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

ABSTRACT

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 favor 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.

***Keywords*:** Baboons; Dominance Rank; Fitness; Reproduction; Sociability; Survival

INTRODUCTION

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

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 (Silk et al. 2003, 2009, 2010, Schülke et al. 2010). For example, both yellow (*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 et al. 2008; Wittig et al. 2008; although see Brent et al. 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). 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 et al. 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 & 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 behavioral 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, 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 et al. 2006). If the value of being sociable lies in the formation of strong social bonds, then one would expect individuals to discriminate in favor 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 non-invasive, and were collected in accordance with the ethical guidelines of the Association for the Study of Animal Behavior. 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 thirty minutes throughout the day from all adult females that could be located within a ten-minute 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 neighbors. In total, 37, 261 scans were collected over the seven-year study period (mean = 1, 774 ± 1, 135 SD scans/subject). Across this sample, we observed 9, 920 dyadic measures of close-proximity, of which 2, 520 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 < 12months, and 10 deaths occurred aged < 24months. 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 behavior 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 8, 000 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 et al. 2006).

Composite sociality index

We used CSIs to measure the strength of the social bonds shared by all female group members for each year of the study. Two behavioral measures were entered into the CSI: the proportion of scans in which each female dyad was (i) grooming and (ii) in 5m 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 behavioral 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 behavioral measures entered into the index).

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

From the 942 potential female dyads present over the seven-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. CSI values greater than one were taken to represent relatively 'strong' social bonds, and CSI values smaller than one are considered to represent relatively 'weak' social bonds, in line with Silk et al. (2006). Following this definition, we calculated the total number of strong (N_{strong}) and weak (N_{weak}) social bonds our study females shared over each year of the study. Our goal was to examine the effect that strong and weak bonds had on individual fitness, so 'non-social' bonds (i.e., dyads with a CSI score of zero) were excluded from the calculation of N_{weak}.

Our calculation of CSI using measures of grooming and proximity is the same as that used by Silk et al. (2006). It is important to note, however, that, in contrast to previous studies on this topic (Silk et al. 2006, 2009, 2010; Schülke et al. 2010), we used CSI to identify the total number of strong and weak bonds each of our females shared with their conspecifics, rather than using the CSI measures to identify an individual's "top partners" (Silk et al. 2009, 2010; Schülke et al. 2010). Previous studies have tended to concentrate their analysis on the consistency and durability of a select number of social bonds, and have ignored the potential influence of weak social bonds. The selection of a particular number or top percentage of social bonds, regardless of their absolute strength, appears to be entirely arbitrary, however, as we could not identify any biologically meaningful criteria used to justify this choice in previous work. In addition, this approach potentially could lead to a particular female's top social partners being those with whom she shares weak social bonds, albeit durable and consistent over time. It also means that one cannot identify females who are less sociable from those that are not, given that all females are allocated three top partners regardless of how frequently they interact. Such an approach would also preclude the possibility of assessing the effect that both strong and weak social bonds have on individual fitness. Restricting the analysis to a predetermined number of bonds therefore eliminates, by definition, the possibility of examining variability in the number of social bonds, regardless of strength, shared by females. Given these concerns, we decided not to identify the top three partners, but simply use higher than average CSI scores and lower than average CSI scores to identify strong and weakly bonded partners as a continuous measure. This approach allowed us to keep bond measures separate, and also means that our sociability measure reflects a female's overall level of sociability.

Statistical analysis

A generalized linear regression was used to test whether N_{strong} predicted N_{weak} (N=122 baboon years of data from 21 females). Female ID nested inside Year was entered as a random effect to control for the fact that a single female was sampled across multiple years.

Three measures of reproductive success were estimated for each female: (i) birth rate: a binomial (yes/no) measure of whether each female gave birth each year or not, (ii) 12-month infant survival: a binomial measure of whether a female's infant survived to 12 months or not, (iii) infant longevity: a binomial measure of whether a female's infant survived each subsequent year postpartum.

Two mixed effects logistic regressions were used to test whether $N_{strong,}$ N_{weak}, or dominance rank predicted either birth rate (N=98 potential cycles for female conception) and 12-month survival (N=46 births). Female ID nested inside Year was entered as a random effect in both models to control for the fact that a single mother could produce more than one infant.

