High early lactational synchrony within baboon groups predicts increased female-female competition and infant mortality

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JCW, ACM, and SCA designed the research; SCA, EAA, and JT administered the long-term research project; SCA, EAA, JT, JCW, and ACM acquired funding; JCW, ILS, JKW, and NHL performed research; JCW analyzed data; JCW, ACM, SCA, EAA, JT, ILS, JKW, and NHL wrote the paper.

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The authors declare no competing interest.

Abstract

In species where multiple breeding females co-reside in a social group, female-female competition may be particularly acute when many females have dependent young at the same time, with potential negative consequences for offspring survival. Here, we used more than four decades of data on wild baboons (*Papio* sp.) in Amboseli, Kenya, to examine the effects of 'early lactational synchrony' (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 energetically demanding for mothers and high-risk for infants, we expected both female-female aggression and protection by males to intensify during this period. In support, when early lactational synchrony was high, rates of female-female agonism increased. High-ranking females increased their time associating with adult males, while the time that low-ranking females associated with adult males decreased. Furthermore, high early lactational synchrony strongly predicted infant mortality, even though periods of high synchrony tended to be brief in duration in this nonseasonally breeding population. This association may result from both aggression among adult females and infanticidal behavior by peripubertal females. These findings provide novel evidence that synchronous reproduction alters competitive regimes and compromises reproductive outcomes even in nonseasonal breeders.

Introduction

Intraspecific competition is an important selective force acting on social behavior, morphology, and life history[1-3]. In many vertebrates, females compete for food, mates, social partners, and other resources, with tactics ranging from mating interference to infanticide[4-10]. Female-female competition can have important fitness effects, as indicated by the association between high dominance rank or increased aggression and higher female reproductive success in many species[11-16]. For group-living species, group demography is expected to shape the dynamics of female-female competition. Specifically, because female reproduction is energetically costly and food resources are often limited, group size, age structure, sex ratio, and female reproductive state should affect the level of female competition and its fitness consequences[17-28]. Among social mammals, female reproductive state is a particularly salient source of variation in competitive landscapes because a female's resource and social requirements depend on whether she is cycling, pregnant, lactating, or reproductively quiescent[29]. Accordingly, shared requirements can promote association by females in similar reproductive states[30], increase competition for reproductive state-specific resources[5], or both.

The importance of 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[3,5]. For example, female topi antelopes (*Damaliscus lunatus*), red deer (*Cervus elaphus*), feral horses (*Equus caballus*), and golden snub-nosed monkeys (*Rhinopithecus roxellana*) display increased rates of aggression and/or disruption of other females' copulations during their short breeding seasons[31-34]. 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, competition, and reproductive timing, which can vary even between closely related, ecologically similar species[35,36].

In this study, we investigated how female-female competition during lactation affects female behavior and infant survival in wild baboons (*Papio* sp.). We hypothesized female-female

competition would intensify in baboon social groups with high 'early lactational synchrony' (a high proportion of females with infants <90 days old) compared to groups with low early lactational synchrony, and that intensified competition would lead to negative fitness-related outcomes for mothers and their dependent offspring. We focused on early lactational synchrony as a predictor of behavior and infant survival because females in early lactation experience a dual challenge: first, increased energetic demands, potentially exacerbated by a clinging infant that can hinder foraging efficiency[37]; and second, the need to protect their vulnerable infants from harassment and infanticide by conspecifics[38-41]. As a result, females with neonates compete for both food[42-44] and adult male associates, who can help buffer mothers and their infants from conspecific harassment and infanticide[6,45-50]. Our study subjects were members of multiple multi-male, multi-female social groups in a wild baboon population (*P. cynocephalus* with significant *P. anubis* admixture[51,52]) in the Amboseli basin of southern Kenya[53]. Females in this population 'inherit' their dominance rank matrilineally and give birth year-round[54-56]. To test our hypothesis, we analyzed group-level rates of female-female agonistic interactions and individual-level infant mortality risk as functions of early lactational synchrony. 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 across all group-days of observation from November 1976 to December 2021. We defined early lactation as the first 90 days of postpartum amenorrhea when a mother had a living infant. In this period, infants are dependent on their mothers for almost all nutrition and transport[37-39,57]. The proportion of females in early lactation 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). The mean proportion of females in early lactation on a given group-day was 0.121 ± 0.102 s.d. (median: 0.105; Fig. S1a) and, on average, groups had 1.96 ± 1.74 s.d. total females in early lactation on any given day (median: 2 females; the number of adult females per group ranged from 3 to 33 adult females; Fig. S1b).

