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Stability of partner choice among female baboons

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In a wide range of taxa, including baboons, close social bonds seem to help animals cope with stress and enhance long-term reproductive success and longevity. Current evidence suggests that female baboons may benefit from establishing and maintaining highly individuated relationships with a relatively small number of partners. Here, we extend previous work on the stability of female baboons' social relationships in three different ways. First, we assess the stability of females' social relationships in two distinct and geographically distant sites using the same method. Second, we conduct simulations to determine whether females' social relationships were more stable than expected by chance. Third, we examine demographic sources of variance in the stability of close social bonds. At both sites, females' relationships with their most preferred partners were significantly more stable than expected by chance. In contrast, their relationships with less preferred partners were more ephemeral, often changing from year to year. While nearly all females experienced some change in their top partners across time, many maintained relationships with top partners for several years. Females that lived in smaller groups and had more close kin available had more stable social relationships than those that lived in larger groups and had fewer close kin available.

A growing body of evidence suggests that close social bonds with same-sex partners help animals cope with stress and enhance long-term reproductive success and longevity. Female rats, *Rattus norvegicus*, that have well-balanced affiliative relationships exhibit lower glucocorticoid levels than those with less symmetric relationships (Yee et al. 2008). In chacma baboons, *Papio hamadryas ursinus*, or *P. ursinus*, grooming relationships enhance females' ability to cope with various sources of stress, such as the immigration of potentially infanticidal males or instability of the dominance hierarchy (Engh et al. 2006a; Crockford et al. 2008; Wittig et al. 2008). Females have lower glucocorticoid levels during months in which they focus their grooming on a small number of partners than in months in which they distribute grooming to a wider subset of group members (Crockford et al. 2008). Females also display marked increases in glucocorticoid levels after a preferred partner dies or disappears from the group (Engh et al. 2006b).

These findings are complemented by evidence suggesting that social bonds confer fitness advantages on individuals (reviewed in: Silk 2007; Seyfarth & Cheney 2012). For example, female house mice, *Mus musculus*, which often share nests with other females and rear their pups communally, reproduce more successfully when they are allowed to choose their nestmates than when nestmates are assigned randomly (Weidt et al. 2008). Well-balanced social relationships also enhance the longevity of female rats (Yee et al. 2008). Female yellow baboons (*Papio hamadryas cynocephalus*, *Papio cynocephalus*) living in the Amboseli basin of Kenya that are more socially integrated into their groups have higher survivorship among their infants than females that are less socially integrated (Silk et al. 2003). Similarly, female chacma baboons in the Moremi Reserve of the Okavango Delta of Botswana that maintained strong bonds with other adult females had higher survivorship among their offspring than females with weaker social bonds (Silk et al. 2009). Moreover, in Moremi, females that had stronger and more consistent relationships with preferred partners lived longer than other females in their group (Silk et al. 2010a). Positive correlations between sociality and reproductive success have also been documented in female horses, *Equus equus* (Cameron et al. 2009) and bottlenose dolphins, *Tursiops truncatus* (Frère et al. 2010), as well as male Assamese macaques, *Macaca assamensis* (Schülke et al. 2010).

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These findings suggest that females gain benefits from establishing and maintaining highly individuated relationships with a relatively small number of partners, rather than interacting less selectively with a wider range of social partners. This has important implications for the proximate mechanisms through which social bonds confer benefits and the ultimate forces that shape the dynamics of close social bonds among female baboons, and by extension, other species that form highly individuated social bonds.

However, there is presently some debate about the temporal stability of social relationships among female baboons. We have previously shown that female yellow baboons in Amboseli and female chacma baboons in Moremi maintain consistent preferences for favoured partners across time. For example, adult females form their strongest ties to their own mothers, and their mothers will be among their top three partners as long as their mothers remain alive (Silk et al. 2006a,b, 2010b). In contrast, chacma baboons in South Africa are reported to show little temporal consistency in female partner choice from month to month (Henzi et al. 2009; but see Seyfarth 1977) or across years (Barrett & Henzi 2002).

Here, we extend our previous analyses to assess the stability of female baboons' social relationships in three ways. First, we assessed the stability of females' social relationships in two distinct and geographically distant sites (Amboseli and Moremi) using the same method. This allowed us to assess the generality of our results across populations. Second, we conducted simulations in which females' partners were chosen at random each year from the set of available females; then, we determined whether female social relationships were more stable than expected by chance, by comparing these simulated patterns of partner stability with observed patterns.

