High early lactational synchrony within baboon groups predicts increased infant mortality

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Abstract

Social group composition can have fitness implications for group members by determining opportunities for affiliative and competitive interactions. Female-female competition may be particularly acute when many groupmates have young infants at the same time, with potential consequences for infant survival. Here, we used decades of data on wild baboons (*Papio* sp.) in Amboseli, Kenya, to examine the effects of 'early lactational synchrony' (here, the proportion of females in a group with an infant <90 days old) on female-female agonistic interactions and infant survival. Because early lactation is an energetically demanding time for mothers and a risky time for infants, we expected early lactational synchrony to produce intensified competition for food and/or male protectors, resulting in more frequent female-female agonistic interactions and high infant mortality. In support of these predictions, we found that the frequency of female-female agonistic interactions increased with increasing early lactational synchrony. Reproductive state affected this relationship: while females in all states (cycling, pregnant, and postpartum amenorrhea) initiated more agonistic interactions when early lactational synchrony was high, only females in postpartum amenorrhea (including, but not limited to, females in early lactation) received more agonistic interactions. Furthermore, while high early lactational synchrony was rare, it strongly predicted infant mortality. This association may result from both aggression among adult females and infanticidal behavior by peripubertal females. These findings provide novel evidence that social dynamics may shape reproductive phenology in a nonseasonal breeder. Specifically, both competition among reproductive females and harassment from nonreproductive females may select against synchronous reproduction.

Significance Statement

Competition between females is a powerful force shaping the behavior and fitness of wild animals, but how it is exacerbated (or mitigated) by the overall composition of social groups is understudied. We asked if female-female competition is enhanced when more females in baboon social groups have young infants, a time that is particularly energetically demanding for mothers and particularly dangerous for their offspring. In these settings, we found that both adult female competitive behavior and infant mortality risk increased. Strikingly, almost all recorded cases of infanticide by adolescent, nulliparous females in our study population occurred on days when many mothers had young infants. These results highlight how social interactions may shape the timing of reproduction in wild social mammals.

Background

Competition between conspecifics is an important selective force acting on social behavior, morphology, and life history (1-3). In many vertebrates, females compete with each other for food, mates, social partners, and other resources, with tactics ranging from mating interference to infanticide (4-10). This competition can have important fitness effects. For example, in many species, high dominance rank or increased aggressive behavior is associated with higher female reproductive success (11-16). Intense female-female competition can even be sufficient to prevent the emergence of group living (17), while moderate female-female competition can shape many aspects of sociality among group-living species, from the differentiation of individual relationships to the structuring of groups according to kinship or dominance hierarchies (18, 19).

For group-living species, group demography is expected to shape the dynamics of female-female competition. Because female reproduction is energetically costly and food

resources are often limited, group size may affect the level of female competition and its fitness consequences (19, 20). Indeed, studies both within and across species report increased rates of agonistic interactions among females with increasing group size (21-26). Other studies have implicated female-female competition as a cause of depressed reproductive success or survival in larger groups (14, 27-29). Although large group size can also benefit females (e.g., via cooperative breeding (30, 31) or advantages in intergroup competition (32, 33)), its relationship with female-female competition highlights one potential "top-down" pathway linking group demography to fitness.

However, group size is not the sole determinant of the intensity of competition: group age structure, sex ratio, and female reproductive state can also modulate competitive intensity because they contribute to body size- and state-dependent variation in energetic demands (34, 35). Among female social mammals, reproductive state is a particularly salient source of variation in competitive landscapes because a female's resource and social requirements vary depending on whether she is cycling, pregnant, lactating, or reproductively quiescent (36). For example, female bottlenose dolphins (*Tursiops aduncus*) avoid male kin in favor of unrelated males while sexually receptive, presumably to minimize the risk of inbreeding (37), but avoid unrelated males while lactating, when the risk of infanticide by unrelated males is high (38). Accordingly, shared requirements can promote association by females in similar reproductive states (39), but shared requirements can also increase competition for food, mates, and/or allomaternal care (5).

The importance of female reproductive state in shaping female-female competition is supported by the observation that conspicuous female-female competition is more frequent among species that exhibit systematically high reproductive synchrony, as expected if females compete over reproductive state-specific resources (3, 5). For example, in topi antelopes (*Damaliscus lunatus*) more than 90% of calves are conceived within an annual 1.5-month period that is marked by aggressive mating interruptions. Similarly, female red deer (*Cervus elaphus*), female feral horses (*Equus caballus*), and female golden snub-nosed monkeys (*Rhinopithecus roxellana*) display increased rates of aggression and/or disruption of other females' copulations during their short breeding seasons (40-43). Even in nonseasonal breeders, individuals can sometimes experience high reproductive synchrony and competition with groupmates. For instance, in chacma baboons, sexually receptive females experience heightened aggression from other sexually receptive females, and also from females who have recently conceived, pointing to competition over mates and paternal investment when females cycle relatively synchronously (6, 44). However, the overall effects of reproductive synchrony on female competition in nonseasonal breeders, and especially the fitness consequences of competition resulting from such synchrony, remain poorly understood. Addressing this gap is important for understanding the relationship between resource availability, resource competition, and reproductive timing, which can vary even between closely related, ecologically similar species (45, 46).

In this study, we investigated how the fitness consequences of female-female competition are affected by one form of reproductive synchrony—early lactational synchrony—in wild baboons (*Papio* sp.), where the importance of female-female competition is well-established. Female-female competition for resources and mates has been studied closely in several baboon species, including chacma (*P. ursinus*), anubis (*P. anubis*), and yellow baboons (*P. cynocephalus*). These species live in large, multimale, multifemale groups characterized by female philopatry and male dispersal (47). Females form stable, linear dominance hierarchies and typically experience nepotistic 'inheritance' of maternal dominance rank (48-50). Rank-

mediated competition for food is likely a prominent force shaping the social behavior of female anubis and yellow baboons because agonistic behaviors are more common among females that experience greater energetic burdens and during periods when food availability is thought to be lower (51-53). Females of both yellow and chacma baboons also compete for mates and/or protective male associates who buffer mothers and their infants from harassment by other adult and immature females (6, 44, 54, 55). Reproductive state influences the rate at which female baboons initiate and receive aggression (6, 44, 51, 52, 56), and previous studies of reproductive synchrony in baboons suggest that the composition of female reproductive states in baboon groups may be an important predictor of competitive behavior (45, 57, 58). Nonetheless, the ultimate consequences of reproductive synchrony for mothers or their infants in baboons and other nonseasonal breeders remains unclear.

