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The benefits of social capital: close social bonds among female baboons enhance offspring survival

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Sociality has evolved in many animal taxa, but primates are unusual because they establish highly differentiated bonds with other group members. Such bonds are particularly pronounced among females in species like baboons, with female philopatry and male dispersal. These relationships seem to confer a number of short-term benefits on females, and sociality enhances infant survival in some populations. However, the long-term consequences of social bonds among adult females have not been well established. Here we provide the first direct evidence that social relationships among female baboons convey fitness benefits. In a group of free-ranging baboons, *Papio cynocephalus ursinus*, the offspring of females who formed strong social bonds with other females lived significantly longer than the offspring of females who formed weaker social bonds. These survival benefits were independent of maternal dominance rank and number of kin and extended into offspring adulthood. In particular, females who formed stronger bonds with their mothers and adult daughters experienced higher offspring survival rates than females who formed weaker bonds. For females lacking mothers or adult daughters, offspring survival was closely linked to bonds between maternal sisters. These results parallel those from human studies, which show that greater social integration is generally associated with reduced mortality and better physical and mental health, particularly for women.

Keywords: social bonds; female relationships; baboons; primates; social capital; fitness

1. INTRODUCTION

Sociality has evolved in many animal taxa, but primates are unusual because they establish highly differentiated bonds with other members of their groups (Cheney & Seyfarth 2007; Dunbar & Schultz 2007; Silk 2007). Female baboons (*Papio cynocephalus* spp.) form strong, equitable and enduring social bonds with particular females in their group (Silk *et al.* 1999; 2006a,b). Indirect evidence suggests that these relationships may be adaptive. First, like other haplorhine primates, baboons have highly developed social cognition, which allows them to track not just their own relationships but also those among other group members (Cheney & Seyfarth 2007). Second, female chacma baboons (*P. c. ursinus*) who concentrate their grooming on a small number of partners have lower glucocorticoid levels and cope better with psychological stressors than females with more diffuse grooming networks (Crockford *et al.* 2008; Wittig *et al.* 2008). When a preferred partner dies, glucocorticoid levels increase and females expand their grooming networks in an apparent attempt to identify new partners (Engh *et al.* 2006). Here we provide

the first direct evidence that social relationships among adult females also have fitness consequences for individuals.

Like other groups of cercopithecine primates, savannah baboon groups are composed of a dominance hierarchy of matriline and varying numbers of unrelated immigrant males (Henzi & Barrett 2003; Swedell & Leigh 2006). Members of high-ranking matriline enjoy a competitive advantage over members of lower-ranking ones, but the magnitude of the effect of dominance rank on female reproductive success, as in most primate species, is generally modest (Altmann & Alberts 2003; Cheney *et al.* 2004). Although females interact with all other group members, they maintain close, long-term bonds with only a few other females, who are usually close kin or peers (Silk *et al.* 1999; Silk *et al.* 2006a,b). The benefits to females of maintaining such bonds, however, are not immediately obvious. Only one previous study, conducted on yellow baboons (*P. c. cynocephalus*) in Amboseli, Kenya, has documented a relation between sociality and a component of fitness. In that study, females who spent more time grooming and associating with other adults experienced higher infant survival (Silk *et al.* 2003a).

The current study extends that analysis in three important ways. First, whereas the Amboseli analysis considered

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infant survival to 1 year, we examine offspring survival into adulthood. Second, the Amboseli study included interactions with adult males, leaving open the possibility that females' associations with males might have driven the results. This is a potentially important consideration, because new mothers often form 'friendships' with adult males in response to the threat of infanticide by immigrant males (Palombit *et al.* 1997). The current study restricts analyses to interactions among adult females (for additional rationale, see §2). Additionally, because infants in this population are at highest risk of infanticide during their first six months of life (unpublished data), we consider the impact of social bonds among females on infant survival after this age. Third, some have argued that, because female baboons are strongly attracted to other females' infants (Altmann 1980; Bentley-Condit & Smith 1999; Silk *et al.* 2003b), the relationship between female sociality and infant survival might simply reflect elevated levels of sociality for mothers of surviving infants rather than benefits derived from sociality (Henzi & Barrett 2007). Here we restrict analyses to interactions among adult females when they do not have young infants.