While daily early lactational synchrony was low on average, periods of high early lactational synchrony were not uncommon. Across the 138 group-years in our 1976-2021 dataset where the group observations were uninterrupted (e.g., the groups were not undergoing a permanent fission and/or were consistently observed across the full year), the mean annual maximum value of early lactational synchrony was 0.320 ± 0.087 s.d.. In other words, an 'average' baboon group in an 'average' year in Amboseli experienced at least some days when approximately one-third of adult females had a <90-day-old infant. This estimate, which corresponds to the 95th percentile value over all group-days, suggests that periods of high early lactational synchrony are a recurring feature of the system (even though they are typically brief in duration: Fig. S2). Therefore, we used 0.320 (the 95th percentile value) as a benchmark of 'high' early lactational synchrony that was met with some regularity (i.e., about once a year).

Baboons in early lactation were centers of female-female competition. To test whether early lactation corresponded to a period of intense competition for female baboons, we next examined changes in behaviors potentially related to competition over either food or males across different stages of the female interbirth interval (see Supplementary Results for a full

description of these behavioral changes). Using behavioral data from focal animal samples collected on adult females from 1999-2021, we found that females in early lactation spent less time foraging than females at any other stage of the interbirth interval (mean percentage of observation time spent foraging: 66.4% ± 12.0% s.d., Table S1, Fig. 1a). Females in early lactation also spent more time within 5 m of at least one adult male than females at any other stage of the interbirth interval (mean percentage of observation time spent with an adult male near neighbor: 25.4% ± 11.0% s.d., Table S1, Fig. 1b), with the exception of females with turgescent sexual swellings in the follicular phase and peri-ovulatory period of the ovarian cycle (who are highly attractive to adult males). Females in early lactation also engaged in agonistic interactions with other adult females at a higher rate than females in any other stage of the interbirth interval (mean agonistic interaction rate: $7.3 \times 10^{-3} \pm 0.011$ s.d. interactions per minute, Table S1, Fig. 1c). On average, females in early lactation were involved in an agonistic interaction with an adult female groupmate once every 2.3 observation hours, while the average across all other female reproductive states was once every 3.1 observation hours.

The relatively high rate of female-female agonistic interactions experienced by early lactating females appeared to be most strongly driven by two sets of interactions: (i) early lactating females initiated high rates of agonistic behavior toward other early lactating females, and (ii) early lactating females received high rates of agonistic behavior from pregnant females (Table S2, Fig. 2). Controlling for the number of potential interaction partners in a given reproductive state, early lactating females initiated agonistic behavior toward other early lactating females at a rate that was 1.6x higher than the rate at which they initiated agonistic behavior toward cycling females, their next most frequent targets (rate of initiation toward early lactating females: $2.6 \times 10^{-4} \pm 1.1 \times 10^{-3}$ s.d. interactions per minute per early lactating female present; rate of initiation toward cycling females: $1.5 \times 10^{-4} \pm 7.7 \times 10^{-4}$ s.d. interactions per minute per cycling female present). Early lactating females received agonistic behavior from pregnant females at a rate that was 1.8x as high as post-early lactation postpartum amenorrhea females, the next most frequent recipients (rate that early lactating females received agonistic behavior from pregnant females: $4.6 \times 10^{-4} \pm 9.9 \times 10^{-4}$ s.d. interactions per minute per pregnant female present; rate that post-early lactation postpartum amenorrhea females received agonistic behavior from pregnant females: $2.5 \times 10^{-4} \pm 1.1 \times 10^{-3}$ s.d. interactions per minute per pregnant female present).

