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Quality versus quantity: do weak bonds enhance the fitness of female baboons?

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There is growing evidence that social bonds have adaptive consequences for individuals in many mammalian species, including savannah baboons. While the majority of studies have shown that the strength of social bonds and the extent of social integration enhance female fitness, several other investigations have suggested that the number of social bonds may sometimes may be more important than the strength or quality of females' social relationships. Here, we examine the impact of the number of strong and weak social bonds on female fertility and longevity in a population of chacma baboons,*Papio ursinus*. We find no evidence that the number of social bonds consistently affects fertility or infant survival to 1 year, but offspring of females with more weak social bonds lived longer than offspring of other females. After discussing several methodological issues that may influence the analyses of the effects of the number of social bonds, we re-examine the relationship between the number of weak and strong social bonds and reproductive performance using procedures that avoid these problems. Again, we find no evidence that the number of weak or strong social bonds affects females' fertility, survival to 1 year. The effects of the number of weak social bonds on infant longevity disappear, and appear to be an artefact of the relationship between the number of weak social bonds and the number of females in the group.

There is growing evidence from a variety of different animal species that social bonds have adaptive consequences for individuals (Seyfarth & Cheney, 2012; Silk, 2007). For example, female humpbacked whales, *Megaptera novaeangliae*, that form the strongest and most stable associations reproduce more successfully than other females (Ramp, Hagen, Palsbøll, Bérubé, & Sears, 2010). In wild horses, *Equus caballus*, the extent of females' social connections to other females is positively related to the survival of their infants (Cameron, Setsaas, & Linklater, 2009). In Assamese macaques, *Macaca assamensis*, males that form strong social bonds are more successful in forming coalitions, achieving high rank and siring more offspring than males with weaker social bonds (Schülke, Bhagavatula, Vigilant, & Ostner, 2010). High eigenvector centrality, a social network measure of the extent to which an individual's social partners are themselves connected to others, is associated with higher female fertility in rhesus macaques, *Macaca mulatta* (Brent et al., 2013).

For female savannah baboons, which live in large female-bonded groups, sociality is also linked to fitness outcomes. In yellow baboons, *Papio cynocephalus*, females that are more socially connected to others have higher survivorship among their infants (Silk, Alberts, & Altmann, 2003) and live longer (Archie, Tung, Clark, Altmann, & Alberts, 2014) than other females. In chacma baboons, *Papio ursinus*, living in the Moremi Game Reserve of Botswana, the average strength of females' dyadic relationships with all other females in the group is linked to the longevity of their offspring (Silk et al., 2009). Females that have strong social bonds also have high eigenvector centrality, which also predicts offspring survival (Cheney, Silk, & Seyfarth, 2016). Females that have the strongest and most stable relationships with their top partners also live longer than other females (Silk et al., 2010a). Taken together, these data suggest that strong and well-differentiated social bonds have important fitness advantages for female baboons.

In contrast to these findings, recent analyses by McFarland and colleagues have suggested that the number of social partners may sometimes be more important than the strength or stability of

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social bonds. In vervet monkeys, *Chlorocebus pygerythrus*, living where winter temperatures sometimes fall below freezing overnight, monkeys who had more social partners were able to maintain their body temperatures better than those with fewer social partners (McFarland et al., 2015). Similarly, in Barbary macaques, *Macaca sylvanus*, the likelihood of surviving a particularly severe winter appeared to be positively related to the amount of time spent feeding and the number of social bonds (McFarland & Majolo, 2013). Finally, in an analysis of South African chacma baboons, McFarland et al. (2017) suggested that infant survival is enhanced by the number of weak bonds that a female forms, while the number of strong bonds enhances fertility (McFarland et al., 2017).

Here, we extend our previous analysis of chacma baboons in Botswana to assess the impact of the number of weak and strong social bonds on female fertility, infant survival and offspring longevity. To enhance comparisons to McFarland et al. (2017), we use the same procedures to categorize social bonds. We find that three related methodological issues may influence these analyses. First, sampling effort biases estimates of the number of social bonds that individuals form. Second, the number of social bonds is positively correlated with group size. Third, the number of weak and strong social bonds are correlated. These factors may affect results of analyses of the impact of the number of social bonds on reproductive performance. We present additional analyses to address these methodological issues.

