

Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons

Elizabeth A. Archie, Jenny Tung, Michael Clark, Jeanne Altmann and Susan C. Alberts

Proc. R. Soc. B 2014 **281**, 20141261, published 10 September 2014

Supplementary data

["Data Supplement"](#)

<http://rspb.royalsocietypublishing.org/content/suppl/2014/09/09/rspb.2014.1261.DC1.html>

References

[This article cites 66 articles, 14 of which can be accessed free](#)

<http://rspb.royalsocietypublishing.org/content/281/1793/20141261.full.html#ref-list-1>

Subject collections

Articles on similar topics can be found in the following collections

[behaviour](#) (1226 articles)

[evolution](#) (1887 articles)

[health and disease and epidemiology](#) (259 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Research



Cite this article: Archie EA, Tung J, Clark M, Altmann J, Alberts SC. 2014 Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc. R. Soc. B* **281**: 20141261. <http://dx.doi.org/10.1098/rsob.2014.1261>

Received: 25 May 2014

Accepted: 13 August 2014

Subject Areas:

behaviour, evolution, health and disease and epidemiology

Keywords:

social relationships, intrasexual competition, longevity, social connectedness, survival

Author for correspondence:

Elizabeth A. Archie
e-mail: earchie@nd.edu

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsob.2014.1261> or via <http://rsob.royalsocietypublishing.org>.

Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons

Elizabeth A. Archie^{1,3}, Jenny Tung^{3,4,5,6}, Michael Clark², Jeanne Altmann^{3,7,8} and Susan C. Alberts^{3,5}

¹Department of Biological Sciences, and ²Center for Social Research, University of Notre Dame, Notre Dame, IN, USA

³Institute of Primate Research, National Museums of Kenya, Nairobi, Kenya

⁴Department of Evolutionary Anthropology, Duke University, ⁵Duke Population Research Institute, Duke University, and ⁶Department of Biology, Duke University, Durham, NC, USA

⁷Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA

⁸Department of Veterinary Anatomy and Physiology, University of Nairobi, Nairobi, Kenya

Social integration and support can have profound effects on human survival. The extent of this phenomenon in non-human animals is largely unknown, but such knowledge is important to understanding the evolution of both lifespan and sociality. Here, we report evidence that levels of affiliative social behaviour (i.e. 'social connectedness') with both same-sex and opposite-sex conspecifics predict adult survival in wild female baboons. In the Amboseli ecosystem in Kenya, adult female baboons that were socially connected to either adult males or adult females lived longer than females who were socially isolated from both sexes—females with strong connectedness to individuals of both sexes lived the longest. Female social connectedness to males was predicted by high dominance rank, indicating that males are a limited resource for females, and females compete for access to male social partners. To date, only a handful of animal studies have found that social relationships may affect survival. This study extends those findings by examining relationships to both sexes in by far the largest dataset yet examined for any animal. Our results support the idea that social effects on survival are evolutionarily conserved in social mammals.

1. Introduction

In the last few decades, there has been considerable interest in understanding how and when social relationships contribute to variation in lifespan [1]. In humans, social integration and support predict both health [2–6] and survival [7–10]. However, comparable studies in non-human animals are rare. To date, only three such studies have been conducted [11–13]. Of these, only two measured social effects on natural adult lifespans, one in captive rats and one in wild baboons [11,12]: both found that some aspects of social relationships enhanced longevity. While few in number, such studies are important because they suggest that social effects on survival may be evolutionarily conserved in social species, perhaps linked by common biological mechanisms [11,12]. In addition, social relationships are thought to be adaptations that evolved in response to selective pressures such as predation, resource acquisition and offspring care. In support, a number of studies have linked social integration or the quality of social bonds to reproductive components of fitness, such as fecundity or offspring survival [14–21]. However in long-lived species, lifespan is also a major fitness component [22,23]. If social integration can predict longevity as well as reproductive success, this suggests an additional, powerful fitness benefit of social relationships and one that likely operates via different mechanisms than social effects on reproduction.

To date, most research on the fitness benefits of social relationships in non-human animals—both for reproduction and for survival—have focused on the benefits of same-sex relationships [11–13,15–21]. By contrast, the fitness benefits of heterosexual social relationships have been largely ignored. However, heterosexual bonds are protective in humans [1,4,24], and two pieces of evidence suggest that they may also be important in other mammals, especially in primates. First, two-thirds of primate genera exhibit permanent, year-round associations between adult males and females, including many non-monogamous species [25,26]. Second, many primate species exhibit close social relationships among adult males and females (sometimes called ‘friendships’) [27–37]. While the primary benefits of such friendships are thought to be reproductive, including bi-parental offspring care and access to potential mates [28,36,38–49], heterosexual friendships may also benefit females directly via reduced harassment, reduced predation risk or stress mitigation [38,39,50–52].

Here, we present the first test of whether a female’s level of affiliative social behaviour (i.e. social connectedness) with both same-sex and opposite-sex conspecifics predicts adult survival in a wild vertebrate. We do so using data spanning 27 years of observations on 204 adult females in the Amboseli baboon population in Kenya. We use a time-varying statistical framework that accounts for age-related changes in individual social connectedness and in the availability of social partners. Our results confirm the importance of female–female social connectedness to female longevity in this species [12] and extend this result to encompass a further independent effect of male–female connectedness on female survival. The strength of these effects motivated us to also investigate the social and demographic factors that predict variation in female social connectedness, a topic of considerable interest in the literature on humans.

2. Material and methods

(a) Study subjects

Study subjects were members of a well-studied population of wild baboons living in the Amboseli ecosystem in southern Kenya [53]. Subjects were females that had survived to reach adulthood, living in eight different social groups over 84 group-years (average years per group = 10.5; range = 2–16 years). Behavioural and demographic data on each group were collected by three experienced observers during 5-h monitoring visits. These visits occurred year round, two to three times per week per group. For 93% of the females in our main dataset (190 of 204), ages were known to within a few days; for the remaining 14 females (born before the onset of behavioural monitoring), birthdates were estimated to within 1 year ($n = 6$), 2 years ($n = 1$) or 3 years ($n = 7$). Death dates were known to be within a few days for females that died before the end of the study period. For females, adulthood was defined by the onset of menarche; males were considered adult when they became higher ranking than all adult females and ranked among the adult males in their social group [54].

