Behav Ecol Sociobiol (2007) 61:1823–1837
DOI 10.1007/s00265-007-0415-1

ORIGINAL PAPER

Divided destinies: group choice by female savannah baboons during social group fission

Russell C. Van Horn · Jason C. Buchan ·
Jeanne Altmann · Susan C. Alberts

Received: 17 July 2006 / Revised: 2 February 2007 / Accepted: 5 May 2007 / Published online: 12 June 2007

Abstract Group living provides benefits to individuals while imposing costs on them. In species that live in permanent social groups, group division provides the only opportunity for nondispersing individuals to change their group membership and improve their benefit to cost ratio. We examined group choice by 81 adult female savannah baboons (*Papio cynocephalus*) during four fission events. We measured how each female's group choice was affected by several factors: the presence of her maternal kin, paternal kin, age peers, and close social partners, her average kinship to groupmates, and her potential for improved dominance rank. Maternal kin, paternal kin, and close social partners influenced group choice by some females, but the relative importance of these factors varied across fissions. Age peers other than paternal kin had no effect on group choice, and average kinship to all groupmates had the same effect on group choice as did maternal kin alone. Most females were subordinate to fewer females after fissions than before, but status improvement did not drive female group choice; females often preferred to remain with social superiors who were their close maternal kin, rather than improving their own social ranks. We suggest that during permanent group fissions, female baboons prefer to remain with close maternal kin if those are abundant enough to influence their fitness; if they have too few close maternal kin then females prefer to remain with close paternal kin, and social bonds with nonkin might also become influential.

Keywords Fission · Fitness · Kinship · Social bonds · Social rank

Communicated by D. Watts

Electronic supplementary material The online version of this article (doi:10.1007/s00265-007-0415-1) contains supplementary material, which is available to authorized users.

R. C. Van Horn (✉) · J. C. Buchan · S. C. Alberts
Department of Biology, Duke University,
P.O. Box 90338, Durham, NC 27708-0338, USA
e-mail: rvanhorn@sandiegozoo.org

J. Altmann · S. C. Alberts
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 long-standing question in behavioral ecology concerns how patterns of group living reflect the costs and benefits of group life (e.g., Krause and Ruxton 2002; Le Galliard et al. 2005). The relative benefits of group living clearly differ among individuals in some species (e.g., Sterck et al. 1997; Kappeler and van Schaik 2002) and can lead them to vary in their propensity for group living (e.g., Jakob 2004). However, when the benefits of group living are large relative to the costs, individuals rarely or never live alone, and group size, rather than propensity for group living, is thought to change in response to the costs and benefits of group living. For example, one model of group living among primates stresses the dynamic tension created when predation risk increases as group size decreases, while intragroup competition for food increases as group size increases (van Schaik 1983). In this model, predation risk sets a minimum viable group size, while intragroup feeding competition sets a maximum viable group size.

In the matrilineal societies typical of many cercopithecine primates, group membership changes over time as individuals are born and die, and as males immigrate and emigrate. However, most females in matrilineal societies do not disperse; when their group's size or composition becomes unfavorable, permanent group fission functions as their only avenue of dispersal (Melnick and Kidd 1983; Dittus 1988; Hamilton and Bulger 1993; Holekamp et al. 1993; Ménard and Vallet 1993; Lefebvre et al. 2003; Widdig et al. 2006). Consequently, group choice during permanent fission is a key opportunity for females to attempt to favorably balance the costs and benefits they accrue through group living. Permanent group fissions have been described in a range of cercopithecine primates (*Cebus olivaceus*, Robinson 1988; *Cercopithecus mitis*, Cords and Rowell 1986; *Macaca fuscata*, Sugiyama 1960; Mizuhara 1964; Furuya 1969; Koyama 1970; Oi 1988; Koyama 2003; *Macaca maurus*, Okamoto and Matsumura 2001; *Macaca mulatta*, Missakian 1973; Chepko-Sade 1974; Cheverud et al. 1978; Chepko-Sade and Olivier 1979; Melnick and Kidd 1981, 1983; Malik et al. 1985; Kapsalis and Berman 1996a, b; Widdig et al. 2006; *Macaca sinica*, Dittus 1988; *Macaca sylvanus*, Ménard and Vallet 1993; Kuester and Paul 1997; Lefebvre et al. 2003; *Macaca thibetana*, Li et al. 1996; *Papio cynocephalus*, Stoltz 1972; Nash 1976; Hamilton and Bulger 1993; Ron et al. 1994; Ron 1996; Henzi et al. 1997; *Presbytis johnii*, Hohmann 1989) and in a few other taxa that have matrilineal societies (*Marmota flaviventris*, Armitage 1987; Armitage and Schwartz 2000; *Nasua narica*, Gompper 1997; *Crocuta crocuta*, Mills 1990; Holekamp and Smale 1995).

In matrilineal societies where maternal kinship is known, permanent fissions of social groups often follow a simple pattern in which groups of maternal kin split from the original social group (Missakian 1973; Cheverud et al. 1978; Chepko-Sade and Olivier 1979; Dittus 1988; Robinson 1988; Mills 1990; Holekamp et al. 1993; Ménard and Vallet 1993; Kuester and Paul 1997; Okamoto and Matsumura 2001; Koyama 2003; Widdig et al. 2006). This pattern is consistent with the hypothesis that a key benefit of group living is the inclusive fitness benefit accrued from living with relatives, and has created an expectation that permanent fissions of matrilineal societies are essentially matrilineal fissions. However, a detailed examination of those data reveals females who left their maternal kin (e.g., Chepko-Sade and Olivier 1979; Koyama 2003; Widdig et al. 2006); these cases cannot be readily explained by the matrilineal fission model. In addition, the fission of groups of yellow-bellied marmots (*M. flaviventris*) always results in females leaving some maternal kin, which illustrates that during fissions an individual's inclusive fitness benefits might not be as influential as its direct fitness benefits (Armitage 1987): The costs of large group size might force females to abandon kin.

During fissions, females' choice of groups should be influenced by any variable that influences their fitness and depends on their groupmates. The fitness of cercopithecine females is influenced by a number of social factors other than maternal kinship, including social rank (e.g., Altmann and Alberts 2003b, 2005) and affiliative social bonds (e.g., Silk et al. 2003). In addition, these females form social bonds with both paternal kin and maternal kin (Widdig et al. 2001; Smith et al. 2003; Silk et al. 2006a), and sometimes with nonkin (Silk et al. 2006a). It seems likely, then, that maternal kinship alone will not predict patterns of female group choice during fissions.

Given the suite of possible influences on fission patterns, we asked about the extent to which several factors, in addition to maternal kinship, influenced the fissions of female savannah baboons (*P. cynocephalus*). Female savannah baboons live in stable, cohesive, matrilineal societies (e.g., Ransom 1981; Smuts 1985; Altmann and Alberts 2003b), and permanent group fissions have been described (e.g., Nash 1976; Ron 1996; Henzi et al. 2000a, b).

First, we examined the role of kinship in group choice during fissions. Kinship can enhance the benefits of group living if individuals direct beneficent behavior toward kin. As described above, maternal kinship has often been seen to influence fission patterns, but only two studies have been able to directly address the role of paternal kinship in permanent group fissions; one study found no effect of paternal kinship on fission patterns (Kuester and Paul 1997), and the other study found evidence for a weaker effect of paternal kinship than maternal kinship (Widdig et al. 2006). We also asked whether the influence of kin upon group choice was altered by the reproductive value of those kin, which might modify the indirect fitness value they represent to a female (Hrdy and Hrdy 1976; Schulman and Chapais 1980; Stearns 1992; Combes and Altmann 2001; but see Horrocks and Hunte 1983; Paul and Kuester 1987).

Second, we addressed whether females might prefer to remain with others of similar age during fissions, as an indirect preference for paternal kin. Paternal kinship can be important during fissions of cercopithecine primates (Melnick and Kidd 1981; Widdig et al. 2006), but unlike maternal kinship there are few behavioral cues to paternal kinship. Theory and observations suggest that age proximity might be an important cue for paternal kinship (Altmann 1979; Alberts 1999; Silk et al. 2006a), thus we asked whether female group choice was influenced by the presence of age peers.

Third, we inquired about the importance of social bonds during fissions. Sociality confers fitness benefits on females (Silk et al. 2003) and social relationships might therefore affect female group choice. However, social bonds among female baboons occur primarily, but not exclusively, with maternal kin (Silk et al. 2004, 2006a). We therefore asked whether females preferentially remained with the kin to whom they were most closely bonded before the fission, and with the nonkin to whom they were most closely bonded before the fission.

Fourth, we asked whether females chose to maximize their postfission social status, because social rank has direct fitness consequences for female baboons (Bulger and Hamilton 1987; Packer et al. 1995; Altmann and Alberts 2003b, 2005; Johnson 2003; but see Cheney et al. 2004). Ron et al. (1994) suggested that female chacma baboons (*Papio hamadryas ursinus*) might improve their social rank during fissions by following the Abandon-Your-Superior (AYS) strategy. In AYS, each female joins a postfission group other than the group containing her immediate social superior, and on average females improve their social rank. As Ron et al. (1994) note, females could improve their rank as much under other strategies as under AYS, but AYS offers the advantage of being a simple rule of thumb that demands relatively little information gathering or processing by female baboons. Given the benefits of social rank and the simplicity of AYS, we asked whether female baboons followed AYS during fission.

