeers (N=18), and true nonkin nonpeers (N=202) are plotted



difference between the paternal sisters and true nonkin. Therefore, we also conducted an analysis in which we included in the “nonkin” category all dyads not related through maternal lines and not known to be related through paternal lines—it probably included some unknown paternal sisters and other paternal relatives. With this much larger sample, the difference between paternal sisters and “nonkin” (i.e., dyads that were not related maternally) was significant (paternal half-sisters: median=0.69, IQ range=0.94, n=41; nonkin: median=0.44, IQ range=0.69, n=1,162; Mann–Whitney U test, Z=−2.839, p<0.005). Females formed significantly stronger bonds with their maternal sisters than with their paternal sisters ($t_{59,41}$=2.587, p=0.011, U=924, Z=−2.001, p=0.045; three dyads excluded).

Effects of age proximity on the strength of social bonds

Paternal kinship and age proximity are confounded because paternal kin tend to be very close in age. In this analysis, the average age difference among pairs of paternal half-siblings was 364±51 days. As noted in the methods, we assigned paternity to only a subset of the adult females in this study (because genetic samples were missing for some of them or their fathers). This means that we do not know exactly how many of the dyads that were less than 1 year apart in age (“peers” hereafter) were actually paternal sisters, but we can get a general idea by considering the 504 pairs of females whose mothers and fathers were both known. Considering the 72 peer dyads with known mothers and fathers, 38% were paternal sisters; in contrast, only 7% of 432 nonpeer dyads with known mothers and fathers were paternal sisters. Thus, peers were more than seven times as likely to be paternal sisters than nonpeers were.

For pairs of females who were not related through maternal lines, the strength of social bonds steadily declined as the age difference between females increased (b=−0.0259±0.0052, t=−4.99, p<0.001, R^2=0.0194, N=1,212; four dyads excluded as outliers; Fig. 2b; see Table 1 for composition of sample). Although this decline was significant, age proximity accounted for only 2% of the variation in the strength of social bonds among females who were not related through maternal lines. This sample includes many dyads for which paternal relatedness was unknown, potentially confounding the effects of paternal relatedness and age proximity. Thus, we repeated the analysis with the 236 pairs of females who were known to be unrelated through maternal or paternal lines. The effects of age proximity were considerably attenuated in this sample ($b=-0.0179\pm0.0099$, $t=-1.81$, $p<0.075$, $R^2=0.0093$, $N=236$), and age proximity explained only half as much of the variation in the strength of social bonds.

One possible explanation of the difference between these two regressions is that the attraction to age mates is at least partly a function of paternal kinship. Overall, the strongest bonds were formed by paternal sisters who were also very close in age (Fig. 2c). To differentiate the effects of age proximity from the effects of paternal relatedness, we divided paternal sisters and true nonkin into two groups: peers and nonpeers. Paternal sisters showed significant preferences for peers over nonpeers ($t_{23,18}=2.712$, $p=0.011$; $U=1{,}292$, $Z=2.049$, $p=0.040$), and true nonkin showed similar preferences for peers over nonpeers ($t_{34,202}=1.1948$. $p=0.056$; $U=2{,}308$, $Z=-3.058$, $p=0.002$). The difference between peers who were paternal sisters and peers who were true nonkin was not statistically significant, but we had little power to detect differences between these groups ($t_{23,34}=1.411$, $p=0.168$, power=0.2001). There were no consistent differences between paternal sisters who were not peers and true nonkin who were not peers; again, the power of these comparisons is very low ($t_{18,202}=-0.315$, $p=0.597$; power=0.0834).

Effects of dominance rank differences on the strength of social bonds

Among baboons, matrilineal kin occupy adjacent ranks, so maternal kinship is closely related to dominance rank differences among females. Therefore, we considered the effects of dominance rank differences on the strength of social bonds among females who were not related through maternal lines. Females who were close in rank but were not maternal kin had significantly stronger bonds than females who occupied more distant ranks ($b=-0.0302\pm0.0064$, $t=-4.74$, $p<0.001$, $R^2=0.0243$, $N=1{,}212$; four dyads excluded as outliers; see Table 1 for composition of sample). Differences in dominance rank explained about 2% of the variation the strength of social bonds among females who were not related through maternal lines. Thus, females were generally attracted to females who occupied similar ranks even when those females were not maternally related. The same pattern emerged when we limited the sample to females who were unrelated through maternal or paternal lines, but the effect was not significant with the considerably smaller sample size, and only half as much variance was explained ($b=0.0220\pm0.0138$. $t=-1.59$, $p=0.117$, $R^2=0.0111$, $N=236$).