Our study subjects were members of multiple social groups in a population of wild baboons (*P. cynocephalus* with significant *P. anubis* admixture: 59-60) in the Amboseli basin of southern Kenya, which has been continuously monitored since 1971 (61). Females in this population give birth year-round, and the first 90 days after birth (hereafter, 'early lactation') constitutes a period of both high energetic demands for mothers and increased risk of harassment from other females towards newborn infants (62, 63). We defined early lactational synchrony as the proportion of adult females in a social group with dependent infants <90 days old. Our main hypothesis was that groups exhibiting high early lactational synchrony would experience intensified intragroup competition, and that intensified competition would lead to negative fitness-related outcomes for both mothers and their dependent offspring. We tested two predictions generated by this hypothesis. First, we predicted that female-female agonistic interactions would increase in frequency with higher lactational synchrony, either for all adult females or for females in specific reproductive states (considering ovarian cycling, pregnant, and postpartum amenorrhea). Second, we predicted that infant survival would be compromised when early lactational synchrony was higher, because increased competition between mothers could negatively impact their dependent offspring. We also examined the most prevalent sources of infant mortality during periods of high early lactational synchrony to gain insight into the specific risks imposed by female-female competition.

Results

Characterizing early lactational synchrony across the study period. We began by measuring the proportion of females in each social group who were in early lactation on each day (i.e., in the first 90 days of postpartum amenorrhea with a living infant), across all group-days of observation from November 1976 to December 2021. This proportion varied considerably across the study period, from group-days on which no females (0.000) were in early lactation to group-days on which more than 70% (0.714) of females were in early lactation (Fig S1). This distribution was heavily skewed toward zero, such that days of high early lactational synchrony were rare, as expected for this nonseasonally breeding species. The mean proportion of females in early lactation on a given group-day was 0.121 (SD: 0.102; median = 0.105, 75th percentile = 0.176 of the group's females per group-day; 95th percentile = 0.316 of the group's females per group-day). On average, groups had 1.96 total females in early lactation on any given day (SD: 1.74 females; median = 2 females, 75th percentile = 3 females, 95th percentile = 5 females; group sizes ranged in our data set from 3 to 33 adult females per group).

Female agonistic behavior. Using behavioral data collected from 1999-2021 (when we could control for observer effort, see Methods), we found that the relative frequency of adult female-female agonistic interactions increased in months when a higher mean proportion of the females in a group were in early lactation. Adult females both initiated relatively more agonistic interactions with other adult females and received relatively more agonistic interactions from other adult females during months when their group had higher mean early lactational synchrony (generalized linear mixed models, GLMMs; agonistic interactions initiated: $\beta = 0.90$, 95% CI: [0.71, 1.08], Tables S1-2; agonistic interactions received: $\beta = 0.66$, 95% CI: [0.49, 0.84], Tables S3-4).

Notably, females of all reproductive states initiated agonistic interactions with other females more frequently when a higher proportion of females were in early lactation (Fig. 1a). Specifically, when we partitioned the dataset by female reproductive state (ovarian cycling, pregnant, or postpartum amenorrhea), we found that females in all three reproductive states initiated more agonistic interactions with all other adult females during group-months of higher mean early lactational synchrony (GLMM for cycling females: $\beta = 0.74$, 95% CI: [0.39, 1.08]; Tables S5-6; for pregnant females: $\beta = 1.48$, 95% CI: [1.11, 1.84]; Tables S7-8; for females in postpartum amenorrhea: $\beta = 0.51$, 95% CI: [0.23, 0.79]; Tables S9-10). For instance, in group-months when mean early lactational synchrony was in the 75th percentile (a mean of 16.5% of females had infants in the first 90 days of life in that month), cycling females were predicted to initiate 8.51% more agonistic interactions compared to when mean early lactational synchrony was in the 25th percentile (a mean of 5.4% of females had infants in the first 90 days of life in that month). Similarly, pregnant females were predicted to initiate 17.8% more agonistic interactions, and females in postpartum amenorrhea were predicted to initiate 5.81% more agonistic interactions, when mean early lactational synchrony was in the 75th versus the 25th percentile.

However, higher early lactational synchrony only predicted an increased frequency of *received* agonistic interactions for females who were in postpartum amenorrhea (GLMM for females in postpartum amenorrhea: $\beta = 1.10$, 95% CI: [0.83, 1.37]; Tables S11-12; for cycling females: $\beta = 0.02$, 95% CI: [-0.16, 0.20]; Tables S13-14; for pregnant females: $\beta = 0.26$, 95% CI: [-0.18, 0.71]; Tables S15-16, Fig. 1b). Specifically, females in postpartum amenorrhea were predicted to receive 13.0% more agonistic interactions in months when mean early lactational synchrony was in the 75th compared to the 25th percentile. Cycling and pregnant females did not receive significantly more or fewer agonistic interactions during months of high versus low mean early lactational synchrony.

We also tested for a relationship between early lactational synchrony and the number of agonistic interactions exchanged within dyads of females in the same reproductive state. In group-months with higher mean early lactational synchrony, pairs of cycling females did not exchange significantly more or fewer agonistic interactions (GLMM; $\beta = 0.18$, 95% CI: [-0.28, 0.64]; Table 1 and S17). However, dyads of pregnant females and females in postpartum amenorrhea exchanged more agonistic interactions in group-months with higher mean early lactational synchrony (GLMM for pregnant females: $\beta = 1.02$, 95% CI: [0.55, 1.48]; for females in postpartum amenorrhea: $\beta = 0.66$, 95% CI: [0.39, 0.92]; Table 1 and S18-19). For instance, when group-months were in the 75th versus the 25th percentile of mean early lactational synchrony, pairs of pregnant females were predicted to exchange 11.92% more agonistic interactions and pairs of females in postpartum amenorrhea were predicted to exchange 7.56% more agonistic interactions.

