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Reevaluating the relationship between female sociality and infant survival in wild baboons

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Over the past few decades, studies have provided strong evidence that the robust links between the social environment, health, and survival found in humans also extend to nonhuman social animals. A number of these studies emphasize the early life origins of these effects. For example, in several social mammals, more socially engaged mothers have infants with higher rates of survival compared to less socially engaged mothers, suggesting that positive maternal social relationships causally improve offspring survival. Here, we show that the relationship between infant survival and maternal sociality is confounded by previously underappreciated variation in female social behavior linked to changes in reproductive state and the presence of a live infant. Using data from a population of wild baboons living in the Amboseli basin of Kenya—a population where high levels of maternal sociality have previously been linked to improved infant survival—we find that infant- and reproductive state-dependent changes in female social behavior drive a statistically significant relationship between maternal sociality and infant survival. After accounting for these state-dependent changes in social behavior, maternal sociality is no longer positively associated with infant survival in this population. Our results emphasize the importance of considering multiple explanatory pathways—including third-variable effects—when studying the social determinants of health in wild populations.

confounds | fitness | maternal behavior | primates | sociality

Significance

In a variety of social animals, females who are more social are shown to have higher rates of infant survival compared to less social females. These associations have been interpreted as evidence that social relationships lead to increased offspring survival. Using long-term data on wild baboons, we demonstrate how these associations are affected by previously underappreciated confounds in maternal social data; specifically, by how females change their social behavior during different reproductive stages and when a live infant is present. After accounting for these confounds maternal sociality is no longer associated with enhanced infant survival in our dataset. These results mandate a closer scrutiny of the causal pathways linking maternal social behavior and infant survival in social mammals.

In social species, social interactions play a major role in determining an animal's access to resources (1–4), exposure to pathogens (5), protection against predators (3, 4, 6, 7), and adoption of novel behaviors (8). Consistent with this idea, the social environment has been linked to health and survival outcomes in a wide variety of social mammals, including humans (9–17). For the dependent young of many species, the social environment is primarily determined by the social relationships of their mothers. For this reason, maternal social traits have been proposed to influence offspring survival, with evidence supporting this link presented in nonhuman primates (18–23), dolphins (24), sheep (25), and horses (26).

Because of their long period of maternal dependence and close evolutionary relationship to humans, nonhuman primates have been a particular focus of studies linking maternal sociality to offspring survival. In the Amboseli baboon population of southern Kenya (an admixed population of yellow, *Papio cynocephalus*, and anubis, *Papio anubis*, baboons), females that spend the most time grooming and in proximity to social partners show the highest relative infant survival over their lifetimes (18). In a long-term study of chacma baboons (*Papio ursinus)* in Botswana, offspring of females with stronger social bonds (i.e., females who have many affiliative interactions with their most frequent social partners; refs. 27–29) also live significantly longer lives (19). In the De Hoop chacma baboons of South Africa, baboon infants whose mothers have many weak bonds (i.e., females who have many partners with whom they interact affiliatively but infrequently) are also more likely to survive the first 12-mo of life than infants whose mothers have fewer weak social bonds (21). In vervet monkeys (*Chlorocebus pygerythrus*) infant survival increases with the number of maternal spatial partners (23). All of these studies suggest that maternal sociality bolsters offspring survival. However, Schneider-Crease et al. (22) recently revealed no significant relationship between maternal sociality and offspring survival in kinda baboons (*Papio kindae*). Meanwhile, in white-faced capuchins (*Cebus imitator*), the offspring of females with the strongest social bonds exhibit higher survivorship than those of less social females during socially stable periods, but lower survivorship during the less stable periods surrounding alpha male turnovers (20). Therefore, associations between maternal sociality and offspring survival within primates appear to vary as a function of species, population, and/or prevailing demographic conditions.

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Importantly, a relationship between maternal sociality and offspring survival could have alternative explanations that do not involve a causal influence of maternal social relationships on offspring survival. All analyses of the relationship between maternal social behavior and infant survival face a key challenge: The amount of time a mother has a living infant may itself drive patterns of female sociality. For example, in a number of primate species, conspecific adult females are attracted to young infants (30–35). This effect could cause mothers with surviving infants to appear more social than mothers whose infants die, simply because they have a socially attractive infant around for a longer time period (36). Under this scenario, instead of female sociality driving infant survival, infant survival would drive estimates of female sociality, providing an alternative explanation for a positive relationship between maternal sociality and offspring survival that would manifest regardless of whether maternal sociality is measured over the lifetime (e.g., ref. 18) or over fixed yearly intervals (e.g., refs. 19–22). Similarly, the relationships females have with males may depend on patterns of infant survival. In many primates, the death of an infant is followed by the rapid resumption of sexual cycling, stimulating male interest in females (37). Mothers with young infants may also spend increased time near adult males to seek protection from harassment and infanticide (e.g., refs. 37 and 38).

Some approaches to avoiding infant-dependent variation in female social relationships in such analyses include discarding maternal social interactions that occur when infants are very young (e.g., less than 100 d: ref. 19) or measuring maternal sociality before an infant is born (23). However, these approaches have limitations. The first approach does not eliminate infant-dependent variation in maternal sociality that occurs after the discarded time window (e.g., cycling resumption following an infant's death). Moreover, both approaches by design eliminate the social interactions that are likely to be the most consequential for infant survival, possibly obscuring any true causal effects of maternal social relationships on offspring survival.

Here, we directly address the potential influence of infant-driven variation in maternal social behavior by measuring and adjusting for the magnitude of this potential confound in a study of baboons living in the Amboseli basin of southern Kenya—a population where higher levels of maternal lifetime sociality have previously been linked to improved infant survival (18). We use an established measure of maternal social behavior (maternal social connectedness, SCI; ref. 13 and *Materials and Methods*) to demonstrate that a female's social interactions with both adult females and adult males are strongly dependent upon her reproductive state along with the age and survival status of any current infant. Next, we demonstrate how the relationships between a female's reproductive state, infant age/presence, and her rates of social interactions produce statistically significant associations between maternal SCI and infant survival that can change in both direction and magnitude depending upon the time interval over which SCI is measured. After accounting for infant- and reproductive state-driven variation in maternal sociality, we find no compelling evidence that sociality positively predicts infant survival in our analysis. Finally, we demonstrate that the same confounds attenuate the original effect reported by Silk et al. (18) and present some post hoc analyses assessing the eco-evolutionary consequences of a trade-off between maternal sociality's effect on adult versus offspring survival.