(b) Measuring female social connectedness

We constructed two individual-based, age-specific indices of adult female social connectedness: one to adult females (SCI-F) and the other to adult males (SCI-M). In studies of the adaptive and health significance of social behaviour, affiliative social connectedness has been measured in a variety of ways (e.g. [1,11–13,15,16–19,40]).

We chose to use ‘composite’ indices of social connectedness (as opposed to ‘dyadic’ indices (e.g. [11,12,17]) because we were interested in the effects of a female’s overall level of affiliative social behaviour, regardless of the presence or quality of particular social bonds in her life. Our indices were very similar to those used in several prior studies in non-human animals [14,16,53], as well as those used to measure structural social integration in many studies in humans (reviewed in [1]). Specifically, social connectedness was measured for each female relative to all other adult females alive in the population in the same year. Following previous studies [12,14,15,54], these indices used data on grooming behaviour, which maintains and strengthens social bonds in baboons and other primates [55,56].

To measure grooming relationships, we chose to use ad libitum observations of grooming [57,58], which included all observed instances of grooming between group members and was the densest dataset available to measure patterns of female affiliation (see the electronic supplementary material). Our sampling protocol was designed to avoid potential biases in the grooming data that could result from uneven sampling of study subjects. Specifically, the great majority of our ad libitum data were collected during random-order focal animal sampling on adult females and juveniles, which ensured that observers continually moved to new locations within the group and observed all adult females and juveniles on a regular rotating basis. Ad libitum grooming frequencies were significantly correlated with hourly rates of grooming from focal animal sampling (see the electronic supplementary material), indicating a lack of strong or systematic bias in the ad libitum data. Nevertheless, we could not assess whether our analysis choices completely eliminated biases introduced by our sampling protocol; therefore, we also consider possible implications of these choices in the Discussion.

From the ad libitum data, we calculated SCI-F and SCI-M for each adult female in each year of her adult life as a composite index of the relative frequency that she groomed and was groomed by adult females or adult males, respectively (see the electronic supplementary material, figure S1). Positive SCI values represent females with relatively high frequencies of grooming for the population in that year; negative values represent females with relatively low frequencies of grooming for that year.

(c) Testing SCI-F and SCI-M as predictors of survival

Data to replicate our analyses have been uploaded to the Dryad data repository. We modelled survival in adult females using Cox proportional hazards models. We employed time-varying covariates in our models because, in the course of testing predictors of SCI-F, we found that older females generally had lower values of SCI-F, making it inappropriate to use a single, average value of lifetime social connectedness. We ran two different models using the *rms* package [59,60] in R [61]. The first model, called the ‘main’ model, included 1968 female-years of data on 204 females with 87 censored records (censored records were females who were still alive when our records ended in 2011; average number of years of data per female = 9.64; range = 1–24 years). The main model included imputed values for some predictor variables in 30% of female-years. Missing values were imputed via multiple imputation [62] and weighted predictive mean matching as implemented via the *aregImpute* function in the *rms* package in R [59,60] (see the electronic supplementary material for additional information on data imputation methods). We performed the full imputation 50 times to create 50 imputed datasets and fit the main Cox proportional hazards model to each of these 50 datasets. Parameters presented in the main model were averaged over the 50 model fits. The second model, called the ‘complete case’

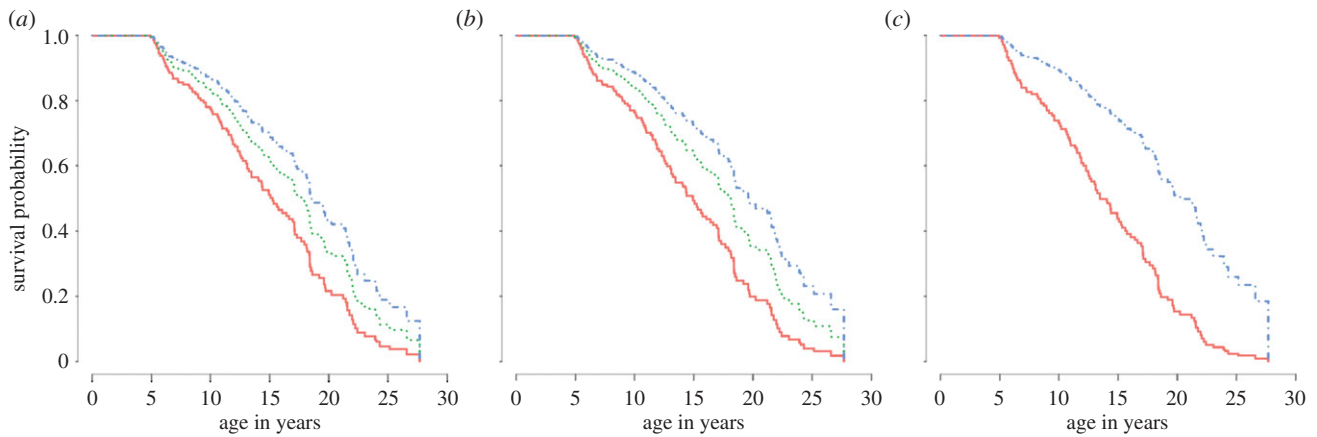


Figure 1. Survival probability for adult female baboons as a function of social connectedness. Plots (a) and (b) depict the effects of SCI-F and SCI-M, respectively; plot (c) depicts the combined effects of female social connectedness to adult females and males. Solid red lines indicate females at the lower 25th percentile for social connectedness, green dotted lines indicate females at the median for social connectedness and blue dashed lines indicate females at the upper 75th percentile for social connectedness. (Online version in colour.)