Females' preferences for maternal kin cannot be explained as an artifact of the similarity in their dominance ranks. Maternal relatedness was a significant predictor of the strength of social bonds among females of known maternal and paternal relatedness who were less than three ranks apart ($b=5.0839\pm0.7037$, $t=7.22$, $p<0.001$, $R^2=0.2818$, $N=225$ dyads; nine dyads excluded) and females who were more distantly ranked ($b=3.8481\pm.8772$, $t=4.39$, $p<0.001$, $R^2=0.1818$; $N=269$; one dyad excluded).

Effects of maternal absence on social bonds among maternal kin

In these analyses, we compared females' relationships with their maternal sisters and maternal aunts when their mothers were present and after their mothers died or joined a different fission product after a group split. There were only five pairs of maternal sisters who lived together in the same group when their mothers were present and absent. Four of these five pairs of females had weaker relationships while their mothers were present than after their mothers were gone. Maternal absence had the opposite effect on the relationships of females with their maternal aunts. Seven of eight females formed stronger ties with their maternal aunts when their mothers were present than after their mothers were gone.

Because there were so few pairs of maternal sisters or maternal aunt–niece dyads who were present before and after the death or departures of their mothers, we also evaluated the effects of maternal presence and absence cross-sectionally across dyads. We compared the average yearly values of the sociality index for each available pair of maternal sisters whose mothers were present with the values for pairs of maternal sisters whose mothers were absent. Maternal sisters without mothers formed stronger bonds than maternal sisters with mothers present (absent: 1.5750 ± 0.2070, $N=34$; present: 1.0284 ± 0.1269, $N=28$; $t=2.251$, $p=0.029$; $U=360$, $Z=-1.648$, $p=0.099$; Fig. 3a).

We followed a very similar procedure to assess the nature of females' relationships with their aunts before and after their mothers' death or departure. We computed the average yearly values of the sociality index for maternal aunt–niece pairs for whom the connecting female (the aunt's sister and niece's mother) was present and compared this with the average yearly values for aunt–niece pairs for whom the connecting female was absent. Maternal aunt–niece pairs formed weaker bonds in the absence of their connecting female (absent: 0.6921 ± 0.2328, $N=19$; present: 0.9362 ± 0.1524, $N=36$; $t=-0.906$, $p=0.369$, power=0.1417; $U=218$, $Z=-2.195$, $p=0.028$; Fig. 3b).

These analyses indicate that females' relationships with their maternal kin were significantly influenced by the presence or absence of their mothers. Maternal absence strengthened females' relationships with their maternal

