

## 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 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.

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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:

$$DSI_{xy} = \frac{\sum_{i=1}^d \frac{f_{ixy}}{\bar{f}_i}}{d}$$

where  $d$  is the number of behaviours that contribute to the index;  $f_{ixy}$  is the rate of behaviour  $i$  for dyad  $xy$ ; and  $\bar{f}_i$  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 (DSI = 0), weak ( $0 < \text{DSI} < 1$ ) or strong ( $\text{DSI} > 1$ ) 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

female identity. Below, we refer to this outcome variable as offspring longevity.

To evaluate the effects of observation time on the number of absent social bonds and the relationship between the number of weak and strong bonds that females formed, we constructed mixed effects linear regression models. Year and female identity were included as random effects variables in these models. We also used a mixed effects linear regression model to evaluate the effects of the number of females in the group on the number of weak and strong bonds that females formed. Female identity was included as a random effects variable. Year was not included as a random effects variable within these models because year and the number of females within groups were collinear.

Below we raise methodological concerns about the procedures used by McFarland et al. (2017), which are partly related to the correlation between the number of social bonds and the number of available partners and collinearity between the number of weak and strong bonds. Collinearity among predictor variables influences the stability of regression coefficients and the width of the associated confidence intervals. To evaluate the extent of collinearity between predictor variables, we calculated the variation inflation factor (VIF) and include the mean value of the VIF in the presentation of results. Although there is no absolute threshold for acceptable values of these measures, VIF values greater than 10 are generally considered to indicate instability in regression estimates and warrant concern (Belsley, Kuh, & Welsch, 2005; Chen, Ender, Mitchell, & Wells, 2003).

All statistical analyses were conducted with STATA 10.0 (Stata-Corp LP, College Station, TX, U.S.A.). Where appropriate, we report means  $\pm$  SE.

## RESULTS

### *Distribution of Social Bonds*

Females formed about twice as many weak social bonds as strong social bonds each year. Females formed weak social bonds ( $0 < \text{DSI} < 1.0$ ) with a mean of  $16.8 \pm 0.3$  females and strong social bonds ( $\text{DSI} > 1$ ) with a mean of  $6.3 \pm 0.2$  partners.

### *Birth Rates*

On average, 43% of the females gave birth each year (range 19–56%). We examined the effects of the number of weak and strong bonds and dominance rank on the likelihood of giving birth in a given year. None of these variables had a significant effect on the likelihood of giving birth (Table 1, Model 1).

### *Infant Survival to 1 Year*

On average, 51% of all infants born each year survived to 1 year of age (range 22–79%). We examined the effects of a female's number of weak and strong social bonds and dominance rank on the

likelihood that her infant would survive to 1 year of age. These analyses exclude the six infants whose mothers did not survive the year of the infant's birth and 12 infants born during the last year of the study whose survival to 1 year of age was unknown. There was no significant effect of the numbers of weak or strong social bonds or female dominance rank on infant survival to 1 year of age (Table 1, Model 2).

### *Offspring Longevity*

The offspring of females that had more weak bonds lived significantly longer than the offspring of females that had fewer weak bonds (Table 2, Model 3). However, the number of strong bonds and female dominance rank did not influence offspring longevity.

### *Methodological Considerations*

To summarize results thus far, when we applied the same methods of analyses as those used by McFarland et al. (2017) to our own data, we found no relationship between a female's fertility and the strength of her social bonds. Our analysis did, however, show a correlation between offspring survival to older ages and the number of weak bonds that females formed.

Consideration of the procedures devised by McFarland and colleagues raise three related methodological concerns that may have influenced this result. First, the probability of observing two animals interact (and being assigned a  $\text{DSI} > 0$ ) is at least partly related to sampling effort (Farine & Whitehead, 2015). Second, the number of weak and strong bonds that females form is related to the number of available partners. Third, when most pairs of females interact, there will be a correlation between the number of weak and strong bonds that females form. We explore the impact of these factors below.

Each year, some females matured and others died. Moreover, sampling was more intensive in some years than in others. This produced considerable variation in the amount of time that females were observed each year. In our data set, there was a strong and nonlinear relationship between observation time and the number of absent bonds (Fig. 1).

Visual inspection of the data in Fig. 1 indicates that the effects of observation time were most pronounced for females observed less than 5 h in a given year. On average, females who were observed less than 5 h had  $9.5 \pm 1.6$  absent bonds, while those who were observed for more than 5 h had  $2.8 \pm 0.2$  absent bonds. The main impact of increasing observation time was to shift social bonds from the absent category to the weak category. Females who were observed for less than 5 h had  $10.5 \pm 1.2$  weak bonds while females who were observed for more than 5 h had  $17.6 \pm 0.3$  weak bonds. Differences in the number of strong social bonds were less pronounced ( $< 5$  h:  $4.8 \pm 0.7$ ;  $> 5$  h:  $6.5 \pm 0.2$ ).