Table 1. Cox proportional hazards model predicting female survival ($N = 204$ females; 1968 female-years of data, 87 censored records). Significant model effects are shown in *italics*.

factors	<i>b</i>	s.e.	<i>z</i>	hazard ratio	<i>p</i>	direction
dominance rank	−0.02	0.02	−0.99	0.98	0.323	—
group size	−0.01	0.01	−0.50	0.99	0.618	—
mother alive versus dead	−0.33	0.27	−1.22	0.72	0.224	—
has adult daughters	0.12	0.30	0.39	1.12	0.696	—
<i>SCI-F^a</i>	<i>−0.42</i>	<i>0.14</i>	<i>−2.90</i>	<i>0.66</i>	<i>0.004</i>	↑ survival with ↑ SCI-F
<i>SCI-M^a</i>	<i>−0.59</i>	<i>0.14</i>	<i>−4.30</i>	<i>0.55</i>	<i><0.001</i>	↑ survival with ↑ SCI-M

^aTo facilitate interpretation, the coefficient (*b*) and hazard ratio for SCI-F and SCI-M reflect the predicted change in the hazard function for the interquartile range of SCI-F and SCI-M (i.e. between the 25th and 75th percentiles), not a change of 1 unit for these variables.

model, excluded all female-years with missing data. This model included 1376 female-years of data on 194 females, with 124 censored records. The complete case model had more censored records than the main model because one or more predictor variables were missing for some females in the final year(s) of their life, forcing us to truncate their data prior to the year of their death ($N = 37$ of 124).

For both the main and the complete case models, females entered the model at adulthood and left the model at death or censorship. For both models, we included the following predictor variables: (i) the female's SCI-F in that year, (ii) her SCI-M in that year, (iii) her average dominance rank in that year, (iv) her average group size (the number of adults of both sexes in the group in that year), (v) whether her mother was still alive and present in the group in that year, and (vi) whether she had adult daughters living in the group that year. For each of these predictors, the validity of the proportional hazards assumption was well supported (electronic supplementary material, table S1). There were no differences in the results from the main and complete case models; in the text, we present the results of the main model because of its added statistical power (see the electronic supplementary material for results of the complete case model).

(d) Identifying predictors of social connectedness

Because we found strong effects of SCI-F and SCI-M on female survival, we conducted further analyses to understand which factors predicted individual SCI-F and SCI-M. Based on prior research, we expected that female social connectedness to adult

females would be correlated with the availability of adult maternal kin, who often form the strongest social bonds in baboon societies [63–66], as well as age, which is associated with declining availability of non-kin social partners [64]. We further predicted that female social connectedness to adult males would be correlated with female dominance rank, based on evidence that male 'friends' may be a limited resource for female baboons [41,50,67].

We modelled SCI-F and SCI-M separately using linear mixed effects models constructed in the *lme4* package in R [68]. Female identity was included in the models as a random variable; we also included the following variables for each female in each year of her adult life: (i) age; (ii) average dominance rank; (iii) average group size; (iv) whether her mother was present in the group; (v) number of her adult maternal sisters in the group; (vi) number of her adult daughters in the group; and (vii) her social connectedness to the other sex (i.e. SCI-M in the case of the SCI-F model and vice versa). We present the results of the full models, but also used stepwise elimination and likelihood ratio tests for subsequent model selection.

3. Results

(a) Social connectedness to adult females and adult males had strong, independent effects on survival

Female social connectedness to both adult males and adult females had powerful effects on survival (figure 1 and table 1;

electronic supplementary material, table S2). Females with SCI-F values at the upper 75th percentile were 34% less likely to die in a given year than females at the lower 25th percentile of SCI-F. These effects were somewhat stronger for female social connectedness to adult males, as females with SCI-M values at the upper 75th percentile were 45% less likely to die in a given year than females at the lower 25th percentile (table 1). These differences in survival translated to strong effects on lifespan; the median lifespan of a female that remained consistently at the upper 75th percentile of SCI-F would be 2 years longer than that of a female who remained consistently at the lower 25th percentile (figure 2; median adult survival at the bottom quartile = 16.4 years; median survival at the top quartile = 18.4 years). For female social connectedness to males, median survival for females at the 75th percentile of SCI-M was 3.3 years longer than for females at the 25th percentile (figure 2; median adult survival at the bottom quartile = 15.3 years; median survival at the top quartile = 18.6 years).

There were no significant interaction effects in the relationship between SCI-F and SCI-M. Hence, female social connectedness to adult females did not influence the survival effects of female connectedness to adult males, or vice versa. Females who were in the bottom quartile of social connectedness to just one sex were 13–26% less likely to die in a given year than females in the bottom quartile of social connectedness to both sexes (incidences of death per female year: 7.5%, 8.9% and 10.2% for females in the bottom quartile of SCI-F, SCI-M, and both SCI-F and SCI-M, respectively).

The effects of SCI-F and SCI-M on survival were also not confounded by variation in female dominance rank, group size or the availability of female maternal kin, which were included in our models. None of these other variables explained significant variation in survival (table 1; electronic supplementary material, table S2). Subsequent analyses indicated that SCI-M was correlated with female dominance rank (see below); hence, we tested whether female dominance rank predicted survival if we removed SCI-M from the model. We found no evidence for this effect (rank effect in a model without SCI-M; $b = -0.003$, $z = -0.18$, $p = 0.85$).

(b) Variation in SCI-F was predicted by the availability of close maternal kin, age and SCI-M

We next examined social and demographic sources of variance in SCI-F and SCI-M. We found significant relationships between SCI-F and four predictor variables (table 2). First, females had higher values of SCI-F when their mothers were alive and when they had more adult daughters. There was a tendency for females with more maternal sisters to have higher SCI-F than females with fewer maternal sisters, but stepwise elimination of non-significant effects indicated that this variable did not significantly improve the model (likelihood ratio test: $p = 0.099$). Second, SCI-F was lower in older than in younger females. Given typical lifetime variation in female SCI-F (average minimum SCI-F = -1.12 ; average maximum SCI-F = 1.11), our model predicted a 19% decline in SCI-F between the ages of 5 and 20. Third, we observed a weak but significant negative relationship between SCI-F and SCI-M, indicating that females who were socially isolated from males were not necessarily isolated from females and that females may, in fact, have experienced a slight trade-off in their social connectedness to males versus females (table 2). Finally, while there was a

