

Female sociality and sexual conflict shape offspring survival in a Neotropical primate

Urs Kalbitzer^{a,1}, Mackenzie L. Bergstrom^a, Sarah D. Carnegie^a, Eva C. Wikberg^{a,b}, Shoji Kawamura^b, Fernando A. Campos^{a,c}, Katharine M. Jack^c, and Linda M. Fedigan^a

^aDepartment of Anthropology and Archaeology, University of Calgary, Calgary, AB, Canada T2N 1N4; ^bDepartment of Integrated Biosciences, University of Tokyo, Kashiwa, Chiba 277-8562, Japan; and ^cDepartment of Anthropology, Tulane University, New Orleans, LA 70118

Edited by Ryne Palombit, Rutgers University, and accepted by Editorial Board Member James O'Connell January 5, 2017 (received for review May 31, 2016)

Most mammals live in social groups in which members form differentiated social relationships. Individuals may vary in their degree of sociality, and this variation can be associated with differential fitness. In some species, for example, female sociality has a positive effect on infant survival. However, investigations of such cases are still rare, and no previous study has considered how male infanticide might constrain effects of female sociality on infant survival. Infanticide is part of the male reproductive strategy in many mammals, and it has the potential to override, or even reverse, effects of female reproductive strategies, including sociality. Therefore, we investigated the relationships between female sociality, offspring survival, and infanticide risk in wild white-faced capuchin monkeys using long-term data from Santa Rosa, Costa Rica. Female capuchins formed differentiated bonds, and bond strength was predicted by kin relationship, rank difference, and the presence of female infants. Most females formed stable bonds with their top social partners, although bond stability varied considerably. Offspring of highly social females, who were often high-ranking females, exhibited higher survivorship during stable periods compared with offspring of less social females. However, offspring of highly social females were more likely to die or disappear during periods of alpha male replacements, probably because new alpha males are central to the group, and therefore more likely to target the infants of highly social, central females. This study shows that female sociality in mammals can have negative fitness consequences that are imposed by male behavior.

social bond | reproductive success | mammal | capuchin | infanticide

In group-living mammals, individuals often form differentiated social relationships with other group members, resulting in variation in their degree of sociality (1). Over the past 14 y, several studies have investigated the fitness consequences of individual variation in sociality. For example, female chacma baboons (*Papio ursinus*) (2) and female yellow baboons (*Papio cynocephalus*) (3) with strong and stable bonds have a longer life expectancy than females with weaker and less stable bonds. More social male and female Barbary macaques (*Macaca sylvanus*) also have a higher chance of survival during adverse conditions, such as very cold winters (4, 5). Although published data with regard to sociality and male reproductive success are rare, Schülke et al. (6) found that male Assamese macaques (*Macaca assamensis*) with strong bonds sire more offspring than do males with weaker bonds. In terms of female sociality and reproductive success, studies on yellow baboons (7), chacma baboons (8), bottlenose dolphins (*Tursiops* sp.) (9), and feral horses (*Equus caballus*) (10) have shown that offspring survival is higher for females with stronger social bonds or better social integration compared with less social females. However, the number of publications on sociality and fitness is still relatively small. Even primate research, which represents a considerable proportion of the literature on this topic, has been limited to species belonging to the Old World monkey tribe of Papionini.

Furthermore, previous studies on female sociality and reproductive success mainly focused on the role of female strategies, but such strategies do not occur in isolation and can be affected by male strategies. Male and female reproductive strategies differ

from one another considerably in most mammals: Female mammals usually invest more energy in each offspring via gestation and lactation, whereas males invest more into intense competition over access to a larger number of receptive females (11). These divergent reproductive strategies can, and do, often result in highly pronounced sexual conflict (11, 12). The killing of dependent offspring by unrelated males, infanticide, is one of several manifestations of sexual conflict that has been reported in many species of social mammals (13–15). The most widely supported explanation for this behavior is that infanticide is a reproductive strategy whereby males can maximize their number of offspring by killing unrelated dependent infants (16). In his review of infanticide across primates, Palombit (16) found that infanticide as a male reproductive strategy coincides with a changeover in the group's alpha male, and is particularly relevant for species showing a high reproductive skew. The killing of dependent infants can induce a female to resume cycling earlier than if the infant survives and open up the possibility that she will reproduce with the new alpha male. For females, losing an infant to male infanticide can destroy substantial reproductive effort within moments and negate female social strategies that would otherwise be beneficial to infant survival, such as forming social bonds with other females.

To extend our knowledge about the adaptive value of female social bonds in mammals, and to investigate whether male infanticide can interfere with female sociality as a strategy that increases infant survival, we analyzed behavioral and life-history data from a population of white-faced capuchin monkeys (*Cebus*

Significance

In group-living mammals, infants of females with strong social relationships sometimes exhibit higher survivorship than infants of less social females, a finding that holds true in our study population of wild white-faced capuchin monkeys. However, as in many mammals, new alpha male capuchins often kill young infants sired by other males. Our long-term research shows that infants of highly social females are at greater risk of dying or disappearing during periods of alpha male replacements than infants of less social females. These findings indicate that new alpha males are more likely to target the infants of more social, and therefore central, females. Our study provides evidence that female sociality can negatively affect offspring survival by increasing the likelihood of infanticide.

Author contributions: U.K. and L.M.F. designed research; M.L.B. and S.D.C. contributed behavioral data; E.C.W. and S.K. analyzed and contributed genetic data; F.A.C. and K.M.J. analyzed life-history data; U.K. conducted statistical analyses; and U.K., M.L.B., S.D.C., E.C.W., S.K., F.A.C., K.M.J., and L.M.F. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. R.P. is a Guest Editor invited by the Editorial Board.