The absolute number of social bonds that females form will be influenced in part by the size of the group and the number of

**Table 1**  
Predictors of birth rate, infant survival to 1 year and offspring longevity

Predictor	Model 1: Birth rate				Model 2: Infant survival to 1 year				Model 3: Offspring longevity			
	Odds ratio	SE	z	P	Odds ratio	SE	z	P	Hazard ratio	SE	z	P
Number of weak bonds	1.2150	0.5489	0.430	0.666	1.1390	0.3588	0.41	0.679	0.8600	0.0568	-2.29	0.022
Number of strong bonds	1.3585	0.8019	0.520	0.604	1.0820	0.2419	0.35	0.724	0.9067	0.0590	-1.46	0.144
Dominance rank	3.4634	13.7835	0.31	0.755	2.1521	4.3634	0.38	0.705	0.6393	0.2946	0.332	0.2591
N	205				85				189			
Mean VIF	1.07				1.25				2.21			

**Table 2**  
Revised analyses of predictors of birth rate, infant survival to 1 year and offspring longevity

Predictor	Model 4: Birth rate				Model 5: Infant survival to 1 year				Model 6: Offspring longevity			
	Odds ratio	SE	z	P	Odds ratio	SE	z	P	Hazard ratio	SE	z	P
Number of weak bonds (standardized)	1.2170	0.4316	0.55	0.580	0.8319	0.6567	-0.23	0.816	1.2401	0.6250	0.43	0.669
Number of strong bonds (standardized)	1.4564	0.3970	1.38	0.168	0.8371	0.5078	-0.29	0.769	1.4798	0.4260	1.36	0.173
Dominance rank	1.4152	0.6938	0.71	0.479	1.9896	1.5157	0.90	0.366	0.7549	0.4789	-0.44	0.658
N	189				83				178			
Mean VIF	2.21				3.56				2.40			

available partners. Moreover, if most females form bonds, there will be a correlation between the number of a female's weak and strong bonds.

These relationships can be seen in our data set. The number of females in the group was positively related to the number of weak social bonds ( $\beta = 0.3096 \pm 0.0624$ ,  $z = 4.96$ ,  $P < 0.001$ ) and to the number of strong bonds ( $\beta = 0.0914 \pm 0.0426$ ,  $z = 2.14$ ,  $P = 0.032$ ) that females formed. The relationships between the number of social bonds and the number of females present became even stronger when we limited the analyses to females observed for more than 5 h (weak:  $\beta = 0.3769 \pm 0.0496$ ,  $z = 7.60$ ,  $P < 0.001$ ; strong:  $\beta = 0.1297 \pm 0.0428$ ,  $z = 3.03$ ,  $P = 0.002$ ). The relationship between the number of weak and strong bonds was not significant when the full data set was used ( $\beta = -0.1550 \pm 0.0941$ ,  $z = -1.65$ ,  $P = 0.100$ ), but when the sample was restricted to females observed for more than 5 h, a significant negative relationship between the number of weak and strong bonds emerged ( $\beta = -0.4640 \pm 0.0745$ ,  $z = -6.23$ ,  $P < 0.001$ ).

We therefore revised McFarland et al.'s procedures to address these methodological considerations. First, we limited analyses of the effects of the number of weak and strong bonds on birth rates, infant survival and offspring longevity to females who were observed for at least 5 h in any given year. This reduced the sample size of female fertility from 205 female-years to 189 female-years, the sample size for infant survival to 1 year from 85 to 83 infants, and the sample size for infant longevity from 181 to 178 infant-years. Second, to avoid the effects of group size on the number of weak and strong bonds that females formed, we standardized these variables within each year so that they had a mean of zero and standard deviation of one. The transformed variables indicate how

many weak or strong bonds that a female had in comparison to the average female in a given year and are independent of group size.

#### Results Based on Revised Procedures

Using the revised procedures, we found no evidence that the number of a female's strong or weak social bonds in a given year influenced the likelihood of giving birth or infant survival to 1 year (Table 2, Models 4, 5). While the number of weak social bonds were associated with increased offspring longevity in the original analysis, this effect disappeared in the revised analysis (Table 2, Model 6).