Materials and methods

Study population

We studied permanent fissions of social groups among wild baboons living in the vicinity of Amboseli National Park in southern Kenya (2°40′S, 37°15′E). Members of this population have been under observation on a near daily basis since 1971 (e.g., Altmann et al. 1985; Alberts and Altmann 2003; Altmann and Alberts 2005). We collected detailed demographic, behavioral, and life history data on all individuals in our study groups (ca. 350 baboons alive at any time). These baboons were individually recognized and habituated to the presence of observers. Birth dates were known within a few days for all females in our study, and social ranks were assigned to each female based on aggressive and submissive behaviors exhibited during dyadic agonistic interactions (Hausfater 1975).

Fission events

Permanent group fissions sometimes begin subtly and develop over long periods of time (Missakian 1973; Dittus 1988; Oi 1988; Hood and Jolly 1995). We considered a fission to begin when adult female groupmates began to forage regularly in spatially disjunct groups or to sleep repeatedly as subgroups in separate groves of trees; we considered the fission to be complete when these subgroups ceased to coalesce to forage or sleep, and instead foraged and slept as independent groups. We have observed four permanent fissions since our observations began in 1971 (Fig. 1; Altmann and Alberts 2003b). Alto's group fissioned between 31 Dec 1988 and 1 Jan 1992; Hook's group fissioned between 1 Jul 1994 and 31 Dec 1994; Lodge group fissioned between 1 Dec 1995 and 31 Dec 1995; and Dotty's group fissioned between 1 Jan 1999 and 31 Jul 1999. Lodge group often foraged at a refuse site associated with a tourist lodge (Altmann and Muruthi 1988; Muruthi et al. 1991), but the other groups did not access supplemental foods; access to abundant food resulted in higher fertility and lower mortality within Lodge group. In addition, provisioning alters primate behavior (e.g., Hill 1999) and might influence fissions (Kuester and Paul 1997). Lodge group therefore served both as an interesting comparison to the other Amboseli groups and as a useful comparison to the many reported fissions of primate groups with access to supplemental food (Furuya 1960, 1968, 1969; Sugiyama 1960; Mizuhara 1964; Koyama 1970; Chepko-Sade 1974; Cheverud et al. 1978; Chepko-Sade and Olivier 1979; Hamilton and Bulger 1993; Hood and Jolly 1995; Li et al. 1996; Kapsalis and Berman 1996a, b; Kuester and Paul 1997; Koyama 2003).

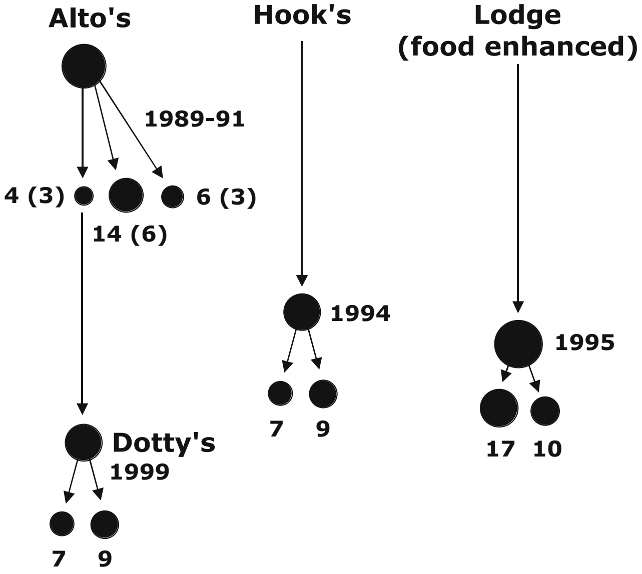

Fig. 1 Fissions among social groups of female baboons in Amboseli. *Areas of points* are proportional to the number of adult females present throughout the fission event. Two females were present as adults during fission of both Alto's group and Dotty's group. *Parenthetical numbers* refer to the number of females not genotyped

Study animals

We analyzed the postfission group choice of all females (n= 81) present throughout their group's fission (Fig. 1) and that fell into either of the two categories: (1) They were reproductively mature when the fission began (76 of 81) or (2) they matured less than 6 months after the fission began (4 of 81) or by the end of the fission (1 of 81), whichever was earlier. Only one dyad was present as adults during two fission events; this dyad remained together during Alto's group fission but split during Dotty's group fission.

Kinship

We knew the mothers of nearly all study females (22 of 24 in Alto's group, 16 of 16 in each of Dotty's group and Hook's group, and 22 of 27 in Lodge group) through long-term field observations (e.g., Altmann et al. 1985; Altmann and Alberts 2005). We then confirmed maternity and assigned paternity using microsatellite genotypes and data on male maturation and dispersal patterns, as in Buchan et al. (2003); see Alberts et al. (2006) for additional details. We were able to assign paternity to nearly half of the study females, although the proportion to which we could assign paternity varied across groups (7 of 14 sampled females in Alto's group, 13 of 16 in Dotty's group, 5 of 16 in Hook's group, and 14 of 27 in Lodge group).

We used these maternity and paternity assignments to construct maternal pedigrees, paternal pedigrees, and combined maternal and paternal pedigrees. We then used these pedigrees to estimate the coefficient of relatedness due to shared maternal descent (r_{mat}), the coefficient of relatedness due to shared paternal descent (r_{pat}), and the overall coefficient of relatedness (r) within dyads. For example, between a pair of individuals known to be maternal half siblings, not paternally related, and not more distant maternal kin, r_{mat}=0.25, r_{pat}=0.0, and r=0.25. Note that r_{mat} and r_{pat} thus differ by definition from R_{m} and R_{p} of Queller and Goodnight (1989). We calculated r_{mat} separately from r_{pat} because female baboons have different cues available for discriminating maternal kin and paternal kin from nonkin (Alberts 1999; Buchan et al. 2003; Smith et al. 2003), and the greater age disparity among maternal kin, relative to that among paternal kin, might alter the relative advantages of associating with each type of kin (Altmann 1979): Females might therefore act differently toward maternal kin and paternal kin during fissions. In addition, females might respond to their overall kinship to groupmates, reflecting combined maternal coancestry and paternal coancestry, rather than either maternal coancestry or paternal coancestry alone. In other words, the influence of r on female group choice might be distinct from the influence of either r_{mat} or r_{pat}.

After using pedigrees to calculate known r_{mat}, r_{pat}, and r for each dyad, we focused on the individual females to assess whether females preferentially remained with close maternal kin or close paternal kin during fissions. We considered only close kin ($r \geq 0.25$) because some evidence suggests that distant kin ($r<0.25$) are not preferred in the way that close kin are preferred across cercopithecines (Koyama 1970; Kapsalis and Berman 1996a; Chapais et al. 1997; Silk et al. 2004, 2006a; but also see Chapais et al. 2001). In addition, because the variation in relatedness (i.e., the expected proportion of alleles identical by descent) among close kin is less than the variation in relatedness among distant kin (Guo 1996; Guo and Xiong 1997), females could have an even greater preference for close kin over distant kin as part of a risk-averse strategy of nepotism.

If females formed postfission groups primarily with kin, the number of their close maternal kin (n_{mat}), close paternal kin (n_{pat}), and combined close kin (n_{kin}) among postfission groupmates would be higher than expected based on random fission events, so we compared each female's postfission n_{mat}, n_{pat}, and n_{kin} to random expectations. Although females cannot increase the *number* of kin they live with as a consequence of group fission, their *mean* pairwise relatedness (i.e., $\bar{r}_{\mathrm{mat}}$, $\bar{r}_{\mathrm{pat}}$, and $\bar{r}$) to groupmates can increase if they preferentially remain with kin and abandon nonkin. We compared $\bar{r}_{\mathrm{mat}}$, $\bar{r}_{\mathrm{pat}}$, and $\bar{r}$ observed for each female in her postfission group to her $\bar{r}_{\mathrm{mat}}$, $\bar{r}_{\mathrm{pat}}$, and $\bar{r}$ expected based on random fission events. For these comparisons we used $\bar{r}_{\mathrm{mat}}$, $\bar{r}_{\mathrm{pat}}$, and $\bar{r}$ calculated from only close kin (r_{mat}, r_{pat}, or $r \geq 0.25$).

We genotyped 71 of the 81 study females; samples were not available for 10 adult females (of 24) in Alto's group. Our pedigree data alone were insufficient to estimate coefficients of relatedness for some dyads because some pedigrees were incomplete, particularly for paternal kin. For cases where our pedigree data were incomplete, we would like to have estimated each dyad's coefficient of relatedness using a molecular estimate of relatedness (e.g., the estimator R of Queller and Goodnight 1989). However, as has been previously demonstrated by several authors (e.g., van de Casteele et al. 2001; Thomas et al. 2002; Wang 2002; Blouin 2003; Kleven et al. 2005; Thomas 2005; Fernández and Toro 2006), and most recently by Csilléry et al. (2006), marker-based estimates of relatedness were highly variable among dyads of known kinship and so were not informative in the absence of pedigree data (not shown). We therefore restricted our analyses to only those dyads for which we knew kinship either from pedigree or demographic data (e.g., we could assign r_{pat}=0 for a pair of females in cases where no mature male was resident in the social group during the conception of both females). That is, if we knew the paternity of focal female A and her groupmates B and C, but not the paternity of groupmate D, then when considering the group choice of female A we would exclude female D from the analyses.