Data deposition: The data reported in this paper have been deposited in the Dryad database at [dx.doi.org/10.5061/dryad.93463](https://doi.org/10.5061/dryad.93463).

¹To whom correspondence should be addressed. Email: urs.kalbitzer@ucalgary.ca.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1608625114/-DCSupplemental.

capucinus imitator) in Santa Rosa, Costa Rica. This species of New World monkey (Platyrrhini) lives in multimale–multifemale groups in which the philopatric females are highly social (17–19). Furthermore, females that groom each other more often also tend to form coalitions more often (19). However, the fitness repercussions of such bonds have not been thoroughly investigated. Males, on the other hand, disperse from their natal group at ~4 y of age and continue to disperse throughout their lives, changing groups at ~4-y intervals (20, 21). This pattern of frequent male movement between groups leads to complete (or near-complete) changeovers in male group members, including alpha males. Infant mortality is significantly greater in the context of alpha male replacements (AMRs) than during times of group stability (18, 22–24).

To clarify the effect of female sociality on infant survival in the context of both male and female reproductive strategies, we investigated the predictors of female bond strength, the stability of female bonds, and the consequences of female sociality for offspring survival in wild capuchin monkeys across periods of varying group stability. Because of the similarities between the capuchin social system and the social system of baboons, we expected that offspring survival would be correlated with female sociality. However, because of the impact of AMRs on infant survival, we expected that female sociality would only have a positive effect on infant survival during times of group stability. Alpha males are usually located centrally within the group (25); therefore, we had earlier postulated that the offspring of more central females would be more vulnerable to aggression by new alpha males than the offspring of more peripheral females (26). Because we predicted that the most social females are also the most central ones, we expected that when infanticide risk is high during AMR periods, highly social females would have poorer infant survival rates than do less social ones.

Results

Predictors of Dyadic Bonds. Female social bonds were highly variable between dyads and within the same dyads over time. The average coefficient of variation (CV) for the dyadic sociality index (*DSI*) was 86% between different dyads within the same year, compared with 67% within the same dyad over different years. This variation in bond strength within and between dyads was significantly related to three of the tested predictor variables: relatedness, dominance rank difference, and presence of female infants (Table 1). Dyads with higher *R*-values (i.e., estimated relatedness) and dyads in which female infants were present showed stronger bonds than did other dyads. Also, dyads with larger differences in rank showed weaker bonds than did dyads with more adjacent rank positions. The presence of male infants and age differences had no effect on bond strength.

Table 1. Predictors of dyadic bond strength

Term	Estimate (SE)	χ^2	<i>P</i>
(Intercept)	−0.356 (0.077)	—	—
<i>R</i> -value	0.207 (0.042)	19.106	<0.001
Age difference	−0.016 (0.043)	0.131	0.717
Rank difference	−0.210 (0.038)	24.988	<0.001
Male infant present	0.053 (0.065)	0.643	0.423
Female infant present	0.240 (0.064)	13.396	<0.001

Results of an LMM with log-transformed *DSI* (+0.1) values as the response variable. The full model was significantly better than the null model ($\chi^2 = 58.810$, *df* = 5, *P* < 0.001). *R*-value, age difference, and rank difference were scaled to a mean of 0 and an SD of 1 before running the model. The original mean ± SD values were as follows: *R*-value = 0.184 ± 0.195, age difference = 6.349 ± 4.745; and rank difference = 0.423 ± 0.249 (*n* = 557 data points from 151 different dyads and 32 different females). Significant results are shown in boldface.

Running the same model with kinship categories instead of *R*-values produced similar results. We found, as before, that kinship ($\chi^2 = 33.079$, *df* = 4, *P* < 0.001), rank differences ($\chi^2 = 18.791$, *df* = 1, *P* < 0.001), and presence of female infants ($\chi^2 = 26.617$, *df* = 1, *P* < 0.001) had a significant effect on bond strength (Table S1). More specifically, mother–daughter dyads formed stronger bonds than did maternal sibs, paternal sibs, and nonkin dyads, but did not differ in bond strength from full-sib dyads (Fig. 1). Full sibs formed stronger bonds than did nonkin dyads, whereas maternal and paternal sibs could not be distinguished from each other or from nonkin dyads.

Number of Top Partners. The *DSI* values of the three strongest bonds per female were, on average, significantly stronger than the mean *DSI* of 1 (results from one-sided *t* tests using log-transformed *DSI* + 0.1 values: first top partner vs. mean *DSI*: *t* = 11.746, *df* = 31, *P* < 0.001; secondary bond partner vs. mean *DSI*: *t* = 7.481, *df* = 31, *P* < 0.001; tertiary bond partner vs. mean *DSI*: *t* = 2.805, *df* = 31, *P* < 0.01; and quaternary bond partner vs. mean *DSI*: *t* = −2.313, *df* = 31, *P* = 0.986; Fig. S1). The three partners with the highest *DSI* values were therefore considered as top partners.

Stability of Bonds with Top Partners. Despite the large temporal variation in bond strength within dyads over years (CV = 67%, discussed above), the comparison between observed partner stability index (*PSI*) values calculated for the top three partners and randomized *PSI* values indicated that observed bonds were more stable than expected by chance (one-sided Wilcoxon test: Wilcoxon test statistic *V* = 133, *P* < 0.05, *n* = 31). However, the difference between observed and randomized *PSI* values was relatively small (mean ± SD: observed *PSI* = 0.382 ± 0.207, simulated *PSI* = 0.309 ± 0.072), and females showed considerable variation in observed bond stability, ranging from 0 to 1, whereas simulated *PSI* values only ranged from 0.206 to 0.430 (Fig. S2). Thus, some female capuchin monkeys formed stable strong bonds, but other females changed their top three partners often.