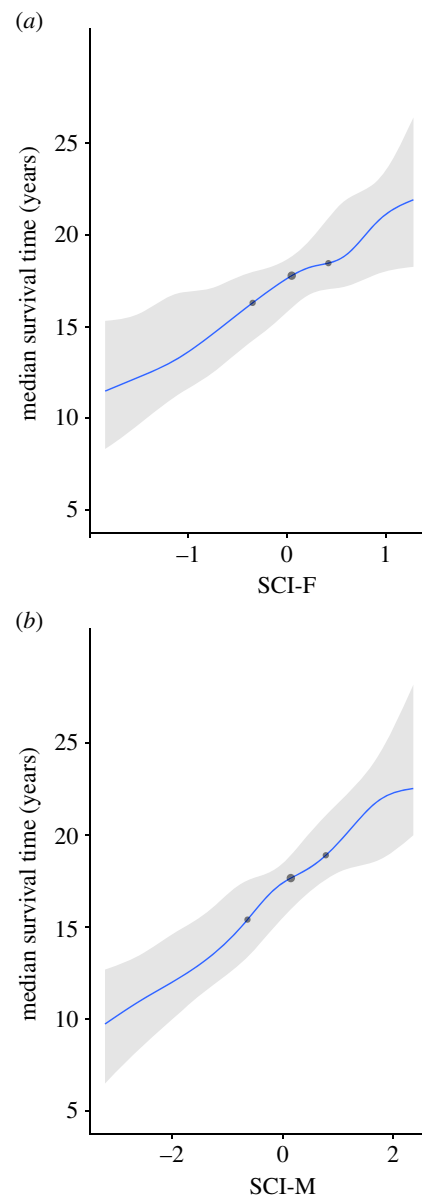


Figure 2. Median adult female survival time as a function of social connectedness to (a) adult females and (b) adult males. Large dots indicate the median values of social connectedness; small, flanking dots indicate the top 75th and lower 25th percentiles of social connectedness. Grey shading indicates 95% CIs. (Online version in colour.)

tendency for high-ranking females to have higher SCI-F than low-ranking females, the addition of this variable did not significantly improve the model's fit to the data (likelihood ratio test: $p = 0.067$).

(c) Variation in SCI-M was predicted by female dominance rank, group size and SCI-F

We found significant relationships between SCI-M and three predictor variables (table 3). First, high-ranking females were more socially connected to males than low-ranking females (figure 3). Given the typical lifetime variation in female SCI-M (average minimum SCI-M = -2.09 ; average maximum SCI-M = 2.08), our model predicts only a modest increase in SCI-M of about 1% for every step up in dominance rank (table 3). However, very high-ranking females (approx. ranks 1–3) appear to experience disproportionately greater access to male social partners than lower ranking females

Table 2. Linear mixed effects model predicting adult females' social connectedness to other adult females (SCI-F; $N = 1376$ female-years of data from 194 females). Significant model effects are shown in *italic*.

fixed effects	<i>b</i>	s.e.	<i>t</i>	<i>p</i>	direction
<i>age</i>	−0.027	0.007	−4.124	<0.001	↑ SCI-F at younger ages
dominance rank	−0.006	0.005	−1.065	0.288	—
group size	−0.002	0.003	−0.790	0.429	—
<i>mother alive versus dead</i>	0.187	0.053	3.522	<0.001	↑ SCI-F with mother alive
number of adult maternal sisters	0.043	0.024	1.757	0.079	—
<i>number of adult daughters</i>	0.270	0.036	7.565	<0.001	↑ SCI-F with ↑ daughters
<i>SCI-M</i>	−0.036	0.017	−2.194	0.028	↑ SCI-F with ↓ SCI-M

Table 3. Linear mixed effects model predicting adult females' social connectedness to adult males (SCI-M; $N = 1376$ female-years of data from 194 females). Significant model effects are shown in *italic*.

fixed effects	<i>b</i>	s.e.	<i>t</i>	<i>p</i>	direction
age	0.011	0.011	1.012	0.352	—
<i>dominance rank</i>	−0.048	0.008	−6.072	<0.001	↑ SCI-M with ↑ rank
<i>group size</i>	0.014	0.004	2.981	0.003	↑ SCI-M in larger groups
mother alive versus dead	0.141	0.083	1.706	0.088	—
number of adult maternal sisters	0.029	0.037	0.792	0.428	—
number of adult daughters	0.009	0.059	0.152	0.879	—
<i>SCI-F</i>	−0.089	0.044	−2.039	0.042	↑ SCI-M with ↓ SCI-F

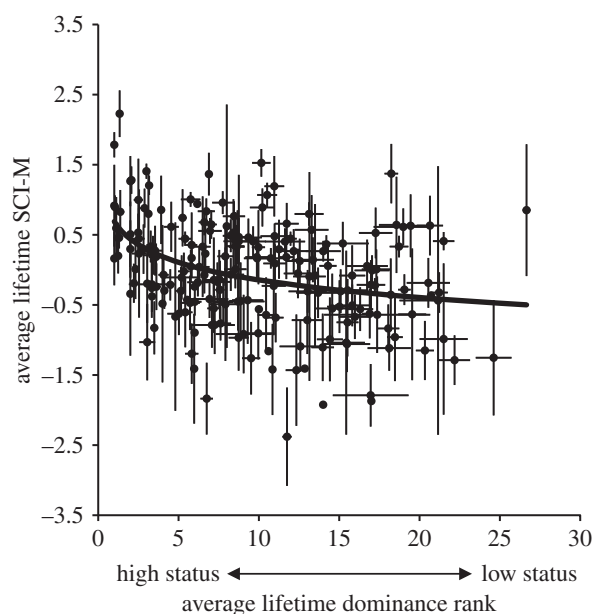


Figure 3. Mean lifetime female social connectedness to adult males (SCI-M) as a function of mean lifetime dominance rank for 194 adult female baboons. Black line depicts a log fit to the data. Error bars represent standard errors of the mean.

(figure 3). Indeed, modelling this relationship using natural log-transformed female rank produced a stronger relationship than when using untransformed rank (AIC for a model with log-transformed rank = 4108.117, AIC for a model with ordinal rank = 4119.665). Second, females living in larger groups had higher values of SCI-M than females in smaller groups (table 3). This result may reflect

differences in the availability of adult males in different sized groups; in our data, smaller groups had fewer adult males per adult female than larger groups (correlation between adult sex ratio and group size: $b = 0.005$, $p < 0.001$). Furthermore, the number of adult males in the group had a much stronger positive effect on SCI-M than did the total number of adults in the group (correlation between number of adult males in the group and SCI-M: $b = 0.046$, $p < 0.001$). Third, we again found a weak, negative relationship between SCI-F and SCI-M such that females with higher SCI-F had slightly weaker SCI-M (table 3).