Group-level female-female competition intensified when early lactational synchrony was high. To determine how group-level synchrony in early lactation was related to the intensity of within-group female-female competition, we aggregated all focal sample data collected from 1999-2021 on adult females by group and day. We then estimated a per-dyad rate of female-female agonistic interactions for every group on every day on which focal samples were conducted. Controlling for group size and cumulative recent rainfall, we found that per-dyad rates of female-female agonism were slightly higher on days with higher early lactational synchrony versus lower early lactational synchrony (generalized linear mixed model, GLMM; $\beta = 0.61$, 95% CI: [0.16, 1.07]; Tables 1 and S3, Fig. 3a). For example, on a group-day characterized by the population median value of early lactational synchrony (10.5% of females in a group in early lactation), any given adult female dyad was predicted to experience an agonistic interaction 3.5×10^{-4} times per minute. On a group-day at the 95th percentile value of early lactational synchrony (32.0% of females in a group in early lactation), any given adult female

dyad was predicted to experience an agonistic interaction 4.0 x 10^{-4} times per minute, a rate increase of 14.3% over the median day.

If high early lactational synchrony intensifies female-female competition over male social partners, high-ranking females should be most successful at staying close to adult males because of their ability to displace lower status females. In support of this prediction, we found that the proportion of time that both early lactating females and pregnant females spent within 5 m of an adult male was predicted by their dominance rank. Higher-ranking females spent more time in close proximity to males than lower-ranking females, and the magnitude of this rank difference increased with higher group-level early lactational synchrony (GLMM for early lactating females: ordinal dominance rank: β = -0.029, 95% CI: [-0.039, -0.019]; early lactational synchrony: β = 0.41, 95% CI: [0.09, 0.72]; interaction term: β = -0.042, 95% CI: [-0.073, -0.011]; Tables 1 and S4; Fig. 3b; GLMM for pregnant females: ordinal dominance rank: β = -0.017, 95% CI: [-0.024, -0.010]; early lactational synchrony: β = 0.66, 95% CI: [0.43, 0.88]; interaction term: -0.065, 95% CI: [-0.092, -0.039]; Tables 1 and S5; Fig. 3c).

To explore the possibility that high early lactational synchrony also intensifies female-female competition over food, we examined the relationship between early lactational synchrony, female dominance rank, and time spent foraging. For both early lactating and pregnant females, we found that high-ranking females, but not low-ranking females, spent less time foraging as early lactational synchrony increased (GLMM for early lactating females: proportional dominance rank: β = 0.01, 95% CI: [-0.18, 0.20]; early lactational synchrony: β = -0.06, 95% CI: [-0.37, 0.25]; interaction term: β = -0.99, 95% CI: [-1.52, -0.46]; Tables S6-7; Fig. 3c; GLMM for pregnant females: proportional dominance rank: β = -0.02, 95% CI: [-0.12, 0.09]; early lactational synchrony: β = -0.02, 95% CI: [-0.25, 0.22]; interaction term: -1.06, 95% CI: [-1.44, -0.68]; Tables S8-9; Fig. 3d). These foraging patterns may represent an indirect consequence of time spent with males: by spending more time with males, high-ranking females may forage more efficiently and/or with fewer interruptions, thus reducing overall time spent foraging.

High early lactational synchrony predicted increased infant mortality risk. 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 infant daily mortality risk during the first 90 days of life (β = 2.68, 95% CI: [1.21, 4.15]; Tables 2 and S10, Fig. 4a). For instance, on days when a group was at the 95th percentile value of early lactational synchrony (32.0% of females in early lactation), an infant's mortality risk was predicted to be 76.5% higher than on days when the group was at the population median value of early lactational synchrony (10.5% of females in early lactation).

Infanticide by females was a common source of infant mortality when early lactational synchrony was high. To understand the most important sources of infant mortality during periods of high early lactational synchrony, we reviewed the most probable causes of death for infants included in the survival analysis (i.e., those that died from 1976-2021). Deaths from infanticide were proportionally more common when early lactational synchrony was high (22.2% of infant deaths on days above 95th percentile value of early lactational synchrony versus 11.5% of infant deaths on days below the 95th percentile value of early lactational synchrony; Fig. 4b-c).