2. MATERIAL AND METHODS

The analysis is based on observations of a group of free-ranging chacma baboons in the Moremi Game Reserve of the Okavango Delta, Botswana from 1992 to 2007 (see Cheney *et al.* 2004; Cheney & Seyfarth 2007 for additional details about the study site). Research was reviewed and approved by the Animal Care and Use Committee at the University of Pennsylvania (Protocol no. 19001). Observations of the study population were initiated in 1978 by the late W. J. Hamilton III and colleagues. From June 1992 to December 2007, the group was observed almost daily by researchers working in collaboration with D.L.C. and R.M.S. Maternal kinship relationships among all group members were known; paternal kinship was available for a subset of individuals. The ages of all females born in the group after 1982 were known.

Almost all deaths among juveniles and adult females are due to suspected or confirmed predation (43/44 = 97%, Cheney *et al.* 2004; see also Busse 1982; Bulger & Hamilton 1987). The causes of individual differences in vulnerability to predation are unclear. However, there is no evidence that low-ranking animals are more susceptible to predation than high-ranking ones (Cheney *et al.* 2004).

Focal samples on adult females (≥ 5.0 years) were collected in 1992–1993 and 2001–2007 using a common protocol. Observations were conducted primarily between 07.00 and 14.00 h. All approaches, vocalizations, social interactions and aggressive interactions involving the focal female were recorded on a continuous basis. The onset and termination of all grooming bouts were recorded, producing information about both the frequency and duration of grooming. The dataset contains approximately 15 300 focal observations of 66 adult females over 251 female years. There were 1174 co-resident adult female dyads in the study group during this period. Behavioural analyses are based on 998 dyads that were observed for at least 10 h (mean, s.e.: 47.15 ± 0.93 h).

Because we were interested in the relation between female–female bonds and offspring survival, we excluded females' interactions with males from the analyses. There are several reasons for hypothesizing that females'

relationships with males do not significantly influence offspring survival in this population, especially after infancy. First, females do not maintain close relationships with males except during lactation, when they form 'friendships' with specific individuals in response to the threat of infanticide (Busse & Hamilton 1981). These bonds are not enduring; they are absent during pregnancy, form only after parturition and cease abruptly after the female resumes sexual cycling or her infant dies (Palombit *et al.* 1997, 2000). Females do not form friendships with the same male in successive lactational periods (Palombit *et al.* 1997; Moscovice *et al.* in preparation). Thus, although some males maintain bonds with real and putative offspring after weaning (Moscovice *et al.* in press), these bonds are not mediated by long-term relationships with those individuals' mothers. Second, although there is variation in the strength of friendships among lactating females and males, long-term demographic records suggest that this variation may have little impact on infant survival. For example, low-ranking and older females tend to form weaker friendships than other females, and sometimes do not form friendships at all, but they do not experience higher infant mortality (Palombit *et al.* 2000; Cheney *et al.* 2004; unpublished data). Moreover, if an immigrant male rises to the top of the male dominance hierarchy and begins to commit infanticide, females with strong relationships with male friends are as vulnerable as those with weaker relationships (Palombit *et al.* 1997, unpublished data). Nonetheless, to avoid any possible confounding influence of male–female friendships on infant survival, our analyses exclude offspring mortality prior to six months of age, when infants are most vulnerable to infanticide. Finally, over a 15-year period only 48% male immigrants ($n = 54$) remained in the group for more than 1 year, and only 19% remained for more than 3 years. Thus, even if females had attempted to establish long-term bonds with specific males, most of these bonds would have been relatively transient.

To control for the effects of the presence of young infants on the mothers' social relationships with other adult females, behavioural analyses excluded all data from females with infants under 100 days of age. This age threshold was set because previous analyses have shown that natal attraction in this population wanes after infants reach this age (Silk *et al.* 2003b).

Following Silk *et al.* (2006a,b), we constructed a composite sociality index (CSI) to characterize the strength of relationships within dyads. To determine what behaviours should be included in the CSI, we tabulated a variety of non-aggressive interactions and vocalizations among adult females. Not all females were present in the study group for the same amounts of time. To adjust for variation in co-residence time, we divided the number of interactions for each dyad by the total amount of time that each female was observed when the other female was co-resident. For grooming, we computed measures based on both the frequency and duration of grooming. Then, we evaluated the magnitude of the correlations in the rates of these behaviours, and retained behaviours that generated the highest correlations: approach, present for grooming, grooming frequency, grooming duration. Grooming frequency was defined as the number of grooming bouts initiated per hour of observation, while grooming duration was the number of minutes spent grooming per hour of observation.