Predictors of Annual Sociality Indices. Overall sociality of each female during each year was significantly related to two of the tested predictor variables (Table 2). First, high-ranking females were more social than low-ranking females [Table 2; plus a Pearson's correlation test between annual sociality indices (*ASI*) and rank indicators: *r* = 0.499 and *P* < 0.001]. Second, adult females with female infants were more social than females without female infants. In accordance with our results on dyadic bond strength, the presence of male infants did not have such an effect.

Sociality and Centrality. Annually calculated centrality values of females ranged from 0.591 to 0.991 (mean ± SD = 0.847 ± 0.094). Thus, despite considerable variation among females, no female was exclusively peripheral. Nevertheless, results from a linear mixed model (LMM) with *ASI* as the predictor variable for centrality values indicate that highly social females were more central than less social females (estimate ± SE: *ASI* = 0.089 ± 0.029, $\chi^2 = 7.319$, *P* < 0.01, *n* = 84 data points from 31 different females and 3 different years; Fig. S3).

Infant Survival. In total, 75 infants were included in this study. Fifty of these infants were at low risk of being killed by a new alpha male, and 76% of these 50 infants survived their first year of life. The other 25 infants were at high infanticide risk and only 44% survived their first year of life (Table S2). Infant survival was significantly predicted by the interaction between *ASI* and infanticide risk, which means that the effect of female sociality on infant survival was dependent on the level of infanticide risk (Fig. 2 and Table 3). In comparison to infants of mothers with a low sociality value, infants of highly social mothers had a higher probability of surviving their first year of life during times of low

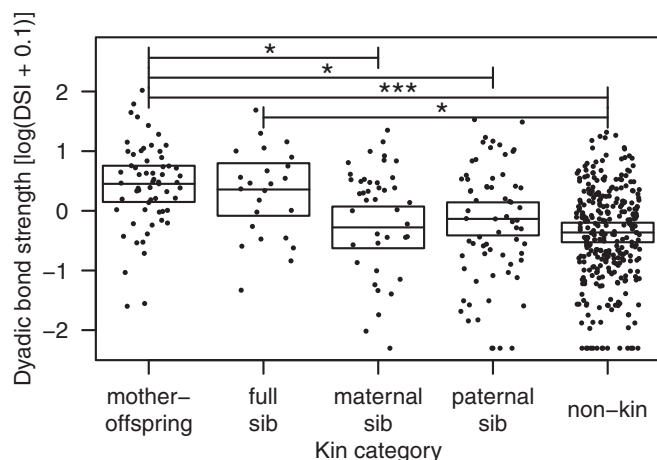


Fig. 1. Differences in bond strength among different kin categories. Each point represents the log-transformed *DSI* (+0.1) value for each dyad during each year in which both females were coresident ($n = 499$ data points from 134 dyads and 32 females; dyads with insufficient information about kin relationships and grandmother-granddaughter dyads, of which only two existed within our dataset, were sorted out). The boxes represent the estimate of the LMM with upper and lower 95% confidence limits for each of the kin categories (assuming mean values for all other variables in the model). The lines and asterisks at the top of the figure denote the significant differences between kin categories. * $P < 0.05$; *** $P < 0.001$ (P values were adjusted using the Tukey method).

infanticide risk but a lower probability of surviving during periods of high infanticide risk. This result was confirmed when we divided the data into two sets: one that only included infants at low infanticide risk and the other that only included infants at high infanticide risk. We ran a generalized linear mixed model (GLMM) with each of these two datasets testing *ASI* as a predictor variable (low infanticide risk, estimate \pm SE: *ASI* = 0.946 ± 0.400 , $\chi^2 = 6.706$, $P < 0.01$; high infanticide risk, estimate \pm SE: *ASI* = -1.180 ± 0.729 , $\chi^2 = 4.799$, $P < 0.05$).

From a lifetime perspective, neither infants of highly social or less social females had a higher survival probability, because a model excluding the interaction between *ASI* and infanticide risk showed no main effect of female sociality (estimate \pm SE: *ASI* = 0.150 ± 0.288 , $\chi^2 = 0.277$, $P = 0.598$; Table S3, model b). Nevertheless, the model confirmed previous results (22, 23) that infants at low infanticide risk show a higher survival probability than infants at high infanticide risk (estimate \pm SE: infanticide risk (low) = 1.601 ± 0.643 , $\chi^2 = 8.008$, $P < 0.01$). Infants of females with stable top-bond partners had no survival advantage either. A model with *PSI* as the predictor variable showed no significant relation between *PSI* and infant survival (estimate \pm SE: *PSI* = 0.478 ± 0.356 , $\chi^2 = 2.266$, $P = 0.132$; Table S3, model c).