A time-dependent cox proportional hazards models with robust standard errors was used to test whether $N_{strong,}$ N_{weak}, or dominance rank predicted 'yearly infant longevity' (N=87 infant years). N_{strong}, N_{weak}, and dominance rank were calculated for each year of an infant's life. We entered mother ID as a cluster option to control for the fact that a single mother could produce more than one infant. All statistical analyses were performed in Stata Statistical Software: Release 14 (StataCorp 2015). We follow Colquhoun (2014) in describing outcomes as indicating weak (P ~0.05), moderate (P~0.01) or strong (P~0.001) evidence for effects.

RESULTS

We calculated yearly CSIs for all female group member dyads over the seven-year study period. The distribution of bond strengths was highly skewed to the left, with many dyads maintaining weaker social bonds (figure 1). N_{weak} was unrelated to N_{strong} (ß±SE=-0.06±0.12, Z=-0.53, P=0.597). Figure 2 illustrates the yearly number of strong and weak social bonds each of our females maintained over the duration of the study (figure 2).

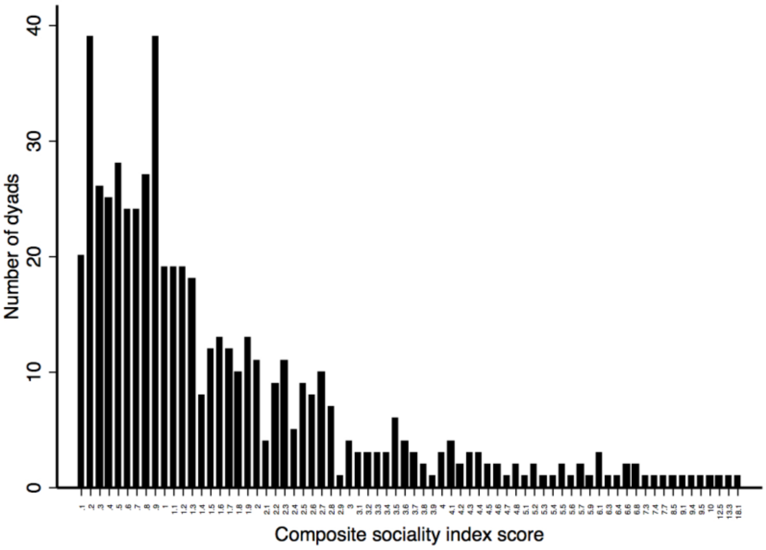

Figure 1. Frequency distribution of composite sociality index (CSI) scores across all adult female baboon dyads. CSI: 1=average, <1=weaker than average bonds (N=258), >1=stronger than average bonds (N=301). CSI scores of zero are not displayed (N=383).

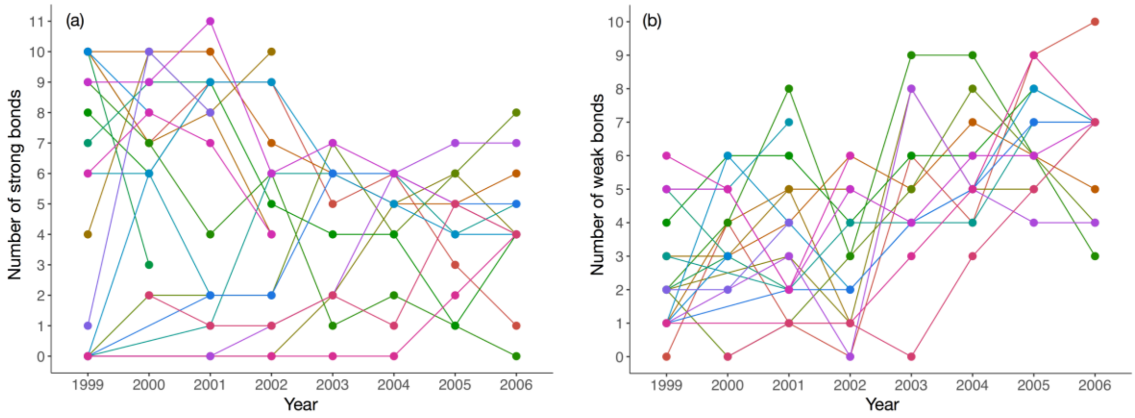

Figure 2. The number of (a) strong, and (b) weak social bonds each female shared over the duration of the study.