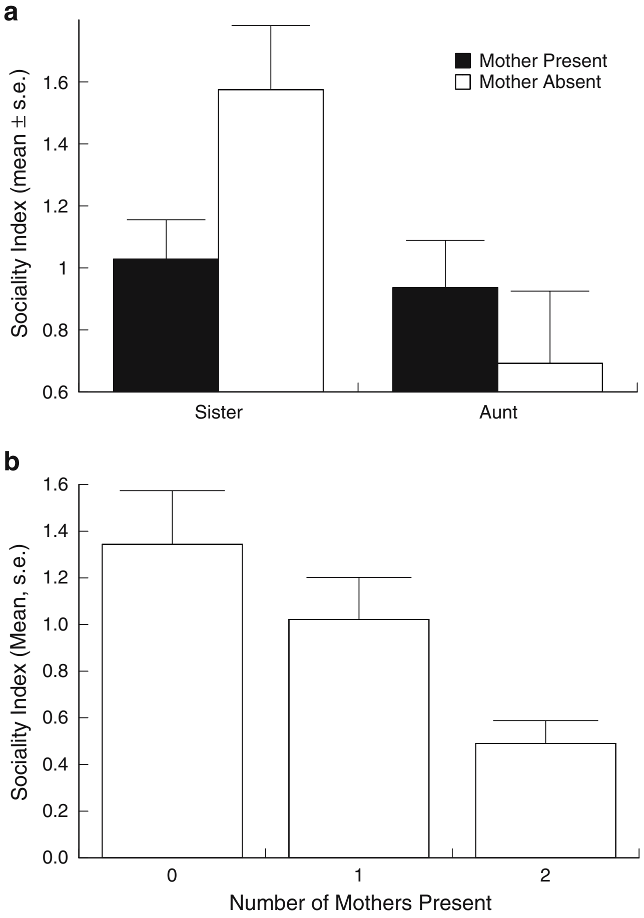


Fig. 3 **a** Effects of mother's presence on the strength of social bonds with maternal kin. On the *left side*, the mean (and standard error) of the sociality index for pairs of maternal sisters when their mothers are present (*N*=28) and absent (*N*=34) is plotted. On the *right side*, the mean (and standard error) of the sociality index for pairs of maternal aunts and nieces when the connecting female (the aunt's sister and the niece's mother) are present (*N*=36) and absent (*N*=19) is plotted. **b** Effect of mothers' presence on the strength of social bonds with paternal sisters. The strength of females' relationships with their paternal half-sisters was strongest when neither of their mothers were present and weakest when both their mothers were present. Here the average number of mothers present is rounded to the nearest integer (no mothers present, *N*=9 dyads; one mother present, *N*=17; both mothers present, *N*=15)

sisters and weakened their relationships with their maternal aunts.

The effects of the availability of maternal kin on the strength of social bonds among paternal sisters

For five pairs of paternal sisters, we were able to compare the strength of social bonds when neither of the females had any mothers of daughters in the same group and when there was one mother or daughter present. In four of these five dyads, females formed stronger bonds with paternal sisters when they had no mothers or daughters present than when there was one mother or daughter present. There were eight pairs of paternal sisters who were observed in years when they had no maternal sisters in their groups and when they had one paternal sister present. Three of these eight pairs of paternal sisters had stronger social bonds when they had no maternal sisters present than when they had one maternal sister present.

To extend the analysis, we evaluated the effects of the availability of maternal kin across dyads. For each pair of paternal sisters each year, we determined whether their mothers were both present, only one was present, or neither was present. For these dyads, we also computed the number of mature daughters and the number of maternal sisters who were present each year. For each available paternal sister dyad, we summed the numbers of mothers available and divided this sum by the number of years in which the pair of paternal sisters was coresident. We followed the same procedure for daughters and maternal sisters. These values represent the average number of mothers, daughters, and maternal sisters who were available to each pair of paternal sisters during the years in which they were coresident. We computed the average value of the sociality index for each pair of paternal sisters by summing the sociality index scores for each year and dividing the sum by the number of years of coresidence.

We then evaluated the relationship between the availability of maternal kin and the strength of social bonds among paternal sisters, controlling for age proximity. Females formed significantly stronger bonds with their paternal sisters when fewer close maternal kin were available (Table 2; Fig. 3b). The number of mothers present among the dyad members, number of daughters present, number of maternal sisters present, and age proximity accounted for 34% of the variation in the strength of social bonds among paternal sisters, although the effect was primarily due to variation in the number of mothers present. When age proximity was dropped from the regression model, the R^2 value dropped to 0.27.

Sources of variability in the number of strong bonds females formed

Females were preferentially attracted to close kin, and the strength of their social bonds was influenced by the availability of preferred types of partners. The availability of preferred types of partners was partly a function of females' ages. Figure 4a shows that the total number of close maternal kin (mothers, daughters, and sisters) stayed relatively constant as females aged, but as females became older, more and more of their mothers and sisters died or joined other groups (after fission), and they were replaced by daughters. Peers were numerous when females were young and steadily declined in number as females aged.

Table 2 Effects of the availability of maternal kin and age proximity on the average strength of social bonds among paternal sisters (N=41 pairs of paternal half-sisters)

Predictor variables	b	Robust SE	t	p
Number of mothers	−0.4859	0.1569	−3.10	0.005
Number of daughters	0.1855	0.4144	0.45	0.659
Number of maternal sisters	−0.0464	0.0833	−0.56	0.583
Age proximity	−0.2165	0.1150	−1.88	0.073

To assess the number of strong social bonds females formed, we identified the sociality index scores that fell within the top 10% of all scores for each group each year and classified these dyads as having "very strong bonds." For each female who was present in a given year, we tabulated (a) the number of very strong bonds she formed, (b) the number of coresident maternal kin (mothers, daughters, and sisters) she had, and (c) the number of coresident peers. We did not include the number of paternal kin available because we had this information for only a subset of females. We matched these data with information about the females' age and dominance rank each year.