Considering the identities of infanticidal individuals, of the six infanticides known or strongly suspected to occur on days when groups exceeded the 95th percentile value of early lactational synchrony (>32.0% of females were in early lactation), all (100.0%) were known or very likely to be cases of infanticide by females living in the same group as the mother. When considering all infanticides committed by within-group females (13 total), 46.2% (six infanticides) occurred on days when groups exceeded the 95th percentile value of early lactational synchrony. This proportion was significantly greater than the proportion of all infant deaths that occurred on days when groups exceeded the 95th percentile value of early lactational synchrony (27/140 deaths, 19.3%; Fisher's exact test: odds ratio = 3.5, $p = 0.04$). Together, these patterns suggest that the relative rise in rates of infanticide during periods of high early lactational synchrony is explained by a rise in infanticidal behavior by females rather than males.

Notably, most cases of infanticide by females could not be attributed to direct competition among adult females for immediate resources. Rather, the vast majority of all within-group infanticides by females (11 of 13; 84.6%) were 'kidnapping' events performed by peripubertal, nulliparous females (Table S11). In these events, an immature 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 two within-group infanticides by females (15.4%) were thought to have occurred during episodes of severe, multiparty aggression that preceded a permanent social group fission. Fully adult females were probably perpetrators in these cases, but their identities are unknown (Table S11).

Discussion

These results provide 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 as well as some enhanced benefits of high female social status, suggesting that early lactational synchrony increases female-female competition over access to protective male associates. High 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. Ultimately, the negative fitness consequences of group-level synchrony in early lactation may select against strong breeding seasonality, even in an environment like Amboseli characterized by highly seasonal resource fluctuations.

Synchrony-related infant mortality risk could be caused by several, co-acting phenomena. First, an increased risk of kidnapping by young, nonreproductive females during periods of high early lactational synchrony contributed to increased mortality overall. Second, the increased rates of aggression mothers experience when early lactational synchrony is high (Fig. 2-3, Tables 1 and S2-3) may compromise the condition of dependent offspring. These two explanations are not mutually exclusive: aggressive contests involving mothers may also grant peripubertal females more opportunities to succeed in kidnapping attempts. Furthermore, while the energy required to produce milk and carry infants likely peaks after the 90-day window investigated here[38,39], new motherhood nonetheless imposes high and rapidly increasing energetic demands and foraging challenges[37,58]. That females in early lactation allocated *less* time to foraging than females in any other reproductive state, potentially due to the constraints on physical mobility imposed by near-constant infant contact[37], suggests that early lactation may be a particularly difficult time to meet increased energetic demands by increasing energy intake. Competition over food may thus arise

when multiple females in the group face these challenges at the same time, potentially reducing maternal and offspring condition.

Female agonistic behavior. Our finding that agonistic interactions between adult females increased with early lactational synchrony (Fig. 3a, Tables 1 and S3) corroborates previous findings in female chacma baboons (*Papio ursinus*) in Tsaobis, Namibia, and female yellow baboons in Mikumi, Tanzania[45,59]. 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[35,45]. On the other hand, researchers in Mikumi cited the reduction of future competition faced by offspring as the most likely explanation for reproductive synchrony-related multiparty attacks[59,60]. In our study, frequent aggression by pregnant females toward early lactating females supports some of the predictions of the 'future competition reduction' hypothesis. However, we believe that competition over available male protectors is a more parsimonious explanation for the observed patterns in Amboseli. Because protective male-female associations often form around the time of conception, peak in early lactation, and can persist until offspring independence[61], the patterns of aggression we observed conform to expectations of competition for male social partners. As Baniel et al.[45] highlight, pregnant, lactating, and ovulating female baboons all potentially benefit from close association with males. Ovulating females may attract males more easily than pregnant or lactating females without the need to engage in much active competition. These dynamics may explain why pregnant females and early lactating females appear to compete with particular intensity for adult males (Figs. 2a-b and 3b-c, Tables 1, S2, and S4-5). Such an explanation avoids the need to invoke more complex cognitive mechanisms involving the projection of future competitive landscapes.