To construct the CSI, the following procedure was followed. For each behavioural measure, the rate for a

particular pair of females was divided by the mean rate for all dyads. The quotients for each dyad were summed across behaviours, and then divided by four, the number of behavioural categories included in the index. Thus, the CSI measures the extent to which each dyad deviated from other dyads. The mean of the CSI is defined as 1, but the values can range from 0 to infinity. Values above 1 represent dyads that had stronger social bonds than the average female dyad in the group; values below 1 represent dyads that had weaker social bonds.

Following Silk *et al.* (2006a,b), we used yearly values of the CSI to identify each females' top three partners each year. These females were designated 'top partners'. To determine how long close social bonds lasted, we tabulated consistency in top partners across years. If female B was among female A's top three partners for three consecutive years, then the duration of the close social bond was defined as 3 years. For consistency with Silk *et al.* (2006b), we allowed a 1-year gap between consecutive years. Thus, if female B was among female A's top partners in year 1, year 2, and year 4, but not year 3, the duration of the close social bond was defined as 4 years.

To assess the effects of sociality on offspring survival, we conducted a multivariate survival analysis using the Cox proportional hazards model. This allowed us to include survivorship data on a number of offspring that were still alive at the end of the study and to examine the effects of several different variables on infant survival simultaneously. In the analyses, the infant is the unit of analysis. Because some females contributed more than one infant to the dataset, we used the cluster option to control for the effects of maternal identity. All statistical analyses were conducted with STATA 10.0. Where appropriate, we report means \pm standard errors. All statistical tests are two-tailed.

3. RESULTS

There was considerable variation in the strength of social bonds among adult females. The median value of the CSI was 0.45; 90% of the values fell between 0.06 and 1.98. The distribution of CSI values was strongly left-skewed, which indicates that many dyads had weak bonds, while a small number of dyads formed especially strong bonds. As in other baboon populations (Silk *et al.* 2006a,b), females formed the strongest (figure 1) and most enduring (figure 2) bonds with close maternal kin, particularly their mothers and adult daughters.

Approximately 75% of all infants born in the group ($n = 188$) were still alive at six months of age; 65% survived to 1 year and 45% survived to 5 years. The offspring of females who formed strong social bonds with other adult females lived significantly longer than the offspring of females with weaker social bonds ($\beta = -0.8540$, $z = -2.01$, $p = 0.045$, $n = 129$ infants; figure 3a). In contrast, offspring longevity was not affected by their mothers' dominance rank ($\beta = -0.2924$, $z = -0.65$, $p = 0.516$) or their own sex ($\beta = 0.0229$, $z = 0.10$, $p = 0.919$). The strength of females' social bonds with their own mothers and adult daughters had particularly strong positive effects on offspring survival ($\beta = -0.0540$, $z = -2.40$, $p = 0.017$, $n = 93$). Females with stronger bonds with their mothers and adult daughters experienced higher offspring survival than those with weaker bonds (figure 3b).

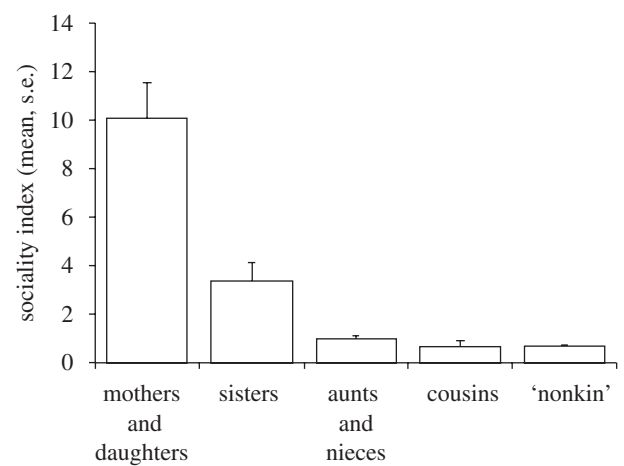


Figure 1. Effects of maternal kinship on the strength of social bonds among adult females. Means and standard errors of the composite sociality index are given for maternal kin (mothers and daughters: $n = 24$ dyads; sisters: 28 dyads; aunts and nieces: 40 dyads; cousins: 18 dyads) and 'nonkin' ($n = 879$ dyads). The 'nonkin' category includes all dyads for which maternal relatedness is less than 0.0625). Means and standard errors are shown.