On average, females formed 1.56±0.05 very strong bonds each year (range=0–6). Females who had more mothers, daughters, or maternal sisters present in the group had more very strong bonds than females who had fewer close maternal kin present (Table 3; Fig. 4b). In contrast, the number of peers present did not significantly affect the number of very strong bonds that females formed each year. Perhaps as a result, although females had fewer peers available as they grew older, age did not affect the number of very strong bonds a female had. In addition, female dominance rank had no consistent effect on the number of very strong bonds females had.

Although females with more close maternal kin had more very strong bonds than females with fewer close maternal kin, most females had at least one very strong bond even when they had no close maternal kin present. For females with no close maternal kin present in a given year, the mean number of very strong bonds was 1.21±0.10. In years when females had no close maternal kin present, they had at least one very strong bond about 70% of the time (89/127 female years).

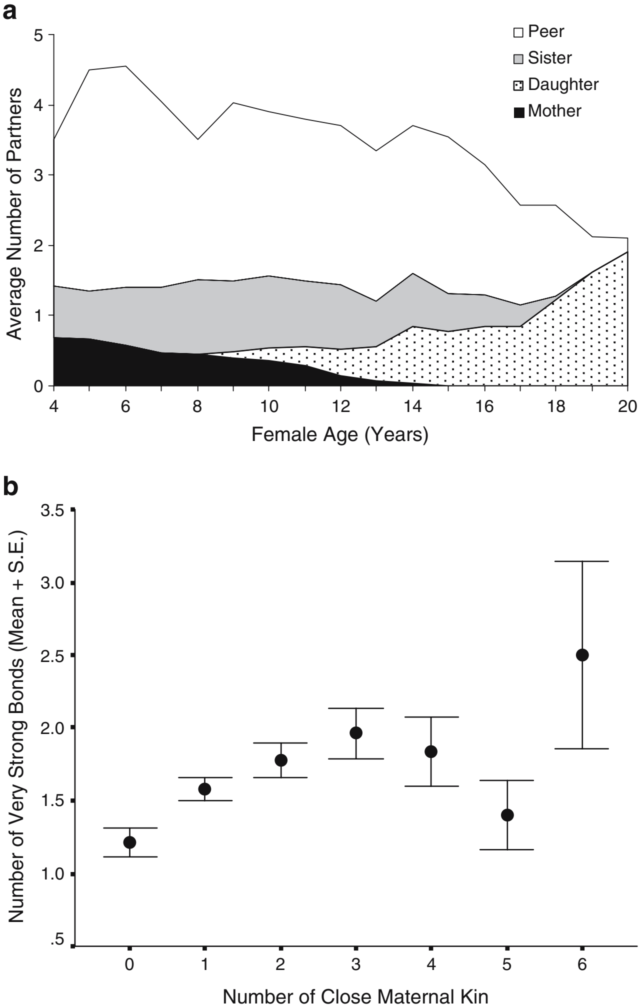


Fig. 4 **a** Changes in the availability of preferred types of partners. Female age is plotted on the *x axis*. The average number of partners of each type (mothers, *black*; maternal sisters, *gray*; daughters, *stippled*; and peers, *white*) that were available to females of a given age is plotted on the *y axis*. Sample is based on 118 adult females over 583 female years. **b** Relationship between availability of preferred partners and the number of very strong bonds females formed. The number of close maternal kin (mothers, daughters, and sisters) is plotted on the *x axis*. The number of very strong bonds females formed is plotted on the *y axis* (sample as in **a**)

Discussion

Previous work has indicated that female baboons who are more socially integrated have more successful reproduction than females who are more solitary (Silk et al. 2003a). The analyses presented here suggest that females achieve this social integration partly through close bonds with other adult females. They formed their strongest bonds with mothers and sisters, and bond strength was a decreasing function of relatedness. Bond strength also decreased with increased age difference, which may reflect the fact that females used age proximity as an indicator of paternal relatedness; females preferred paternal sisters over nonkin. Females actively compensated for the loss or absence of preferred partners by strengthening their relationships with others, and they compensated for the loss of maternal relatives by strengthening bonds with paternal sisters. They showed strikingly different responses to their sisters than to their aunts when they lost their mothers, strengthening bonds with maternal sisters in the absence of their mother,

Table 3 Sources of variation in the number of very strong bonds that females formed each year (N=583 female years)

Predictor variables	b	Robust SE	Z	p
Number of mothers and daughters	0.1085	0.0471	2.30	0.021
Number of maternal sisters	0.0671	0.0327	2.05	0.040
Number of peers	0.0186	0.0255	0.73	0.466
Female's age	0.0017	0.0093	0.18	0.857
Female's rank	−0.0090	0.0068	−1.32	0.187

but weakening bonds with aunts, indicating the importance of very close relatives (r=0.25) more than even slightly more distant ones (r=0.125).