Because maternal rank and *ASI* were highly correlated (discussed above), we did not include rank in the original GLMM testing for the effect of sociality on infant survival. When we replaced *ASI* with rank in this model, we obtained similar results: The interaction between rank and infanticide risk was significantly related to infant survival ($\chi^2 = 4.287$, $P < 0.05$; Fig. S4 and Table S3, model d). Infants of high-ranking mothers showed a higher chance of survival when they were at low infanticide risk (estimate \pm SE: rank = 0.788 ± 0.429 , $\chi^2 = 4.711$, $P < 0.05$). However, we did not detect a significant effect of rank on survival of infants at high risk (estimate \pm SE: rank = -0.774 ± 1.445 , $\chi^2 = 0.994$, $P = 0.319$). Similar to sociality, a model excluding the interaction between rank and infanticide risk did not indicate a lifetime effect of rank on infant survival (estimate \pm SE: rank = 0.338 ± 0.300 , $\chi^2 = 1.321$, $P = 0.250$; Table S3, model e).

The comparison of different model fits indicated that sociality accounted for components of variation in infant survival not explained by rank. The model with both interactions included (*ASI*:infanticide risk + rank:infanticide risk) was significantly better than the model only including the interaction rank:infanticide risk ($\chi^2 = 7.589$, $df = 2$, $P < 0.05$; Table S3, models d and f). However, the model with both interactions included was not significantly better than the model only including the interaction *ASI*:infanticide risk ($\chi^2 = 1.551$, $df = 2$, $P = 0.4605$; Table S3, models a and f). Thus, although sociality explained variation in infant survival distinct from the effect of rank, the addition of rank did not significantly increase the explanatory value of the model.

Discussion

Female white-faced capuchin monkeys form highly variable social bonds with other females, and variation in individual sociality has consequences for offspring survival. Similar to other highly social mammals (27–30), the strength of social bonds was associated with relatedness and rank differences (also ref. 31). Furthermore, “natal attraction,” a phenomenon shown in numerous studies whereby females with infants form stronger bonds than females without infants (e.g., refs 32, 33), was also exhibited by females in our study population, but this effect was limited to mothers with female infants. Perhaps such is the case because female offspring usually stay in the group, and therefore represent prospective bond partners, whereas males emigrate as subadults or adults (18, 26). Alternatively, females may simply have fewer opportunities to interact with male offspring because adult males in this species show great interest in infants (34), particularly in male infants (35).

As predicted from studies of other species (7–10), variation in overall female sociality was associated with variation in offspring survival in white-faced capuchins. This effect, however, was dependent on male behavior; we observed a positive effect of maternal sociality on infant survival only for infants at low male infanticide risk, whereas infants born during periods of high infanticide risk (shortly before or after an AMR) had a higher chance of survival if their mothers were less social females. Infants at low infanticide risk and born to highly social females may benefit from having better access to preferred food resources and the protection provided by group males against predators. Additionally, infant white-faced capuchin monkeys often acquire supplementary milk from other females [i.e., allonursing (18, 19, 36)], and infants of highly social females may have more opportunities to engage in allonursing. Furthermore, our results show that highly social females are found significantly more often in the center of the group; therefore, their infants may be less vulnerable to predators (8).

However, alpha males are usually central to the group as well (25), and if the resident alpha male is defeated and disperses, the central females will slowly start to accept the presence of the new alpha male by grooming him when he approaches (18). During the period of accepting the new alpha male, the offspring of these resident females [which are rarely weaned before 1 y, and are therefore close to their mother (36)] experience high rates of

Table 2. Predictors for *ASI*

Term	Estimate (SE)	χ^2	P
(Intercept)	0.458 (0.031)	—	—
Rank	0.147 (0.025)	16.617	<0.001
Male infant present	−0.047 (0.065)	0.465	0.495
Female infant present	0.134 (0.062)	4.027	<0.05

Results from an LMM with *ASI* as the response variable. The full model was significantly better than the null model ($\chi^2 = 24.639$, $df = 3$, $P < 0.001$). Rank was scaled to a mean of 0 and SD of 1 before running the model. The original mean \pm SD of rank was 0.500 ± 0.330 ($n = 149$ data points from 32 females and 7 different years). Significant results are shown in boldface.

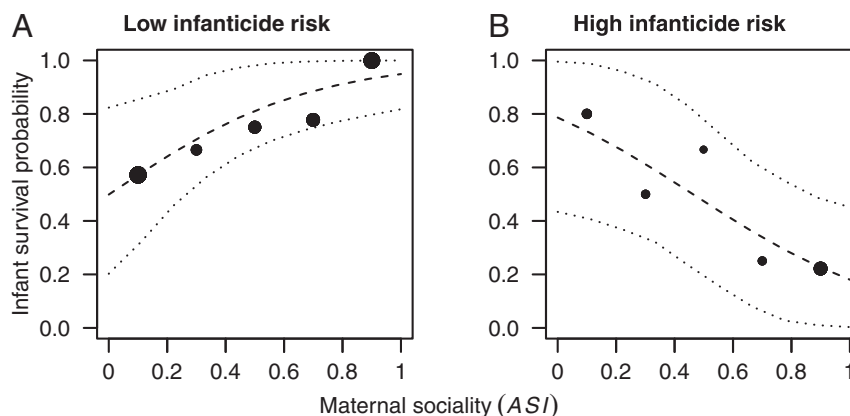


Fig. 2. Effect of female sociality on infant survival for infants at low risk of infanticide (A; $n = 50$ infants) and infants at high risk of infanticide (B; $n = 25$ infants). The circles (●) show the observed survival probability, summarized for five equally large intervals of ASI , and the area of the circles is proportional to the (square rooted) number of infants included in each of these intervals. The dashed lines show the survival probability predicted by the GLMM, and the dotted lines depict the bootstrapped 95% confidence intervals (number of bootstraps = 1,000). The GLMM was calculated with ASI scaled to a mean of 0 and SD of 1 but shown here on the original scale from 0 to 1.

wounding, death, and disappearance (this study and refs. 22–24). Alternative explanations, such as increased predation pressure or feeding competition, cannot account for this pattern. A previous study showed that infant survival was much lower during periods of AMRs compared with ecologically comparable periods of group stability (22). Furthermore, annual rainfall, a proxy for resource availability, is not a significant predictor of infant survival in our population (23). Therefore, it appears that the central positions of highly social females are responsible for the higher vulnerability of their dependent infants during and after AMR periods (26). Offspring of less social females, on the other hand, may benefit from the peripheral position of their mothers during high-risk times.