Results

Maternal Social Behavior Strongly Depends on Reproductive State and Infant Presence. Social connectedness of adult female baboons to other females (SCI-F, a nondyadic measure of grooming frequency, the primary affiliative social behavior in baboons) tends to peak for mothers with infants in the first 6 mo of life (Fig. 1*A* and *SI Appendix*, Table S1). This pattern is consistent with the idea that having a young living infant increases a mother's social interactions with other females (e.g., by attracting other females to groom with her). Females stop experiencing this peak in grooming interactions if their infants die in the first year of life (*SI Appendix*, Fig. S1*A*).

SCI-M peaks during the prepregnancy period when females are sexually cycling, and steadily declines from pregnancy through the first year of a surviving infant's life (Fig. 1*B* and *SI Appendix*, Table S2). If an infant dies, the mother's connectedness to males returns to prepregnancy levels as she resumes cycling (*SI Appendix*, Fig. S1*B*).

Associations between the presence of a live infant, reproductive state, and maternal SCI could confound an apparent effect of

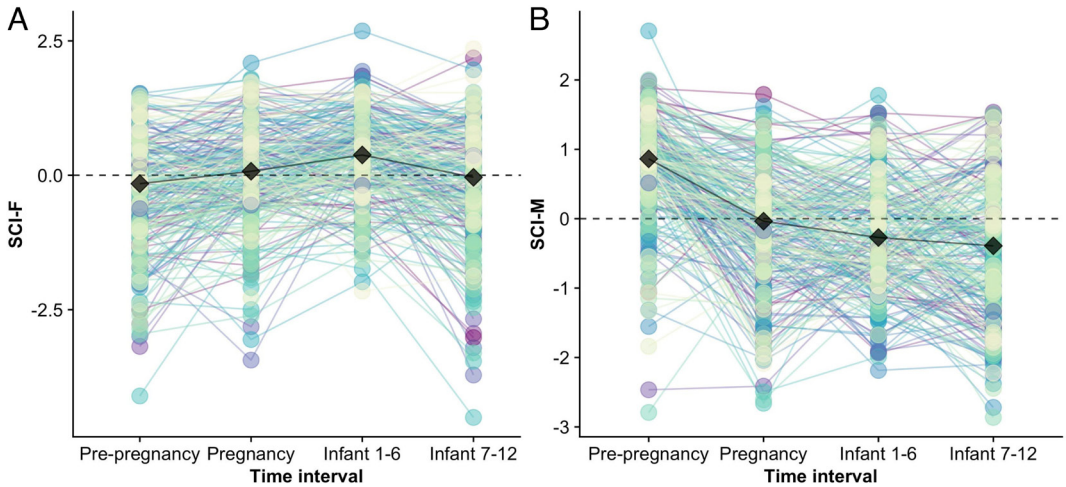

Fig. 1. Comparison of (*A*) social connectedness to females (SCI-F) and (*B*) social connectedness to males (SCI-M) for mothers with infants who survived to 1 y across four 6-mo time intervals (6 mo prior to pregnancy, pregnancy, 1 to 6 mo following birth, and 7 to 12 mo following birth). Black diamonds show the median for each time interval. Each series of connected dots represents a single infant ID for 257 unique infant births (n = 146 unique mothers) where behavioral data for the mother was available for all four time intervals and the mother did not have a young infant (less than 6 mo old) from a previous pregnancy during the prepregnancy period.

maternal sociality on infant survival. The same concern affects analyses using alternative measures of social integration such as the dyadic sociality index (DSI, which captures the strength of a females top three social bonds based on grooming data; refs. 39 and 40) and the composite sociality index (CSI, which combines data on grooming and proximity with individuals of both sexes; ref. 18), which are also correlated with reproductive state and infant presence (albeit less so for CSI; *SI Appendix*, Figs. S2 and S3). These patterns indicate that the association between infant status, reproductive state, and maternal sociality are not unique to SCI, our specific social measure of interest.

The Relationship between Maternal Sociality and Infant Survival Varies Depending on When Maternal Sociality Is Measured. After confirming that mothers experience patterns of social behavior that depend on infants and reproductive state, we investigated the effects of this relationship on the association between maternal social behavior and infant survival. To do so, we analyzed the link between the probability of infant mortality within the first year of life and, in separate models, SCI-F and SCI-M measured during four different time intervals. These time intervals included i) the fixed 6-mo window after an infant's conception (i.e., the pregnancy period in baboons, where gestation lasts an average of 6 mo; ref. 41), ii) the fixed 6-mo window beginning with the infant's live birth, iii) the fixed 6-mo window beginning 6 mo after an infant's birth, and iv) a "shifting time window" that represented the 6 mo prior to each infant's death or—for infants that survived—their first birthday. The shifting time window was designed to exclude any maternal social behavior occurring after (and possibly as a result of) an infant's death while also capturing key parts of the infant's life which were likely critical to its survival. The other time intervals occurred over the same fixed window relative to birth for all mothers, regardless of infant outcome, and thus more closely paralleled approaches taken in previous studies connecting maternal sociality to infant survival (e.g., refs. 19, 21, and 23).