METHODS

Study Group

Analyses were based on almost daily observation of a group of free-ranging chacma baboons in the Moremi Game Reserve of the Okavango Delta, Botswana between June 1992 and December 2007 (see Cheney et al., 2004, for additional details). During this period, the group varied in size from 56 to 87, with a range of 26–38 adult and subadult females (>4 years). The ages and maternal kin relationships of all females in the group were known. Predation (by leopards, *Panthera pardus*, and lions, *Panthera leo*) was the primary cause of mortality among adult females, and confirmed or suspected infanticide by immigrant males was the primary cause of death among infants (Cheney et al., 2004).

Ethical Note

Research was reviewed and approved by the Animal Care and Use Committee at the University of Pennsylvania (Protocol No. 19001). All animal protocols followed the Guidelines for the treatment of animals for teaching and research recommended by ASAB/ABS (2014).

Data Collection

Focal samples on all subadult and adult females in the group were collected in 1992–1993 and 2001–2007 using a common observation protocol. Observations were conducted primarily between 0700 and 1400 hours. 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.

Assessment of Female Dominance Ranks

We used the direction of approach–retreat interactions to assess female dominance rank, and constructed dominance hierarchies in which females were ordered so as to minimize the number of reversals (Silk, Seyfarth, & Cheney, 1999). The females formed a linear, matrilineal dominance hierarchy. There were few changes in the relative ranks of matrilines over the course of the study period (Engh, Hoffmeier, Cheney, & Seyfarth, 2006), although changes in the relative ranks of females within matrilines occurred as females rose in rank above their older sisters (Bergman, Beehner, Cheney, & Seyfarth, 2003).

Following McFarland et al. (2017), we calculated the proportion of females dominated by each female. This was calculated as: $(N-d)/(N-1)$, where N is the total number of adult females in the group and d is the ordinal rank of a particular female. Thus, the highest-ranking female in the group is ranked 1, while the lowest-ranking female is ranked 0. The analyses are based on females' rank in January of each year.

Measurement of Social Bonds

To assess the strength of social bonds, we calculated the dyadic sociality index (DSI) for each dyad in each year (Silk, Cheney, & Seyfarth, 2013). The DSI was computed by the following formula:

$$\mathrm{DSI}_{xy} = \frac{\sum_{i=1}^{d} \frac{f_{ixy}}{\overline{f}_i}}{d}$$

where d is the number of behaviours that contribute to the index; f_{ixy} is the rate of behaviour i for dyad xy; and $\overline{f}_i$ is the mean rate of behaviour i across all dyads. The values of this index range from $0 \rightarrow \infty$, with a mean of 1.0. High DSI values represent dyads that have stronger ties than the average dyad, and low DSI values represent dyads that have weaker ties than the average dyad. McFarland et al. (2017) referred to this measure as the 'composite sociality index', but in Silk et al. (2013), we defined the composite sociality index as an aggregate measure of social interactions with all partners, and use the term dyadic sociality index for the measure described here.

The DSI was based on the approaches, grooming solicitations, grooming frequency and 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 (for more details, see Silk et al., 2010b).

Following McFarland et al. (2017), we categorized social bonds as absent ($\mathrm{DSI} = 0$), weak ($0 < \mathrm{DSI} < 1$) or strong ($\mathrm{DSI} > 1$) and tabulated the number of absent, weak and strong bonds that each female formed each year.

Statistical Analyses

Following McFarland et al. (2017), we evaluated the effects of dominance rank and the number of social bonds on the likelihood that a female would give birth in a given year (scored as 1 = give birth, 0 = no birth) and the likelihood that her infant would survive the first year of life (1 = survive, 0 = not survive). In both of these analyses, we used a mixed effects logistic regression model. Year and female identity were included as random effects variables.

To evaluate the effects of a female's dominance rank and her number of social bonds on offspring survival from one year to another (up to 7 years, following McFarland et al., 2017), we conducted a time-dependent Cox proportional hazards model. For each year of an offspring's life, yearly values for maternal dominance rank and the number of weak and strong social bonds were entered. Because some females contributed multiple offspring to the data set, we used the cluster option to control for the effects of