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The 'strength of weak ties' among female baboons: fitness-related benefits of social bonds

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Studies across a range of species have shown that sociability has positive fitness consequences. Among baboons, both increased infant survival and adult longevity have been associated with the maintenance of strong, equitable and durable social bonds. However, not all baboon populations show these patterns of bonding. South African chacma baboons, *Papio ursinus*, in the Drakensberg Mountains and De Hoop Nature Reserve show cyclical variation in social relations across time, with strong bonds formed only during certain times of the year. Using long-term data from the De Hoop baboons, we tested whether social relations influence female reproductive success in our study group in a manner similar to other baboon populations. Our results show that the number of strong bonds a female maintained predicted birth rate, and that the number of weak bonds a female possessed predicted infant 12-month survival and infant longevity. Fitness-related benefits of sociability were, however, independent of female dominance rank, and there was no relationship between the number of weak and strong bonds a female maintained. One possible explanation for the influence of weak as well as strong bonds in our study group may be that variation in demographic and ecological conditions across populations may favour the use of different social strategies by females. In our sample, weak bonds as well as strong bonds appear to be instrumental to achieving fitness-related benefits.

Social relationships, as identified through the quality and patterning of interactions among group members over time (Hinde, 1979), can alleviate the negative effects of intragroup competition on individual fitness by improving the health, longevity and offspring survival of more sociable individuals (Armitage & Schwartz, 2000; Cameron, Setsaas, & Linklater, 2009; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Silk, Alberts, & Altmann, 2003; Silk et al., 2010, 2009; Smith & Christakis, 2008). Social behaviour is therefore argued to be evolutionarily adaptive, with the most reproductively successful animals being those that are best able to navigate their social environment (Brent et al., 2013; Silk, 2007).

Various measures have been used to describe the degree to which individuals are integrated in to their social group; including social relationship (i.e. bond) strength, number, or a combination of these measures. Among primates, it has been argued that the maintenance of a small number of strong and enduring social bonds has the largest impact on individual fitness (Schülke et al., 2010; Silk et al., 2003, 2009, 2010). For example, both yellow baboon, *Papio cynocephalus*, and chacma baboon, *Papio ursinus*, females with strong and consistent bonds to particular individuals experienced increased longevity and higher offspring survival than females with fewer bonds (Silk et al., 2009, 2010). Observations from these same chacma baboons have also shown that females with more focused grooming networks experience lower glucocorticoid levels, which was interpreted to suggest that social bonds reduce chronic psychosocial stress, and so have an impact on individual fitness (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008; Wittig et al., 2008; although see Brent, Chang, Gariépy, & Platt, 2014 for a criticism of the idea that stress reduction can be viewed as the ultimate explanation for social relationship formation, rather than a proximate factor influencing their maintenance).

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Collectively, these findings have led to the suggestion that the value of sociability lies mainly in the formation of a small number of strong and consistent social bonds, rather than the formation of a more extended social network.

Data from two other chacma baboon populations in South Africa, however, suggest that such patterns may not be universal: bond stability was shown to fluctuate in a cyclical fashion. Specifically, during the food-scarce season across two ecologically distinct populations, females formed both 'constant companionships' and 'brief associations' (which map approximately onto Silk and colleagues' notion of strong and weak bonds), whereas during the food-abundant season of each year, females formed only brief associations and 'casual acquaintances' (Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009). There was also some suggestion that females in these populations formed strong bonds with others on a contingent basis: when strong bonds between individuals dissolved and subsequently reformed, they were not necessarily between the same animals.

It is also possible that strong and weak bonds serve distinct roles. For example, McFarland and Majolo (2013) have shown that, in Barbary macaques, *Macaca sylvanus*, the number of social bonds, but not their strength, predicted survival through a particularly harsh winter. Similarly, McFarland et al. (2015) recently demonstrated that the number of social bonds, but not their strength, predicted thermoregulatory efficiency among female vervet monkeys, *Chlorocebus pygerythrus*. In both cases, the behavioural flexibility afforded by a broader social network of weaker social bonds was suggested to provide physiological (i.e. energetic and thermal) benefits and so similarly exert an impact on individual fitness. If correct, this would suggest that, under some ecological circumstances, there is no simple trade-off between the number and quality of social bonds: a few strong bonds may not necessarily compensate for a large number of weak bonds if the two serve different functions. Under such circumstances, it will pay individuals to invest the effort required to ensure as many individuals as possible are incorporated into their networks in order to receive the associated benefits of both strong and weak connections. That is, female reproductive success may be influenced by the formation of a certain minimum number of bonds above some threshold, rather than by their strength per se.