We used binomial Generalized Linear Models (GLMs) implemented in R to test the relationship between SCI-F and SCI-M measured over each of the four time intervals and infant survival, controlling for other variables that could influence infant survival (maternal social rank, age, parity, group size, and sexual receptivity; see *Materials and Methods*). In these models the outcome was scored as 1 (if the infant died within 1 y) or 0 (if the infant survived). The total number of infants included in these analyses varied between 824 and 923 depending on the time interval of interest. This variation in sample sizes was a result of gaps in behavioral data for some mothers during some time intervals when behavioral sampling was constrained (e.g., if groups ranged outside of the study area or demographic events decreased sampling opportunities; see sample sizes reported in *SI Appendix*, Tables S3–S10). In all datasets, approximately 20% of infants died before their first birthday (range 19 to 24%).

The relationship between SCI-F and infant survival varied dramatically in direction and magnitude depending on when SCI-F was measured (Fig. 2). When SCI-F was measured over the fixed 6-mo window directly following a live birth, SCI-F positively predicted survival: Infants born to mothers with higher SCI-F experienced lower mortality rates than infants born to mothers with a lower SCI-F (coefficient = −0.208; odds ratio (OR) = 0.812; P = 0.013; Fig. 2 and *SI Appendix*, Table S4). In contrast, when measured over the shifting time window, which excludes all time periods after an infant's death, higher SCI-F negatively predicted survival: Infants born to mothers with higher SCI-F experienced higher mortality rates compared to infants born to mothers with a lower SCI-F (coef = 0.374; OR = 1.454; P = <0.001; Fig. 2 and *SI Appendix*, Table S6). SCI-F showed no statistically significant relationship with infant survival when measured over the pregnancy period (coef = −0.125; OR = 0.882; P = 0.109; Fig. 2 and *SI Appendix*, Table S3) or 7 to 12 mo after an infant's birth (coef = 0.109; OR = 1.116; P = 0.240; Fig. 2 and *SI Appendix*, Table S5).

These conflicting results are consistent with expectations if adult females' attraction to infants—and by extension, to their mothers (Fig. 1*A*)—accounts for the observed link between infant survival and maternal sociality with other females. Specifically, measuring SCI-F during the six months following birth means that females whose infants survive the entire 6-mo period appear more social than females whose infants die during that period, because surviving infants attract social attention for longer than infants that die in their first 6 mo. When SCI-F is measured during the shifting time window, however, mothers with infants who die within the first year of life appear more social because their SCI-F is measured when their infants are young and most likely to attract social attention.

Similar to SCI-F, the link between SCI-M and infant mortality depended upon the time interval over which SCI-M was measured (Fig. 2). When measured during the 6 mo following birth, higher SCI-M was associated with somewhat lower infant mortality (coef = −0.229; OR = 0.795; P = 0.048; Fig. 2 and *SI Appendix*, Table S8). On the other hand, when measured during the 7 to 12 mo following birth or using the shifting time window, higher SCI-M was associated with considerably higher infant mortality (coef = 0.656; OR = 1.928; P = <0.001; Fig. 2 and *SI Appendix*, Table S9 and coef = 0.607; OR = 1.834; P = <0.001; Fig. 2 and *SI Appendix*, Table S10, respectively). SCI-M did not predict infant mortality when measured during pregnancy

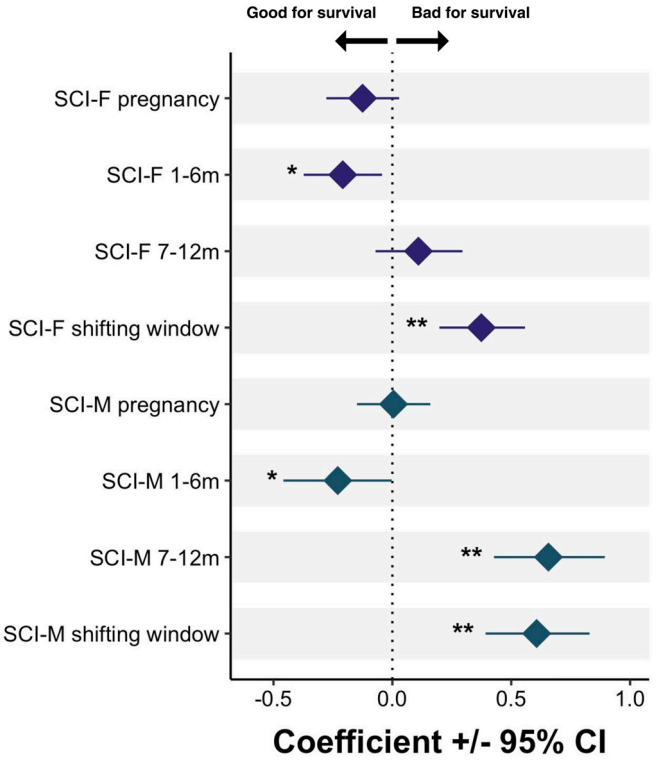

Fig. 2. Infant survival as a function of maternal social connectedness to females and to males (SCI-F and SCI-M) measured over different time intervals relative to infant birth; a coefficient (i.e., the natural logarithm of the odds ratio) = 0 (shown by vertical dashed line) indicates no effect of the social measure of interest on infant survival. See *SI Appendix*, Tables S3–S10 for full model results and sample sizes. *P < 0.05; **P < 0.01.

(coef = 0.005; OR = 1.005; $P = 0.952$; Fig. 2 and *SI Appendix*, Table S7).

As with the SCI-F results, results with SCI-M are consistent with the idea that the reproductive state-dependent nature of female relationships with males affects the apparent relationship between SCI-M and infant survival. Specifically, high levels of sociality with males may be negatively associated with infant survival when measured 7 to 12 mo after birth because mothers with surviving infants of this age typically have not yet resumed sexual cycling (42) and are less social with adult males than females in any other reproductive state (Fig. 1*B*). In contrast, mothers whose infants die resume sexual cycling and return to their prepregnancy levels of social interactions with adult males soon after infant death, resulting in high levels of social interactions with males 7 to 12 mo after their (nonsurviving) infants' births (*SI Appendix*, Fig. S1*B*). Similarly, when using the shifting time window, SCI-M for mothers whose infants survive is measured when those mothers are least likely to be interacting with adult males (i.e., when their infants are older but the mothers are often not yet cycling).