If being highly social has a negative effect on infant survival during AMR periods, why do females not adjust their sociality accordingly? Overall, sociality appears to be relatively variable over time, and it would be reasonable to assume that lactating or pregnant females could become less social (and therefore more peripheral) during takeover times. The observation that infants of highly social females are at higher risk of infanticide during such periods, however, suggests that females either cannot or choose not to do so. Other fitness benefits of high sociality could make it worthwhile to remain highly social despite the high infanticide risk. The results of the main-effect models indicate that neither strategy, being highly social or less social, results in a long-term benefit with regard to infant survival. Thus, high sociality could provide advantages for female capuchins other than maximizing infant survival, such as increasing longevity, which has been shown for female baboons (2). Because long-lived iteroparous organisms should prioritize individual survival over the survival of any particular offspring, high sociality may be favored by selection for pregnant or lactating females even during AMRs if the benefits in terms of adult female survival are sufficiently strong.

Rank was positively correlated with individual sociality indices; therefore, it is not surprising that we detected a similar effect of rank on infant survival depending on infanticide risk. An association (usually positive) between maternal rank and offspring survival is prevalent in many mammalian species (37, 38), but was not documented in previous studies of our study population (39). In the present study, we were able to detect this link because we determined infanticide risk by assessing conception time and birth date in relation to AMR events instead of using (rarely) confirmed instances of infanticide, and we included the interaction between infanticide risk and rank (or sociality) in our models. The idea that maternal rank can affect the risk for infants of being attacked by

infanticidal males has been suggested before (26, 40) but, to our knowledge, not yet systematically tested. Our study shows that the explicit consideration of infanticide risk is a promising approach to studying the fitness consequences of both sociality and rank in mammalian species that exhibit male infanticide.

The comparison of different models indicated that sociality explained variation in infant survival distinct from rank as an explanation for variation in infant survival. However, the reverse was not the case in white-faced capuchin monkeys. Rank positions in our population are relatively stable [about one rank change per female every 2.34 y as a result of active challenge (41)]. In contrast, bond strength was highly variable and individual sociality showed more variation over time than rank positions (Fig. S5). As outlined above, pregnant and lactating females seem not to be able to adapt their sociality during AMR periods, at least not sufficiently to mitigate the higher mortality risk to infants. Such an inability to adapt would be expected for a stable trait, such as rank, but not for an apparently highly dynamic trait, such as sociality. Therefore, future studies evaluating how females of different rank positions and in different reproductive stages change their social behavior during the establishment of new alpha males would help to clarify why highly social females do not simply become less social during periods of high infanticide risk.

Our study contributes to the understanding of fitness implications of sociality in mammals by providing another example of the relationship between female sociality and offspring survival. In particular, it provides much needed data on a Neotropical primate by providing evidence that an association between sociality and

Table 3. Predictors of infant survival

Term	Estimate (SE)	χ^2	<i>P</i>
(Intercept)	-0.205 (0.469)	—	—
Infanticide risk (low)	1.768 (0.711)	—*	—
<i>ASI</i>	-1.013 (0.509)	—*	—
<i>ASI</i> :Infanticide risk (low)	2.067 (0.718)	11.369	<0.001

Results from a GLMM with infant survival (first year of life) as the response variable. The full model was significantly better than the null model ($\chi^2 = 19.445$, $df = 3$, $P < 0.001$). Infanticide risk is a binary variable with two categories: high risk and low risk. *ASI* was scaled to a mean of 0 and SD of 1 before running the model. The original mean \pm SD of *ASI* was 0.535 ± 0.360 ($n = 75$ infants). Significant results are shown in boldface.

*Because the interaction including this term is significant, the *P* value for the main effect is not interpretable.

offspring survival exists in a nonhuman primate species outside Papionini, making more generalizable the claim that there are fitness consequences of sociality. More importantly, however, we have shown how male behavior, namely, infanticide during AMRs, can periodically render sociality as a female reproductive strategy disadvantageous. This study also confirms that female–female bonds seem not to represent an effective strategy in reducing male infanticide risk; instead, they can even increase this risk. To our knowledge, no other studies have demonstrated such a trade-off for female sociality in a group-living mammal.

Materials and Methods

The research reported in this study adhered to the laws of Costa Rica, the United States, and Canada, and complied with protocols approved by the Área de Conservación Guanacaste, by Tulane University's Institutional Animal Care and Use Committee, and by the Canada Research Council for Animal Care through the University of Calgary's Life and Environmental Sciences Animal Care Committee.

Behavioral Observations and Life-History Data. We derived data on the social behavior of females, and the dates of birth, death, or disappearance of females and infants from the long-term Santa Rosa Primate dataset (39). This project began in Costa Rica in 1983, and since its onset, life-history data have been collected on a continuous basis from females in several study groups. For this study, we considered females to be adult once they reached the age of 5 y, which is the youngest age at which females become pregnant (42).