4. Discussion

(a) Social effects on survival

Our results represent the first demonstration in a non-human animal that a female's level of affiliative social behaviour with both same-sex and opposite-sex individuals predicts her survival. Specifically, high levels of social connectedness to adult males reduced the risk of death of adult female baboons by 45% or more, and social connectedness to adult females reduced the risk of death by 34% or more. Compared with the large literature on social relationships and survival in humans (e.g. [1,7, 8–10]), studies that test the association between social behaviour and survival in animals are extremely rare.

To date, there have been only three such studies [11–13]. First, among 44 wild female baboons in Botswana, females with stronger, more persistent and more stable female–female social bonds led longer lives than females with weaker, transient and unstable bonds [12]. Second, in a

sample of 28 juvenile wild male dolphins, individuals with higher eigenvector centrality (a combined measure of direct and indirect associations) in a social network of juvenile males were more likely to survive the juvenile period than males with lower eigenvector centrality [13]. Finally, among 49 female Sprague-Dawley rats, reciprocity in affiliative relationships with other females was protective against all-cause mortality in a laboratory setting [11].

A unique component of our study was the inclusion of affiliative behaviour with opposite-sex individuals. Heterosexual relationships are relatively common in social species [27–37,44,68–70], but prior research on the evolutionary import of these relationships has focused on reproductive components of fitness, including protection from infanticide and male mating privileges [28,36,38–49]. Our results suggest an additional, powerful fitness benefit of male–female relationships for female baboons: increased survival. Additional support for this idea has been found in the wild baboons in Botswana discussed above. Specifically, in that population, female mortality was highest when the group had many females and comparatively few males [50]. Interestingly, the number of males in the group did not predict offspring survival, suggesting that adult female survival is a key benefit of mixed sex social groups [50].

Our results also lend insight into the direction of causality in social effects on survival. If unhealthy individuals lack the energy or motivation to seek social relationships, poor health may cause both social isolation and mortality. This scenario predicts that females who were isolated from one sex would also be isolated from the other sex. However, we found that females were rarely isolated from both sexes, and if anything females experienced a slight trade-off such that females with strong connectedness to one sex had slightly weaker connectedness with the other sex. Thus, poor health was not an obvious driver of the connection between social isolation and mortality, and females may preferentially allocate social efforts towards one sex or another in different contexts.

While social behaviour is clearly linked to survival, major questions remain about the behavioural mechanisms that mediate these effects. To date, studies vary considerably in their measures of social support, ranging from detailed measures of the strength and quality of individual social bonds to composite measures of individual social integration and experience. Despite this heterogeneity, the associations of these measures with human mortality risk are remarkably robust [1]. Most studies in humans have relied on composite indices, including ‘structural’ measures of individual integration into social networks or communities or ‘functional’ measures of perceived or received social support [1]. Both types of composite measures predict stress reactivity and health [2,3,6,71,72], and structural measures of social connectedness are more strongly associated with survival than functional measures [1].

However, the use of composite measures of social integration, including the social connectedness index used in our study, can make it challenging to identify the behavioural mechanisms that underlie the links between social connectedness and survival. For instance, high values of composite indices can result when individuals have either a few high-quality social bonds or numerous bonds of average strength. Hence, although our approach is highly comparable to studies in humans, it does not distinguish between the

relative roles of relationship quality and quantity. The use of ad libitum data to construct our composite index also raises the possibility that social integration may act in part via spatial positioning within a group. If so, more centrally positioned individuals would be observed interacting more frequently than more peripheral individuals, both because central individuals would have more opportunities to interact and because observation schedules would place observers in the centre of the group more frequently. This hypothesis could be explicitly tested in future work. However, we note that such an explanation could not account for the effects of both social connectedness to males and connectedness to females: because these effects were independent, it is not possible to explain both effects by spatial positioning.

Animal studies have the potential to make considerable progress on the behavioural mediators of social effects on survival, including both of the possible mechanisms we have raised here: relationship quality versus quantity and centrality in grouping patterns [11,12,15,17,18]. However, to our knowledge, no study has yet compared the relative survival and reproductive benefits of these phenomena, making this area a critical issue for future research.

(b) Social and demographic predictors of social connectedness

In several species, female–female competition for access to males, both as mates and as social partners, can be important to female fitness (reviewed in [73,74]). Some of the strongest evidence for this phenomenon comes from studies of female baboons [50,67,75]. Here, we found that higher female social connectedness to males was predicted by higher female dominance rank. This result suggests that male baboons are a limited, monopolizable resource for females, and females who effectively compete for access to males may experience higher survival, as well as reproductive benefits [38,41,50]. However, in our data, we did not observe a direct effect of female rank on survival. This result is surprising because Amboseli represents a relatively harsh environment for baboons, and prior work in Amboseli has found persistent effects of female rank on fertility and age at maturity [76,77]. In addition, high rank is associated with survival benefits for female baboons in Mikumi, Tanzania and in the Okavango Delta in Botswana [12,78]. We interpret the lack of an effect of rank on female survival in Amboseli with caution because female rank and social connectedness are both, of course, estimated with some error. Nevertheless, our results provide further evidence that social connectedness and/or positive social bonds can be more important than dominance rank in determining female survival, even in harsh environments.

In baboons, female intrasexual competition seems to be most intense when sexually cycling females are ovulating—perhaps because males who are mate guarding one female can no longer serve as an effective ‘friend’ to another. For instance, Huchard & Cowlishaw [75] found that female baboons experienced the highest rates of aggression from other females when they were at peak sexual swelling (i.e. most likely to be ovulating) and that females being guarded by an adult male experienced more aggression from other females than did unguarded females. Similarly, female baboons experience the highest risk of physical injury

during ovarian cycling, especially during the days of peak sexual swelling [79,80].

We also found that demographic factors predicted female social connectedness to males: females in larger groups had higher SCI-M, probably because larger social groups had more male-biased sex ratios than smaller groups. These results are interesting in light of prior results by Cheney *et al.* [50], who reported that rates of female–female aggression were higher, and female–female social bonds were less stable, in social groups with relatively female-biased sex ratios. Hence, group size (via sex ratio) seems to influence social options for females, and in turn may influence social effects on longevity.

