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Report

Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons

Joan B. Silk,[1,2,*] Jacinta C. Beehner,[3,4] Thore J. Bergman,[3,5] Catherine Crockford,[6] Anne L. Engh,[7] Liza R. Moscovice,[9] Roman M. Wittig,[6] Robert M. Seyfarth,[8] and Dorothy L. Cheney[7]

[1]Department of Anthropology
[2]Center for Society and Genetics
University of California, Los Angeles, Los Angeles, CA 90095, USA
[3]Department of Psychology
[4]Department of Anthropology
[5]Department of Ecology and Evolutionary Biology
University of Michigan, Ann Arbor, MI 48109 USA
[6]School of Psychology, University of St. Andrews, St. Andrews KY16 9JP, UK
[7]Department of Biology
[8]Department of Psychology
University of Pennsylvania, Philadelphia, PA 19104, USA
[9]Department of Biology, Binghamton University, Binghamton, NY 13902, USA

Summary

Longevity is a major component of variation in fitness in long-lived iteroparous species [1–4]. Among female baboons, variation in breeding lifespan accounts for approximately 50% of the variation in lifetime fitness [5, 6]. However, we know little about the causes of variation in longevity in primates or other long-lived mammals. Savannah baboons form strong, equitable, and enduring relationships with specific female partners, particularly with close relatives and agemates [7–10]. The quality of females' social relationships influences their ability to cope with stressful events [11–13] and is associated with variation in female reproductive success [9, 14]. Here we show that dominance rank and the quality of close social bonds have independent effects on the longevity of female chacma baboons (*Papio hamadryas ursinus*). High-ranking females live longer than lower-ranking females. In addition, females who form stronger and more stable social bonds with other females live significantly longer than females who form weaker and less stable relationships. These data extend our understanding of the adaptive value of social bonds in baboons and complement a growing body of evidence that indicates that social bonds have adaptive value in a range of taxa, from mice to humans [9, 14–19].

Results and Discussion

The analyses focus on a group of free-ranging baboons in the Moremi Game Reserve in the Okavango Delta of Botswana studied continuously over a 16 year period [6, 20]. Previous analyses indicate that infants and juveniles suffer the highest rates of age-specific mortality, whereas adults experience relatively low mortality [6]. Predation is the major source of mortality for adults in this population [6].

Behavioral measures were derived from focal observations of adult females conducted regularly using a common protocol over a 7 year period, from 2001 to 2007. The number of adult females ($\geq$5 years of age) in the group during this period varied from 23 to 32, with an average of 27.4. Only females who were present in the group for at least 2 years were included in these analyses (n = 44).

All approaches, vocalizations, and affiliative 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 grooming initiations and the duration of grooming bouts.

We constructed a composite sociality index (CSI) to characterize the strength of affiliative relationships among females when they did not have young infants and to identify females' top three partners in each year [9, 10]. The CSI was constructed as follows: $(A_{ij}/A_{ave} + P_{ij}/P_{ave} + G_{ij}/G_{ave} + D_{ij}/D_{ave})/4$. The first term represents the hourly rate of approaches for dyad *ij* divided by the average hourly rate of approaches for all dyads, the second term represents grooming, the third represents grooming initiations, and the last represents grooming duration. These values are summed and divided by 4. The CSI measures the extent to which each dyad deviated from other dyads in a given year. The mean of the CSI is defined as 1, but the values can range from 0 to infinity. High values of the CSI represent dyads that had stronger social bonds than the average female dyad in the group in a given year, and low values of the sociality index represent dyads that had weaker social bonds. We used CSI scores to identify each female's top three partners in each year.

To assess the consistency of females' relationships with their top three partners, we used the following procedure. For each female, we tabulated the number of different females that were among her top three partners across years. This value, U, could range from 3 to 3Y, where Y is the number of years that the female was present (range 2–7). We assessed the consistency of females' relationships as $C = (3Y - U)/(3Y - 3)$. The possible values of C range from 1 for females who had the same three partners across years to 0 for females who had three different partners each year.

Females varied considerably in the strength and consistency of their relationships with their top partners, and this variation contributed significantly to variation in longevity. The value of the CSI for females' top three partners averaged 7.30 ± 0.56 (range: 1.38–14.41). Although females in this group show strong preferences for closely related females [9, 10], some females established strong bonds with unrelated individuals. Thus, there was a trend for females with more relatives in the group to have stronger social bonds with their top partners (Table 1). Female dominance rank had no effect on the strength of females' relationships with their top three partners (Table 1).

There was also considerable variation in the consistency of females' relationships with their top partners from year to year (mean = 0.37 ± 0.03, range 0–0.67). The consistency of females' relationships was positively related to the number

*Correspondence: joansilk@gmail.com

Table 1. Sources of Variation in the Strength and Consistency of Relationships

	Strength[a]				Consistency[b]			
	β	Standard Error	t Statistic	p Value	β	Standard Error	t Statistic	p Value
Mothers and daughters present	1.7880	0.9378	1.91	0.064	0.1509	0.0354	4.26	<0.001
Dominance rank	0.0867	2.0972	0.04	0.967	−0.0232	0.1062	−0.22	0.828

[a] Regression with robust standard errors: $F_{2,41} = 1.87$, $p = 0.169$, $R^2 = 0.07$.
[b] $F_{2,41} = 9.29$, $p = 0.0005$, $R^2 = 0.18$.

of close relatives that they lived with, but not to their dominance rank (Table 1). Importantly, the lack of consistency in some females' relationships appeared to result from instability in the relationships themselves rather than stochastic demographic events. In 79% of cases in which females switched partners from one year to the next, their previous year's partners were still present in the group.