We analyzed behavioral and life-history data from 32 adult females residing in three different groups: Los Valles (LV), Cerco de Piedra (CP), and Guanacaste (GN). For the LV and CP groups, we included data from 2005 until 2011, and for the GN group, we included data from 2007 until 2011. Each female provided between 1 and 7 y of data (mean \pm SD = 4.7 ± 1.9 y), totaling to 149 female years. Groups included five to 11 females, resulting in 151 coresident dyads during this study period, and 557 data points if each dyad is counted once per year.

We derived information on social bonds from behavioral data collected during focal sample observations. During each study year, data were collected from each group for between 4 and 12 mo, and between 2.5 and 55.1 h per individual (mean \pm SD = 13.7 ± 13.7 h), resulting in 5–107.7 h of observation time per dyad per year (mean \pm SD = 22.5 ± 22 h). We calculated sociality indices per year (discussed below); thus, interannual variation in focal hours should not bias these indices, although indices may be more precise in years with more focal data.

Dominance Ranks and Kin Relationship. We calculated ranks for each year separately, based on focal and ad libitum data using the I&SI (i.e., minimizing number and strength of inconsistencies in dominance matrices) method (41). We then scaled ranks from 0 (lowest rank in the group) to 1 (highest rank in the group) by calculating $1 - \frac{\text{Rank} - 1}{\text{Ranks in group} - 1}$.

We used two different estimates to assess dyadic relatedness. First, we calculated *R*-values from genotypes at 20 short tandem-repeat loci (43). These values do not always fit the expected values for kin categories (44), but are well-suited as continuous predictor variables to estimate in general the effect of relatedness on social behavior. To obtain a better understanding of how kin relationships would affect social bonds, we established different kin categories, including mother–daughter, full sibs, maternal sibs, paternal sibs, and maternal grandmother–granddaughter dyads. We considered all other dyads as “nonkin.” We determined members of kinship categories from known mother–daughter relationships and from paternal relationships determined via parentage analysis (34).

Dyadic Bond Strength. To make our results comparable to the results of previous studies, we closely followed the procedures described by Silk et al. (30) to determine social bonds in baboons and calculated the *DSI*, considering approaches and grooming (*SI Materials and Methods, Method S1: Calculation of DSI*).

Predictors of Bond Strength. To investigate the determinants of bond strength, we ran LMMs; we included *R*-values, age, rank differences within dyad, and the number of male and female infants younger than 1 y present in the dyad as predictor variables. We considered infants as “present” if they were in the group for at least 20% of the time during which the *DSI* was assessed for their mother. We then recalculated the model using kin categories instead of *R*-values to obtain a better understanding as to how kinship affects social bonds, and to test whether maternal kinship is more important than paternal kinship.

Number of Top Partners and Stability of Top Bonds. For each female, we calculated averaged *DSI* values for each partner rank (*SI Materials and Methods, Method S2: Calculation of Average DSI Values for Each Partner Rank*). We then used a one-sided *t* test with log-transformed values ($+0.1$) to test whether the averaged *DSI* for each partner rank was stronger than the average *DSI* in the group, the latter of which was 1 by definition (because dyadic rates of every behavior were divided by the average rate within the group). We defined all *DSI* partner ranks significantly stronger than 1 as “top partners.”

Using the number of top partners, we calculated the *PSI* as defined by Silk et al. (45), but corrected the index for small group sizes (*SI Materials and Methods, Method S3: Calculation of the PSI and Simulated PSI Values*). The resulting *PSI* values range from 0 to 1; 0 means that the female had the maximum number of different top partners, and 1 means that a female always kept her top partners and bonds were thus highly stable over time. To determine whether bonds were more stable than expected by chance, we simulated random *PSI* values (45) (*SI Materials and Methods, Method S3: Calculation of the PSI and Simulated PSI Values*). Then, we compared simulated *PSI* values of each female with the observed *PSI* values using a Wilcoxon signed rank test. We used a one-sided test because we were specifically interested in whether females would form more stable bonds than expected by chance.

Predictors of Sociality. In addition to dyadic values, we were interested in assessing whether females varied with regard to sociality in general and in investigating the predictors and consequences of this variation. To obtain such values, previous studies (2, 8) calculated a lifetime sociality index by averaging *DSI* values with the top three partners during the entire study for each female. Our results indicated that females had stronger than average bonds with the top three partners, but there was a lot of variation over time with regard to bond stability and many females had highly unstable top partners. Therefore, we calculated *ASI* instead of a lifetime sociality index by averaging the top three partners each year. We scaled these values within each group and each year from 0 (the least social female) to 1 (the most social female). The resulting *ASI* reflects whether a female was more or less social compared with other females in the same group during a specific year. This approach might also be more appropriate if the basic ability to form strong bonds (compared with the ability to form very long-lasting strong bonds) is important.

We then used an LMM to test if *ASI* is related to the annual rank of a female and/or the presence of male or female infants during each year.

Sociality and Centrality. To test whether highly social females are also more central to the group, we used data on spatial position collected during focal observations, which were available from 31 females in 3 different years (2009, 2010, and 2011). During each 10-min focal session, the position relative to the group's center (1 = central, 0.5 = intermediate, 0 = peripheral) was noted every 2.5 min, resulting in five data points per focal session. We averaged these values for each focal observation, resulting in a centrality index ranging from 0 (completely peripheral) to 1 (completely central). Based on these values, we calculated average centrality values for each female per year.