Although kinship is a symmetrical link between two females, the value of each female to the other is not necessarily symmetrical. The indirect fitness value of a female to her kin is influenced not only by her pedigree position, but also by other factors, including her potential for future reproductive success. This potential, her age-specific reproductive value (RV), is the current value of her estimated future contribution to the population (Stearns 1992; Caswell 2001), and it might modify the value she represents to her kin (Hrdy and Hrdy 1976; Schulman and Chapais 1980; Combes and Altmann 2001). For instance, a postreproductive mother (r_{mat}=0.5, RV=0) would be of less potential indirect fitness value to a female than a paternal half sister in her reproductive prime (r_{pat}=0.25, RV=1.86). Therefore, to assess whether females maximized their potential postfission indirect fitness benefits, rather than either their postfission number of kin or their $\bar{r}$ among groupmates, we used RV for different ages of females in this population that we calculated in an earlier analysis (Alberts and Altmann 2003). We determined the potential indirect fitness benefits to each female from the other females in her group by taking the mean, across her groupmates, of the individual products of their pairwise r and their RV, for maternal kin (r_{mat}), for paternal kin (r_{pat}), and for all close kin (r). We then compared each female's postfission observed and expected potential indirect fitness benefits.

Age proximity

Baboons might use age proximity as a cue for paternal kinship (i.e., to differentiate paternal half siblings from nonkin; Alberts 1999), and age proximity affects the strength of social bonds in rhesus macaques (*M. mulatta*; Widdig et al. 2001) and baboons (Smith et al. 2003; Silk et al. 2006a). However, females also bias their behavior toward paternal kin age peers relative to nonkin age peers (Widdig et al. 2001; Smith et al. 2003). Female group choice might therefore be influenced by age proximity as a proxy for paternal kinship, or females might prefer to remain with paternal sisters who are coincidentally their age peers. We addressed these alternatives by examining whether females preferentially remained with paternal sisters among their age peers, and with nonkin age peers among nonkin. For each study female we classified as her age peers any females who were no more than 365 days younger or older than her, and we determined which of these age peers were her paternal sisters and which were not her kin. We then compared each female's observed and expected number of paternal sister age peers ($\text{peer}_{\text{patsis}}$) and nonkin age peers ($\text{peer}_{\text{nonkin}}$) after fission. We excluded the nongenotyped females in Alto's group from consideration as nonkin to ensure that we did not include unidentified paternal sisters as nonkin.

Social bonds

Sociality has fitness consequences for female baboons (Silk et al. 2003), and might therefore influence which dyads remain together during fission events. As in Silk et al. (2006a), we measured the strength of social bonds with a sociality index (SI) derived from data on the occurrence of grooming and being groomed, and spatial proximity (within 5 m), where $\text{SI} = \left[\left(G_{ij}/G_{xy}\right) + \left(P_{ij}/P_{xy}\right)\right]/2$. G and P are the frequencies of grooming or spatial proximity, respectively. These frequencies have been adjusted to account for differences in the number of days that females coresided. G_{ij} is the adjusted frequency of grooming for baboon dyad i and j; G_{xy} is the mean adjusted frequency of grooming for all dyads in group x in year y. Similarly, P_{ij} is the adjusted frequency of spatial proximity for baboon dyad i and j; P_{xy} is the mean adjusted frequency of spatial proximity for all dyads in group x in year y. Data on grooming and proximity were collected from point samples conducted at 1-min intervals during 10-min focal animal samples (Altmann 1974). SI for a dyad reflects the extent to which that dyad is above or below average in the amount of time it spends grooming or in proximity to each other; dyads with high SI are those that spend more time than average grooming and in spatial proximity (Silk et al. 2006a). See Silk et al. (2006a) for more details on SI.

SI can change over time (Silk et al. 2006b), so we measured SI for each pair of females during the calendar year before onset of fission for three of the four fissions (i.e., 1988 for Alto's group, 1993 for Hook's group, and 1998 for Dotty's group); SI data were not available for Lodge group. SI values were available for 22 adult females in Alto's group, 13 adult females in Dotty's group, and 15 adult females in Hook's group. The strength and stability of social bonds is influenced by kinship (Silk et al. 2004, 2006a, b), so for each female we identified her three strongest social bonds among kin, and her three strongest social bonds among nonkin. To test the hypotheses that kin and nonkin social bonds were retained at random, for each female we compared her postfission observed and expected number of these social partners (n_{kinbond} and $n_{\text{nonkinbond}}$, respectively). Across groups, 19 of the 50 females for whom we had SI data did not have three close kin groupmates; we asked whether these females retained their existing social bonds to close kin. Again, we excluded the nongenotyped females in Alto's group from consideration as nonkin to ensure that we did not include unidentified paternal sisters as nonkin.

Social rank

Social rank often confers fitness benefits on adult female baboons and other primates (see review in Silk 1987; for Amboseli baboons, see Altmann and Alberts 2003a, b, 2005). We therefore evaluated whether females used group choice to maximize their social rank. We assigned an ordinal social rank (e.g., 1, 2, and 3 with 1 being the highest social status) to each adult female at the beginning of fission events, based on the outcome of prior agonistic encounters (Hausfater 1975). We then compared each female's observed postfission rank to her rank expected after random fission. Observed female rank relationships were linear and stable over time, as is the norm for females in this population (e.g., Hausfater et al. 1982; Samuels et al. 1987); only one female (of 81) changed rank relative to other females during fissions: She dropped two ranks over several months. We therefore assumed no changes in relative ranks among females when generating expected postfission ranks. Note that an individual's expected postfission rank measured on an ordinal scale, as in this analysis, is merely the product of group size and the expected dominance rank based on a relative scale (e.g., Beehner et al. 2006). Consequently, our results on social rank would not differ if we used relative rank rather than ordinal rank.

We also tested the specific hypothesis that females followed the AYS strategy (Ron et al. 1994). We noted, for each female except the highest-ranked female of each fission event (i.e., females without immediate superiors to abandon), whether she joined the same postfission group as her immediate superior. We then compared the observed rate of AYS to the rate expected from random fission. The rate at which AYS would randomly occur is the probability that the superior will not be in the same postfission group as the focal female. While the probability of random AYS will sometimes be 0.5, as suggested in Ron et al. (1994), this will be uncommon. Rather, the probability of random AYS is the ratio of [the number of females who do not belong to the same postfission group as the focal female] to [the number of other females in the fission event]. For example, the probability that a female in Alto's group would randomly abandon her superior when joining the smallest (n=4) postfission group is 0.87 (i.e., 20 of 23) while the chance that a female in Lodge group would randomly abandon her superior when joining the larger postfission group (n=17) is 0.385 (i.e., 10 of 26).

Immediate social superiors might often be close maternal kin because the dominance hierarchy of female baboons is matrilineal in nature (Hausfater et al. 1982). Given the influence of maternal kinship on social bonds (Silk et al. 2006a, b) and reproductive fitness (Silk et al. 2003), females might be less likely to follow AYS if those superiors were close maternal kin. To see whether kinship influenced the rate of AYS, we compared the observed and expected rates of AYS among females who would thereby abandon close maternal kin, and among other females.

Comparing observed and expected values

We assessed the degree to which each female's postfission parameters (e.g., n_{mat} and $\bar{r}_{\mathrm{mat}}$) differed from those expected after random fission. For parameters that involved counts of females, such as n_{mat}, we calculated each female's expected postfission value as the product of her prefission value and the proportion of her prefission groupmates who joined her postfission group. For parameters that did not involve count data (i.e., r values), we could not calculate exactly each female's expected postfission value, so we estimated these values via random permutations. To do so, we used POPTOOLS 2.6.2 (Hood 2004) to generate random postfission groupings for each female by sampling her prefission groupmates without replacement to create two groups (or three groups, for Alto's group fission) of the same sizes as the observed postfission groups; we then calculated the mean parameter value for the focal female in the group whose size was equal to that of her observed postfission group. We repeated this process 10,000 times for each female to generate each female's theoretical distribution of postfission values.

We then compared the differences between the observed postfission values and the expected mean values after random fission (see Tables S1 and S2) based on either direct calculation (for n_{mat} and other count data) or from permutations (for r values) as described above, with two-tailed Wilcoxon signed-rank tests (Zar 1999) for each fission event. For example, to test the hypothesis that $\bar{r}$ changed randomly as a result of the fission of Dotty's group, we ran permutations on the values for each of the 16 females in Dotty's group (Fig. 2). We then used Wilcoxon test to assess the significance of the differences between the observed $\bar{r}$ values and the mean $\bar{r}$ values from each corresponding set of permutations. We excluded females without the relevant type of close kin when comparing observed and expected r values (e.g., when comparing observed and expected values of $\bar{r}_{\mathrm{mat}}$ we excluded females who had no close maternal kin). It was straightforward to calculate the probability that AYS would occur randomly, so we used two-tailed binomial tests (Zar 1999) to determine whether AYS occurred as expected by random chance. We tested this for females both with and without close maternal kin as immediate superiors. All α=0.05.