Infant survival. Using data collected from 1976-2021, we next employed a time-varying Cox proportional hazards model to test whether infant survival was compromised when early lactational synchrony was high. Controlling for other covariates thought to explain infant mortality (maternal death, maternal rank, maternal age, group size, and rainfall), early lactational synchrony strongly predicted infants' daily mortality risk during the first year of life ($\beta = 4.45$, 95% CI: [3.46, 5.44]; Table 2 and S20, Fig. 2b). For instance, on days when a group was in the 75th percentile of early lactational synchrony (17.6% of females in a group were in early lactation that day), infants were predicted to have a 75.2% increased risk of mortality relative to days when the group was in the 25th percentile (5.0% of females in a group were in early lactation that day). We also tested the same covariates in a Cox proportional hazards model predicting daily infant survival up to 90 days after birth (coincident with the period in which their mothers would be in early lactation). This model produced qualitatively similar results (Tables S21-22).

Infanticide. To understand which sources of infant mortality were most prevalent during periods of high early lactational synchrony, we reviewed the most probable causes of death for infants included in the survival analysis (i.e., from 1976-2021). Deaths from infanticide were proportionally more common when early lactational synchrony was high (16.4% of infant deaths on days in the top quartile of early lactational synchrony versus 7.27% of all infant deaths; Figs. 2c and S2). Further, of the 37 potentially infanticidal deaths that occurred during this period, 22 occurred on days with very high early lactational synchrony (>80th percentile for all group-days; Table S23). When we limit these potential infanticides to those that were directly observed or strongly suspected with corroborating evidence (n = 24; see Methods) and were performed by females in the same group as the mother and infant (n = 14), 12 (85.7%) occurred on days when groups were in the top quartile of early lactational synchrony overall. This was significantly greater than the proportion of all infant deaths that occurred in the top quartile of early lactational synchrony (109/300 deaths, 36.3%; Fisher's exact test: odds ratio = 10.4, 95% CI: [2.3, 97.8], $p = 0.0003$). The vast majority of these within-group infanticides by females (11 of 14; 78.6 %) were attributed to female "kidnapping" events, in which a female separated an infant from its mother for an extended period of time and the infant subsequently died from starvation, dehydration, and/or rough handling. The remaining three within-group infanticides by females (21.4%) were thought to have occurred during episodes of severe, multiparty aggression that preceded a permanent social group fission. Although infanticide by females accounts for a substantial fraction of infant mortality during high synchrony periods, all 11 of the fatal female kidnappings were performed by peripubertal, nulliparous females (Table S23). Hence, these fatal kidnappings are not examples of direct competition among adult females for immediate resources. In contrast, the three infanticides thought to be the result of severe, multiparty aggression probably involved fully adult females, although the identities of the perpetrators are unknown (Table S23).

Discussion

These results provide considerable evidence that group composition, specifically the proportion of adult females in early lactation, influences female-female competition and infant survival in baboons. Higher levels of early lactational synchrony were linked to more frequent agonistic interactions between adult females, suggesting that early lactational synchrony increases intragroup, female-female competition over food and/or access to protective male

associates. High early lactational synchrony predicted an increased frequency of agonistic interactions initiated by adult females in all reproductive states. However, high early lactational synchrony only predicted a higher frequency of received agonistic interactions for females in postpartum amenorrhea, suggesting that lactating females disproportionately bear the costs of high synchrony. At the dyadic level, pairs of pregnant females and pairs of females in postpartum amenorrhea also exchanged more agonistic interactions when early lactational synchrony was higher, but pairs of cycling females did not.

Early lactational synchrony also strongly predicted infant mortality. Notably, infanticides, especially those performed by peripubertal females, were overrepresented in periods of high early lactational synchrony relative to infant deaths overall. Taken together, these results suggest that infant baboons are more likely to die in highly synchronous periods. This increased risk may be caused by two phenomena. First, the increased risk of kidnapping by young, nonreproductive females during periods of high early lactational synchrony contributed substantially to the mortality we measured, either immediately or on future days due to the costs of prolonged maternal separation. Second, the increased rates of aggression directed towards females in postpartum amenorrhea when early lactational synchrony was high may decrease the viability of dependent offspring. These two explanations are not mutually exclusive: increased rates of aggression overall may also grant peripubertal females more opportunities to succeed in kidnapping attempts. Therefore, the negative fitness consequences of group-level synchrony in lactation may select against strong breeding seasonality, even in an environment characterized by highly seasonal resource fluctuations.

Female agonistic behavior. Our finding that agonistic interactions between adult females increased with early lactational synchrony corroborates previous findings in female chacma baboons in Tsaobis, Namibia, and female yellow baboons in Mikumi, Tanzania (44, 57). Researchers in Tsaobis have argued that a positive correlation between aggression and group-level reproductive synchrony reflects competition for mates and access to paternal care (44, 45). On the other hand, researchers in Mikumi cited the reduction of the future competition faced by offspring as the most likely explanation for reproductive synchrony-related multiparty attacks (57, 58). In our study, increased aggression by pregnant and cycling females toward females in postpartum amenorrhea supports some of the predictions of the "future competition reduction" hypothesis. However, we believe that competition over current food resources or available male protectors are more parsimonious explanations for the observed patterns in Amboseli. Because high early lactational synchrony should increase group-level energetic demand and therefore average daily group travel distances (34, 64), females of all reproductive states will incur the energetic costs of high early lactational synchrony. Additionally, because protective male-female associations often form around the time of conception, peak in early lactation, and can persist until offspring independence (65), the patterns of aggression we observed also conform to expectations of competition for male social partners. As Baniel et al. (44) highlight, pregnant, lactating, and ovulating female baboons all potentially benefit from close association with males. This observation, combined with the peak in male-female association during early lactation, may explain why females in postpartum amenorrhea are the most frequent recipients of synchrony-related agonistic behavior from other adult females. Such an explanation avoids the need to invoke more complex cognitive mechanisms involving the projection of future competitive landscapes.