Evidence from Moremi demonstrates that the sudden loss of preferred partners is stressful to female baboons (Engh et al. 2006). In that study, females who lost a close relative to predation experienced higher levels of glucocorticoids in the weeks that followed their loss. Females also responded to the loss of preferred partners by increasing the amount of time they spent grooming and by expanding the number of females that they groomed. Females' hormone levels returned to baseline levels within 2 months of the loss of the partner (Engh et al. 2006). In Laikipia, Kenya, female baboons showed significantly higher rates of self-directed behavior when there were no other individuals within 10 m than when there was at least one other baboon 5 to 10 m away, suggesting that females are most anxious when they are isolated from other group members (Castles et al. 1999). Taken together, these data suggest that social bonds play an important role in baboon females' lives, and the ability to adjust to disruptions in their social networks may have both short-term and long-term consequences for females.

Chapais and his colleagues (Chapais 2001, 2005; Chapais and Bélisle 2004) hypothesized that high rates of interaction among some categories of maternal kin might confer no inclusive fitness benefits and occur only as a by-product of their common attraction to a third party. If that is the case, then we might expect ties to deteriorate in the absence of the connecting female. In Amboseli, females' ties to their maternal sisters became stronger in their mothers' absence. This indicates that females actively seek out their sisters as social partners, and their bonds with their maternal sisters are not simply a passive by-product of their relationship with their mother. In contrast, females' relationships with their aunts tended to become weaker when their mothers were not present. This raises the possibility that the relationship between aunts and nieces is mainly an artifact of their common attraction to the more closely related female, the niece's mother and the aunt's sister, who links them together. This interpretation is supported by evidence that the relatedness threshold for nepotistic biases hovers around 0.25 in macaques (Chapais et al. 1997, 2001; Widdig et al. 2002). However, it is possible that the females in our study groups would actively maintain aunt–niece relationships if they did not have more closely related maternal kin available. As Fig. 4a indicates, the loss of a mother or a sister is commonly accompanied by the gain of a daughter. Further work is needed to determine how the availability of alternative social partners influences the nature of social bonds among various categories of maternal kin.

In Amboseli, females showed preferences for unrelated females who hold adjacent ranks. Similar patterns were documented among female baboons in Moremi, although information about paternal relatedness was not available (Silk et al. 1999; see also Kapsalis 2003). The basis for the attraction to females who hold similar ranks is unclear because female baboons in Amboseli do not seem to exchange grooming for coalitionary support (Silk et al. 2004), and adult females in Moremi rarely form coalitions or compete for grooming partners (Silk et al. 1999). Moreover, there was no evidence that females in Moremi groomed more equitably with females who occupied adjacent ranks (Silk et al. 1999). Elevated rates of grooming and association among females who occupy similar dominance ranks might reflect low-ranking females' anxiety about associating with considerably higher-ranking females. However, whereas females showed higher levels of self-directed behavior when they were near higher-ranking females than lower-ranking females, there was no evidence that females experienced less stress when they were with females who were closer to their own rank (Castles et al. 1999). Thus, the function of females' attraction to females of similar rank remains unclear.

In contrast to the results of Smith et al. (2003), in which paternal sisters and maternal sisters exhibited social bonds of similar strength, the larger sample of paternal sisters in the current analysis exhibited social bonds that were intermediate in strength between those of maternal sisters and true nonkin. This is similar to the result presented by Widdig et al. (2001) for provisioned rhesus monkeys on Cayo Santiago. The difference between our current results and those of Smith et al. (2003) supports their hypothesis that differences in the extent of maternal and paternal kin biases among baboons in Amboseli and rhesus macaques on Cayo Santiago might reflect a contingent response to differences in the size and composition of maternal kin networks. By chance, relatively few of the females that Smith et al. studied had close maternal kin available. Our analysis demonstrates that females in Amboseli formed stronger ties to their paternal sisters when few close maternal kin (particularly mothers and daughters) were available. Although the sources of variation within populations are not necessarily the same as the sources of variation across populations or species, our data suggest that demographic conditions contribute to observed differences in the strength of social bonds among paternal sisters.