Sample sizes, and therefore statistical power, varied across our analyses, both because we did not have measurements for all parameters for all females in each fission (e.g., we have no measure of n_{pat} for the non-

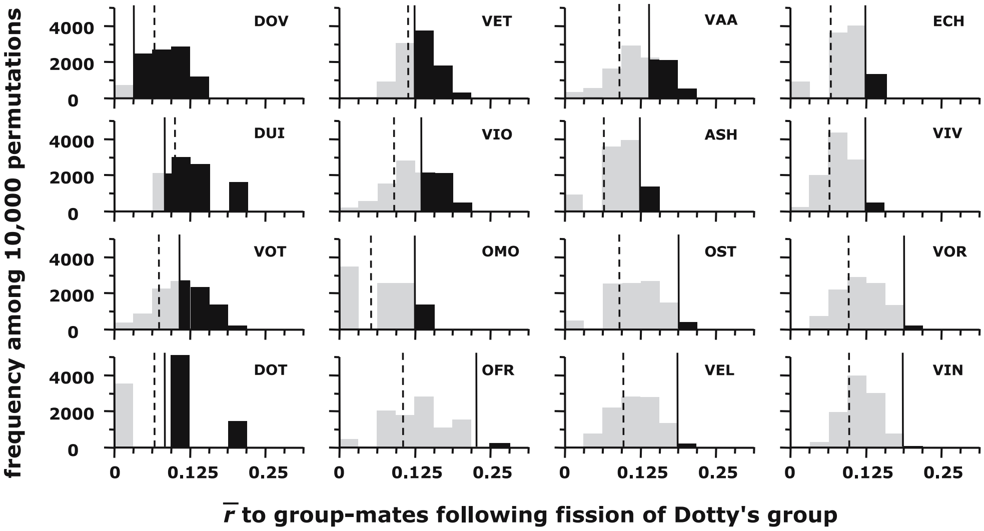

Fig. 2 Illustration of our use of permutations, showing observed and expected postfission $\bar{r}$ to groupmates after fission of Dotty's group. Each *graph* includes results for one adult female. *Solid vertical lines* indicate observed postfission $\bar{r}$; *dashed vertical lines* indicate $\bar{r}$ (expected) from 10,000 permutations of prefission groupmates (see text). *Black bars* indicate $\bar{r}$ – values from permutations that were larger than observed values. Comparison across females of observed $\bar{r}$ to expected $\bar{r}$ with two-tailed Wilcoxon signed-rank test indicated that observed $\bar{r}$ differed from that expected by random chance ($T_{-}=7$, $p<0.001$, $n=16$). These results are summarized in Table 1, line 18

genotyped females in Alto's group) and because females with tied values are excluded from Wilcoxon signed-rank tests (Zar 1999). Given that we could not increase sample sizes and boost statistical power, and that post hoc power analyses provide no more information than do sample sizes and *p* values (Colegrave and Ruxton 2003; see also Hoenig and Heisey 2001; Colegrave and Ruxton 2005; Johnson 2005), we stress that readers should note sample sizes when comparing observed values and expected values.

Results

Kinship

Based on known and assigned pedigree relationships, the number of known kin and the distribution of their relatedness varied widely among females and among groups, both before and after fissions (Fig. 3). Before the fissions, females in Dotty's group and Lodge group had more close maternal kin (i.e., mothers, daughter, and maternal sisters) than did females than in Alto's group and Hook's group. Females had slightly more close paternal kin (i.e., paternal sisters) than close maternal kin before they fissioned (Table 1). Lodge group was extreme in this regard, with one cohort of 13 paternal sisters.

After fissioning, females from Dotty's group and Lodge group stayed with far more close maternal kin than expected by chance (Fig. 3, Tables 1 and S3). In fact, no female from the Lodge group left close maternal kin. In contrast, females from Alto's group and Hook's group split from close

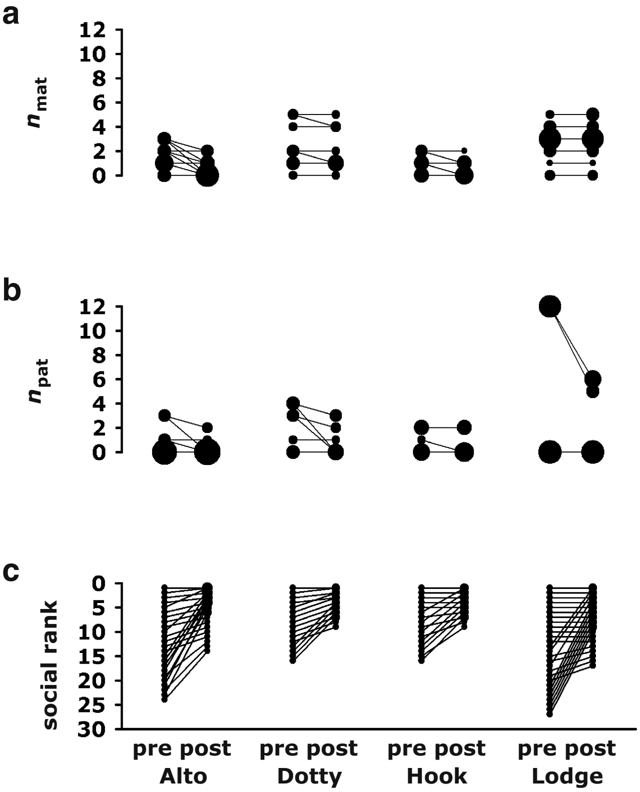

Fig. 3 Impact of fissions on female baboons in Amboseli. *Areas of points* are proportional to the number of adult females with that value. *Lines* connect points for individual females. **a** Number of each female's close ($r \geq 0.25$) maternal kin (n_{mat}) among her groupmates. **b** Number of each female's close paternal kin (n_{pat}) among her groupmates. **c** Each female's social rank, where smaller values indicate higher social rank

Table 1 Observed pre- and postfission mean values (±SD) among female savannah baboons, with values expected by random fission or simulated expected postfission values from 10,000 permutations of groupmates without replacement (random) for several variables: number ($\overline{n}_{\mathrm{mat}}$) of close maternal kin, r from close maternal kin ($\overline{r}_{\mathrm{mat}}$), number ($\overline{n}_{\mathrm{pat}}$) of close paternal kin, r from close paternal kin ($\overline{r}_{\mathrm{pat}}$), combined kinship ($\overline{r}$), number of paternal sister age peers ($\overline{\mathrm{peer}}_{\mathrm{patsis}}$), number of nonkin age peers ($\overline{\mathrm{peer}}_{\mathrm{nonkin}}$), number of coresident three strongest social bonds among kin ($\overline{n}_{\mathrm{kinbond}}$), number of coresident three strongest social bonds among nonkin ($\overline{n}_{\mathrm{nonkinbond}}$), and social rank

	Group	Prefission	Postfission	Random	(Post)-(Random)		
$\overline{n}_{\mathrm{mat}}$[a]	Alto	1.79±0.86	0.74±0.81	0.69±0.49	$T_-=82$	$n=19$	$p=0.311$
	Dotty	**2.57±1.65**	**2.36±1.65**	**1.30±0.93**	**$T_-=0$**	**$n=14$**	**$p<0.001$**
	Hook	1.40±0.52	0.80±0.63	0.67±0.25	$T_-=22$	$n=10$	$p=0.313$
	Lodge	**3.08±0.93**	**3.09±0.93**	**1.63±0.71**	**$T_-=0$**	**$n=24$**	**$p<0.001$**
$\overline{r}_{\mathrm{mat}}$[a]	Alto	0.03±0.02	0.04±0.05	0.03±0.02	$T_-=89$	$n=19$	$p=0.414$
	Dotty	**0.06±0.03**	**0.10±0.06**	**0.06±0.03**	**$T_-=8$**	**$n=14$**	**$p=0.002$**
	Hook	0.04±0.02	0.03±0.03	0.04±0.03	$T_+=18$	$n=10$	$p=0.188$
	Lodge	**0.04±0.02**	**0.09±0.04**	**0.04±0.02**	**$T_-=0$**	**$n=24$**	**$p<0.001$**
$\overline{n}_{\mathrm{pat}}$[a]	Alto	2.00±1.07	1.00±0.93	0.96±0.63	$T_-=16$	$n=8$	$p=0.422$
	Dotty	3.09±1.14	1.82±1.17	1.42±0.49	$T_-=17$	$n=11$	$p=0.087$
	Hook	**1.75±0.46**	**1.50±0.93**	**0.82±0.25**	**$T_-=3$**	**$n=8$**	**$p=0.020$**
	Lodge	12.00±0.00	5.65±0.51	5.65±1.68	$T_+=40$	$n=13$	$p=0.368$
$\overline{r}_{\mathrm{pat}}$[a]	Alto	0.02±0.01	0.02±0.02	0.02±0.01	$T_-=15$	$n=8$	$p=0.371$
	Dotty	0.05±0.02	0.07±0.05	0.05±0.02	$T_-=16$	$n=11$	$p=0.074$
	Hook	**0.03±0.01**	**0.06±0.04**	**0.03±0.01**	**$T_-=3$**	**$n=8$**	**$p=0.020$**
	Lodge	**0.12±0.00**	**0.13±0.05**	**0.12±0.00**	**$T_-=21$**	**$n=13$**	**$p=0.047$**
$\overline{r}$	Alto	0.03±0.02	0.04±0.05	0.03±0.02	$T_-=128$	$n=22$	$p>0.50$
	Dotty	**0.09±0.02**	**0.14±0.05**	**0.09±0.02**	**$T_-=7$**	**$n=16$**	**$p<0.001$**
	Hook	0.04±0.02	0.05±0.05	0.04±0.02	$T_-=40$	$n=15$	$p=0.1384$
	Lodge	**0.10±0.05**	**0.15±0.08**	**0.10±0.05**	**$T_-=28$**	**$n=27$**	**$p<0.001$**
$\overline{\mathrm{peer}}_{\mathrm{patsis}}$	Alto	3.00±0.00	1.50±1.00	0.78±0.62	NA	$n=4$	NA
	Dotty	2.60±0.84	1.90±1.20	1.18±0.39	$T_-=11$	$n=10$	$p=0.053$
	Hook	**1.60±0.55**	**1.60±0.55**	**0.70±0.15**	**$T_-=0$**	**$n=5$**	**$p=0.031$**
	Lodge	4.67±0.99	2.00±0.85	2.29±0.94	$T_+=18$	$n=12$	$p=0.055$
$\overline{\mathrm{peer}}_{\mathrm{nonkin}}$	Alto	3.25±1.48	1.58±1.44	1.27±0.82	$T_-=28$	$n=12$	$p=0.212$
	Dotty	1.00±0.00	1.00±0.00	0.53±0.00	NA	$n=2$	NA
	Hook	2.15±1.07	0.92±0.86	0.98±0.50	$T_-=44$	$n=13$	$p=0.473$
	Lodge	**1.77±0.66**	**0.53±0.62**	**0.92±0.46**	**$T_+=35$**	**$n=17$**	**$p=0.025$**
$\overline{n}_{\mathrm{kinbond}}$[b]	Alto	2.40±0.75	1.10±1.21	1.14±0.72	$T_+=88.5$	$n=20$	$p=0.273$
	Dotty	**2.77±0.44**	**2.310±0.751**	**1.28±0.25**	**$T_-=0$**	**$n=13$**	**$p<0.001$**
	Hook	2.64±0.63	1.43±1.09	1.23±0.31	$T_-=35$	$n=12$	$p=0.400$
$\overline{n}_{\mathrm{nonkinbond}}$[b]	Alto	3	1.33±1.23	1.38±0.71	$T_+=36$	$n=12$	$p=0.425$
	Dotty	**3**	**0.62±0.65**	**1.39±0.13**	**$T_+=5.5$**	**$n=13$**	**$p=0.002$**
	Hook	**3**	**2.20±0.86**	**1.31±0.35**	**$T_-=10$**	**$n=15$**	**$p=0.001$**
Rank	Alto	12.50±7.07	5.63±4.02	5.32±3.48	$T_-=86.5$	$n=22$	$p=0.105$
	Dotty	8.50±4.76	4.56±2.48	4.50±2.06	$T_-=49$	$n=14$	$p=0.428$
	Hook	8.50±4.76	4.56±2.48	4.40±2.10	$T_-=45$	$n=14$	$p=0.335$
	Lodge	14.00±7.94	7.67±4.66	6.98±3.21	$T_-=128$	$n=26$	$p=0.120$