Similarly, our dyadic analysis revealed that increased aggression in periods of high early lactational synchrony is not strictly linked to competition over resources sought exclusively by new mothers. Rather, dyads of both pregnant females and females in postpartum amenorrhea exchanged more agonistic interactions in these periods. This observation lends support to the hypothesis of competition over food, as both pregnant females and females in postpartum amenorrhea must invest energy in growing offspring. However, it does not rule out the hypothesis of competition over access to male associates: unlike females in other reproductive states, fertile, cycling females may attract males without engaging in much active competition. Nevertheless, we note that the potential hypotheses (i.e., competition over current vs. future resources; competition over food vs. male associates) are not mutually exclusive and may be dependent on other characteristics (e.g., rank, social bonds).

Infant survival and female infanticide. An unexpected and striking observation was the rise in infanticidal behavior by peripubertal females during periods of high early lactational synchrony. We suggest that synchrony-related infanticidal behavior by peripubertal females is not directly related to competition. If infanticide serves to reduce current competition, we would expect parous females rather than peripubertal (i.e., non-reproductive, nulliparous) females to commit infanticide when early lactational synchrony is high, especially because nulliparous females are unlikely to conceive in close temporal proximity to the births of the infants they target. Contrary to this expectation, parous females rarely engage in kidnapping, even when they have no current infants of their own. Furthermore, if infanticide serves to reduce future competition, neither peripubertal nor parous females should restrict their infanticidal attacks to periods of high early lactational synchrony, because the intensity of competition in the future is unlikely to be predictable at any given time and because female baboons compete with more individuals than their immediate birth cohort.

One explanation for the increased rates of kidnapping by peripubertal females during periods of high early lactational synchrony is that the unusual abundance of young infants may spur higher-than-usual interest in infants on the part of peripubertal females. If so, the probability that interactions with infants escalate to kidnapping may increase. A second possibility is that, because infants of lower-ranking mothers are likely more easily kidnapped than infants of higher-ranking mothers, high early lactational synchrony may simply increase the probability that any given peripubertal female has access to infants of lower-ranking mothers. However, a *post hoc* analysis casts some doubt on this second possibility: during periods of high early lactational synchrony, an early lactating mother was *less* likely to have a higher-ranking peripubertal female as her nearest neighbor than during other periods (see Supplementary Methods; GLMM: $\beta = -1.29$, 95% CI: [-2.37, -0.21], Tables S24-S25). This pattern suggests that mothers avoid the most probable kidnappers in their group when early lactational synchrony is high, especially since early lactational synchrony did not predict whether early lactating mothers were likely to have *lower*-ranking peripubertal females as their nearest neighbors (GLMM: $\beta = -0.12$, 95% CI: [-0.77, 0.52], Tables S26-S27).

While the drive to kidnap infants in peripubertal females is not likely directly related to competition among adult females, adult female competition could interact with the interest of peripubertal females in infants if the increased rates of agonistic interactions between adult females make kidnapping attempts more likely to be successful. Furthermore, the relationship between infant kidnapping and early lactational synchrony may be compounded if some mother-

infant pairs are competitively excluded from receiving male protection because of the unusually high number of new mothers per male in the group.

Conclusions. The patterns of female aggression, infant survival, and female infanticide reported here provide new evidence that group-level synchrony in female reproductive state can negatively impact breeding success at the individual level, even in a non-seasonal breeder. First, an increase in the proportion of females with young infants was associated with higher relative frequencies of adult female-female agonistic behavior, indicating intensified competition. Additionally, this synchrony predicted higher infant mortality, likely due to a combination of infanticidal behavior by peripubertal females and the downstream effects of female-female competition and aggression. These results set the stage for future studies testing the proximate factors shaping female aggression, the underlying mechanisms motivating female interactions with non-offspring infants, and the roles of inter- and intrasexual social interactions in shaping the timing of reproduction.

Methods

Study site and subjects. This population of wild baboons lives in the Amboseli basin, a semi-arid short-grass savannah ecosystem at the northern base of Mt. Kilimanjaro in southern Kenya. The basin experiences an annual dry season from June to October when virtually no rain falls, followed by a highly variable wet season from November to May when the amount of rainfall varies greatly from year to year (67). The baboon population has been continuously monitored by the Amboseli Baboon Research Project (ABRP) since 1971 (61). Over the course of the study's history, the number of habituated social groups monitored at any one time has ranged from one to six, and the groups have undergone multiple fissions and fusions since the late 1980s. See Supplementary Methods for additional details on daily demographic, behavioral, and ecological monitoring by ABRP.

Female reproductive states. In our analyses, we considered both individual female reproductive states and a group-level metric of reproductive state similarity as important predictors of individual behavior. We identified four female reproductive states (see Supplementary Methods for details, also (66)). (i) Ovarian cycling lasted from the first day a female's sex skin was turgescent after menarche or her last live birth to either the next onset of pregnancy or death. (ii) Pregnancy lasted from the first day a female's sex skin was deturgescent in her last sexual cycle preceding a known pregnancy to the day before she gave birth, experienced a spontaneous abortion, or died. (iii) Postpartum amenorrhea lasted from the day a female gave birth or experienced a spontaneous abortion to the next day her sex skin was turgescent or she died. (iv) Early lactation refers to a subset of the period of postpartum amenorrhea, specifically the first 90 days of postpartum amenorrhea with a live infant. Any female who was in early lactation was, by definition, in postpartum amenorrhea, but postpartum amenorrhea typically extends long past the first 90 days (mean ± SD length of postpartum amenorrhea: 322 ± 87 days, (66)). Throughout, we use the term early lactational synchrony to refer to the proportion of adult females in a group that were in early lactation, i.e., had an infant <90 days old. See the Supplementary Methods for further information on how early lactational synchrony was calculated.