The number of strong bonds that females formed varied within a rather narrow range. The total number of very strong bonds that we identified is clearly an artifact of the fact that we defined them as the top 10% of all social bonds. However, our definition did not seriously constrain the extent of variation among females, and it was possible for a few females to have had a number of strong bonds and for others to have had none. Nonetheless, few females had very large social networks, and few females had no very strong bonds. Ecological constraints may limit females' ability to maintain social relationships with multiple partners (Henzi et al. 1997). Moreover, if female baboons do not rely on coalitionary support from many different partners to maintain their dominance ranks or gain access to resources (Henzi and Barrett 1999), then a small and dense social network may be sufficient to serve females' needs. The fact that the majority of females formed very strong bonds with at least one partner, even if they had no close maternal kin in the group, suggests that females may need a minimum number of partners to satisfy their social needs.

The social lives of female baboons revolve around a tight core of close associates with whom they form stable and equitable relationships (Silk et al. 2006). Females show pronounced preferences for close kin, including mothers, daughters, and maternal and paternal sisters. Females also prefer to groom and associate with unrelated age mates and those who are close to their own rank. Both the size and composition of females' social networks are strongly influenced by demographic factors. Females adjust to variation in the availability of preferred types of partners, forming stronger ties with their sisters when closer kin (mothers and daughters) are unavailable. Even in the absence of close maternal kin, most females form strong social bonds with at least one partner. Taken together, these data contribute to a growing of body of evidence that social bonds have adaptive value for female baboons.

Acknowledgments We thank the Office of the President of Kenya and the Kenya Wildlife Service for permission to work in Amboseli. The staff of Amboseli National Park provided valuable cooperation. The members of the pastoralist communities of Amboseli and Longido and the Institute for Primate Research in Nairobi provided local sponsorship. We thank R.S. Mututua, S.N. Sayialel, and J.K. Warutere for their expert assistance in data collection, and S. Combes and D. Onderdonk for database support. Jason Buchan, Russ Van Horn, and Kerri Smith performed genetic analyses for assignment of paternal kin. We appreciate valuable comments on the manuscript from Louise Barrett, Bernard Chapais, Dorothy Cheney, and Robert Seyfarth, and Anja Widdig. This project was supported by grants to J.B.S. from the National Geographic Society, the L.S.B. Leakey Foundation, the UCLA Academic Senate, and the National Science Foundation (BCS-0003245); by grants to J.A. by the Chicago Zoological Society and the National Science Foundation (IBN-9985910 and its predecessors); and by a grant to S.C.A. from the National Science Foundation (IBN-0322613). This research protocol was approved by the Chancellor's Animal Research Committee of the Office of the Protection of Research Subjects at the University of California, Los Angeles (ARC no. 99-075-02). The final drafts of this paper were prepared when J.B.S. was visiting the Large Animal Research Group in the Department of Zoology and the Leverhulme Center for Human Evolutionary Studies at the University of Cambridge. She thanks her hosts for their hospitality and fellowship.

References

Alberts SC, Buchan JC, Altmann J (2006) Sexual selection in wild baboons; from mating opportunities to paternity success. Anim Behav (in press)

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

Arnold W (1990) The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behav Ecol Soc 27:239–246

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

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

Boonstra R, Hogg I (1988) Friends and strangers: a test of the Charnov–Finerty hypothesis. Oecologia 77:95–100

Buchan JC, Alberts SC, Silk JB, Altmann J (2003) True paternal care in a multi-male primate society. Nature 425:179–181

Buchan JC, Archie, EA, Van Horn RC, Moss CJ, Alberts SC (2005). Locus effects and sources of error in noninvasive genotyping. Mol Ecol Notes 5:680–683

Castles DL, Whiten A, Aureli F (1999) Social anxiety, relationships and self-directed behaviour among wild female olive baboons. Anim Behav 58:1207–1215

Chapais B (2001) Primate nepotism: what is the explanatory value of kin selection? Intl J Primatol 22:203–229

Chapais B (2005) Kinship, competence and cooperation in primates. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans: mechanisms and evolution. Cambridge University Press, Cambridge, pp 47–64

Chapais B, Bélisle P (2004) Constraints on kin selection in primate groups. In: Chapais B, Berman C (eds) Kinship and behavior in primates. Oxford University Press, Oxford, pp 365–386