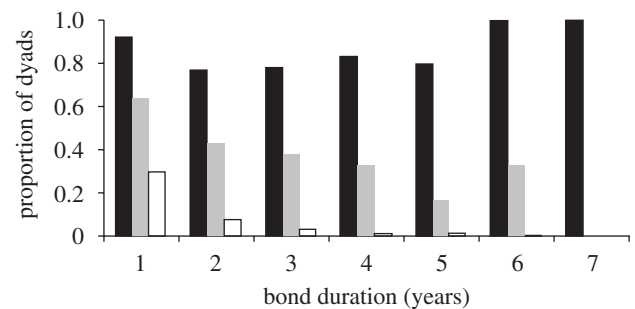


Figure 2. Stability of females' close social bonds. The duration of close social bonds for dyads composed of mothers and daughters (black bars); maternal sisters (gray bars), and females who are not related through maternal lines (white bars) is shown here. Initial sample sizes for kin categories are given in figure 1. For each type of dyad, the proportion of dyads that maintained close social bonds for a given number of years is plotted on the y-axis. The values were obtained by dividing the number of dyads that maintained a close social bond for at least x years by the total number of dyads that were coresident for x or more years. Mothers and daughters were very likely to maintain close social bonds for as long as they lived together in the group.

Among yellow baboons, females' social relationships with their maternal sisters are generally weaker and less stable than their relationships with their own mothers and adult daughters (Silk *et al.* 2006a,b). In the chacma group, the strength of females' bonds with their sisters varied, but this variation had no influence on offspring survival when their mother or adult daughters were present during their reproductive years, ($\beta = -0.0328$, $z = -0.37$, $p = 0.709$, $n = 89$). However, for females who had no mother or adult daughters, offspring survival was linked to the strength of their relationships with their sisters ($\beta = -0.1477$, $z = -1.95$, $p = 0.051$, $n = 23$).

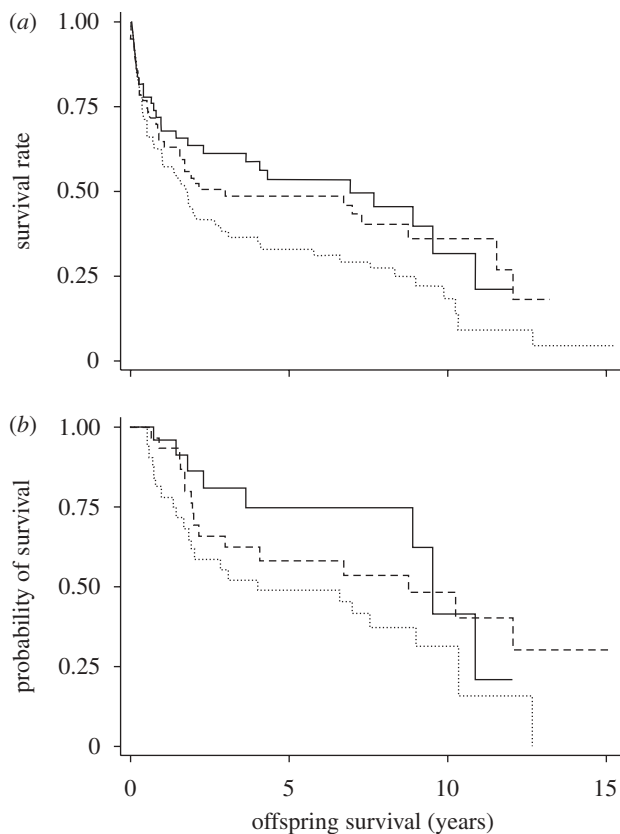


Figure 3. Effects of maternal sociality on offspring survival. For the purposes of illustration here, females were ranked according to the strength of their social bonds to (a) all adult females or (b) to their own mothers and adult daughters, and then divided into three equal groups. Offspring of females with the strongest social bonds are depicted by a solid black line, offspring of females with intermediate bonds by a dashed line, and offspring of females with the weakest bonds by a dotted line. Note that sample sizes decline as longevity increases.

Thus, the strength of females' relationships with their closest living relatives enhanced offspring survival.