There was weak evidence to suggest that birth rate was positively related to N_{strong} (ß±SE=0.30±0.15, Z=2.03, P=0.042). Birth rate was unrelated to both N_{weak} (ß±SE=0.19±0.16, Z=1.20, P=0.231) and dominance rank (ß±SE=-0.05±0.07, Z=-0.69, P=0.493). There was moderate evidence to suggest that 12-month infant survival was positively related to N_{weak} (ß±SE=1.41±0.63, Z=2.22, P=0.026). 12-month infant survival was also unrelated to both N_{strong} (ß±SE=1.13±0.59, Z=1.90, P=0.058) and dominance rank (ß±SE=0.02±0.187, Z=0.14, P=0.892).

There was also moderate evidence to suggest that infants whose mothers maintained a larger N_{weak} experienced a lower hazard of dying (HR±SE=0.70±0.11, Z=-2.28, P=0.023; figure 3*a*). Hazard of dying was unrelated to both N_{strong} (HR±SE=0.90±0.11, Z=-0.82, P=0.410; figure 3*b*) and dominance rank (HR±SE=1.05±0.08, Z=0.66, P=0.508).

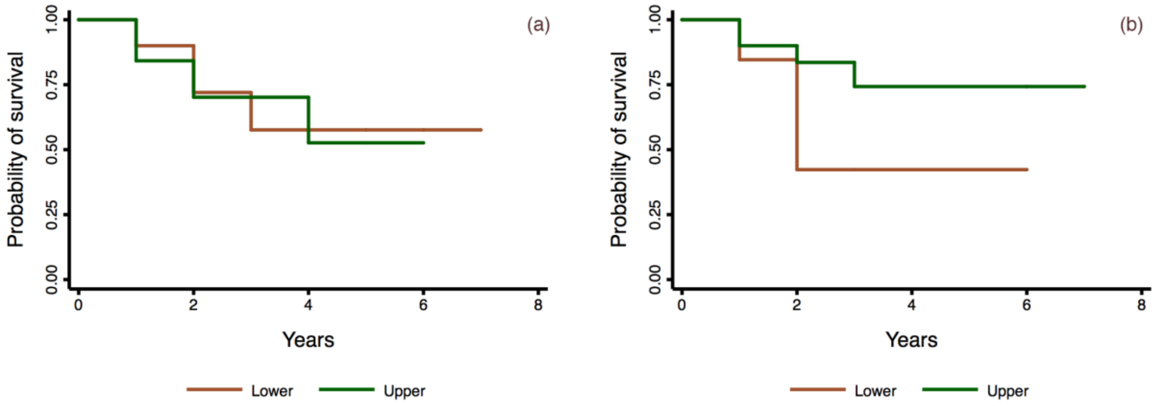

Figure 3. Survivorship curves illustrating the influence of (a) strong and (b) weak social bonds on infant longevity. For purposes of illustration, infants were categorized according to the number of bonds their mothers shared and clustered into the lower and upper half of the group distribution.

DISCUSSION

A strong emphasis has been placed on inter-individual variability in the maintenance of strong social bonds when attempting to partition the reproductive fitness benefits associated with social integration (Armitage & Schwartz 2000; Silk et al. 2003, 2009, 2010; Smith & Christakis 2008; Cameron et al. 2009; Schülke et al. 2010). Our findings agree with previous work demonstrating an effect of bondedness on fitness-related traits, but add an extra dimension by considering the influence of both weak and strong bonds. In our study group, female chacma baboons invested in a broad network of weaker social bonds, with only a few dyads displaying especially strong social relationships; a finding also reported in yellow baboons (Silk et al. 2006). There was no relationship between the number of weak and strong bonds that a female possessed, suggesting that, in our study, there is no necessary trade-off between the number of weak versus strong bonds. That is, a larger number of strong bonds does not preclude females from investing in a number of weak bonds, nor does it suggest that females form weak bonds to compensate for a lack of strong bonds. Instead, it may imply that, as suggested in the introduction, strong and weak bonds serve distinct functions.