Comparisons between postfission observed values and expected values were assessed with two-tailed Wilcoxon signed-rank tests; statistically significant results ($p<0.5$) are indicated in bold. Sample sizes indicate only the females considered in statistical tests; these tests consider only females for whom values were not tied, and therefore they also consider only females who possessed the parameter of interest (e.g., a female without close paternal kin would not be included in r_{pat}).

[a] Close kin were those with $r_{\mathrm{mat}} \geq 0.25$, $r_{\mathrm{pat}} \geq 0.25$, or $r \geq 0.25$.

[b] We counted only the three strongest bonds with close kin and the three strongest bonds with nonkin among prefission groupmates. However, females often had fewer than three close kin groupmates, resulting in n_{kinbond} values of less than three.

maternal kin as expected by chance. Consequently, postfission $\overline{r}_{\mathrm{mat}}$ to groupmates was significantly higher than expected for females from Dotty's group and Lodge group, but not for females from Alto's group or Hook's group (Tables 1 and S3). Adjusting r_{mat} with RV produced the same results (data not shown) as from r_{mat} alone.

As with close maternal kin, females from different groups varied in their behavior toward close paternal kin during fissions. However, females did not behave in the same way to close paternal kin as they did to close maternal kin (Fig. 3). Females from Hook's group joined postfission groups with more close paternal kin (n_{pat}) than expected, and females from Dotty's group did so as well (Tables 1 and S3). However, females from Alto's group and Lodge group split from close paternal kin as expected by random chance. Females from Hook's group experienced an increase in $\bar{r}_{\mathrm{pat}}$ after fission, and females from Lodge group also did so even though they did not preferentially remain with close paternal kin. Females from Dotty's group showed a similar result in $\bar{r}_{\mathrm{pat}}$ (Tables 1 and S3), but postfission $\bar{r}_{\mathrm{pat}}$ was as expected for females from Alto's group. Adjusting r_{pat} with RV generated the same results (data not shown) as from r_{pat} alone.

Some patterns in $\bar{r}_{\mathrm{pat}}$ were potentially artifacts of bias for coincident maternal kinship. Four of the 17 (23.5%) close paternal kin dyads in Dotty's group were also distant maternal kin and 8 of the 78 (10.3%) close paternal kin dyads in Lodge group were full siblings, so the apparent increase in $\bar{r}_{\mathrm{pat}}$ after fissions of those groups might be due to the preferential maintenance of n_{mat}. However, none of the close paternal kin dyads in Hook's group (n=11) were also maternal kin, so a bias for maternal kin as groupmates cannot explain the unexpectedly high n_{pat} and $\bar{r}_{\mathrm{pat}}$ after fission of Hook's group.

It appeared as though females in groups where close maternal kin were more abundant (e.g., Dotty's group and Lodge group) were more likely to remain with them than females in groups where there were fewer close maternal kin (e.g., Alto's group and Hook's group). To examine this we conducted a post hoc analysis into whether the difference between individuals' observed and expected postfission n_{mat} could be explained by their prefission n_{mat}. Across all groups, we found a significant association between prefission n_{mat} and the observed deviation from the expected postfission n_{mat} (Fig. 4a; Spearman's ρ=0.691, n=67, p<0.001). In other words, females with few close maternal kin in their original group joined postfission groups where they had fewer close maternal kin than expected, and vice versa. The same was not true for close paternal kin. Across all groups, there was no association between prefission n_{pat} and the observed deviation from expected postfission n_{pat} (Fig. 4b; Spearman's ρ=0.087, n=40, p=0.592): The degree to which females had more or fewer close paternal kin than expected in their postfission groups was independent of the number of close paternal kin they had in their original group.

Changes in n_{kin} were similar to the changes in n_{mat}: Females from Dotty's group and Lodge group had higher than expected postfission n_{kin} (Dotty's: T_{-}=11.5, n=16, p< 0.001; Lodge: T_{-}=83.0, n=26, p=0.009), while the postfission n_{kin} values from Alto's group and Hook's group were as expected by chance (Alto's: T_{-}=117.5, n=22, p=0.387; Hook's: T_{-}=35.0, n=15, p=0.0.0844). Patterns of changes in $\bar{r}$ were similar to those in $\bar{r}_{\mathrm{mat}}$. In particular, postfission $\bar{r}$ was higher than expected for females from Dotty's group and Lodge group, but not for females from Alto's group or Hook's group (Tables 1 and S3). Adjusting $\bar{r}$ by RV (data not shown) generated the same results as from $\bar{r}$ alone. The similarity between results for $\bar{r}$ and $\bar{r}_{\mathrm{mat}}$ did not arise artifactually as a result of our more complete knowledge of maternal kinship than paternal kinship. If better knowledge of maternal kinship led us to overemphasize its effect, then

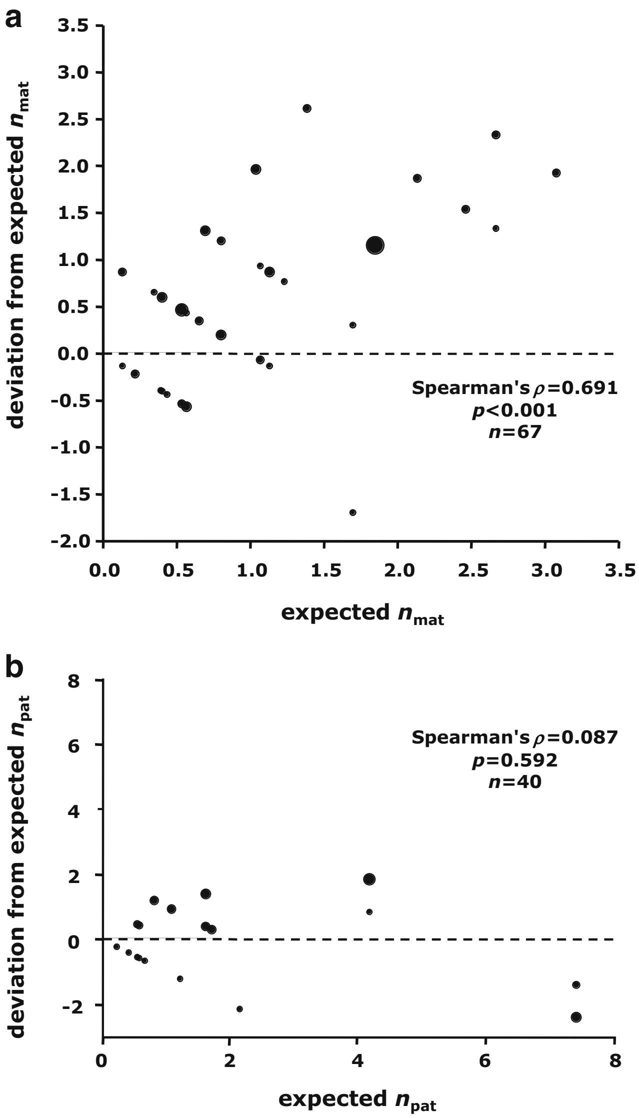

Fig. 4 Relationships, for all females pooled across the fissions, of the expected postfission number of close kin (r≥0.25) and females' postfission deviation from expected numbers of close kin. *Areas of points* are proportional to the number of females with that value. **a** Number of close maternal kin (n_{mat}). **b** Number of close paternal kin (n_{pat}). Note that a female's possible deviation from expected postfission values increases with the number of kin she had before the fission, so random fissions would produce a horizontal V-shaped cloud of data pointing to the left, centered on y=0. Note the different scales on both axes

$\overline{r}_{\mathrm{mat}}$ values should have accounted for a larger fraction of $\overline{r}$ values in Dotty's group and Lodge group, where we saw an effect of maternal kinship on group choice, than in Alto's group and Hook's group, where maternal kinship did not appear influential. This was not the case: $\overline{r}_{\mathrm{mat}}$ values (based on close kin) accounted for a smaller fraction of $\overline{r}$ values (based on close kin) in Dotty's group (64.9%) and in Lodge group (44.7%), than in Alto's group (87.7%) and in Hook's group (97.1%).