Statistical approach. We took an information theoretic approach to all analyses, which were conducted in R v4.0.3 (68). We began by constructing "full models" that included all likely covariates. We then used the *dredge* function in the *MuMIn* R package (69) to acquire Akaike's information criterion (AIC_c) values for all models with all possible combinations of fixed effects included in the full model (70, 71). All candidate models within 2 AIC_c values of the candidate model with the lowest AIC_c value were selected as the best-fitting models. We used *MuMIn*'s *model.avg* function to obtain a weighted average of the best-fitting models (those within 2 AIC_c of the best model) and estimate effect sizes for individual fixed effects. If a fixed effect was left out of a particular candidate model, then a weighted effect size of zero was included in the calculation of the overall weight-averaged effect size for that fixed effect. We considered fixed effects significant when the 95% confidence interval of their weight-averaged effect size did not overlap zero. Cox proportional hazards models were constructed using the *coxph* function from the package *survival* (72) and GLMMs were constructed using the package *glmmTMB* (73).

Female agonistic behavior. To test the prediction that early lactational synchrony is associated with increased adult female-female competition, we aggregated data collected from October 1999 to December 2021 on all intragroup dyadic agonistic interactions occurring between adult females in which either one female displayed aggressive behaviors and the other displayed submissive behaviors or in which one female spatially displaced the other. We then tallied, for each female in each month of her adult life (each "female-month"), the number of agonistic interactions that she initiated (i.e., interactions in which she displayed aggressive behavior or she spatially displaced the other female). Next we tallied, for each female in each month of her adult life, the number of agonistic interactions she received (i.e., interactions in which she displayed submissive behavior in response to aggression or she was spatially displaced). We restricted our behavioral analysis to 1999-2021 because this was the period of time during which we were best able to control for observer effort. Specifically, we calculated these tallies only for female-months in which our records of observation times were of the highest quality, and during which observers were with the female's group for at least 30 hours. We also assigned each female-month to one of three reproductive states (cycling, pregnant, or postpartum amenorrhea), as described above. When a female transitioned from one reproductive state to another or changed social group membership within a calendar month, we split that female-month at the date of transition, and counted agonistic interactions before the transition as belonging to the first state or social group, and those after the transition to the second state or social group. Thus, each count is informative of a female in one social group and in one reproductive state. For counts of agonistic interactions both initiated and received, our sample sizes reflected 21,321 unique female-reproductive state-group-months for 278 individual females in 14 social groups.

We then used these counts of agonistic interactions initiated and received as response variables in two negative binomial GLMMs with log link functions. We chose to model these counts as negative binomial distributions because they were overdispersed. In both models, we included the following fixed effects: (i) the average proportion of adult females in the group who were in early lactation for that month, (ii) the female's proportional dominance rank, (iii) the female's age, (iv) the female's reproductive state (cycling, pregnant, or postpartum amenorrhea), (v) season, and (vi) a measure of observer effort to control for variation in observation intensity across the study period (see Supplementary Methods). In both models, we controlled for variation in the duration of female reproductive state-group-months (e.g., due to transitions in

reproductive state) by including an offset term which was calculated as the the log-transformed number of days in the month in which the female was in her present group and reproductive state. We included individual ID and group ID as random effects to control for repeated sampling of females and groups. In all models presented in the main text, we did not include a fixed effect of group size because group size is strongly negatively correlated with our measure of observer effort. However, to assess the potential role of group size, we built an alternative model structure which instead incorporated observer effort into the offset term and included group size as a fixed effect (see Supplementary Methods and Results), which produced similar results (Tables S28-49).

To determine if females in different reproductive states experienced different consequences of early lactational synchrony, we partitioned the agonistic interaction dataset by the reproductive state of the female in question, resulting in 6,861 female-months for 273 cycling females in 14 social groups, 6,095 female-months for 254 pregnant females in 14 social groups, and 8,365 female-months for 245 postpartum amenorrhea females in 14 social groups. For each of these three datasets, we again modeled the monthly counts of agonistic interactions either initiated or received using negative binomial GLMMs with log link functions (see also Supplementary Methods), but removing the female reproductive state term. We included all other fixed and random effects that were included in the overall agonism models, as well as the log-transformed offset term for the number of days in the month in which the female was a member of her group and in her present reproductive state.

To investigate the relationship between early lactational synchrony and agonistic interactions at the dyadic level, we identified all possible pairs of females that were in the same reproductive state in each social group and each month and tallied the total number of agonisms they exchanged in that month (cycling: N=23,547 dyad-months across 3,703 dyads in 14 groups; pregnant: N=18,677 dyad-months across 2,746 dyads in 14 groups; postpartum amenorrhea: N=35,975 dyad-months across 2,891 dyads in 14 groups). We constructed Poisson GLMMs with a log link function predicting the total number of agonistic interactions exchanged in each dyad-group-month for each of these three reproductive states (see Supplementary Methods). We chose to model these counts using a Poisson distribution because, unlike in the previous agonism models, the count data for agonistic interactions exchanged within dyads were not overdispersed. As fixed effects in all three models we included: (i) the average proportion of adult females in the group who were in early lactation for that month, (ii) the absolute value of the difference between the two females' proportional ranks, (iii) season, and (iv) observer effort. We also included the logged number of days in the month that both females were present in the group and in the same state as an offset term, as well as dyad ID and group ID as random effects to control for repeated sampling of dyads and groups.

Because only one observer typically collects observational data on any given day, we are not able to record all true occurrences of agonistic interactions. Observed interaction counts per capita are therefore typically low, especially in large groups (mean ± SD of agonistic interactions initiated = 1.82 ± 3.06; mean ± SD of agonistic interactions received = 1.82 ± 2.64). Therefore, while interpreting the results of these models, even small effect sizes for our count response variables can indicate meaningful differences in the relative frequencies of agonistic interactions.