Notably, high early lactational synchrony not only predicted more frequent female-female aggression, but also strengthened the extent to which social status was associated with enhanced resource access (Fig. 3b-c). Adult males were monopolized by high-ranking females to a greater extent during periods of higher early lactational synchrony than otherwise. This effect may also have influenced female foraging patterns, as high-ranking females also spent less time foraging when early lactational synchrony was higher (Fig. 3d-e). One potential explanation for this observation is that, as the benefits of male protective services (e.g., less frequent harassment) were disproportionately allocated to high-status females, those females were able to forage more efficiently. Alternatively or in addition, if males buffer females against conflicts with group mates[47], high-ranking females could use their enhanced access to males specifically to reduce conflict, even if doing so imposes some foraging costs. Either way, we note that competition over current versus future resources and competition over food versus male associates are not mutually exclusive explanations for female agonistic behavior.

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. While it is tempting to hypothesize that synchrony-related infanticidal behavior by peripubertal females is a tactic of direct competition with adult females, this hypothesis suffers from some logical flaws. Specifically, 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,

314 even when they have no current infants of their own. Furthermore, if infanticide serves to reduce
315 the number of future competitors for the perpetrator or their offspring, neither peripubertal nor
316 parous females should restrict their infanticidal attacks to periods of high early lactational
317 synchrony, because the current number of young infants is unlikely to be a reliable predictor of
318 future competition.
319 The drive to kidnap infants in peripubertal females is therefore unlikely to be directly
320 related to competition among adult females. However, adult female competition could interact
321 with the interest that peripubertal females commonly show in infants, if the frenetic nature of
322 some aggressive interactions makes kidnapping attempts more likely to be successful.
323 Furthermore, the relationship between infant kidnapping and early lactational synchrony may be
324 compounded if some mother-infant pairs are competitively excluded from receiving male
325 protection because the number of new mothers per male in the group is unusually high.
326 Whether early lactational synchrony itself increases interest in infants among peripubertal
327 females remains an open question. It is possible that an unusual abundance of young infants may
328 spur higher-than-usual interest in infants on the part of peripubertal females. If so, the probability
329 that interactions with infants escalate to kidnapping may increase. An additional possibility is
330 that, because infants of lower-ranking mothers are likely more easily kidnapped than infants of
331 higher-ranking mothers, high early lactational synchrony may simply increase the probability
332 that any given peripubertal female has access to infants of lower-ranking mothers. However, a
333 *post hoc* analysis casts some doubt on this second possibility: during periods of high early
334 lactational synchrony, an early lactating mother was *less* likely to have a higher-ranking
335 peripubertal female as her nearest neighbor than during other periods (see Supplementary
336 Methods; GLMM: $\beta = -1.29$, 95% CI: [-2.37, -0.21], Tables S12-S13). This pattern suggests that
337 mothers avoid the most probable kidnappers in their group when early lactational synchrony is
338 high. In support of this possibility (as opposed to general maintenance of distance from
339 peripubertal females), early lactational synchrony did not predict whether early lactating mothers
340 were likely to have *lower*-ranking peripubertal females as their nearest neighbors (GLMM: $\beta = -$
341 0.12, 95% CI: [-0.77, 0.52], Tables S14-S15).
342
343 *Conclusions.* The patterns of female aggression, infant survival, and female infanticide
344 reported here provide new evidence that group-level synchrony in female reproductive state can
345 alter group-level competitive regimes and negatively impact female breeding success, even in a
346 nonseasonal breeder. First, an increase in the proportion of females with young infants was
347 associated with higher rates of adult female-female agonistic behavior and increased
348 monopolizability of male social partners, indicating intensified competition. Additionally,
349 increased early lactational synchrony predicted higher infant mortality, likely due to a
350 combination of infanticidal behavior by peripubertal females and the downstream effects of
351 female-female competition for males and/or food.
352 The potential for demographic variability to affect competitive regimes and the potential
353 for subsequent variation in competitive regimes to affect fitness outcomes should be investigated
354 in a broader range of group-living species. Among social mammals, within-group female-female
355 competition and female infanticide are widespread[7], despite the prevalence of female philopatry
356 and female-biased kinship[62,63]. Therefore, species in which philopatric females engage in
357 reproductive competition with behavioral tactics up to and including infanticide[7,64] are of
358 particular interest. We suggest that future studies should focus on the proximate factors shaping
359 female aggression, the underlying mechanisms motivating juvenile and adult 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 nearly no rain falls, followed by a highly variable season from November to May when the amount of rainfall varies greatly from month to month and year to year[65]. The baboon population has been continuously monitored by the Amboseli Baboon Research Project (ABRP) since 1971[53]. 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 the 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 three 'major' female reproductive states (see Supplementary Methods for details, also[66]), each of which can be subdivided further into finer-grained 'minor' reproductive states (Fig. 1):