Infant-Dependent and Reproductive State-Dependent Trends in Maternal Social Behavior Explain the Relationship between Infant Survival and Maternal Sociality Measured Over Multiple Time Intervals. To determine whether infant-dependent and reproductive state-dependent changes in female social behavior could account for the associations between maternal sociality and infant survival in our observed datasets, we used a data randomization procedure that forced independence between maternal sociality and infant survival. In this data randomization (hereafter the "Randomization of SCI Values"), maternal SCI-F and SCI-M values were assigned randomly to the infant outcomes used in our analysis above. These randomly assigned SCI values were then changed systematically over time depending only on the infant outcome: For each month that an infant was alive, their mother was assigned an SCI value consistent with that of a female with a live infant of that given age range, but if an infant died the mother's SCI value was changed for all remaining months to be consistent with that of a mother with no infant (see further explanation below). Because these SCI scores were randomly assigned and only increased and decreased based on what happened to the assigned infant outcome, any relationship between maternal SCI and survival in this dataset would reflect an effect driven by infant-dependent trends in maternal social behavior (i.e., reverse causality), as opposed to maternal social behavior causally influencing infant survival. If the confound of infant-dependent trends in maternal social behavior was sufficient to account for the observed links between maternal sociality and infant survival, then we expected randomized SCI data to generate effects comparable to those obtained with the observed data.

To randomize SCI-F values, we randomly sampled SCI-F trajectories, with replacement, from the set of trajectories shown in Fig. 1*A* (where infant death never occurred). We then matched these trajectories one-by-one to infant–mother pairs in the observed dataset, which included cases where the infant died (randomization procedure visualized in *SI Appendix*, Fig. S4). For all infant outcomes in the observed dataset, we assigned the pregnancy SCI-F value from the randomly sampled trajectory from Fig. 1*A* to serve as the mother's SCI during pregnancy months. For infant outcomes where the infant survived to 12 mo of age, we assigned SCI-F values from the randomly sampled trajectory for the 6 mo following birth and the 7 to 12 mo following birth to serve as the maternal SCI-F for those months. For infant outcomes where the infant died, we followed the same procedure as for surviving infants with one exception: For all months following the infant's death, we assigned the maternal SCI-F value to match that of the prepregnancy SCI-F value from the randomly sampled SCI-F trajectory (because a female's prepregnancy SCI-F values closely match her SCI-F values after the loss of her infant, *SI Appendix*, Fig. S1). We repeated this procedure across all observed infant outcomes 1,000 times, resulting in 1,000 datasets with randomized SCI-F values.

We randomized SCI-M values as described above for SCI-F, but with an additional control for patterns in sexual cycling (since sexual cycling attracts social attention from males; see *SI Appendix*, Fig. S5) using data from *SI Appendix*, Fig. S6 (randomization procedure visualized in *SI Appendix*, Fig. S7). For all months after birth where a female had a live infant and had not resumed cycling, we assigned her the SCI-M value from the randomly sampled female trajectory where the sampled female had a live infant and also had not yet resumed cycling. For months after birth where a female had a live infant and had resumed sexual cycling, we assigned the SCI-M values from the randomly sampled trajectory during prepregnancy. For cases in which an infant died, we assigned the mother the prepregnancy SCI-M value from the randomly sampled trajectory, starting 2 mo after the infant's death (reflecting the rapid resumption of cycling in baboons after infant death; ref. 43). Once a mother was assigned a prepregnancy SCI-M value following the resumption of sexual cycling (induced by infant loss or otherwise) she was assigned that value for four consecutive months (reflecting the mean cycling length before the next conception; ref. 43). After 4 mo she was then assigned the pregnancy SCI-M value from the randomized trajectory.

We averaged the randomized monthly SCI values described above to get a mean SCI-F and SCI-M value for each infant's mother during pregnancy, the 6 mo following birth, the 7 to 12 mo following birth, and the shifting time window. We then ran parallel binomial GLMs on the randomized datasets to estimate the association between SCI measured over each time interval and infant survival, controlling for the same fixed effects as in analyses with the observed data. The sample size for each time interval matched the sample of infant outcomes for the complementary analyses with real data reported in *SI Appendix*, Tables S3–S10.

After repeating the process above across 1,000 randomized datasets, we found that in many cases the distribution of effect sizes generated from analyses with randomized data did not center on zero, suggesting that infant-dependent and reproductive state-dependent changes in maternal social behavior indeed present a detectable confound over these time intervals (Fig. 3 and *SI Appendix*, Table S11). Furthermore, for both SCI-F and SCI-M, we found that all of the observed effect sizes fell within the distribution of effect sizes generated from randomized datasets, indicating the observed effect sizes could be explained by infant-dependent and reproductive state-dependent changes in maternal social behavior (Fig. 3 and *SI Appendix*, Table S11). In several cases the observed effects fell within the tails of the distributions (Fig. 3 *A*–*C*, *F*, and *G*) making these effects less likely to be entirely explained by the confound than cases where effects fell within the center of the distributions. Among cases where the observed coefficients fell within one tail of a distribution, effects generated from SCI-F and SCI-M measured 7 to 12 mo after birth were the least likely to be entirely explained by the confound: Less than one percent of coefficients from randomized data were larger than the observed coefficient (Fig. 3 *C* and *G* and *SI Appendix*, Table S11), in the direction of higher maternal sociality during this time interval being associated with *higher* infant mortality. Overall, these results suggest that infant-dependent and