Finally, we observed that older female baboons had weaker connections to other females than younger females, but females did not experience a parallel loss of social connectedness with age to males. This suggests that age-related declines in SCI-F were unlikely to be caused by declines in health and energy with age. Instead, demographic factors could explain the loss of female–female relationships. While the availability of maternal kin does not decline with age in baboons [64], older females have fewer same-aged peers than do younger females, and peers are among the most preferred social partners [64,66]. In addition, as females age, the composition of their social partners shifts to comprise a greater proportion of adult daughters. As these daughters age, they begin to have adult daughters of their

own, perhaps leaving less time for social interactions with their mothers.

Ethics statement. All protocols were non-invasive, adhered to the laws and guidelines of Kenya (Kenya Research Permit numbers NCST RRI/12/1/SS011/1543 to E.A.A., NCST/RCD/12B/012/57 to J.T., NCST 5/002/R/777 to S.C.A. and NCST 5/002/R/776 to J.A.) and were approved by the Animal Care and Use Committees at the University of Notre Dame (13-030), Duke University (A0840903) and Princeton University (1689).

Data accessibility. Data sets on female social connectedness and survival are deposited in Dryad (<http://datadryad.org/>). Data identifier: doi:10.5061/dryad.bt348.

Acknowledgements. We thank the Kenya Wildlife Services, Institute of Primate Research, National Museums of Kenya, National Council for Science and Technology, members of the Amboseli-Longido pastoralist communities, Tortilis Camp and Ker & Downey Safaris for their assistance in Kenya. Particular thanks to R. S. Mututua, S. Sayialel, and J.K. Warutere, V. Somen and T. Wango in Kenya, and K. Pinc, D. Onderdonk, C. Markham, T. Fenn, N. Learn, L. Maryott, P. Onyango and J. Gordon in the US.

Funding statement. We are grateful for the helpful comments of two anonymous reviewers. We gratefully acknowledge the support of the National Science Foundation and the National Institutes of Health, especially the National Institute on Aging, for the majority of the data represented here: grants from the past 15 years include IBN 9985910, IBN 0322613, IBN 0322781, BCS 0323553, BCS 0323596, DEB 0846286, DEB 0846286, DEB 0846532, IOS 0919200, IOS 1053461, R01AG034513 and P01AG031719. We are also grateful to the Princeton Center for the Demography of Aging (P30AG024361), Duke University, Princeton University and the Max Planck Institute for Demographic Research.

References

- Holt-Lunstad J, Smith TB, Layton JB. 2010 Social relationships and mortality risk: a meta-analytic review. *PLoS Med.* **7**, e1000316. (doi:10.1371/journal.pmed.1000316)
- Cacioppo JT, Hawkley LC. 2003 Social isolation and health, with an emphasis on underlying mechanisms. *Perspect. Biol. Med.* **46**, 539–552. (doi:10.1353/pbm.2003.0049)
- Seeman TE. 1996 Social ties and health: the benefits of social integration. *Ann. Epidemiol.* **6**, 442–451. (doi:10.1016/S1047-2797(96)00095-6)
- Waldron I, Hughes ME, Brooks TL. 1996 Marriage protection and marriage selection—prospective evidence for reciprocal effects of marital status and health. *Soc. Sci. Med.* **43**, 113–123. (doi:10.1016/0277-9536(95)00347-9)
- Berkman LF, Glass T. 2000 Social integration, social networks, social support, and health. In *Social epidemiology* (eds LF Berkman, I Kawachi), pp. 137–173. New York, NY: Oxford University Press.
- Uchino BN. 2006 Social support and health: a review of physiological processes potentially underlying links to disease outcomes. *J. Behav. Med.* **29**, 377–387. (doi:10.1007/s10865-006-9056-5)
- Smith KP, Christakis NA. 2008 Social networks and health. *Annu. Rev. Sociol.* **34**, 405–429. (doi:10.1146/annurev.soc.34.040507.134601)
- Berkman LF, Melchior M, Chastang JF, Niedhammer I, Leclerc A, Goldberg M, Cohort G. 2004 Social integration and mortality: a prospective study of French employees of Electricity of France-Gas of France. *Am. J. Epidemiol.* **159**, 167–174. (doi:10.1093/aje/kwh020)
- Berkman LF, Syme SL. 1979 Social networks, host-resistance, and mortality: a 9-year follow-up study of Alameda County residents. *Am. J. Epidemiol.* **109**, 186–204.
- House JS, Landis KR, Umberson D. 1988 Social relationships and health. *Science* **241**, 540–545. (doi:10.1126/science.3399889)
- Yee JR, Cavigelli SA, Delgado B, McClintock MK. 2008 Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary tumors and lifespan. *Psychosom. Med.* **70**, 1050–1059. (doi:10.1097/PSY.0b013e31818425fb)
- 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. (doi:10.1016/j.cub.2010.05.067)
- Stanton MA, Mann J. 2012 Early social networks predict survival in wild bottlenose dolphins. *PLoS ONE* **7**, e47508. (doi:10.1371/journal.pone.0047508)
- Silk JB, Alberts SC, Altmann J. 2003 Social bonds of female baboons enhance infant survival. *Science* **302**, 1231–1234. (doi:10.1126/science.1088580)
- 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. (doi:10.1098/rsbp.2009.0681)
- Cameron EZ, Setsaas TH, Linklater WL. 2009 Social bonds between unrelated females increase reproductive success in feral horses. *Proc. Natl Acad. Sci. USA* **106**, 13 850–13 853. (doi:10.1073/pnas.0900639106)
- Frere CH, Krutzen 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. USA* **107**, 19 949–19 954. (doi:10.1073/pnas.1007997107)
- Weidt A, Hofmann SE, König B. 2008 Not only mate choice matters: fitness consequences of social partner choice in female house mice. *Anim. Behav.* **75**, 801–808. (doi:10.1016/j.anbehav.2007.06.017)
- McDonald DB. 2007 Predicting fate from early connectivity in a social network. *Proc. Natl Acad. Sci. USA* **104**, 10 910–10 914. (doi:10.1073/pnas.0701159104)
- Berghanel A, Ostner J, Schroder U, Schulke O. 2011 Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. *Anim. Behav.* **81**, 1109–1116. (doi:10.1016/j.anbehav.2011.02.009)
- Silk JB. 2007 Social components of fitness in primate groups. *Science* **317**, 1347–1351. (doi:10.1126/science.1140734)
- Clutton-Brock TH. 1988 Reproductive success. In *Reproductive success studies of individual variation in contrasting breeding systems* (ed. TH Clutton-Brock), pp. 472–485. Chicago, IL: University of Chicago Press.