(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. Subdivisions of ovarian cycling include 'flat' (days when females do not exhibit any sexual swelling), 'turgescence-follicular' (lasting from the first day a female's sex skin was turgescent to the sixth day before her sex skin became deturgescent), 'turgescence-ovulation' (lasting from the fifth day before a female's sex skin became deturgescent to the day before her sex skin became deturgescent), and 'deturgescence-luteal' (lasting from the first day a female's sex skin was deturgescent to the last day any swelling was discernible)[67].

(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, spontaneously aborted her pregnancy, or died. Pregnancy was subdivided into three 60-day trimesters (mean ± SD duration of pregnancy: 178 ± 6 days[66]; first trimester: day 1-60; second trimester: day 61-120; third trimester: day 121-parturition).

(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. The duration of postpartum amenorrhea is far more variable than the duration of pregnancy (mean ± SD duration of postpartum amenorrhea: 322 ± 87 days[66]). For the first 360 days of postpartum amenorrhea, we defined 90-day subdivisions of equal length ('early lactation': day 1-90; 'early-mid lactation': day 91-180; 'late-mid lactation': day 181-270; 'late lactation': day 271-360). We pooled all females who had not yet resumed cycling more than 360 days after giving birth into a single subdivision: 'post-year postpartum amenorrhea'. While milk production may continue beyond 360 days after birth, Altmann[39] estimated that yearling baboons were, on average, capable of intaking adequate amounts of energy and protein from independent foraging by this age. He provides 35 weeks as a rough estimate of peak milk volume production by baboon mothers in Amboseli, corresponding to our 'late-mid lactation' category.

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 to be biologically meaningful 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].

Characterizing competition-related behavior. Because we suspected that early lactation would be a particularly competitive time for adult females, we calculated three competition-related metrics from data collected during 10-minute focal animal samples from October 1999 to December 2021 for females in each of the 12 'minor' reproductive states (see Supplementary Methods for more details on focal sampling). These were the: (i) mean proportion of observation time spent foraging, (ii) mean proportion of observation time spent within 5 m of at least one adult male, and (iii) mean rate of agonistic interactions. Foraging time was defined as the sum of time spent feeding and time spent walking while not feeding, as in[65,74,75]. Male neighbors were considered adults once they attained a higher dominance rank than at least one other adult male[76]. We calculated agonistic interaction rate by summing the number of intragroup dyadic agonistic interactions occurring between a focal female and a nonfocal adult female and dividing it by the number of minutes in the focal sample. Agonistic interactions were only included in this rate if either one female displayed aggressive behaviors and the other displayed submissive behaviors or if one female spatially displaced the other. For all three metrics, we obtained 95% confidence intervals via nonparametric bootstrapping. In total, we analyzed data from 60,665 focal samples collected on 270 adult females in 14 social groups. Sample sizes for each of the 12 'minor' reproductive states are given in Table S16.

Different explanations for female-female aggression (e.g., competition over food vs. mates, current competition vs. future competition reduction) offer different predictions about how females in different reproductive states should participate in agonistic interactions[42]. Therefore, we also calculated mean rates of agonistic interactions initiated by and received from females in each of four mutually exclusive reproductive states: cycling, pregnant, early lactation, and the entire period of postpartum amenorrhea following early lactation. However, because there is considerable variation in the presence and number of females in a given reproductive state in a given group at any time, these rates are subject to variation in group composition. Therefore, for each focal sample, we first divided the number of agonistic interactions initiated

toward or received from a nonfocal female in the reproductive state of interest by the number of minutes in the sample. Next, we divided this 'observed' rate of interaction by the number of nonfocal females in the reproductive state of interest that were present in the focal group on the day of the sample to acquire a 'corrected' rate of interaction controlling for group composition. Again, we calculated 95% confidence intervals for these corrected interaction rates with nonparametric bootstrapping.