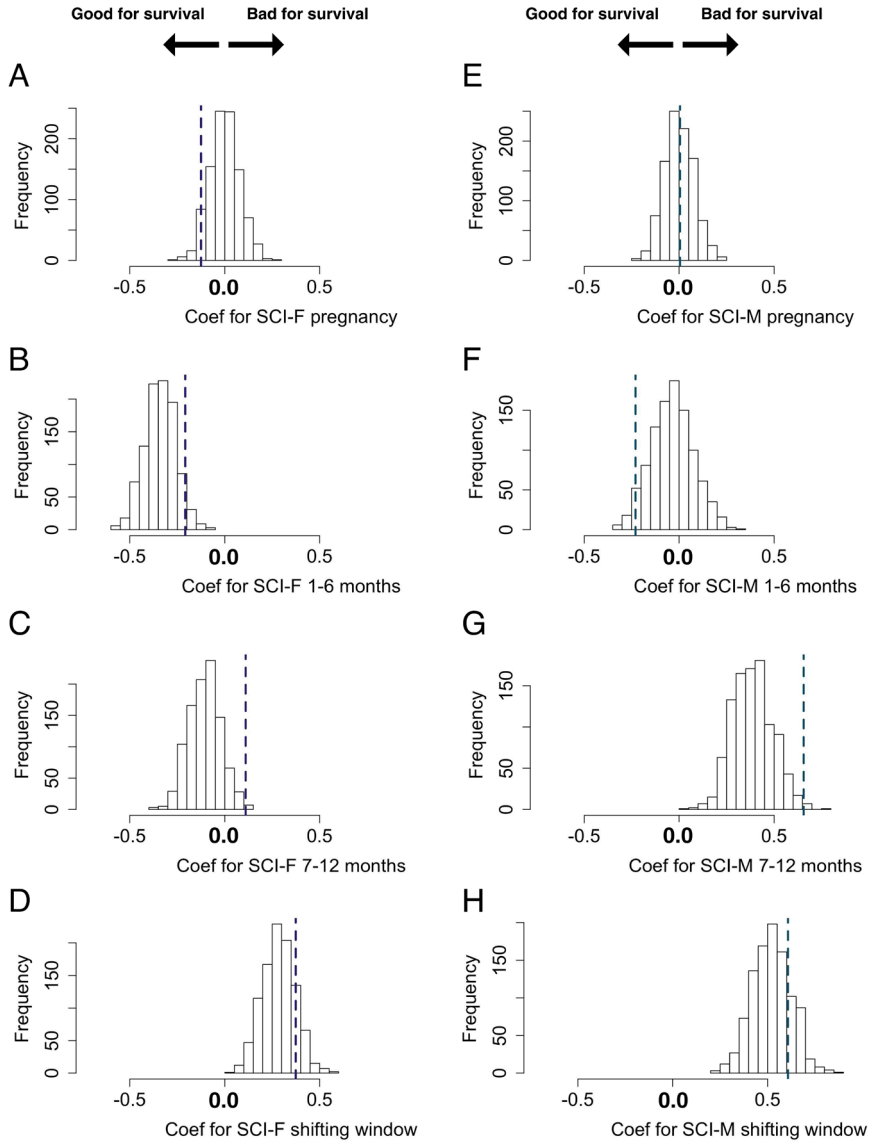

Fig. 3. Results of the Randomization of SCI Values analysis. Histograms show the distribution of coefficients (i.e., the natural logarithm of the odds ratio) from binomial GLMs using randomized SCI data; vertical dashed lines show coefficients from GLMs with observed data (Fig. 2). *Left* column shows SCI-F estimated over (*A*) pregnancy, (*B*) the 6 mon following birth, (*C*) the 7 to 12 mo following birth, and (*D*) a shifting data window (6 mo prior to infant death or first birthday depending on survival outcome). *Right* column shows SCI-M estimated over (*E*) pregnancy, (*F*) the 6 mo following birth, (*G*) the 7 to 12 mo following birth, and (*H*) a shifting data window. Negative coefficients mean high SCI is associated with low risk of mortality and thus high survival, while positive coefficients mean high SCI is associated with high risk of mortality and thus low survival. If an observed coefficient (dashed line) is to the *left* of the distribution of permuted coefficients, then high maternal sociality is associated with high infant survival after accounting for the confounding effect of infant and reproductive variation in maternal social behavior. If an observed coefficient is to the *right* of the distribution, then high maternal sociality is associated with high infant mortality after accounting for the confound. See *SI Appendix*, Table S11 for median coefficient values and variances associated with distributions of coefficients from analyses on randomized datasets.

reproductive state-dependent patterns in maternal behavior are sufficient to produce nonzero associations between maternal sociality and infant survival when they are not taken into account, and that any evidence for maternal sociality having a consistent positive effect on infant survival is weak at best.

As a complementary test of this hypothesis, we conducted a second data randomization (hereafter the "Randomization of Time Intervals") that was designed to avoid (rather than quantify) any potential confound. Here, we randomly sampled, with replacement, the age at death for infants who died within 1 y, and assigned that age as the last day of the 6-mo time interval used to calculate SCI for infants who survived. This approach avoids both the problem of sampling maternal behavior that occurs after an infant has died and the problem of measuring SCI at later ages for infants who survive. We then calculated maternal SCI-F and SCI-M over the 6 mo prior to either the true death date (for dead infants) or the randomly sampled death date (for surviving infants). We analyzed data from 100 of these randomized datasets using GLMs that paralleled those applied above. Each randomized dataset included between 766 and 793 infant outcomes, depending on the number of infants whose mothers had complete behavioral data available for the sampled 6-mo time interval. These analyses provided no evidence that SCI-F or SCI-M predict infant survival (mean coef = −0.025; mean OR = 0.975; 0% of *P*-values < 0.05 and mean coef = −0.029; mean OR = 0.971; 0% of *P*-values < 0.05, respectively; distribution of coefficients are shown in *SI Appendix*, Fig. S8 *A* and *B*). Rerunning this analysis using Bayesian Regression Models (44) that allowed for the flexible

inclusion of random effects (maternal identity, hydrological year, and group identity; see *Materials and Methods*) produced qualitatively similar results (*SI Appendix*, Fig. S9 *A* and *B*).