Age peers

Females differed greatly in the numbers of age peers (i.e., females born within 365 days of themselves) they had in their prefission groups, but many of these age peers were not close paternal kin. Only 54.1% (59 of 109) of genotyped age peer dyads across fissions were paternal sisters, and only 50.5% (51 of 101) of paternal sister dyads were age peers. Consequently, if females simply chose to remain with age peers they might remain with some of their paternal sisters, but abandon many other paternal sisters. Females with paternal sister age peers in Hook's group always remained with them after the fission, and females from Dotty's group preferentially remained, though not significantly, with them (Tables 1 and S3). In contrast, females from Lodge group split, though not significantly, from their paternal sister age peers. There were too few known paternal sister age peers in Alto's group to analyze. Females from Lodge group split from their nonkin age peers more often than expected, while females from Alto's group and Hook's group left their nonkin age peers as expected; there were too few nonkin age peers in Dotty's group to analyze (Tables 1 and S3).

Social bonds

Social bonds and kinship interacted differently across groups. Before fission, the strongest social bonds to kin were stronger than the strongest social bonds to nonkin (Table S4). The strongest social bonds to kin were preferentially retained during fission by females from Dotty's group (Tables 1 and S3), but the evidence suggests that it was the female kin that were retained preferentially rather than the social bonds; the strongest social bonds to kin were not preferentially retained by females from either Alto's group or Hook's group. In contrast, females from Hook's group did preferentially retain their strongest social bonds to nonkin (Tables 1 and S3).

Social rank

Most females did not follow AYS, that is, they did not abandon their immediate social superiors more often than expected based on random fission. Most females had close maternal kin as immediate superiors (63 of 79 ranks, 79.7%), and the tendency for many females to preferentially remain with close maternal kin reduced the rate at which they followed AYS. In particular, females from Dotty's group with close maternal kin as immediate superiors followed AYS less often (2 of 13 females, 15.4%) than expected by chance (51.8%, $p=0.008$). Similarly, females from Lodge group with close maternal kin as immediate superiors also followed AYS less often (4 of 23 females, 17.4%) than expected by chance (49.0%, $p=0.002$). However, females from Alto's group with close maternal kin as immediate superiors followed AYS as often (13 of 18 females, 72.2%) as expected by chance (62.8%, $p=0.285$). Similarly, females from Hook's group with close maternal kin as immediate superiors followed AYS as often (3 of 9 females, 33.3%) as expected by chance (52.6%, $p=0.206$). Among females whose immediate superiors were not close maternal kin, the observed rate of AYS across fissions (8 of 16 females, 50%) was not different than expected by chance (expected AYS of 53.7%, $p=0.445$), although sample sizes were too small to analyze fissions separately.

Most females (68 of 83 ranks, 81.9%) improved their social status during fissions (Fig. 3). However, because fissions did not alter social rank order, and postfission groups were by definition smaller than prefission groups, most females would rise in status by chance. In fact, there was no evidence that individual females joined postfission groups that raised their ranks above those expected by chance (Tables 1 and S3).

Discussion

Group choice by female savannah baboons illustrates the importance of local variability and contingency, as has been stressed by others (e.g., Henzi et al. 2000a, b). Although Dotty's group and Hook's group had the same number of females, and their fissions took the same amount of time, females in those groups made very different choices. In contrast, although Dotty's group and Lodge group had quite different characteristics (Dotty's group was unprovisioned and much smaller than the provisioned Lodge group), females from both Dotty's and Lodge groups were strongly influenced by maternal kinship. Females in provisioned groups could have more maternal and paternal kin than in unprovisioned groups. Provisioning might thereby create ideal conditions for group choice during fission, in that females might be able to choose between joining a group composed entirely (or primarily) of kin vs a group composed of nonkin. However, these conditions probably rarely occur in unprovisioned groups, where the alternate choices that a female faces might not include such large contrasts as can occur in a provisioned group. In addition, in unprovisioned groups a female might face less favorable choices. For example, if there must be a threshold number of maternal kin for them to be influential, then females with too few maternal kin might instead maximize whatever other factor is to their benefit (e.g., paternal kinship). It could also be that sometimes once fissioning begins, a subset of females with shared interests quickly forms a cohesive clique, leaving excluded females to form an ad hoc subgroup based on their lack of alternatives. This might account for our inability to explain female group choice during the fission of Alto's group; a few females might have chosen their groupmates during that fission, but most might have been forced to make the best of a bad job.

Given the importance of maternal kin to female cercopithecines living in matrilineal societies (e.g., Hrdy and Hrdy 1976; Melnick and Pearl 1987; Silk et al. 2006a, b) one might expect that females with few maternal kin would be especially likely to remain with those kin, and that females with more maternal kin could afford to leave some of them if doing so brought other benefits. It is surprising to note that females did not preferentially retain close maternal kin as groupmates when they had few such kin (e.g., Alto's group and Hook's group). Rather, females hoarded close maternal kin when such kin were abundant (e.g., Dotty's group and Lodge group). This inverse relationship between the size of a group of maternal kin and the likelihood that the kin group divided (Fig. 4a) suggests that a minimum number of kin were required before they could act as a cohesive unit, or quorum, as in the fission of a spotted hyena (*C. crocuta*) social group (Holekamp et al. 1993). Similarly, Armitage and Schwartz (2000) suggested that female yellow-bellied marmots sometimes defer dispersal until they accumulate enough female kin to split off as a separate new matriline. Perhaps when groups contain multiple matrilines it is most necessary for females to remain with maternal kin when there is an increased probability of being opposed by a large coalition of maternally related females. When groups contain few matrilines, or there is a low risk of being opposed by a large coalition of maternal kin, maternal kinship may be less influential than other factors (e.g., social bonds of males and females among chacma baboons).

We should expect that fission patterns would not be fully explained by maternal kinship because maternal kinship is not the only social effect on female fitness (Altmann and Alberts 2003b, 2005; Silk et al. 2003). Maternal kin do, however, appear to take precedence over paternal kin in fissions of matrilineal groups, when a threshold number of maternal kin are present. Although paternal kinship has rarely been examined during fission events, it has been found to be less influential than maternal kinship (Kuester and Paul 1997; Widdig et al. 2006). Our incomplete knowledge of paternity reduces our ability to detect an influence of paternal kinship on group choice; in spite of this we detected an effect of paternal kin on female group choice.

Patterns of changes in overall kinship measured as $\overline{r}$ were similar to those from maternal kinship, again suggesting that when kinship mattered, maternal kinship was more important than was paternal kinship. The lack of increase in $\overline{r}$ after the fission of Hook's group could have occurred because the increase in $\overline{r}_{\mathrm{pat}}$ was counterbalanced by those females' disregard for n_{mat}. A similar random change in overall relatedness after fission, due to differential retention of maternal kin and paternal kin, was suggested for wild rhesus macaques (Melnick and Kidd 1983). In any case, our results for $\overline{r}$ support the conclusion that kinship had a greater influence on females from Dotty's group and Lodge group than females from Alto's group and Hook's group. The role of kinship in female group choice was not obviously altered by the reproductive value of individual group mates. This indicates either that females could not assess the reproductive value of other females, or that the primary value of kin to a female was through their impact on her direct fitness, not through their impact on her indirect fitness.

Kinship and age proximity together influenced group choice, although females did not prefer to remain with age peers per se. Paternal kinship among age peers was more salient to females from Hook's group than was age proximity, and age proximity itself was not an attractant for females in any fission.

Social bonds were not as important as kinship during fissions. Grooming and associative bonds have not always been preferentially maintained during fissions of matrilineal groups (e.g., Ron et al. 1994; Okamoto and Matsumura 2001), and their retention could have been confounded by kinship (e.g., Cords and Rowell 1986). For females from Dotty's group the salient feature of preferred social partners was their kinship, but for females from Hook's group the value of social partners was either the social bond itself or an unmeasured factor that increased their social affiliation (e.g., mutual social bonds with a third party).

Smaller group size might be a key benefit of permanent fissions to female savannah baboons, as smaller group size enhances their reproduction (Altmann and Alberts 2003a; Davidson et al., unpublished data), probably reduces their competition for resources, and often improves their social status. Most females in every fission gained social rank, but these gains merely reflected smaller group sizes: Most females did not maximize their postfission social rank nor did they follow AYS. On the contrary, females from Dotty's group and Lodge group preferred to remain with their immediate social superior when those superiors were close maternal kin. When describing the use of AYS by female chacma baboons, Ron et al. (1994) noted high rates of aggression but almost no coalitionary support among these females who may have had few close maternal kin. Perhaps in chacma baboons, where social groups are smaller and coalitionary support appears to play little or no role in females' social lives (Barrett et al. 1999; Henzi and Barrett 2003; Silk et al. 2004), females are able to independently maintain their individual social rank. However, where the social rank of a female savannah baboon partially depends on the support of maternal kin (e.g., Walters 1980; Horrocks and Hunte 1983; Silk et al. 2004), then individual females are not generally free to maximize their social rank. Typically, when status has played a role in fissions of matrilineal groups, kin with adjacent social ranks have split off as coherent blocks and jointly improved their social status (e.g., Oi 1988; Barton et al. 1996; Widdig et al. 2006).

Female group choice could have been influenced by a factor beyond the scope of this study: males. In some fissions of matrilineal groups, females' mating histories or social bonds with particular males have been important (Nash 1976; Li et al. 1996; Henzi et al. 2000a, b). Indeed, in some baboon populations, fission may occur as a response to the threat of infanticide, that is, females may leave a social group in the company of the father of their offspring when a new, potentially infanticidal male joins the group (e.g., Hamilton and Bulger 1993; Henzi et al. 2000a, b; reviewed in Henzi and Barrett 2003). Perhaps males mattered to females from Hook's group, to whom maternal kin appeared unimportant. If the primary influence on those females was the presence of a male with whom the female had conceived offspring or with whom she had a strong social bond, this might produce the apparent preference for close paternal kin, for paternal sister age peers, and for nonkin social partners (i.e., if some females were mutually bonded to a focal male or were herded by a focal male).