Infant survival. To test our prediction that high early lactational synchrony is associated with an increased risk of infant death, we used a Cox proportional hazards model with time varying covariates to predict the daily risk of infant death in the first year of life (see

Supplementary Methods). Our covariates were: (i) the proportion of adult females in early lactation on each day of the infant's life; (ii) group size; (iii) whether or not the infant's mother was dead; (iv) maternal proportional rank; maternal age as a (v) linear and (vi) quadratic term; and the (vii) cumulative total rainfall that fell in the last 90 days. If an infant lived at least a day after its mother's death (n = 19 infants), then the covariate data for maternal rank and age were entered as the mother's rank and age on her death date. These post-maternal death data points were rare, constituting 0.05% of the total dataset. In total, 1,323 infants born between November 1976 and December 2021 were included in this analysis, of whom 300 died in the first year of life, and 87 were right censored because observations on them ceased before they reached their first birthday. We restricted our survival analyses to this period because rainfall data were not recorded before November 1976. To determine if the effect of early lactational synchrony on infant survival differed when infants themselves had early lactating mothers, we ran another Cox proportional hazards model predicting the daily risk of infant death from the day of birth until the infant was 90 days old using the same covariates. This model included 1,304 infants born between November 1976 and December 2021 (140 deaths in the first 90 days of life; 30 infants were right censored).

Infanticide risk. After observing a negative relationship between early lactational synchrony on infant survival, we sought to investigate the causes of death for infants who died during periods of high early lactational synchrony (see Supplementary Methods for information on how we assigned causes of death and confidence in the assigned causes). Of the 300 infant deaths included in our survival analysis, causes of death with our highest confidence level could be assigned to 75 individuals.

Following this assignment process, we visualized the relative proportion of each cause of death for (i) all infants, (ii) those infants who died on days in the lowest quartile of early lactational synchrony across all infant death days (< 0.076 of females in the group in early lactation, n = 72 deaths), and (iii) those infants who died on days in the highest quartile of early lactational synchrony across all infant death days (> 0.222 of females in the group in early lactation, n = 75 deaths, Fig. S1). In this assessment, any infant whose cause of death was not assigned with our highest level of confidence was considered to have died of an unknown cause. Infanticide deaths appeared to be overrepresented during the periods of highest early lactational synchrony, relative to all deaths and relative to deaths that occurred in the lowest quartile of early lactational synchrony. This observation led us to review field notes related to each infanticide death to determine the most likely actors (male or female) and contexts (within-group or between-group) of infanticide when early lactational synchrony was high (Table S21). In assigning causes of death, we use the definition of infanticide proposed by Digby (74) and more recently invoked by Lukas and Huchard (7): "an act that makes a direct or significant contribution to the immediate or imminent death of conspecific young." This definition includes acts of physical aggression toward infants and acts such as kidnappings that cause infants to die via "enforced neglect" (7). It thus focuses on the ultimate consequences of interactions with conspecific young, regardless of proximate motivation.

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Tables & Figures

Table 1. GLMM results for the models predicting monthly agonistic interactions observed within dyads of cycling females (n = 23,547 dyad-months), pregnant females (n = 18,677 dyad-months), and females in postpartum amenorrhea (n = 35,975 dyad-months). Dyad ID and group ID were included as random effects in all three models. The results for cycling dyads and pregnant dyads reflect model averaging of candidate models that were within 2 AIC_c units of the top candidate model, but no other candidate models were within 2 AIC_c units of the top model for postpartum amenorrhea dyads (see Tables S17-19 for the top 20 candidate models for all three reproductive states). Significant fixed effects are indicated in bold. Model predictions are presented to aid interpretation of estimates and were calculated for the extreme values[1] of each significant fixed effect, while holding values for other fixed effects constant at their observed median value.

Dyad type	Fixed effect	Estimate	Std. Error	95 % CI	Model predictions
Cycling – cycling	(intercept)	-5.59	0.16	[-5.91, -5.27]	–
	Season (dry vs. wet)	**-0.10**	**0.03**	**[-0.17, -0.03]**	Dyads of cycling females exchanged 0.22 observed agonistic interactions per month in the dry season vs. 0.20 observed agonistic interactions per month in the wet season
	Rank difference	**0.55**	**0.09**	**[0.37, 0.72]**	Dyads of cycling females exchanged 0.18 observed agonistic interactions per month when they had the least rank difference vs. 0.31 observed agonistic interactions per month when they had the greatest rank difference
	Early lactational synchrony	0.18	0.24	[-0.28, 0.64]	–
	Observer effort	**0.54**	**0.04**	**[0.47, 0.61]**	Dyads of cycling females exchanged 0.14 observed agonistic interactions per month when observer effort was least intense vs. 4.06 observed agonistic interactions when observer effort was most intense
Pregnant – pregnant	(intercept)	-5.30	0.17	[-5.62, -4.98]	–
	Season (dry vs. wet)	-0.02	0.04	[-0.10, 0.05]	–
	Rank difference	**0.22**	**0.10**	**[0.04, 0.41]**	Dyads of pregnant females exchanged 0.20 observed agonsistic interactions per month when they had the least rank difference vs.

					0.25 observed agonistic interactions per month when they had the greatest rank difference
	Early lactational synchrony	**1.02**	**0.24**	**[0.55, 1.48]**	Dyads of pregnant females exchanged 0.20 observed agonistic interactions per month when early lactational synchrony was the lowest vs. 0.32 observed agonistic interactions per month when early lactational synchrony was the highest
	Observer effort	**0.29**	**0.04**	**[0.21, 0.36]**	Dyads of pregnant females exchanged 0.18 observed agonistic interactions per month when observer effort was least intense vs. 0.94 observed agonistic interactions when observer effort was most intense
Postpartum amenorrhea – postpartum amenorrhea	(intercept)	-5.41	0.13	[-5.66, -5.16]	–
	Season (dry vs. wet)	**-0.19**	**0.02**	**[-0.23, -0.14]**	Dyads of PPA females exchanged 0.23 observed agonistic interactions per month in the dry season vs. 0.19 observed agonistic interactions per month in the wet season
	Rank difference	**0.55**	**0.07**	**[0.41, 0.70]**	Dyads of PPA females exchanged 0.19 observed agonistic interactions per month when they had the least rank difference vs. 0.33 observed agonistic interactions per month when they had the greatest rank difference
	Early lactational synchrony	**0.66**	**0.13**	**[0.39, 0.92]**	Dyads of PPA females exchanged 0.21 observed agonistic interactions per month when early lactational synchrony was the lowest vs. 0.29 observed agonistic interactions per month when early lactational synchrony was the highest
	Observer effort	**0.40**	**0.03**	**[0.35, 0.45]**	Dyads of PPA females exchanged 0.18 observed agonistic interactions per month when observer effort was least intense vs. 1.77 observed agonistic interactions when observer effort was most intense

[1]The minimum and maximum values for each significant fixed effect that we observed in our dataset were: i) season = [dry, wet] (binary), ii) rank difference = [0.03, 1.00], iii) mean early lactational synchrony = [0, 0.47], iv) observer effort = [0.03, 6.27].