Maternal Sociality and Infant Survival. To assess the effect of sociality on infant survival, we calculated a GLMM using the binomial response of whether the infant survived its first year of life (Yes/No). The predictor variables included were *ASI*, male infanticide risk, and the interaction *ASI*:infanticide risk to test whether the effect of maternal sociality on infant survival depends on the level of infanticide risk. We considered infants to be “at high risk” if one of the following two conditions applied: (i) The infant was younger than 1 y during an AMR, or (ii) the infant was born during the 5.5 mo following the establishment of a new alpha male, which is the gestation length for this species (46), and we can thus assume that the infant was not sired by the new alpha male. Because dominance rank and *ASI* were highly correlated, we did not include rank in these models, but we ran alternative models using rank instead of *ASI*. To test for long-term effects of maternal sociality, rank, and partner stability on infant survival, we calculated models that included sociality, rank, or *PSI*, but not the interactions with infanticide risk.

To investigate whether the effect of sociality on infant survival simply reflects the effect of rank or, vice versa, rank simply reflects the effect of sociality, we compared different models using χ^2 tests. Earlier, we did not calculate the model with both sociality and rank because these two variables were highly correlated. Here, however, we compared the model with both of these variables with the models with either sociality or rank included to investigate whether the addition of the second variable would significantly increase the model fit, and therefore the variation explained by the respective variable (sociality or rank).

Statistical Analyses. We conducted all statistical analyses in R version 3.1.2 (47). We used the function “t.test” to conduct *t* tests, and the function “wilcox.test” to conduct a Wilcoxon signed rank test. We used the lme4 package version 1.1-11 (48) to calculate LMMs (function “lmer”) and GLMMs (function “glmer”), with respective response and test variables. All model procedures and the establishment of *P* values are described in detail in *SI Materials and Methods, Method S4: Model Procedures*. To conduct pairwise comparisons of *DSI* values between different kin categories, we used the function “lsmeans” from the package lsmeans version 2.20-23 (49) with the “Tukey” method to adjust for multiple testing. We used the function “anova” with the argument “test = ‘chisq’” to conduct χ^2 tests for the comparison of (nested) models.

ACKNOWLEDGMENTS. We thank the Costa Rican National Park Service and Administrators of the Área de Conservación Guanacaste (especially R. Blanco Segura) for permission to conduct research in the park since 1983. We thank

Dr. J. Addicott, who designed and developed the Primate Adaptations to Changing Environments (PACE) database that made these analyses possible, and we thank the many students and field assistants who collected life-history data over the years, particularly S. Cheves Hernandez and M. Myers. We also thank Ryne Palombit and three anonymous reviewers for their valuable comments. This project was funded by the Eyes High Postdoctoral program of the University of Calgary (U.K.); the Leakey Foundation (M.L.B., K.M.J., and F.A.C.); Alberta Innovates (M.L.B., S.D.C., and F.A.C.), the Animal Behaviour Society (M.L.B.), the International Primatological Society and Sigma Xi (M.L.B. and S.D.C.); Japan Society for the Promotion of Science Grants JSPS 15H2421 (to S.K.) and JSPS 24-02739 (to E.C.W.); the American Society of Primatologists (F.A.C.); the Louisiana Board of Regents, Nacy Maggioncalda Foundation, National Geographic Society, Newcomb Institute, and the Stone Center for Latin American Studies at Tulane University (K.M.J.); the Natural Sciences and Engineering Research Council of Canada (S.D.C. and L.M.F.); and the Canada Research Chairs Program (L.M.F.).