We estimated mean agonistic interaction rates from the perspectives of individual initiators and recipients separately. For example, to estimate the mean rate of agonistic interactions initiated by cycling females toward pregnant females (Fig. 2a), we only used data from focal samples collected on cycling females. Similarly, to estimate the mean rate of agonistic interactions received by pregnant females from cycling females (Fig 2b), we only used data from focal samples collected on pregnant females. Counterintuitively, these mean rates were not equal at the individual level; mean rates calculated from the initiator's perspective were always almost lower than mean rates calculated from the receiver's perspective. This is because there was higher interindividual skew in the rate of interaction initiation than there was in the rate of interaction reception (Fig. S3). Specifically, there were more females who initiated agonistic interactions at relatively low rates than there were females who received agonistic interactions at relatively low rates, suggesting that a small number of aggressive females initiate a disproportionately large number of agonistic interactions. This is consistent with a despotic, linear dominance hierarchy, as low-ranking females have fewer available groupmates against whom they can win agonistic contests.

Group-level female-female competition. To test the prediction that early lactational synchrony is associated with increased adult female-female competition at the group level, we first aggregated focal samples collected on adult females by group and day. We used these samples to estimate, for every group on every day that focal samples were collected, the group's per female-female dyad agonistic rate. We counted the total number of female-female agonistic interactions that were observed during a focal sample and that included the focal female as a participant. Interaction data collected during a single focal sample were therefore representative of the interactions between the focal female and all other adult females in her group. For example, during one 10-minute focal sample on an adult female in a group that contained 10 adult females in total, the observer was functionally observing nine female-female dyads (one for each focal female + other female combination). Thus, such a sample represents 90 'dyad-minutes' of observation effort. For each group-day, we then divided the count of female-female agonistic interactions observed during focal sampling by the total number of dyad-minutes observed during focal sampling on that day for our daily estimate of group-level female-female agonistic interaction rate. With this approach, we acquired a total sample size of 8,655 group-days from 14 social groups, with one group-level interaction rate estimate for each group-day. On average, 7.0 focal samples were collected each group-day, and 1,039.8 dyad-minutes were observed. Focal sampling captured at least one female-female agonistic interaction on 24.8% of group-days.

We then used these daily counts of female-female agonistic interactions as the response variable in a negative binomial GLMM with a log-link function. We chose to model these count data with a negative binomial distribution because they were overdispersed. In the model, we included the following fixed effects: (i) the proportion of adult females in the group who were in early lactation on that day, group size as a (ii) linear and (iii) quadratic term, and (iv) the