Reproductive State and Infant-Dependent Trends in Maternal Social Behavior Explain the Effect of Lifetime Maternal Sociality on Infant Survival. The present analysis was motivated in part by results from Silk et al. (18), who showed that, in Amboseli, more socially integrated mothers experience higher infant survivorship. Silk et al. (18) used the individual mother (i.e., a female's lifetime success at producing surviving infants) as the unit of analysis while the analyses reported above used the infant as the unit of analysis. Furthermore, Silk et al. (18) used a lifetime estimate of the CSI, which combines data on female social relationships with both males and females (captured by grooming and proximity to others during focal points; see *SI Appendix, Methods*), as the measure of maternal sociality. This approach contrasts with the measures we used above, which were summarized over short time intervals, were sex-specific (SCI-F and SCI-M), and were based only on grooming data. These differences could mitigate the influence of the confound described above. To test this possibility, we recreated the analysis reported by Silk et al. (18) using an expanded dataset that included an additional 22 y of more recently collected behavioral and demographic data. A total of 295 adult females were included in our recreation, compared to 108 in ref. 18. See *SI Appendix, Methods* for more details about our recreation.

We conducted three analyses on the expanded dataset. First, following Silk et al. (18), we analyzed the relationship between a mother's lifetime relative infant survival and her lifetime CSI (an estimate of her tendency to groom with and be in proximity to other adults). In this analysis, we recovered a similar pattern to the original paper: Higher maternal sociality was associated with higher relative infant survival (B = 0.095; $P = 0.027$) (Fig. 4*A*), although the effect size was smaller than originally estimated (original paper reports B = 0.321; $P = 0.015$).

Next, we repeated the analysis twice more, first removing time periods from the CSI calculation in which mothers had infants less than 1 y old, and second removing all time periods except pregnancy (when females typically do not have young infants and all share the same reproductive state). These two analyses limit the measures of maternal social behavior to periods when the mother's behavior is least likely to be influenced by the presence of an attractive infant or by sexual cycling. In neither of these analyses did the relationship between maternal CSI and offspring mortality reach statistical significance (removing time periods where mothers had infants less than 1 y of age: B = 0.031, $P = 0.268$, n = 256, Fig. 4*B*; restricting the analysis to periods of pregnancy: B = 0.025, $P = 0.332$, n = 268, Fig. 4*C*). These results support the idea that the original result reported by Silk et al. (18) is primarily explained by infant-dependent and reproductive state-dependent trends in maternal social behavior.

Effects of Sociality on Adult Survival Outweigh Effects of Sociality on Offspring Survival. Our analysis revealed some limited evidence that mothers who are highly social during certain periods of their infant's early life may experience modestly reduced offspring survival (Fig. 3 *C* and *G*). At the same time, high SCI and DSI scores are associated with higher survival for adult female baboons themselves (10, 13, 16), even after controlling for the percentage of days females spend with a young infant (45). If maternal sociality does indeed have opposing effects on infant and maternal survival, how is this trade-off between the two outcomes ultimately balanced? To probe this question, we built a simple matrix projection model based on the life cycle of female baboons. The model's parameters were chosen to roughly match the life history of our study population, and infant and adult female survival rates were assumed to be a function of SCI (males were not explicitly modeled; see *SI Appendix, Methods* for details).

Our primary goals were to determine what values of SCI maximize λ_1—the long-term per capita growth rate (the estimate of female fitness generated by the model; see *SI Appendix, Methods*)—and to understand how the relationship between SCI and λ_1 changes depending on how SCI affects infant survival versus adult survival in our model. If λ_1 is greatest when SCI is relatively high, this result would indicate that high levels of maternal sociality confer net fitness benefits for females. If λ_1 is greatest when SCI is relatively low, this result would indicate that low levels of maternal sociality confer net fitness benefits (and conversely that high levels of maternal sociality impose net fitness costs).

We found that the effect of SCI on overall female fitness (λ_1) depends almost entirely on how SCI affects adult female survival, regardless of the outcome for infants (Fig. 5). In Fig. 5, both of

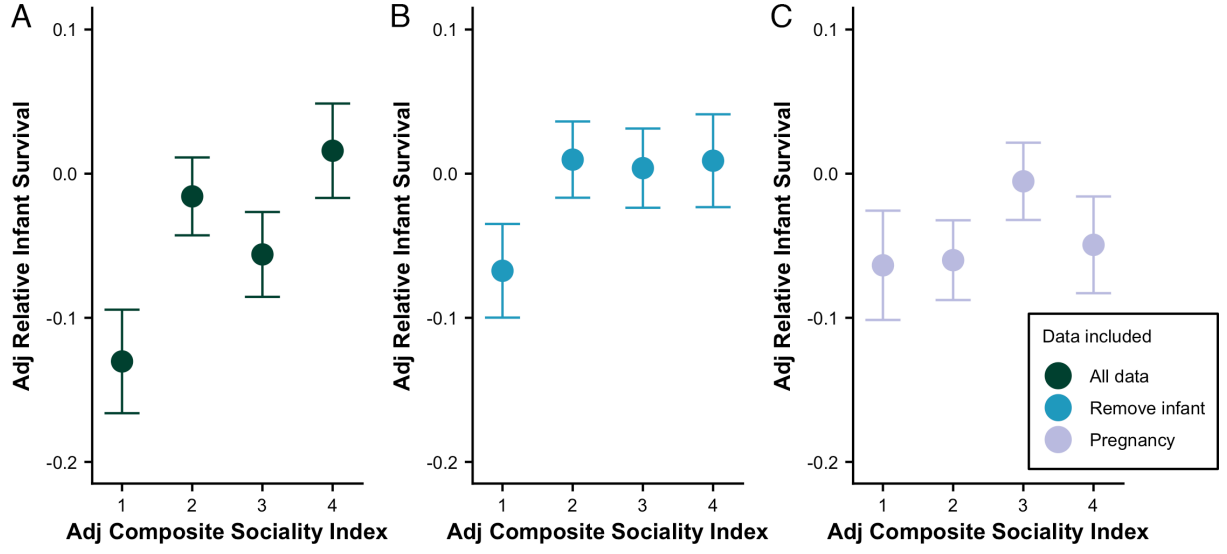

Fig. 4. Recreation of figure 1 in ref. 18 using an updated dataset (1984 to 2022), showing the relationship between a mother's lifetime CSI score and relative infant survival. Panels from left to right show estimates: (*A*) including all data from mothers' adult lives (green), (*B*) removing periods in the CSI calculation when mothers had a young infant less than 1 y old (blue), and (*C*) only including data from periods of pregnancy (purple) in the CSI calculation.