Chapais B, Gauthier C, Prud'homme J, Vasey P (1997) Relatedness threshold for nepotism in Japanese macaques. Anim Behav 53:1089–1101

Chapais B, Savard L, Gauthier C (2001) Kin selection and the distribution of altruism in relation to degree of kinship in Japanese macaques (*Macaca fuscata*). Behav Ecol Sociobiol 49:493–502

Chen X, Ender PB, Mitchell M, Wlls C (no date) Regression with STATA. http://www.ats.ucla.edu/stat/stata/webbooks/reg

Combes S, Altmann J (2001) Status change during adulthood: life-history by-product or kin selection based on reproductive value? Proc R Soc Lond B Biol Sci 268:1367–1373

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

Christal J, Whitehead H (2001) Social affiliations within sperm whale (*Physeter macrocephalus*) groups. Ethology 107:323–340

Dobson FS, Jacquot C, Baudoin C (2000) An experimental test of kin association in the house mouse. Can J Zool 78:1806–1812

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

Fairbanks LM (1980) Relationships among adult females in captive vervet monkeys: testing a model of rank-related attractiveness. Anim Behav 28:853–859

Gerlach G, Bartmann S (2002) Reproductive skew, costs, and benefits of cooperative breeding in female wood mice (*Apodemus sylvaticus*). Behav Ecol 13:408–418

Greenwood PJ (1980) Mating systems, philopatry, and dispersal in birds and mammals. Anim Behav 28:1140–1162

Hackländer K, Möstl E, Arnold W (2003) Reproductive suppression in female Alpine marmots, *Marmota marmota.* Anim Behav 65:1133–1140

Hayes LD, Solomon NG (2004) Costs and benefits of communal rearing to female prairie voles (*Microtus ochrogaster*). Behav Ecol Sociobiol 56:585–593

Hamilton WD (1964) The genetical evolution of social behavior. I and II. J Theor Biol 7:1–52

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

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

Henzi SP, Lycett JE, Piper SE (1997) Fission and troop size in a mountain baboon population. Anim Behav 53:525–535

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

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, Krebs CJ (1993) Influence of female relatedness on the demography of Townsend's vole populations in spring. J Anim Ecol 62:536–550

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

Mappes T, Ylonen H, Viitala J (1995) Higher reproductive success among kin groups of bank voles (*Clethrionomys glareolus*). Ecology 76:1276–1282

McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Matriarchs as repositories of social knowledge in African elephants. Science 292:491–494

Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. Mol Ecol 7:639–655

Morin PA, Chambers KE, Boesch C, Vigilant L (2001) Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). Molec Ecol 10:1835–1844

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

Navidi W, Arnheim N, Waterman MS (1992) A multiple-tubes approach for accurate genotype of very small DNA samples by using PCR: statistical considerations. Am J Hum Genet 50:347–359

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*). Behav Ecol Sociobiol 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

Rusu A, Krackow S (2004) Kin-preferential cooperation, dominance-dependent reproductive skew, and competition for mates in communally nesting female house mice. Behav Ecol Sociobiol 56:298–305

Schino G (2001) Grooming, competition and social rank among female primates: a meta-analysis. Anim Behav 62:265–271

Seyfarth RM (1977) A model of social grooming among adult female monkeys. J Theor Biol 65:671–698

Seyfarth RM (1983) Grooming and social competition in primates. In: Hinde RA (ed) Primate social relationships: an integrated approach. Sinauer, Sunderland, pp 182–190

Silk JB (1982) Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. Behaviour 79:162–188

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

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, Cheney DL, Seyfarth RM (1996) The form and function of post-conflict interactions among female baboons. Anim Behav 52:259–268

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

Silk JB, Rendall D, Cheney DL, Seyfarth RM (2003b) Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. Ethology 109:627–644

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, Alberts SC, Altmann J (2006) Social relationships among adult female baboons (*Papio cynocephalus*) II: sources of variation in the quality and stability of social bonds. Behav Ecol Sociobiol. DOI 10.1007/s00265-006-0250-9

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

Taberlet P, Griffin S, Goossens B, Questiau S, Manceau V, Escoravage N, Waits LP, Bouvet J (1996). Reliable genotyping of samples with very low DNA quantities using PCR. Nucleic Acids Res 24:3189–3194

Waser PM, Jones WT (1983) Natal philopatry among solitary mammals. Q Rev Biol 58:355–390

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 U S A 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