23. Pusey A. 2012 Magnitude and sources of variation in female reproductive performance. In *Evolution of primate societies* (eds JC Mitani, J Call, P Kappeler, R Palombit, JB Silk), pp. 343–366. Chicago, IL: University of Chicago Press.
24. Staehelin K, Schindler C, Spoerri A, Stutz EZ, Grp SNCS. 2012 Marital status, living arrangement and mortality: does the association vary by gender? *J. Epidemiol. Commun. Health* **66**, e22. (doi:10.1136/jech.2010.128397)
25. Wilson EO. 1975 *Sociobiology*. Cambridge, UK: Belknap.
26. van Schaik CP, Kappler PM. 1997 Infanticide risk and the evolution of male–female associations in primates. *Proc. R. Soc. Lond. B* **264**, 1687–1694. (doi:10.1098/rspb.1997.0234)
27. Smuts BB. 1985 *Sex and friendship in baboons*. New York, NY: Aldine Transaction.
28. Seyfarth RM. 1978 Social relationships among adult male and female baboons. II. Behavior throughout the female reproductive cycle. *Behaviour* **64**, 227–247. (doi:10.1163/156853978X00044)
29. Takahata Y. 1982 Social relations between adult males and females of Japanese monkeys in the Arashiyama B troop. *Primates* **23**, 1–23. (doi:10.1007/BF02381434)
30. Mason JH. 1994 Mating patterns, mate choice, and birth season heterosexual relationships in free-ranging rhesus macaques. *Primates* **35**, 417–433. (doi:10.1007/BF02381951)
31. Paul A, Kuester J, Amemann J. 1996 The sociobiology of male–infant interactions in Barbary macaques, *Macaca sylvanus*. *Anim. Behav.* **51**, 155–170. (doi:10.1006/anbe.1996.0013)
32. Bercovitch FB. 1991 Mate selection, consortship formation, and reproductive tactics in adult female savanna baboons. *Primates* **32**, 437–452. (doi:10.1007/BF02381935)
33. O'Brien TG. 1991 Female–male social interactions in wedge-capped capuchin monkeys: benefits and costs of group living. *Anim. Behav.* **41**, 555–567. (doi:10.1016/S0003-3472(05)80896-6)
34. Wrangham RW. 1979 On the evolution of ape social systems. *Soc. Sci. Inform.* **18**, 335–368. (doi:10.1177/053901847901800301)
35. Machanda ZP, Gilby IC, Wrangham RW. 2013 Male–female association patterns among free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *Int. J. Primatol.* **34**, 917–938. (doi:10.1007/s10764-013-9707-7)
36. Ostner J, Vigilant L, Bhagavatula J, Franz M, Schulke O. 2013 Stable heterosexual associations in a promiscuous primate. *Anim. Behav.* **86**, 623–631. (doi:10.1016/j.anbehav.2013.07.004)
37. Massen JJM, Sterck EHM. 2013 Stability and durability of intra- and intersex social bonds of captive rhesus macaques (*Macaca mulatta*). *Int. J. Primatol.* **34**, 770–791. (doi:10.1007/s10764-013-9695-7)
38. Nguyen N, Van Horn RC, Alberts SC, Altmann J. 2009 'Friendships' between new mothers and adult males: adaptive benefits and determinants in wild baboons (*Papio cynocephalus*). *Behav. Ecol. Sociobiol.* **63**, 1331–1344. (doi:10.1007/s00265-009-0786-6)
39. Hrdy SB. 1979 Infanticide among animals: review, classification, and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.* **1**, 13–40. (doi:10.1016/0162-3095(79)90004-9)
40. Palombit RA, Seyfarth RM, Cheney DL. 1997 The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Anim. Behav.* **54**, 599–614. (doi:10.1006/anbe.1996.0457)
41. Moscovice LR, Di Fiore A, Crockford C, Kitchen DM, Wittig R, Seyfarth RM, Cheney DL. 2010 Hedging their bets? Male and female chacma baboons form friendships based on likelihood of paternity. *Anim. Behav.* **79**, 1007–1015. (doi:10.1016/j.anbehav.2010.01.013)
42. Weingill T. 2000 Infanticide and the value of male–female relationships in mountain chacma baboons. *Behaviour* **137**, 337–359. (doi:10.1163/156853900502114)
43. Lemasson A, Palombit RA, Jubin R. 2008 Friendships between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback experiments. *Behav. Ecol. Sociobiol.* **62**, 1027–1035. (doi:10.1007/s00265-007-0530-z)
44. Palombit RA. 2000 Infanticide and the evolution of male–female bonds in animals. In *Infanticide by males and its implications* (eds CP van Schaik, CP Janson), pp. 239–268. Cambridge, UK: Cambridge University Press.
45. Seyfarth RM. 1978 Social relationships among adult male and female baboons. I. Behavior during sexual consortship. *Behaviour* **64**, 205–226.
46. Kulik L, Muniz L, Mundry R, Widdig A. 2012 Patterns of interventions and the effect of coalitions and sociality on male fitness. *Mol. Ecol.* **21**, 699–714. (doi:10.1111/j.1365-294X.2011.05250.x)
47. Massen JJM, Overduin-de Vries AM, de Vos-Rouweler AJM, Spruijt BM, Doxiadis GGM, Sterck EHM. 2012 Male mating tactics in captive rhesus macaques (*Macaca mulatta*): the influence of dominance, markets, and relationship quality. *Int. J. Primatol.* **33**, 73–92. (doi:10.1007/s10764-011-9552-5)
48. Langergraber KE, Mitani JC, Watts DP, Vigilant L. 2013 Male–female socio-spatial relationships and reproduction in wild chimpanzees. *Behav. Ecol. Sociobiol.* **67**, 861–873. (doi:10.1007/s00265-013-1509-6)
49. Langos D, Kulik L, Mundry R, Widdig A. 2013 The impact of paternity on male–infant association in a primate with low paternity certainty. *Mol. Ecol.* **22**, 3638–3651. (doi:10.1111/mec.12328)
50. Cheney DL, Silk JB, Seyfarth RM. 2012 Evidence for intrasexual selection in wild female baboons. *Anim. Behav.* **84**, 21–27. (doi:10.1016/j.anbehav.2012.03.010)
51. Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL. 2006 Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Anim. Behav.* **71**, 1227–1237. (doi:10.1016/j.anbehav.2005.11.009)
52. Beehner JC, Bergman TJ, Cheney DL, Seyfarth RM, Whitten PL. 2005 The effect of new alpha males on female stress in free-ranging baboons. *Anim. Behav.* **69**, 1211–1221. (doi:10.1016/j.anbehav.2004.08.014)
53. Runcie DE, Wiedmann M, Archie EA, Altmann J, Wray GA, Alberts SC, Tung J. 2013 Social environment influences the relationship between genotype and gene expression in wild baboons. *Phil. Trans. R. Soc. B* **368**, 20120345. (doi:10.1098/rstb.2012.0345)
54. Silk J, Cheney D, Seyfarth R. 2013 A practical guide to the study of social relationships. *Evol. Anthropol.* **22**, 213–225. (doi:10.1002/evan.21367)
55. Silk JB. 2012 The adaptive value of sociality. In *Evolution of primate societies* (eds JC Mitani, J Call, P Kappeler, R Palombit, JB Silk), pp. 552–564. Chicago, IL: University of Chicago Press.
56. Cords M. 2012 The behavior, ecology, and social evolution of cercopithecine monkeys. In *Evolution of primate societies* (eds JC Mitani, J Call, P Kappeler, R Palombit, JB Silk), pp. 91–112. Chicago, IL: University of Chicago Press.
57. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–267. (doi:10.1163/156853974X00534)
58. Alberts SC, Altmann J. 2011 Monitoring guide for the Amboseli Baboon Research Project. See <http://www.amboselibaboons.nd.edu/downloads/>.
59. Harrell F. 2014 rms: regression modeling strategies. R package v. 4.1–1. See <http://www.CRAN.R-project.org/package=rms>.
60. Therneau. 2014 A package for survival analysis in S. R package v. 2.37–7. See <http://www.CRAN.R-project.org/package=survival>.
61. Team RC, and . 2013 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. (<http://www.R-project.org>)
62. Little RJA, Rubin DB. 2002 *Statistical analysis with missing data*, 2nd edn. New York, NY: Wiley and Sons.
63. Silk JB, Alberts SC, Altmann J. 2006 Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behav. Ecol. Sociobiol.* **61**, 197–204. (doi:10.1007/s00265-006-0250-9)
64. 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. (doi:10.1007/s00265-006-0249-2)
65. Silk JB, Alberts SC, Altmann J. 2004 Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Anim. Behav.* **67**, 573–582. (doi:10.1016/j.anbehav.2003.07.001)
66. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010 Female chacma baboons form strong, equitable, and enduring social bonds. *Behav. Ecol. Sociobiol.* **64**, 1733–1747. (doi:10.1007/s00265-010-0986-0)