This result is also intriguing given that the time available for the servicing of social relationships is limited (Dunbar et al. 2009; Marshall et al. 2012), and individuals that invest more time in grooming particular individuals have been argued to do so at the expense of generating a broader social network (Dunbar 1992). Our results suggest that this need not be the case, although it is possible that the large variability seen across years in the number of weak and strong bonds (figure 2) may reflect shifts in time budget demands within and between females across time. In humans, Granovetter (1973) argued that the value of weak ties (i.e., bonds) lay in the formation of bridges between individual social networks, enabling connections between a wider range of people than strong ties. Comparable ‘indirect relationships’ are also observed among non-human primates, in the sense that two animals that do not themselves interact can be connected by a third with whom they do (Brent 2015), albeit within networks generally restricted to group mates. Weak bonds between may therefore increase overall levels of social integration by enhancing these indirect relationships; something that can be tested using social network measures of centrality and comparing these to the patterns of bondedness identified using CSI. That is, females with a larger number of weak social bonds, as measured by CSI, should also occupy more central positions in the social network as measured by, for example, alpha or eigenvector centrality (Brent 2015).

With respect to reproductive success indicators, our results show that broad social networks of relatively weak bonds provide fitness-related benefits, supporting similar findings in our own previous work on baboons, macaques and vervets (Henzi et al. 2009; McFarland & Majolo 2013; McFarland et al. 2015). Both infant survival to one year and infant longevity were predicted by a female's number of weak social bonds, but were not predicted by the number of strong bonds a female possessed. In addition, there was some evidence to suggest that female birth rate was influenced by the number of strong bonds she possessed, but was not related to weak bonds. In both cases, there was no influence of dominance on these fitness-related traits.

The idea that weak and strong social bonds serve different functions and, hence, the relative importance of strong versus weak bonds might differ across ecological and demographic contexts (including group-size effects) thus warrants more detailed consideration. For example, the De Hoop baboons differ from the Kenyan and Botswanan populations previously studied in a number of respects: they experience significant cold stress (Weingrill et al. 2004), variable feeding competition throughout the year (Henzi et al. 2009), low predation risk, and a moderate risk of infanticide. It may be the case, therefore, that the value of weak social bonds to De Hoop females reflects their specific ecology, whereas strong bonds alone enhance female reproductive success at other sites. Alternatively, as Silk and colleagues' used a different analytical approach, and did not explicitly consider the influence of weak bonds on female reproduction, it is possible that – given the similarities in the distribution curves of bond strengths across populations (Silk et al. 2006) – weak bonds may also augment strong bonds in these populations, and it is their combined effect that influences reproductive success. That is, the use of an individual's "top-partners" as an estimate of sociability potentially conflates strong and weak bonds, and analyses based on particular strong bonds might actually represent a proxy for the combined effect of weak plus strong social bonds.

We have shown previously that baboons at De Hoop and the Drakensberg tend to form only weaker social bonds during the season of food abundance, and both strong and weak social bonds when food was scarce (Henzi et al. 2009). The collinearity between social bond strength and food abundance, therefore, makes it difficult to assess any effect of sociability on individual fitness, independent of ecology. As baboons are not seasonal breeders, however, there is no necessary or consistent link between the presence of infants and recurrent ecological conditions that could, for example, influence survival to twelve months. That is, even though ecological conditions may influence the formation of weak versus strong bonds in some or other way, and these bonds influence fitness measures, any such ecological effect is not an alternative explanation, but part and parcel of why sociability exerts its fitness-related effects (Barrett et al. 1999; Barrett & Henzi 2002; Henzi et al. 2003; Henzi & Barrett 2007). The link between ecology, bondedness and fitness-related traits is undoubtedly complex, and it is also possible that ecology may directly influence infant survival in ways that are not mediated by female sociality: further analyses designed to tease out these possibilities is now possible, having established that social bondedness potentially can be linked to female reproductive success.

The lack of any effect of strong social bonds on infant survival, and a weak influence on birth rate stands in contrast to other baboon populations, although it should be remembered that strong social bonds potentially carry costs as well as benefits. For example, social network position can influence the transmission of pathogens within a group. An elevated risk of disease transmission is thought to be a major cost of group living, especially for social species such as primates (Altizer et al. 2003; Nunn & Altizer 2006). Individuals more centrally embedded in their social network, or those that possess a larger social network, tend to be prone to greater pathogen load than those individuals that are more socially isolated (MacIntosh et al. 2012; Rimbach et al. 2015; Wren et al. 2016). If possessing more strong social bonds increases an individual's chance of pathogen transmission, due to longer and more intense periods spent in close proximity, the formation of strong bonds may not always exert a positive influence on female reproductive success: mounting an immune response comes at an energetic cost that may impact female survival, fecundity and fertility, and, if infants are similarly affected, offspring survival.