Females who had the strongest relationships with their top partners also had the most consistent relationships ($r = 0.6097$, $p < 0.0001$, $n = 44$). Because of the high correlation between these variables, we used principal component analysis to combine these variables into a single measure of relationship quality. Female dominance rank was unrelated to relationship quality ($r = 0.0622$, $p = 0.6882$, $n = 44$).

Relationship quality and high dominance rank jointly influenced female longevity (Cox proportional hazards model: Wald $\chi^2 = 15.85$, $p = 0.0004$, $n = 44$). High-ranking females lived significantly longer than lower-ranking females ($\beta = -1.6682 \pm 0.7916$, $z = -2.11$, $p = 0.034$). In addition, females who had stronger and more consistent relationships with their top partners lived significantly longer than other females ($\beta = -0.4324 \pm 0.1497$, $z = -2.89$, $p = 0.004$; Figure 1). This effect was stronger than that related to dominance rank. The effects of relationship quality held when we controlled statistically for the presence of close maternal kin.

These findings indicate that relationship quality and dominance rank have independent effects on female longevity, that relationship quality has stronger effects on longevity than does dominance rank, and that the development of strong and consistent social bonds may partially offset fitness loss because of low dominance rank. The fact that most females' partner changes were not the result of the death of a close partner suggests that some females were more strongly motivated or more skilled in maintaining relationships with favored partners over time. Natural selection may have favored in baboons—and, by extension, in other primates—mechanisms that promote the maintenance of close and enduring social bonds. Previous work indicates that pairs of female baboons that have the most equitable grooming relationships also have the strongest and most enduring social bonds [8]. The mechanisms that contribute to grooming reciprocity among females may be favored because they enhance relationship quality and thereby extend females' life spans and increase their lifetime fitness.

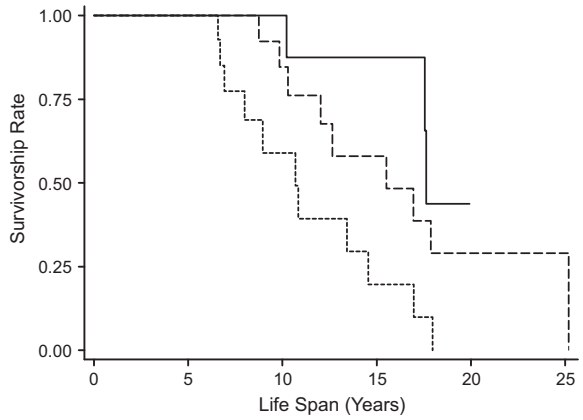

Figure 1. Females with Strong and Consistent Stable Bonds Live Longer than Females with Weaker and Less Consistent Social Bonds

For the purposes of the illustration, females were divided into three groups based on relationship quality. The solid line represents females in the top third, the dashed line represents females in the middle third, and the dotted-dashed line represents females in the bottom third.

Our findings parallel evidence showing that social integration enhances longevity in humans in a range of cultural settings [18, 19, 21–24]. In humans, social support has important effects on cardiovascular, endocrine, and immune system function [25]. Social ties seem to buffer the short-term effects of stress and may enhance the efficacy of anabolic processes involved in somatic maintenance and repair [25]. In both humans and baboons, social ties seem to reduce adrenocortical activity [11–13, 25, 26], suggesting that these responses may be based on homologous processes. Taken together, these data suggest that the human motivation to form close and enduring social bonds has a long evolutionary history.

Experimental Procedures

The analyses focus on one group of free-ranging baboons in the Moremi Game Reserve in the Okavango Delta of Botswana. This group was habituated in the late 1970s by William J. Hamilton and his colleagues, who continued observations of the group into the 1980s. From June 1992 through December 2007, the group was observed almost daily by a series of researchers working in collaboration with Dorothy Cheney and Robert Seyfarth. For more information about the study population and site, see [20].

Information about births and deaths was derived from demographic records collected almost daily during the study period; see [6]. For the purposes of these analyses, females were considered to be adult when they reached the age of 5 years.

Dominance ranks among adult females were determined by the direction of approach-retreat interactions [9, 10]. Females were assigned yearly ranks according to the proportion of females dominated in January of each year (relative rank). The proportion of females dominated was calculated as $(N - d)/(N - 1)$, where N is the total number of adult females in the group each year and d is the ordinal rank of a particular female. The highest-ranking female in the group is ranked 1, and the lowest-ranking female in the group is ranked 0. Values were averaged across years.

All statistical analyses were conducted with STATA 11.0 (Statcorp 2009). Two-tailed tests of significance were used throughout.

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