Third, we examined demographic sources of variance in partner stability. Previous analyses revealed that female baboons form the strongest relationships with their mothers and sisters, and with agemates (Silk et al. 2006a,b, 2010b). However, the availability of these preferred types of partners could affect the stability of partner preferences and could explain apparent differences between social groups or populations of female baboons in the formation of stable relationships. That is, it is possible that baboons have stable partner 'preferences', but the opportunity to sustain relationships with preferred partners from one year to the next is limited by demographic factors. The stability of close social bonds may reflect a compromise between the preferences that guide partner choice and demographic factors that constrain the ability of individuals to exercise those preferences. The number of adult females within a group is likely to affect the stability of females' associations because the chance of having the same top partner from one year to the next by chance is higher when there are fewer potential partners than when there are many potential partners. Because females form the strongest bonds with close kin, particularly their mothers and daughters, the availability of close kin is also likely to influence the stability of social bonds. Finally, if females compete for access to preferred partners, then we might expect high-ranking females, which generally have priority of access to resources, to have more stable social bonds than lower-ranking females.

METHODS

Amboseli

The study site is located in the Amboseli Basin, which straddles the border between Kenya and Tanzania and lies at the foot of Mount Kilimanjaro. Data are derived from observations of 137 adult female baboons living in six well-habituated groups over a 16-year period (Table 1). Alto's group has been monitored since 1971, and Hook's group has been monitored since 1980. Both of these groups shifted their ranges in response to deteriorating ecological conditions and subsequently fissioned (Fig. 1a). Alto's group fissioned into Dotty's group and Nyayo's group (for more details about the study groups, see Altmann & Alberts 2003). The fission took several years to complete and was followed by a period of limited behavioural (but not demographic) data collection in the newly formed groups. As a consequence of the paucity of focal behavioural observations during this period, focal samples were available for only three females both in Alto's group and in one of the daughter groups. Hook's group fissioned into Linda's group and Weaver's group, but there was no lull in focal behavioural observations during the fission. Fourteen females were observed both in Hook's group and in one of the two daughter groups. All procedures were approved by the Institutional Animal Care and Use Committee of Duke University (Protocol number A028-12-02).

Table 1
Numbers of adult female baboons observed in each group in Amboseli and Moremi

Group	Years analysed	Average number of adult females present each year	Total number of females in sample
Amboseli			
Alto	5	21.6	34
Dotty	7	12.3	21
Nyayo	4	15.3	16
Hook	11	20.9	38
Linda	5	10.8	14
Weaver	5	12.4	14
Moremi	7	29.1	49

Grooming and proximity maintenance are widely considered to provide meaningful measures of social relationships among nonhuman primates and they make up the major components of female baboons' social time. Focal samples conducted on adult females provided information about grooming partners and spatial proximity. Females were sampled on a random schedule during daylight hours. At 60 s intervals within each 10 min focal sample, the activity of the focal female and the identity of her nearest neighbour within 5 m were recorded.

Dyads that had high rates of grooming also had high rates of association, so we used the frequency of grooming and proximity to compute a composite sociality index ($\mathrm{CSI_A}$) for each dyad in each year:

$$\frac{\left(\frac{G_{ij}}{G_{xy}}+\frac{P_{ij}}{P_{xy}}+\right)}{2}$$

The first term in the numerator is the adjusted frequency of grooming for dyad *ij* in year *y* divided by the mean adjusted frequency of grooming for all dyads in group *x* in year *y*. The second term in the numerator is the adjusted frequency of proximity for dyad *ij* divided by the mean frequency of proximity for all dyads in group *x* in year *y*. The $\mathrm{CSI_A}$ measures the extent to which each dyad deviated from other dyads. The mean of the $\mathrm{CSI_A}$ is defined as 1, but the values can range from 0 to infinity. High values of the $\mathrm{CSI_A}$ represent dyads that had stronger social bonds than the average female dyad in the group in the same year, and low values of the $\mathrm{CSI_A}$ represent dyads that had weaker social bonds (for more details about observation and analysis procedures, see Silk et al. 2006a,b).

Moremi

The study site is located in the Moremi Game Reserve in the Okavango Delta of Botswana. The data are derived from focal samples on 49 adult females collected over a 7-year period in one well-habituated group (Table 1). The number of adult females in the study group ranged from 25 to 35 (Fig. 1b). For more details about the study site and the history of the study population, see Cheney &