Table 2. Model-averaged estimates for the best-fitting models ($\Delta AIC_c < 2$) predicting the daily risk of all-cause infant mortality up to one year after birth (Cox proportional hazards model, total infants = 1,323; died = 300, censored = 87; top 20 candidate models shown in Table S20). Significant covariates are indicated in bold. Model predictions are presented to aid interpretation of estimates and were calculated for the extreme observed values[1] for each significant predictor variable for a 10-day-old infant, while holding values for other fixed effects constant at their observed median value.

Fixed effects	Estimate (hazard ratio)[2]	Std. Error	95 % CI	Model predictions
Maternal death	**5.47 (236.51)**	**0.16**	**[5.14, 5.79]**	Infants had a 0.008% chance of dying on a day when their mother was alive vs. a 1.963% chance on a day when she was dead
Early lactational synchrony	**4.45 (85.63)**	**0.51**	**[3.46, 5.44]**	Infants had a 0.005% chance of dying on a day when early lactational synchrony was lowest vs. a 0.122% chance on a day when it was highest
Maternal age	**-0.42 (0.65)**	**0.07**	**[-0.57, -0.28]**	Infants had a 0.008% chance of dying on a day when their mother was the median age vs. a 0.053% chance on a day when she was the oldest age
Maternal age^2	**0.016 (1.02)**	**0.003**	**[0.011, 0.021]**	Infants had a 0.008% chance of dying on a day when their mother was the median age vs. a 0.024% chance on a day when she was the youngest age
Maternal rank	**-0.37 (0.69)**	**0.18**	**[-0.72, -0.02]**	Infants had a 0.010% chance of dying on a day when their mother was the lowest-ranking female vs. a 0.007% chance of dying on a day when she was the highest-ranking female
Group size	-0.004 (1.00)	0.003	[-0.010, 0.003]	–
Cumulative rainfall	-0.00009 (1.00)	0.00035	[-0.00078, 0.00061]	–

[1]The minimum and maximum values for each significant predictor variable that we observed in our dataset were: i) maternal death = [mother alive, mother dead] (binary), ii) early lactational synchrony = [0.00, 0.71], iii) maternal age = [4.75, 24.50], iv) maternal rank= [0.00, 1.00].

[2]A positive coefficient or a hazard ratio >1 means that higher values of the predictor (or the presence of the predictor in the case of maternal death) are associated with higher mortality hazard (lower infant survival), and negative coefficients or a hazard ratio <1 mean that higher values of the predictor are associate with lower mortality hazard (higher infant survival).

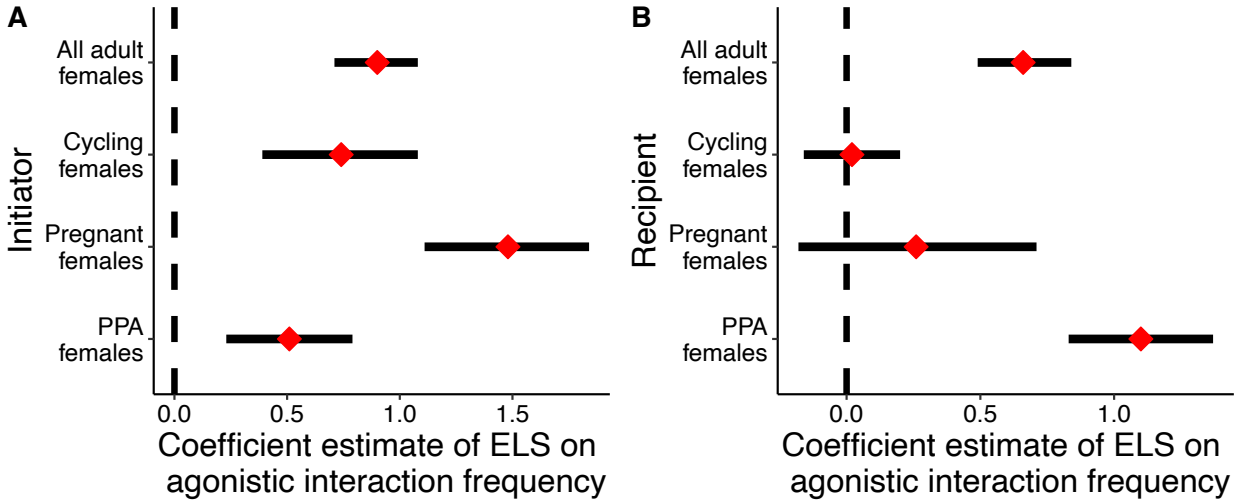

Figure 1. (A) Females in all reproductive states initiated agonistic interactions with other adult females at higher rates when early lactational synchrony (ELS) was high, but (B) only females in postpartum amenorrhea received agonistic interactions from other adult females at higher rates when early lactational synchrony was high. Red diamonds depict the β coefficient estimates for the fixed effect of mean early lactational synchrony from negative binomial generalized linear mixed models predicting the relative frequencies of agonistic interactions (A) initiated by all adult females, cycling females, pregnant females, and females in postpartum amenorrhea (PPA females) and (B) received by all adult females, cycling females, pregnant females, and PPA females. Horizontal black bars indicate the 95% confidence intervals of these estimates. We interpret effects as significant if their 95% confidence intervals do not overlap zero (indicated by the vertical dotted line). Note that while 'early lactational synchrony' on the x-axis labels refers to the proportion of adult females in a group who had a live infant <90 days old, the term 'PPA females' on the y-axes refers to all females in postpartum amenorrhea, not only those with live infants <90 days old (see Methods).