Simple decision rules can allow animals to make adaptive choices quickly with little information (Todd and Gigerenzer 2000), and modeling suggests that simple rules can lead to consensus among individuals (Seeley and Visscher 2004; Couzin et al. 2005). However, if females cannot distinguish the values of alternative groups, or if conflicting interests among females prevents them from reaching a quorum, it might be difficult for females to coalesce into new groups. Fission events often begin with the unobtrusive formation of socially disjunct cliques within a spatially cohesive group, before the more obvious spatial separation that finalizes permanent group fission (Missakian 1973; Dittus 1988; Oi 1988; Hood and Jolly 1995). Perhaps the initial period of social dissolution indicates the necessary interval of information gathering before the finality of spatial separation. Spatial separation during permanent group fissions typically takes several months to years, especially among unprovisioned groups, although it can occur quite quickly (Furuya 1968, 1969; Missakian 1973; Chepko-Sade 1974; Cords and Rowell 1986; Dittus 1988; Oi 1988; Ménard and Vallet 1993; Li et al. 1996; Okamoto and Matsumura 2001). We make no claims here as to whether subgroups of female baboons reach consensus on postfission group membership, or respond to the formation of distinct and separate quorums (see Seeley and Visscher 2004), and we do not speculate as to the cues used by individuals during group choice. However, if the length of time required for a fission event is indicative of the difficulty that individuals have in collecting information, reaching consensus, or forming a quorum, then this might explain why fissions were quicker in the Lodge group than in the unprovisioned groups. The contrast in value between groups could have been greater for females in Lodge group (e.g., join a group composed nearly entirely of maternal kin vs a group not composed of maternal kin), which might require less time for information gathering and consensus building (a group composed nearly entirely of close maternal kin would likely form a consensus quicker than a group composed of maternal kin and nonkin) or building a quorum (the cluster of close maternal kin might be large enough to form a new group without including nonkin). This is also consistent with simpler patterns of female group choice in Lodge group and in other provisioned groups (e.g., Cheverud et al. 1978; Kuester and Paul 1997; Koyama 2003) than in the unprovisioned Amboseli groups.

Many explanations have been proposed for why matrilineal groups split (reviewed in Chapman and Pavelka 2005). Most reported fissions of matrilineal groups, especially among provisioned groups, have occurred when unusually large group size, high density, or environmental stress led to increased intragroup competition for food, which could be reduced through fission; fissions might also occur when individuals do not have sufficient time to maintain the requisite social networks (Sugiyama 1960; Furuya 1968, 1969; Chepko-Sade and Olivier 1979; Mohnot et al. 1981; Malik et al. 1985; Dittus 1988; Mills 1990; Dunbar 1992; Holekamp et al. 1993; Ménard and Vallet 1993; Barton et al. 1996; Li et al. 1996; Henzi et al. 1997). In addition, unusually high intragroup competition for resources sometimes manifests itself as rank reversal among females (Dittus 1988), so that rank instability presages fission. At Amboseli no single explanation or indicator clearly applied across fissions. Fissions in Amboseli were not preceded by rank reversals among females nor did they lead to rank reversals among females. Prefission group size varied widely, suggesting that group size itself was not a consistent trigger for fission (i.e., there was no consistent maximum group size). This in turn suggests two nonexclusive scenarios; addressing these is beyond the scope of this paper. First, different constraints and pressures may have applied in different groups. Second, time constraints or feeding competition may not have been sufficient conditions for fission, although they may have been necessary conditions for fission. In other words, the likelihood of fission may rise with increased costs due to ecological pressures, as others have suggested (e.g., Dunbar 1992; Henzi et al. 1997), but permanent group fission may require more than just the presence of increased costs in a large group. Fission may also require the presence of a subgroup of individuals with mutually shared interests, for whom the most profitable option is to leave the original group. Variation in the nature of these interests among individuals may drive the variation in group choice during fissions.

Acknowledgements This work was supported by NSF BCS-0323553, NSF IBN-0322613, its predecessors, and the Chicago Zoological Society. We thank many Kenyans for their assistance: the Office of the President, Republic of Kenya, the Kenya Wildlife Services, its Amboseli staff and Wardens, the Institute of Primate Research, the National Museums of Kenya, and the members of the Amboseli–Longido pastoralist communities. Particular thanks go to the Amboseli fieldworkers who contributed to sample and data collection, especially to R. Mututua, S. Sayialel, and J. Warutere. D. Onderdonk and L. Gerber provided database assistance. J. Silk provided the SI data, and K. Smith identified some paternal relationships in Hook's group. Helpful comments were provided by R. Davidson and several others at Duke University: E. Archie, C. Fitzpatrick, J. Hollister-Smith, D. Loisel, J. Tung, A. Widdig, Y. Zhu, and members of the Drea lab. David Watts, Peter Henzi, and an anonymous reviewer provided helpful comments on an earlier version of this manuscript. All protocols were noninvasive and comply with relevant regulations in Kenya (Kenya Research Permit MOEST 13/001/33C 179) and the United States (Duke University IACUC protocol A180-03-05).

References

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

Alberts SC, Altmann J (2003) Matrix models for primate life history analysis. In: Kappeler PM, Pereira ME (eds) Primate life history and socioecology. University of Chicago Press, Chicago, IL, USA, pp 66–102

Alberts SC, Buchan JC, Altmann J (2006) Sexual selection in wild baboons: from mating opportunities to paternity success. Anim Behav 72:1177–1196

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267

Altmann J (1979) Age cohorts as paternal sibships. Behav Ecol Sociobiol 6:161–164

Altmann J, Alberts SC (2003a) 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: human fertility behavior in biodemographic perspective. The National Academies Press, Washington, DC, USA, pp 140–169

Altmann J, Alberts SC (2003b) Variability in reproductive success viewed from a life-history perspective in baboons. Am J Hum Biol 15:401–409

Altmann J, Alberts SC (2005) Growth rates in a wild primate population: ecological influences and maternal effects. Behav Ecol Sociobiol 57:490–501

Altmann J, Muruthi P (1988) Differences in daily life between semiprovisioned and wild-feeding baboons. Am J Primatol 15:213–221

Altmann J, Hausfater G, Altmann SA (1985) Demography of Amboseli baboons, 1963–1983. Am J Primatol 8:113–125

Armitage KB (1987) Social dynamics of mammals: reproductive success, kinship and individual fitness. Trends Ecol Evol 2:279–284

Armitage KB, Schwartz OA (2000) Social enhancement of fitness in yellow-bellied marmots. Proc Natl Acad Sci USA 97:12149–12152

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

Barton RA, Byrne RW, Whiten A (1996) Ecology, feeding competition and social structure in baboons. Behav Ecol Sociobiol 38:321–329

Beehner JC, Bergman TJ, Cheney DL, Seyfarth RM, Whitten PL (2006) Testosterone predicts future dominance rank and mating activity among male chacma baboons. Behav Ecol Sociobiol 59:469–479

Blouin MS (2003) DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. Trends Ecol Evol 18:503–511

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

Bulger J, Hamilton WJI (1987) Rank and density correlates of inclusive fitness measures in a natural chacma baboon (*Papio ursinus*) troop. Int J Primatol 8:635–650

Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer, Sunderland, MA, USA

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

Chapman CA, Pavelka MSM (2005) Group size in folivorous primates: ecological constraints and the possible influence of social factors. Primates 46:1–9

Cheney DL, Seyfarth RM, Fischer J, Beehner J, Bergman T, Johnson SE, Kitchen DM, Palombit RA, Rendall D, Silk JB (2004) Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. Int J Primatol 25:401–428

Chepko-Sade BD (1974) Division of group F at Cayo Santiago. Am J Phys Anthropol 41:472

Chepko-Sade BD, Olivier TJ (1979) Coefficient of genetic relationship and the probability of intragenealogical fission in *Macaca mulatta*. Behav Ecol Sociobiol 5:263–278

Cheverud JM, Buettner-Janusch J, Sade D (1978) Social group fission and the origin of intergroup genetic differentiation among the rhesus monkeys of Cayo Santiago. Am J Phys Anthropol 49:449–456

Colegrave N, Ruxton GD (2003) Confidence intervals are a more useful complement to nonsignificant tests than are power calculations. Behav Ecol 14:446–450

Colegrave N, Ruxton GD (2005) What hypothesis tests are not: a reply to Johnson. Behav Ecol 16:325

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

Cords M, Rowell TE (1986) Group fission in blue monkeys of the Kakamega Forest, Kenya. Folia Primatol 46:70–82

Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. Nature 433:513–516

Csilléry K, Johnson T, Beraldi D, Clutton-Brock T, Coltman D, Hansson B, Spong G, Pemberton JM (2006) Performance of marker-based relatedness estimates in natural populations of outbred vertebrates. Genetics 173:2091–2101

Dittus WPJ (1988) Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. Anim Behav 36:1626–1645

Dunbar RIM (1992) Time: a hidden constraint on the behavioral ecology of baboons. Behav Ecol Sociobiol 31:35–49

Fernández J, Toro MA (2006) A new method to estimate relatedness from molecular markers. Mol Ecol 15:1657–1667

Furuya Y (1960) An example of fission of a natural troop of Japanese monkey at Gagyusan. Primates 2:149–179

Furuya Y (1968) On the fission of troops of Japanese monkeys. I. Five fissions and social changes between 1955 and 1966 in the Gagyusan troop. Primates 9:323–350