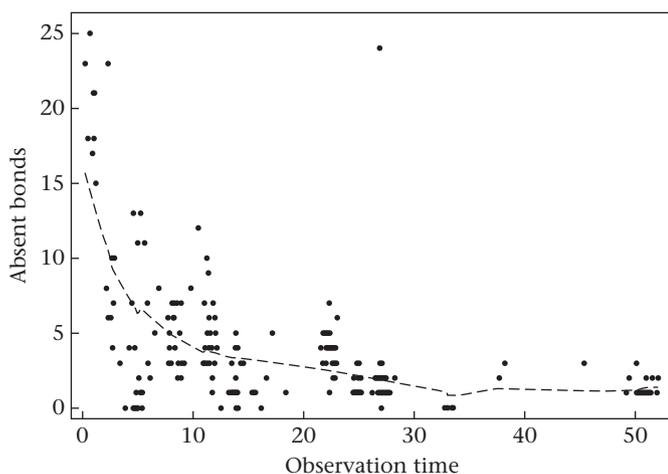
This suggests that the original result may have been confounded by the correlation between the number of weak social bonds and group size. To examine this possibility, we examined the effects of the number of females present on offspring longevity, and we compared the Akaike's information criterion (AIC) value for this model with the AIC value of the original model presented in Table 1. Offspring longevity was significantly higher when there were more females present in the group (hazard ratio =  $0.8223 \pm 0.0271$ ,  $z = -5.95$ ,  $P < 0.001$ ;  $N = 181$  infant-years). The AIC value for this model was substantially lower than the AIC for the original model (306 versus 337).

#### DISCUSSION

For female chacma baboons in Moremi, the numbers of weak and strong social bonds had no consistent impact on birth rates, infant survival to 1 year or offspring longevity. Taken together with our previous findings (Cheney et al., 2016; Silk et al., 2009), the data suggest that the reproductive success of females in this population of baboons is more strongly affected by the strength, stability and structure of their social bonds than by their number.

The difference between our results and the results obtained by McFarland et al. (2017) might reflect differences in the ecological conditions at the two sites. McFarland et al.'s study was conducted at the De Hoop Nature Reserve in the Cape Province of South Africa (34.43°S, 20.55°E) while Moremi is located approximately 1600 km northeast in the Okavango Delta (19.37°S, 23.05°E). Ecological differences between these two sites might affect the benefits females derive from social bonds (McFarland et al., 2017). To test this hypothesis it will be necessary to specify how ecological conditions (such as thermoregulatory challenges, seasonality or food distribution) and social or demographic conditions (including the number of competitors and the size of matriline) are expected to influence the benefits females derive from the number and quality of their social relationships, collect the relevant data and construct appropriate statistical analyses.

It is possible, however, that apparent differences in the effects of the number of weak and strong bonds at the two sites may result from methodological issues. Our analyses show that estimates of the number of absent and weak social bonds were affected by sampling effort. In our study group, only 10% of all dyads ( $N = 5887$ )



**Figure 1.** The number of absent social bonds in relation to hours of observation time per year. A nonparametric LOESS regression, which provides a locally weighted prediction based on the original data points (bandwidth = 0.8), is plotted along with the original data.

that were observed for more than 5 h in a given year failed to form bonds (DSI = 0). By contrast, at De Hoop, 41% of all dyads ( $N = 942$ ) were never observed in close proximity and never groomed during scan samples, and had a DSI of 0. This is a striking difference, particularly because close proximity was defined as 5 m in De Hoop and 2 m in Moremi. The authors report considerable variation in the number of scan samples per subject across study period (mean  $\pm$  SD =  $1774 \pm 1135$  scans/subject, McFarland et al., 2017, p. 102), but do not address the possibility that sampling effort might have affected their estimates of the numbers of weak and strong bonds that females formed.

Our results also suggest that correlations between the number of weak social bonds and the number of females in the group may confound the results of analyses based on the number of weak social bonds. Our analysis suggested a correlation between the number of a female's weak social bonds and offspring longevity (but not with infant survival, as McFarland et al. found). However, when we standardized the number of weak social bonds so that it was independent of the number of females present, this effect disappeared. Additional model comparisons suggested that the number of females in the group is a better predictor of offspring longevity than the number of weak bonds that females form.

Our analyses also suggest that problems may arise from categorizing social bonds as absent, weak or strong. When sampling effort is sufficient, most pairs of females will be observed to associate or interact at some point, even if they do not do so often, and their DSI scores will be greater than 0. This will create a positive relationship between the number of available partners and the number of social bonds – particularly weak social bonds – that females form, as we observed in our data. There will also be negative correlations between the number of weak and strong social bonds. This makes it difficult to distinguish between the effects of the number of social bonds and the effects of group size, or to distinguish between the effects of weak and strong social bonds.

We are still in the early stage of efforts to understand how social relationships influence individual fitness. Some analyses have focused on the impact of variation in aggregate rates of interaction (e.g. Archie et al., 2014; Cameron et al., 2009; Silk et al., 2003), while others have examined the effects of variation in the stability and structure of dyadic relationships (Brent et al., 2013; Cheney et al., 2016; Gilby et al., 2013; Silk et al., 2010a) and the number of social partners (McFarland & Majolo, 2013; McFarland et al., 2017). The use of different metrics in different populations makes it difficult to determine how robust these patterns are or to understand why certain aspects of sociality are more important in one setting than in another. Attempts to faithfully replicate analyses in different populations and taxa will play an important role in this process and contribute to a deeper and more comprehensive understanding of the adaptive value of social bonds.

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