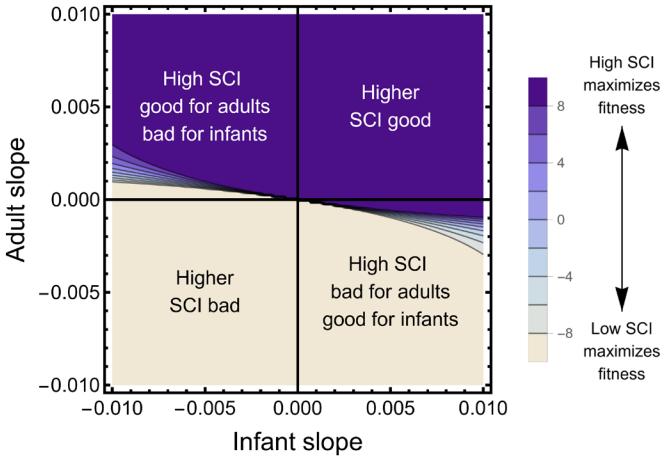

Fig. 5. Colored landscape showing the SCI score that maximizes λ_1 (female fitness) in our matrix projection model. Dark colors correspond to cases where relatively high values of SCI improve female fitness, while light colors correspond to cases in which high values of SCI reduce female fitness (see color legend). Axes show the slope of infant survival (*x* axis) and adult survival (*y* axis) as a function of SCI when SCI = 0 (the population mean). More positive slopes correspond to a greater beneficial influence of high SCI on survival and more negative slopes correspond to a greater detrimental influence of high SCI on survival.

the top quadrants (where SCI is *positively* associated with adult survival) are almost entirely dark in color, indicating that high SCI *improves* fitness (λ_1) when high SCI is good for adult survival (positive values on the *y* axis), regardless of the effect of SCI on infant survival (the *x* axis). Meanwhile both of the bottom two quadrants (where SCI is *negatively* associated with adult survival) are almost entirely light in color indicating that high SCI *reduces* fitness (λ_1) when high SCI is bad for adult survival (negative values on the *y* axis), regardless of the effect of SCI on infant survival. Notably, exceptions occur where the effects of SCI on adult survival are quite weak (i.e., the adult slope is close to zero): In these cases, the infant slope becomes more influential in determining how SCI affects female fitness. The fact that SCI mainly influences fitness based upon its effects on adult survival likely follows from there being more adults in the population than infants at any given time.

Discussion

We found no strong evidence that maternal sociality is causally associated with improved infant survival in our infant-wise analysis. We instead found that apparent relationships between maternal sociality and infant survival are more parsimoniously explained by infant-dependent and reproductive state-dependent trends in a mother's social behavior. As a result, the direction of the relationship between maternal social behavior and infant survival changes depending on the time interval during which maternal sociality is captured.

Our results further suggest that infant-dependent and reproductive state-dependent differences in maternal social behavior can generate a spurious relationship between maternal sociality and infant survival not only when maternal sociality is measured in the first 6 mo of an infant's life, but even in the 7 to 12 mo following a birth. Specifically, Fig. 3 *C* and *G* demonstrate that the distribution of effect sizes from analyses with randomized SCI-F and SCI-M data do not center on zero, indicating that removing data for the first 100 d following a birth as done by Silk et al. (19) would not be enough to completely eliminate the effect of this confound in our population. Furthermore, controlling for this confound not only affects conclusions from infant-wise analyses, but also strongly attenuates the original effect reported by Silk et al. (18), who used lifetime estimates of maternal sociality and infant survival (Fig. 4). Notably, when tested separately as predictors of relative infant survival in ref. 18, proportion of time being groomed was the only one of the three social components of CSI that was a significant predictor of survival on its own (i.e., time spent grooming and time spent in proximity to others were not significant predictors), suggesting that the amount of time mothers spend being groomed by others drives the apparent relationship between CSI and infant survival. This further supports the idea that infants and certain reproductive states (e.g., sexual cycling) that attract high levels of social attention directed at the mother contribute to the original result.

After accounting for variation in individual behavior driven by reproductive state and infants, our analyses with data from the Randomization of SCI Values produced some limited evidence that more social mothers may experience higher infant mortality (Fig. 3 *C* and *G*). A negative association between infant survival and maternal sociality captured over certain time periods could have multiple, non-mutually exclusive explanations. High levels of maternal social interactions could result in increased exposure to pathogens (46, 47), increased stress (48), reduced time spent feeding (31), or increased vulnerability to fatal kidnappings or infanticide (20, 49, 50). Furthermore, a high frequency of social interactions between mothers and other females may result in rough handling of infants by other females, which in turn is associated with signs of distress in infants in Amboseli (38), and with lower survival in several other nonhuman primate populations (49, 51). On the other hand, maternal sociality may be negatively associated with infant survival if less healthy mothers or infants attract more social attention. For example, kin and other close social partners might groom more with a female if that female or her infant are experiencing illness or injury (52). In this case, maternal social behavior would not contribute directly to infant survival, but rather unhealthy mothers and infants would receive more social attention.