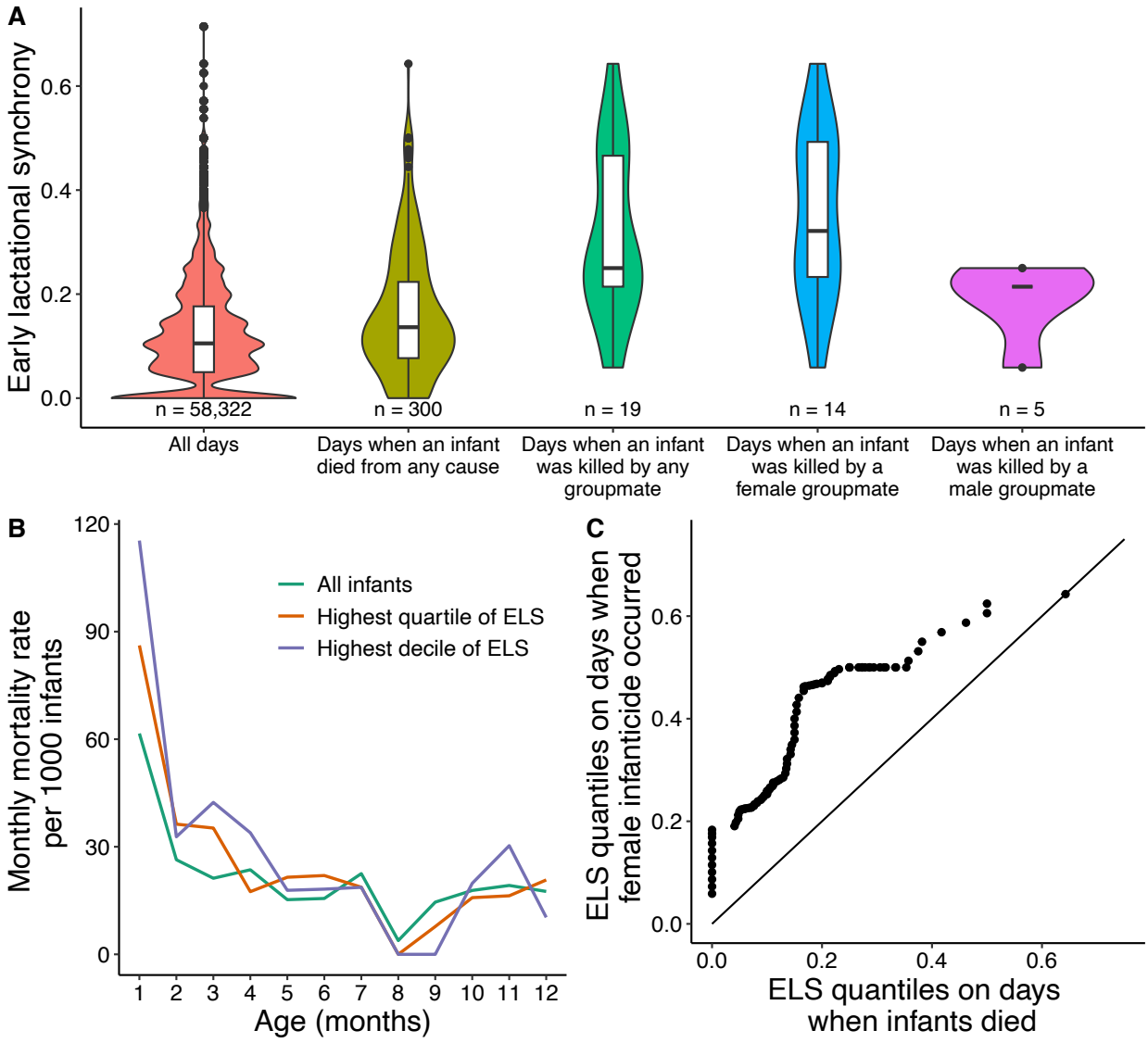

Figure 2. The relationship between early lactational synchrony (ELS), infant mortality, and infanticide. A) The distribution of early lactational synchrony across the study period and in subsets of days when infants died or were killed by infanticide. The y-axis shows the daily proportion of adult females in early lactation as a function of different partitions of our data on the x-axis: all group-days between 1976 and 2021, group-days on which infants less than 1 year old died, group-days on which infants less than 1 year old were killed by a groupmate, group-days on which infants less than 1 year old were killed by a female groupmate, and group-days on which infants less than 1 year old were killed by a male groupmate. Violin plots depict probability densities of the data on each category of group-day, while the overlaid boxplots depict the median values and interquartile ranges. Infanticides were only included in counts for this figure if they were directly observed or strongly suspected with corroborating evidence (see Methods). B) Lactational synchrony predicts infant mortality risk. Monthly mortality rates per 1000 infants are depicted with values calculated across all infants (green line), for infants in groups-months in which mean early lactational synchrony was in the highest quartile relative to

other infants in the same month of life (orange line), and for infants in groups-months in which mean early lactational synchrony was in the highest decile relative to other infants in the same month of life (purple line). Early lactational synchrony was modeled as a continuous, daily, time-varying variable in our survival analysis; monthly mean values and quartiles are used for visualization purposes. C) The distribution of early lactational synchrony is higher on days when infants are killed by females than on days when infants die by any cause. This quantile-quantile plot compares the distribution of early lactational synchrony on female infanticide days with the distribution of early lactational synchrony across all infant death days. The solid, black line depicts the expected relationship if female infanticide was equally likely on all infant death days. Almost all points fall above the line, indicating that days on which infants are killed by females tend to have higher early lactational synchrony relative to days on which infants die from any cause.