Furuya Y (1969) On the fission of troops of Japanese monkeys. II. General view of troop fission of Japanese monkeys. Primates 10:47–69

Gompper ME (1997) Population ecology of the white-nosed coati (*Nasua narica*) on Barro Colorado Island, Panama. J Zool (Lond) 241:441–455

Guo SW (1996) Variation in genetic identity among relatives. Hum Hered 46:61–70

Guo S-W, Xiong M (1997) Genes preserved in relatives. Hum Hered 47:138–154

Hamilton WJ, Bulger J (1993) Origin and fate of a one-male savanna baboon group formed by fissioning. Int J Primatol 14:131–143

Hausfater G (1975) Dominance and reproduction in baboons (*Papio cynocephalus*): a quantitative analysis, vol 7. S. Karger, Basel

Hausfater G, Altmann J, Altmann S (1982) Long-term consistency of dominance relationships among female baboons (*Papio cynocephalus*). Science 217:752–755

Henzi P, Barrett L (2003) Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. Evol Anthropol 12:217–230

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

Henzi SP, Barrett L, Weingrill A, Dixon P, Hill RA (2000a) Ruths amid the alien corn: males and the translocation of female chacma baboons. S Afr J Sci 96:61–62

Henzi SP, Lycett JE, Weingrill A, Piper SE (2000b) Social bonds and the coherence of mountain baboon troops. Behaviour 137:663–680

Hill DA (1999) Effects of provisioning on the social behaviour of Japanese and rhesus macaques: implications for socioecology. Primates 40:187–198

Hoenig JM, Heisey DM (2001) The abuse of power: the pervasive fallacy of power calculations for data analysis. Am Stat 55:19–24

Hohmann G (1989) Group fission in Nilgiri langurs (*Presbytis johnii*). Int J Primatol 10:441–454

Holekamp KE, Smale L (1995) Rapid change in offspring sex ratios after clan fission in the spotted hyena. Am Nat 145:261–278

Holekamp KE, Ogutu JO, Frank LG, Dublin HT, Smale L (1993) Fission of a spotted hyena clan: consequences of female absenteeism and causes of female emigration. Ethology 93:285–299

Hood GM (2004) Poptools version 2.6.2. Availble at http://www.cse.csiro.au/poptools

Hood LC, Jolly A (1995) Troop fission in female Lemur catta at Berenty Reserve, Madagascar. Int J Primatol 16:997–1015

Horrocks JA, Hunte W (1983) Rank relations in vervet sisters: a critique of the role of reproductive value. Am Nat 122:417–421

Hrdy SB, Hrdy DB (1976) Hierarchical relations among female hanuman langurs (Primates: Colobinae, *Presbytis entellus*). Science 193:913–915

Jakob EM (2004) Individual decisions and group dynamics: why pholcid spiders join and leave groups. Anim Behav 68:9–20

Johnson SE (2003) Life history and the competitive environment: trajectories of growth, maturation, and reproductive output among chacma baboons. Am J Phys Anthropol 120:83–98

Johnson DH (2005) What hypothesis tests are not: a response to Colegrave and Ruxton. Behav Ecol 16:204–205

Kappeler PM, van Schaik CP (2002) Evolution of primate social systems. Int J Primatol 23:707–740

Kapsalis E, Berman CM (1996a) Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) I. Criteria for kinship. Behaviour 133:1209–1234

Kapsalis E, Berman CM (1996b) Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) II. Testing predictions for three hypothesized organizing principles. Behaviour 133:1235–1263

Kleven O, Jacobsen F, Robertson RJ, Lifjeld JT (2005) Extrapair mating between relatives in the barn swallow: a role for kin selection? Biol Lett 1:389–392

Koyama N (1970) Changes in dominance rank and division of a wild Japanese monkey troop in Arashiyama. Primates 11:335–390

Koyama NF (2003) Matrilineal cohesion and social networks in *Macaca fuscata*. Int J Primatol 24:797–811

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, New York, NY, USA

Kuester J, Paul A (1997) Group fission in Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. Int J Primatol 18:941–966

Lefebvre D, Ménard N, Pierre JS (2003) Modelling the influence of demographic parameters on group structure in social species with dispersal asymmetry and group fission. Behav Ecol Sociobiol 53:402–410

Le Galliard J-F, Ferrière R, Dieckmann U (2005) Adaptive evolution of social traits: origin, trajectories, and correlations of altruism and mobility. Am Nat 165:206–224

Li J, Wang Q, Han D (1996) Fission in a free-ranging Tibetan macaque troop at Huangshan Mountain, China. Chin Sci Bull 41:1377–1381

Malik I, Seth PK, Southwick CH (1985) Group fission in free-ranging rhesus monkeys of Tughlaqabad, northern India. Int J Primatol 6:411–422

Melnick DJ, Kidd KK (1981) Social group fission and paternal relatedness. Am J Primatol 1:333–334

Melnick DJ, Kidd KK (1983) The genetic consequences of social group fission in a wild population of rhesus monkeys (*Macaca mulatta*). Behav Ecol Sociobiol 12:229–236

Melnick DJ, Pearl MC (1987) Cercopithecines in multimale groups: genetic diversity and population structure. In: Smuts BB, Cheney DL, Seyfarth R, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, IL, USA, pp 121–134

Ménard N, Vallet D (1993) Dynamics of fission in a wild Barbary macaque group (*Macaca sylvanus*). Int J Primatol 14:479–500

Mills MGL (1990) Kalahari hyaenas: comparative behavioral ecology of two species. Unwin Hyman, London

Missakian EA (1973) The timing of fission among free-ranging rhesus monkeys. Am J Phys Anthropol 38:621–624

Mizuhara H (1964) Social changes of Japanese monkey troops in the Takasakiyama. Primates 5:27–52

Mohnot SM, Gadgil M, Makwana SC (1981) On the dynamics of the Hanuman langur population of Jodhpur (Rajasthan, India). Primates 22:182–191

Muruthi P, Altmann J, Altmann S (1991) Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. Oecologia 87:467–472

Nash LT (1976) Troop fission in free-ranging baboons in the Gombe Stream National Park, Tanzania. Am J Phys Anthropol 44:63–78

Oi T (1988) Sociological study on the troop fission of wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island. Primates 29:1–19

Okamoto K, Matsumura S (2001) Group fission in Moor macaques (*Macaca maurus*). Int J Primatol 22:481–493

Packer C, Collins DA, Sindimwo A, Goodall J (1995) Reproductive constraints on aggressive competition in female baboons. Nature 373:60–63

Paul A, Kuester J (1987) Dominance, kinship and reproductive value in female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. Behav Ecol Sociobiol 21:323–331

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. Evolution 43:258–275

Ransom TW (1981) Beach troop of the Gombe. Bucknell University Press, Lewisburg, PA, USA

Robinson JG (1988) Demography and group structure in wedge-capped capuchin monkeys, *Cebus olivaceus*. Behaviour 104:202–232

Ron T (1996) Who is responsible for fission in a free-ranging troop of baboons? Ethology 102:128–133

Ron T, Henzi P, Motro U (1994) A new model of fission in primate troops. Anim Behav 47:223–226

Samuels A, Silk JB, Altmann J (1987) Continuity and change in dominance relationships among female baboons. Anim Behav 35:785–793

Schulman SR, Chapais B (1980) Reproductive value and rank relations among macaque sisters. Am Nat 115:580–593

Seeley TD, Visscher PK (2004) Quorum sensing during nest-site selection by honeybee swarms. Behav Ecol Sociobiol 56:594–601

Silk JB (1987) Social behavior in evolutionary perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, IL, USA, pp 318–329

Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. Science 302:1231–1234

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, Altmann J, Alberts SC (2006a) Social relationships among adult female baboons (*Papio cynocephalus*). I. Variation in the strength of social bonds. Behav Ecol Sociobiol 61:183–195

Silk JB, Alberts SC, Altmann J (2006b) Social relationships among adult female baboons (*Papio cynocephalus*). II. Variation in the quality and stability of social bonds. Behav Ecol Sociobiol 61:197–204

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

Smuts BB (1985) Sex and friendship in baboons. Aldine, Hawthorne, NY, USA

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Stoltz LP (1972) The size, composition and fissioning in baboon troops (*Papio ursinus* Kerr, 1792). Zool Afr 7:367–378

Sugiyama Y (1960) On the division of a natural troop of Japanese monkeys at Takasakiyama. Primates 2:109–148

Thomas SC (2005) The estimation of genetic relationships using molecular markers and their efficiency in estimating heritability in natural populations. Philos Trans R Soc Lond B 360:1457–1467

Thomas SC, Coltman DW, Pemberton JM (2002) The use of marker-based relationship information to estimate the heritability of body weight in a natural population: a cautionary tale. J Evol Biol 15:92–99

Todd PM, Gigerenzer G (2000) Précis of *Simple heuristics that make us smart*. Behav Brain Sci 23:727–741

van de Casteele T, Galbusera P, Matthysen E (2001) A comparison of microsatellite-based pairwise relatedness estimators. Mol Ecol 10:1539–1549

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87:120–144

Walters J (1980) Interventions and the development of dominance relationships in female baboons. Folia Primatol 34:61–89

Wang J (2002) An estimator for pairwise relatedness using molecular markers. Genetics 160:1203–1215

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 USA 98:13769–13773

Widdig A, Nürnberg P, Bercovitch FB, Trefilov A, Berard JB, Kessler MJ, Schmidtke J, Streich WJ, Krawczak M (2006) Consequences of group fission for the patterns of relatedness among rhesus macaques. Mol Ecol 15:3825–3832

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, Upper Saddle River, NJ, USA