Because females formed the strongest bonds with their close maternal kin, the relationship between a female's social bonds and offspring survival might simply have reflected the fact that females who had close kin in the group tended to form strong social bonds. However, the average number of close female kin present in the group had no significant effect on offspring survival (mothers, daughters, and sisters: $\beta = -0.0385$, $z = -0.41$, $p = 0.680$; mothers and daughters: $\beta = -0.1531$, $z = -0.70$, $p = 0.485$; $n = 129$).

4. DISCUSSION

These results demonstrate that females' bonds with other females enhanced reproductive success independent of infant attractiveness or long-term bonds with specific males. Females who formed the strongest social bonds with other adult females had the highest survivorship among both daughters and sons—at least after the age of high infanticidal risk. These benefits persisted into offspring adulthood, were unrelated to female dominance rank and increased quantitatively with the strength of a female's social bonds. Although females formed the

strongest bonds with their closest kin, the mere presence of kin seemed to be less important to offspring survival than the quality of these bonds. The causes for the variation in the strength of females' bonds with close kin remain unclear and are currently being investigated.

A number of proximate mechanisms might contribute to the relationship between a female's social bonds and her offspring's survival. First, predation is the primary cause of juvenile and adult mortality for Okavango baboons (Cheney *et al.* 2004). Females with stronger and more secure social bonds may be less spatially peripheral while they are feeding during the day and perching in sleeping trees at night, and they and their offspring may be less vulnerable to predators. Second, females with strong social bonds may be better shielded from social conflict and therefore able to feed more efficiently (Silk *et al.* 2003a). Third, females who have more focused social networks experience lower glucocorticoid levels than other females and seem better able to overcome social stressors (Crockford *et al.* 2008; Wittig *et al.* 2008). These advantages may extend to their offspring. Data from a wide variety of species have shown that maternal exposure to environmental and social stressors can have detrimental impacts on their offspring's growth rates, longevity, organization of the hypothalamic–pituitary–adrenal pathway, and behaviour (Bernardo 1996; Sanchez 2006; Onyango *et al.* 2008; Weinstock 2008).

Primates have evolved complex, well-differentiated social relationships that are supported by specialized cognitive abilities (Byrne & Whiten 1988; Cheney & Seyfarth 1990, 2007; Dunbar 2003). Our data provide the first direct indication that such relationships among females have been favoured by natural selection. Large brains and sophisticated cognitive abilities may have been favoured because they enable individuals to cooperate and compete more effectively with both related and unrelated group members. Cercopithecine primate females live in societies with extremely stable matrilineal dominance hierarchies, in which high-ranking females enjoy priority of access to resources. Nevertheless, reproductive skew among females is relatively low (reviewed in Cheney *et al.* 2004), suggesting that females may have developed alternative strategies to enhance their reproductive success. While females may have little ability to alter their own dominance status, they may have considerable control over the size and quality of their social networks. For female baboons, the ability to forge strong and enduring social bonds may generate more reproductive benefits than high rank.

Female baboons form bonds with non-kin when relatives are not available (Silk *et al.* 2006a,b). Recent research has indicated that similar close bonds among unrelated females also occur in species that do not exhibit female philopatry, including in particular chimpanzees (*Pan troglodytes*). Contrary to previous assumptions, it is now evident that social bonds among female chimpanzees are as well-differentiated, stable and long-lasting as those among males, even when they involve unrelated partners (Langergraber *et al.* in press; Lehmann & Boesch 2009; Mitani 2009; see also Williams *et al.* 2002; Gilby & Wrangham 2008). Although it is not yet known whether females derive reproductive benefits from these associations, they may function in part to reduce competition for food and space (Kahlenberg *et al.* 2008; Langergraber *et al.* in press; Lehmann & Boesch 2009).

In humans, greater social integration is generally associated with reduced mortality and better physical and mental health, particularly for women (Thorsteinsson & James 1999; Taylor *et al.* 2000; Kendler *et al.* 2005). As with baboons, the strength and quality of these bonds are more important than their number (Seeman 1996; Hill & Dunbar 2003). Similarly, the help that women receive from their own mothers and adult daughters (the 'grandmother' effect; Hawkes 2004; Lahdenpera *et al.* 2004; Volland *et al.* 2005; Sear & Mace 2008) appears to have a significant influence on offspring fitness. It therefore seems possible that the capacity and motivation to establish and nurture close social relationships with other females have been under strong selective pressure in the primate lineage for many millions of years.

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