Having said this, and although increased pathogen load is often cited as being detrimental to individual fitness (e.g., Lehman 1993), a more recent study suggests that increased exposure to certain types of pathogen may actually enhance host resistance to infection, and reduce the impact of infection on individual fitness (Ezenwa et al. 2016). In these circumstances, strong social bonds/and or a wide social network may enhance females' immune systems. This patterns of findings thus suggests that observed differences in the formation and patterning of social relationships between species and populations, and their differential effects on individual fitness-related traits, may reflect, not only ecological differences in feeding competition and climatic factors, but also the prevalence of certain pathogens.

Taken together, our findings are in line with previous work demonstrating the fitness-related benefits of sociability in female baboons. Our findings augment this previous work in a novel way, however, by showing that these benefits are not dependent on the formation of strong social bonds alone, but also reflect the influence of weak bonds. This suggests that females may reap long-term fitness-related benefits by forming strong and weak bonds in ways that enable them to both embed themselves in strong, predictable network structures, while at the same time, retaining the ability to use social bonds (of grooming and proximity) to respond contingently to current circumstances. In other words, it seems reasonable to suggest that females may be opportunistic in their formation of strong and weak bonds, varying investment in partners across time in relation to shifts in group demography and composition, as well in response to changes in reproductive state, health status and ecological conditions.

ACKNOWLEDGMENTS

Thanks to Cape Nature Conservation for permission to work at De Hoop, and to all the graduate students and field assistants who contributed to our long-term data-base. [redacted] was supported by NSERC Canada Research Chair and Discovery Programs; [redacted] was supported by the NRF (South Africa) and NSERC Discovery Grants during the writing of this manuscript. We are grateful to one anonymous reviewer and, in particular, Lauren Brent for invaluable feedback on earlier drafts of our manuscript.

REFERENCES

Akaike H. 1974 A new look at the statistical model identification. Automatic Control, IEEE Transactions on **19**, 716-723.

Altizer S, Nunn CL, Thrall PH, Gittleman JL, Antonovics J, Cunningham AA, Cunnningham AA, Dobson AP, Ezenwa V, Jones KE, Pedersen AB. 2003 Social organization and parasite risk in mammals: integrating theory and empirical studies. *Ann. Rev. Ecol. Evol. Syst.* 517-547.

Altmann J. 1974 Observational study of behavior: sampling methods. *Behavior* **49**, 227-266.

Armitage KB, Schwartz OA. 2000 Social enhancement of fitness in yellow-bellied marmots. *Proc. Natl. Acad. Sci.* **97**, 12149-12152.

Barrett L, Henzi SP, Weingrill A, Lycett JE, Hill RA. 1999 Market forces predict grooming reciprocity in female baboons. *Proc. Roy. Soc. Lond. B* **266**, 665–670.

Barrett L, Henzi SP. 2002 Constraints on relationship formation among female primates. *Behaviour*, **139**, 263-289.

Brent LJ. 2015 Friends of friends: are indirect connections in social networks important to animal behaviour? *Anim. Behav.* **103**, 211-222.

Brent LJ. et al. 2013 Genetic origins of social networks in rhesus macaques. *Sci. Rep.* **3**.

Brent LJ, Chang SW, Gariépy JF, Platt ML. 2014 The neuroethology of friendship. *Ann. N. Y. Acad. Sci.* **1316**, 1-17.

Cameron EZ, Setsaas TH, Linklater WL. 2009 Social bonds between unrelated females increase reproductive success in feral horses. *Proc. Natl. Acad. Sci.* **106**, 13850-13853.

Colquhoun D. 2014 An investigation of the false discovery rate and the misinterpretation of p values. *R. Soc. Open. Sci*. **1**, 140216.

Crockford C. et al. 2008 Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Horm. Behav.* **53**, 254-265.

De Vries H, Stevens JMG, Vervaecke H. 2006 Measuring and testing the steepness of dominance hierarchies. *Anim. Behav.* **71,** 585-592.