67. Palombit RA, Cheney DL, Seyfarth RM. 2001 Female–female competition for male ‘friends’ in wild chacma baboons, *Papio cynocephalus ursinus*. *Anim. Behav.* **61**, 1159–1171. (doi:10.1006/anbe.2000.1690)
68. Emery NJ, Seed AM, von Bayern AMP, Clayton NS. 2007 Cognitive adaptations of social bonding in birds. *Phil. Trans. R. Soc. B* **362**, 489–505. (doi:10.1098/rstb.2006.1991)
69. Seyfarth RM, Cheney DL. 2012 The evolutionary origins of friendship. *Annu. Rev. Psychol.* **63**, 153–177. (doi:10.1146/annurev-psych-120710-100337)
70. Massen JJM, Sterck EHM, de Vos H. 2010 Close social associations in animals and humans: functions and mechanisms of friendship. *Behaviour* **147**, 1379–1412. (doi:10.1163/000579510X528224)
71. Coe CL, Laudenslager ML. 2007 Psychosocial influences on immunity, including effects on immune maturation and senescence. *Brain Behav. Immun.* **21**, 1000–1008. (doi:10.1016/j.bbi.2007.06.015)
72. Hawkley LC, Thisted RA, Masi CM, Cacioppo JT. 2010 Loneliness predicts increased blood pressure: 5-year cross-lagged analyses in middle-aged and older adults. *Psychol. Aging* **25**, 132–141. (doi:10.1037/a0017805)
73. Rosvall KA. 2011 Intrasexual competition in females: evidence for sexual selection? *Behav. Ecol.* **22**, 1131–1140. (doi:10.1093/beheco/arr106)
74. Stockley P, Bro-Jorgensen J. 2011 Female competition and its evolutionary consequences in mammals. *Biol. Rev.* **86**, 341–366. (doi:10.1111/j.1469-185X.2010.00149.x)
75. Huchard E, Cowlishaw G. 2011 Female–female aggression around mating: an extra cost of sociality in a multimale primate society. *Behav. Ecol.* **22**, 1003–1011. (doi:10.1093/beheco/arr083)
76. Charpentier MJE, Tung J, Altmann J, Alberts SC. 2008 Age at maturity in wild baboons: genetic, environmental and demographic influences. *Mol. Ecol.* **17**, 2026–2040. (doi:10.1111/j.1365-294X.2008.03724.x)
77. Altmann J, Alberts SC. 2003 Intraspecific variability in fertility and offspring survival in a nonhuman primate: behavioral control of ecological and social sources. In *Offspring: the biodemography of fertility and family behavior* (eds KW Wachter, Ra Bulatao), pp. 140–169. Washington, DC: National Academy Press.
78. Wasser SK, Norton GW, Kleindorfer S, Rhine RJ. 2004 Population trend alters the effects of maternal dominance rank on lifetime reproductive success in yellow baboons (*Papio cynocephalus*). *Behav. Ecol. Sociobiol.* **56**, 338–345. (doi:10.1007/s00265-004-0797-2)
79. MacCormick HA, MacNulty DR, Bosacker AL, Lehman C, Collins DA, Packer C. 2012 Male and female aggression: lessons from sex, rank, age, and injury in olive baboons. *Behav. Ecol.* **24**, 683–691.
80. Archie EA, Altmann J, Alberts SC. 2014 Costs of reproduction in a long-lived female primate: injury risk and wound healing. *Behav. Ecol. Sociobiol.* **68**, 1183–1193. (doi:10.1007/s00265-014-1729-4)