Given the above reasoning, we hypothesize that weak bonds, as well as strong bonds, can potentially have an impact on individual fitness, and that the relative importance of such bonds may vary accordingly to ecological conditions. Here, we examine the effect of social integration on three fitness-related traits in baboons (i.e. birth rate, 12-month infant survival and infant longevity), and assess the relative contribution of strong and weak social bonds as defined by a composite sociality index (CSI: Silk, Altmann, & Alberts, 2006). If the value of being sociable lies in the formation of strong social bonds, then one would expect individuals to discriminate in favour of fewer, stronger social relationships, and that these strong bonds would predict reproductive success, as in other populations. If the value of sociability is linked to broader social integration, however, then one would expect individuals to spread their social investment more evenly across the group, investing in a wider network of weaker social bonds. If the latter is true, we would expect that the number of weak social bonds would also predict aspects of reproductive success.

METHODS

Data Collection

We used demographic data collected between May 1998 and August 2007 from all adult females living in a wild troop of chacma baboons on the De Hoop Nature Reserve, South Africa (34.43°S, 20.55°E). Across this study period, the number of adult females observed in the group ranged from 13 to 21 (median = 15), largely reflecting the maturation of females into the adult cohort. All females lived on a completely natural diet and were recognized individually from natural markings. Data were purely observational and noninvasive, and were collected in accordance with the ethical guidelines of ASAB/ABS. All procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocol: 0702) and conformed to the legal requirements of South Africa. Data are archived on Figshare (McFarland et al., 2017).

Instantaneous scan data used in the current study were collected between January 1999 and December 2006 (Altmann, 1974). Data were collected every 30 min throughout the day from all adult females that could be located within a 10 min time window. Data were collected on whether a female was engaged in one of four mutually exclusive activities: grooming, resting, foraging or moving. Data were also collected on the direction of grooming, the proximity of female group members, and the identities of all grooming partners and nearest neighbours. In total, 37 261 scans were collected over the 7-year study period (mean ± SD = 1774 ± 1135 scans/subject). Across this sample, we observed 9920 dyadic measures of close proximity, of which 2520 were dyadic grooming interactions.

We recorded the dates of birth ($N = 47$) and death ($N = 18$) of all infants born during the study (range 1–6 infants/female). Six of the 18 infant deaths occurred aged <12 months, and 10 deaths occurred aged <24 months. We excluded one female and her infant from the analyses, as this mother died before her infant reached 12 months of age. Assessing this infant's overall survival in relation to their biological mother's social behaviour is therefore invalid. We followed all infants born during this study, including those born in the final year of data collection, for at least 12 months after birth to establish 12-month survival data.

We collected data ad libitum on the occurrences of all aggressive interactions exchanged by adult females. In total, we recorded over 8000 instances of aggression. These data were used to calculate monthly David's scores for each individual, allowing average ranks to be assigned to each female for each year of the study (De Vries, Stevens, & Vervaecke, 2006).

Composite Sociality Index

We used composite sociality indices (CSIs) to measure the strength of the social bonds shared by all female group members for each year of the study. Two behavioural measures were entered into the CSI: the proportion of scans in which each female dyad was (1) grooming and (2) in 5 m close proximity but not grooming. To control for the fact that not all females were present in the study group for the same amount of time, these proportions were divided by the total number of months that the two members of each dyad co-resided in the group. These adjusted dyadic behavioural measures (x_i) were divided by the group's mean for these same measures (m_i). These values were summed across all group member dyads, and divided by two (i.e. the number of behavioural measures entered into the index).

$$\mathrm{CSI} = \frac{\sum_{i=1}^{2} \frac{x_i}{m_i}}{2}$$

From the 942 potential female dyads present over the 7-year study period, 383 dyads (41%) had a CSI score of zero (i.e. did not exchange grooming or maintain close proximity) and thus reflect the absence of a social bond. The number of strong and weak social bonds were calculated for the remaining 559 group member dyads.