Dunbar RIM, Korstjens AH, Lehmann J. 2009. Time as an ecological constraint. *Biol. Rev.* **84**, 413–429.

Dunbar RIM. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behav. Ecol. Sociobiol*. **31**, 35–49.

Ezenwa VO, Ghai RR, McKay AF, Williams AE. 2016 Group living and pathogen infection revisited. *Curr. Opin. Behav. Sci.* **12**, 66-72.

Frère CH, Krützen M, Mann J, Connor RC, Bejder L, Sherwin WB. 2010 Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proc. Natl. Acad. Sci.* **107**, 19949-19954.

Granovetter MS. 1973 The strength of weak ties. *Am. J. Sociol.* **78**, 1360-1380.

Henzi SP, Barrett L, Gaynor D, Greeff J, Weingrill T, Hill RA. 2003 The effect of resource competition on the long!term allocation of grooming by female baboons: Evaluating Seyfarth's model. *Anim. Behav.* **66**, 931–938.

Henzi SP, Barrett L. 2007 Coexistence in female-bonded primate groups. *Adv. Study Behav.* **37**, 43-81.

Henzi SP, Lusseau D, Weingrill T, van Schaik CP, Barrett L. 2009 Cyclicity in the structure of female baboon social networks. *Behav. Ecol. Sociobiol.* **63**, 1015-1021.

Hinde RA. 1979 *Towards understanding relationships*. London: Academic Press.

Lehmann T. 1993 Ectoparasites: direct impact on host fitness. *Parasitol. Today* **9**, 8–13.

Marshall HH, Carter AJ, Rowcliffe JM, Cowlishaw G. 2012 Linking social foraging behaviour with individual time budgets and emergent group-level phenomena. *Anim. Behav.* **84**, 1295-1305.

McFarland R, Majolo B. 2013 Coping with the cold: predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biol. Lett.* **9**, 20130428.

McFarland R, Fuller A, Hetem RS, Mitchell D, Maloney SK, Henzi SP, Barrett L. 2015 Social integration confers thermal benefits in a gregarious primate. *J. Anim. Ecol.* **84**, 871-878.

McFarland R, Murphy D, Lusseau D, Henzi SP, Parker JL, Pollet TV, Barrett L. 2017 Data from: The strength of weak ties among female baboons: fitness-related benefits of social bonds. Figshare. (http://dx.doi.org/10.6084/m9.figshare.1572325).

Nunn C, Altizer SM. 2006 Infectious diseases in primates: behavior, ecology and evolution. Oxford: Oxford University Press.

Schülke O, Bhagavatula J, Vigilant L, Ostner J. 2010 Social bonds enhance reproductive success in male macaques. *Curr. Biol.* **20**, 2207-2210.

Silk JB. 2007 The adaptive value of sociality in mammalian groups. *Phil. Trans. R. Soc. B* **362**, 539-559.

Silk JB, Alberts SC, Altmann J. 2003 Social bonds of female baboons enhance infant survival. *Science* **302**, 1231-1234.

Silk JB, Altmann J, Alberts SC. 2006 Social relationships among adult female baboons (*Papio cynocephalus*) I: variation in the strength of social bonds. *Behav. Ecol. Sociobiol.* **61**, 183–195.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2009 The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc. R. Soc. B* **276**, 3099-3104.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010 Strong and consistent social bonds enhance the longevity of female baboons. *Curr. Biol*. **20**, 1359-1361.

Smith KP, Christakis NA. 2008 Social networks and health. *Annu. Rev. Sociol*. **34**, 405-429.

StataCorp. 2015 Stata Statistical Software: Release 14. College Station, TX: StataCorp LP.

Weingrill T, Gray DA, Barrett L, Henzi SP. 2004 Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Horm. Behav.* **45**, 259-269.

Wittig RM et al. 2008. Focused grooming networks and stress alleviation in wild female baboons. *Horm. Behav*. **54**, 170-177.

HIGHLIGHTS

- Baboon birth rate is positively predicted by the number of strong bonds shared.
- 12-month infant survival is positively predicted by the number of weak bonds shared.
- Infant longevity is positively predicted by the number of weak bonds shared.
- There is no simple trade-off between the number and quality of social bonds.
- Social strategies are linked to ecological and demographic variability.