- Seyfarth RM, Silk JB, Cheney DL (2012) Variation in personality and fitness in wild female baboons. *Proc Natl Acad Sci USA* 109(42):16980–16985.
- Silk JB, et al. (2010) Strong and consistent social bonds enhance the longevity of female baboons. *Curr Biol* 20(15):1359–1361.
- 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 Biol Sci* 281(1793):20141261.
- McFarland R, Majolo B (2013) Coping with the cold: Predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biol Lett* 9(4):20130428.
- Lehmann J, Majolo B, McFarland R (2016) The effects of social network position on the survival of wild Barbary macaques, *Macaca sylvanus*. *Behav Ecol* 27(1):20–28.
- Schülke O, Bhagavatula J, Vigilant L, Ostner J (2010) Social bonds enhance reproductive success in male macaques. *Curr Biol* 20(24):2207–2210.
- Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. *Science* 302(5648):1231–1234.
- Silk JB, et al. (2009) The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proc R Soc B Biol Sci* 276(1670):3099.
- Frère CH, et al. (2010) Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proc Natl Acad Sci USA* 107(46):19949–19954.
- Cameron EZ, Setsaas TH, Linklater WL (2009) Social bonds between unrelated females increase reproductive success in feral horses. *Proc Natl Acad Sci USA* 106(33):13850–13853.
- Trivers R (1972) Parental investment and sexual selection. *Sexual Selection and the Descent of Man*, ed Campbell BG (Heinemann, London), pp 136–179.
- Parker GA (1979) Sexual selection and sexual conflict. *Sexual Selection and Reproductive Competition in Insects*, eds Blum MS, Blum NA (Academic, New York), pp 123–166.
- Hrdy SB (1974) Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol (Basel)* 22(1):19–58.
- Lukas D, Huchard E (2014) Sexual conflict. The evolution of infanticide by males in mammalian societies. *Science* 346(6211):841–844.
- Opie C, Atkinson QD, Dunbar RIM, Shultz S (2013) Male infanticide leads to social monogamy in primates. *Proc Natl Acad Sci USA* 110(33):13328–13332.
- Palombit RA (2012) Infanticide: Male strategies and female counterstrategies. *The Evolution of Primate Societies*, eds Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (Univ of Chicago Press, Chicago), pp 432–468.
- Fragaszy DM, Visalberghi E, Fedigan LM (2004) *The Complete Capuchin: The Biology of the Genus Cebus* (Cambridge Univ Press, Cambridge, UK), 1st Ed.
- Perry S (2012) The behavior of wild white-faced capuchins. *Adv Stud Behav* 44:135–181.
- Perry S (1996) Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *Am J Primatol* 40(2):167–182.
- Jack KM, Fedigan L (2004) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*: Part 1: Patterns and causes of natal emigration. *Anim Behav* 67(4):761–769.
- Jack KM, Fedigan L (2004) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*: Part 2: Patterns and causes of secondary dispersal. *Anim Behav* 67(4):771–782.
- Fedigan LM (2003) Impact of male takeovers on infant deaths, births and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. *Int J Primatol* 24(4):723–741.
- Fedigan LM, Carnegie SD, Jack KM (2008) Predictors of reproductive success in female white-faced capuchins (*Cebus capucinus*). *Am J Phys Anthropol* 137(1):82–90.
- Jack KM, Fedigan LM (2016) Infant mortality in white-faced capuchins: The impact of alpha male replacements. *Am J Phys Anthropol* 159(S62):183.
- Hall CL, Fedigan LM (1997) Spatial benefits afforded by high rank in white-faced capuchins. *Anim Behav* 53(5):1069–1082.
- Fedigan LM, Jack KM (2013) Sexual conflict in white-faced capuchins. *Evolution's Empress*, eds Fisher ML, Garcia JR (Oxford Univ Press, New York), pp 281–303.
- Archie EA, Moss CJ, Alberts SC (2006) The ties that bind: Genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proc Biol Sci* 273(1586):513–522.
- Frère CH, et al. (2010) Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Anim Behav* 80(3):481–486.
- 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(2):197–204.
- 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(2):183–195.
- Perry S, Manson JH, Muniz L, Gros-Louis J, Vigilant L (2008) Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. *Anim Behav* 76(1):187–199.
- Bădescu I, Scotte P, Ting N, Wikberg EC (2015) Female parity, maternal kinship, infant age and sex influence natal attraction and infant handling in a wild colobine (*Colobus vellerosus*). *Am J Primatol* 77(4):376–387.
- Manson JH, Rose LM, Perry S, Gros-Louis J (1999) Dynamics of female-female relationships in wild *Cebus capucinus*: Data from two Costa Rican sites. *Int J Primatol* 20(5):679–706.
- Sargeant EJ, Wikberg EC, Kawamura S, Jack KM, Fedigan LM (2016) Paternal kin recognition and infant care in white-faced capuchins (*Cebus capucinus*). *Am J Primatol* 78(6):659–668.
- Sheller CR, King Z, Jack K (2009) The effects of infant births on male-female relationships in *Cebus capucinus*. *Am J Primatol* 71(5):380–383.
- Sargeant EJ, Wikberg EC, Kawamura S, Fedigan LM (2015) Allonursing in white-faced capuchins (*Cebus capucinus*) provides evidence for cooperative care of infants. *Behaviour* 152(12–13):1841–1869.
- Ellis L (1995) Dominance and reproductive success among nonhuman animals: A cross-species comparison. *Ethol Sociobiol* 16(4):257–333.
- Majolo B, Lehmann J, de Bortoli Vizioli A, Schino G (2012) Fitness-related benefits of dominance in primates. *Am J Phys Anthropol* 147(4):652–660.
- Fedigan LM, Jack KM (2012) Tracking neotropical monkeys in Santa Rosa: Lessons from a regenerating Costa Rican dry forest. *Long-Term Field Studies of Primates*, eds Kappeler PM, Watts DP (Springer, Berlin), pp 165–184.
- Cheney DL, et al. (2004) Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *Int J Primatol* 25(2):401–428.
- Bergstrom ML, Fedigan LM (2010) Dominance among female white-faced capuchin monkeys (*Cebus capucinus*): Hierarchical linearity, nepotism, strength and stability. *Behaviour* 147(7):899–931.
- Carnegie SD, Fedigan LM, Ziegler TE (2011) Social and environmental factors affecting fecal glucocorticoids in wild, female white-faced capuchins (*Cebus capucinus*). *Am J Primatol* 73(9):861–869.
- Wikberg EC, et al. (2014) The effect of male parallel dispersal on the kin composition of groups in white-faced capuchins. *Anim Behav* 96:9–17.
- Van Horn RC, Altmann J, Alberts SC (2008) Can't get there from here: Inferring kinship from pairwise genetic relatedness. *Anim Behav* 75(3):1173–1180.
- Silk JB, Alberts SC, Altmann J, Cheney DL, Seyfarth RM (2012) Stability of partner choice among female baboons. *Anim Behav* 83(6):1511–1518.
- Carnegie SD, Fedigan LM, Melin AD (2011) Reproductive seasonality in female capuchins (*Cebus capucinus*) in Santa Rosa (Área de Conservación Guanacaste), Costa Rica. *Int J Primatol* 32(5):1076–1090.
- R Core Team (2014) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna). Available at www.R-project.org/. Accessed January 27, 2015.
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1):1–48.
- Lenth R (2015) lsmeans: Least-Squares Means. Available at: cran.r-project.org/packages/lsmeans/index.html. Accessed April 14, 2016.
- Bolker BM, et al. (2009) Generalized linear mixed models: A practical guide for ecology and evolution. *Trends Ecol Evol* 24(3):127–135.