Notably, a potentially harmful effect of higher maternal sociality on infant survival was only supported over some time intervals used in our analyses. Analyses from our Randomization of Time Intervals approach did not support an effect of SCI on infant survival in either direction. Moreover, when SCI-F was measured over pregnancy and SCI-M was measured over the 6 mo following a birth, the results from our Randomization of SCI Values were suggestive in the opposite direction: High SCI may be associated with slightly higher survival (Fig. 3 *A* and *F*). The direction of these results with SCI-F are consistent with findings of Blersch et al. (23) who found a positive relationship between maternal social connectedness and infant survival when measuring social relationships during pregnancy in an attempt to avoid the confound of infant attractiveness. The result in Fig. 3*F* also matches expectations if male social partners protect from infanticide when infants are very young. Importantly, such results could also be explained by reverse causality if, for example, mothers tend to socialize more when they are healthier (and thus more likely to have a healthy infant). Regardless, given that we show maternal sociality has a neutral and occasionally even negative relationship with infant survival when quantified over other time periods, our results suggest that high maternal sociality does not provide universal fitness benefits for infants overall, at least in our population.

Furthermore, according to the results of our matrix projection model, any negative or positive effects of maternal sociality on infant survival are unlikely to strongly influence selection for maternal social behavior if maternal social relationships improve

adult female survival. Specifically, even if maternal sociality directly affects both adult and infant outcomes, the survival benefits or costs that a mother experiences from being social outweigh the benefits or costs experienced by her infants. In other words, if being social enhances adult female survival then selection should not act to reduce female sociality, even if maternal social relationships pose potential risks to infants. Consistent with adult survival having an outsized effect on fitness, previous findings suggest longevity is more important than fecundity for lifetime reproductive success in the Amboseli baboons (53).

Conclusion

We have shown that the manner in which a female baboon's social interactions are affected by her reproductive state and whether she has a live infant can lead to the erroneous inference that maternal sociality improves infant survival. Specifically, the way a female's social behavior changes depending upon her reproductive state and infant status generates a correlation between maternal sociality and infant survival that varies in both direction and magnitude depending on when sociality is measured relative to an infant's birth or death. Correcting for reproductive state and infant-related variation in maternal sociality can attenuate, eliminate, or even reverse the direction of maternal sociality-infant survival correlations. We believe that this confound is the best explanation for previous results reported from our study system, where high levels of maternal sociality were interpreted as a driver of enhanced infant survival (18). Furthermore, results from a simple matrix projection model suggest that selection is unlikely to favor reduced female sociality, even if being social has negative effects for offspring, so long as being social provides a survival advantage to adult females themselves.

Taken together our results provide no strong support for a positive effect of maternal sociality on infant survival after accounting for variation in female social behavior driven by changes in reproductive state and the presence of a live infant. In fact, the most compelling evidence for an association between maternal sociality and offspring survival was found in the 7 to 12 mo following birth, when maternal sociality may be linked to reduced rather than increased infant survival in the Amboseli baboon population. This evidence that more social mothers may experience worse infant survival is suggestive rather than definitive: The strength of the relationship between high maternal sociality and poor infant survival varies across the time periods in which we measured maternal sociality (Fig. 3). Importantly, female state-dependent patterns of social interaction occur in other primate species (e.g., refs. 34, 54, and 55), suggesting that our findings may generalize to other analyses. Consequently, our results mandate a closer scrutiny of the causal pathways linking maternal social behavior and infant survival in other nonhuman primate populations.

Materials and Methods

Estimating the Relationship between Infant Survival and Maternal Sociality, Measured Over Different Time Intervals.

Study system and subjects. Data for this analysis come from a long-term study of baboons (*P. cynocephalus* and *P. anubis*) in the Amboseli basin of southern Kenya. This population has been under continuous observation since 1971 (56). All study subjects in our dataset were live infants born into study groups between July of 1983 (when behavioral data began being collected systematically and consistently in our population) and December of 2020.

Maternal sociality. Maternal SCI (the social connectedness index, our measure of maternal sociality) with females (SCI-F) and with males (SCI-M) were calculated separately for each time interval using grooming data collected during "representative interaction sampling" (*SI Appendix, Methods*) by averaging the residuals from two linear regressions: i) log grooms given by the focal individual per day to other groupmates, regressed on log observer effort (i.e., the number of focal follows per adult female in the group divided by the number of days; see extended description in *SI Appendix, Methods*); and ii) log grooms received by the focal individual per day, regressed on log observer effort (13). These values were z-scored within population and year and used as our final measures of SCI.

Testing the relationship between SCI and infant survival. We tested whether SCI-F or SCI-M predicted infant survival in separate models using binomial GLMs implemented with the glm function from R. Each model included one maternal social measure (SCI-F or SCI-M) measured over one of four time intervals. The outcome was scored according to whether the infant died (1) or survived (0). Given that the purpose of our analysis was to interrogate the previously reported linear effects of maternal sociality on infant survival and that no explicit hypotheses exist to support a nonlinear relationship between sociality and infant survival, we did not explore the possibility of nonlinear relationships in our analyses.

Several variables are already known or suspected to influence offspring survival in this population (18, 57). To control for the possible influence of these variables on infant survival, we also measured them over the time intervals of interest and included them as additional fixed effects in our GLMs. These additional fixed effects were i) the relative proportion of adult females a given mother outranked in her group, ii) maternal age, iii) maternal age squared, iv) whether the infant of interest was the mother's first birth (1 = true; 0 = false), and v) group size. In models with SCI-M we also included the absolute proportion of days over the 6-mo time interval in which the mother was experiencing menstrual cycling as a fixed effect, to control for the ephemeral social relationships that arise between adult males and females when females are sexually cycling (58, 59). In all models, continuous fixed effects were scaled by subtracting the mean and dividing by the SD to ensure model convergence. We initially used mixed models including the random effects of maternal identity, hydrological year, and group identity in addition to fixed effects. However, these variables explained little to no variance leading to issues of singular fit and thus uninterpretable results. These terms were therefore dropped from all final analyses. Analyses of residuals with DHARMa (60) indicated acceptable model fits.

Data, Materials, and Software Availability. Anonymized Data and Code data have been deposited in Duke Research Data Repository (https://doi.org/10.7924/r46d63h7p) (61).

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