497 cumulative rainfall that fell in the previous 90 days. To control for variation in the number of
498 dyad-minutes observed in a given group on a given day, we included an offset term which was
499 calculated as the log-transformed number of dyad-minutes observed that day. We also included
500 group identity as a random effect to control for repeated sampling of groups. Because observers
501 recorded no female-female agonistic interactions on a majority of group-days, we used the
502 *check_zeroinflation* function in the R package *performance*[77] to test whether the model was
503 significantly zero-inflated. However, no zero-inflation was detected (observed number of zeros =
504 6,512; predicted number of zeros = 6,515; ratio = 1.00).
505 After determining that early lactational synchrony was positively correlated with a
506 group's per-dyad female-female agonistic interaction rate, we sought to test if this rise in
507 aggression could be better explained by either competition over male social partners or food. To
508 do so, we constructed four binomial GLMMs with logit link functions, each of which tested the
509 relationship between early lactational synchrony and either the proportion of observation time
510 that females spent within 5 m of an adult male or the proportion of observation time that females
511 spent foraging. We tested these two response variables with two models each: one including data
512 from focal samples conducted on females in early lactation (n = 7,640 focal samples on 235
513 females) and one including data from focal samples conducted on pregnant females (n = 16,991
514 focal samples on 250 females). We examined behavior during these two reproductive states
515 because females in these states were the most frequent agonistic interaction partners of females
516 in early lactation.
517 For the two models predicting time spent in close proximity to males, we included four
518 fixed effects: (i) the proportion of adult females in the group who were in early lactation, (ii) the
519 focal female's ordinal dominance rank, (iii) an interaction term between (i) and (ii), and (iv)
520 group size. We modeled an interaction between early lactational synchrony and dominance rank
521 to test whether dominance rank-related differences in time spent with adult males would become
522 stronger when early lactational synchrony was higher, a prediction based on the hypothesis that
523 early lactational synchrony intensifies competition over access to males. In these models, we
524 quantified female dominance with ordinal ranks (as opposed to proportional ranks) because prior
525 research in this population indicated that ordinal rank is a better predictor of competition over
526 density-dependent resources (including females' social connectedness to males)[78]. AIC
527 comparisons also favored ordinal rank (early lactating females' time with males: ΔAIC for
528 ordinal rank vs. proportional rank = -78.8; pregnant females' time with males: ΔAIC for ordinal
529 rank vs. proportional rank = -21.7). In both models, we also included individual identity and
530 group identity as random effects.
531 For the two models predicting time spent foraging, we included the same fixed and
532 random effects, but we added a term for cumulative rainfall over the previous 90 days and we
533 substituted proportional rank for ordinal rank. In contrast to ordinal rank, proportional rank is a
534 better predictor of competition for density-independent resources in this population (such as
535 distributed food resources)[78]. Consistent with previous findings, AIC comparisons favored
536 proportional rank over ordinal rank (early lactating females' time with males: ΔAIC for
537 proportional rank vs. ordinal rank = -17.6; pregnant females' time with males: ΔAIC for
538 proportional rank vs. ordinal rank = -21.0)
539
540 *Infant survival.* To test our prediction that high early lactational synchrony is associated
541 with an increased risk of infant death, we used a Cox proportional hazards model with time
542 varying covariates to predict the daily risk of infant death in the first 90 days of life. 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 died on or before that day; (iv) maternal ordinal 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 = 2 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 extremely rare: in no case did an infant under 90 days old survive more than 2 days post-maternal death. In total, 1,304 infants born between November 1976 and December 2021 were included in this analysis, of whom 140 died in the first 90 days of life, and 30 were right-censored because observations on them ceased before they reached 90 days old. We restricted our survival analyses to this period because rainfall data were not recorded before November 1976.

Infanticide risk. After observing a negative relationship between early lactational synchrony and 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 140 infant deaths included in our survival analysis, causes of death with our highest confidence level could be assigned to 45 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 that were below the 95th percentile value of early lactational synchrony (<32.0% of females in the group in early lactation, n = 113 deaths), and (iii) those infants who died on days that were above 95th percentile value of early lactational synchrony (>32.0% of females in the group in early lactation, n = 27 deaths, Fig. 3c). 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 were overrepresented among deaths on days that were above the 95th percentile value of early lactational synchrony, relative to all deaths and relative to deaths on days below the 95th percentile value. 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 S11). In assigning causes of death, we use the definition of infanticide proposed by Digby[79] 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.

Alternative metrics of lactational synchrony. Our analyses of both agonistic behavior and infant survival rely on the assumption that the 90-day period after birth is particularly relevant to female-female competition. To further interrogate this assumption beyond our primary analyses of competition-related behavior above, we constructed several alternative statistical models for the analyses predicting agonistic interaction rates and infant survival. In each of these models, we replaced the early lactational synchrony fixed effect with a term for group-level synchrony in one of the other 'minor' reproductive states included in postpartum amenorrhea (early-mid lactation, late-mid lactation, and late lactation). These were calculated analogously to our

calculation of early lactational synchrony (e.g., the proportion of adult females in a group that were in early-mid lactation on a given day). We found no evidence that synchrony in any other stage of postpartum amenorrhea besides early lactation was associated with either increased female-female competition or increased infant mortality risk. The detailed results of these alternative models can be found in the Supplementary Results (Tables S17-28).

Data Availability

Data and code necessary to reproduce analyses are currently available for reviewers at: http://datadryad.org/share/Uq_1gh4eJtVrQb3UxM_7vsKHT5BiSxkpFqXu7FBXpkM. These data and code will be made publicly available at Dryad Data Repository upon publication.

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References

1 Wilson, A. J. Competition as a source of constraint on life history evolution in natural populations. *Heredity* **112**, 70-78 (2014).

2 Judge, K. A. & Bonano, V. L. Male weaponry in a fighting cricket. *PLoS One* **3**, e3980 (2008).
3 Emlen, S. T. & Oring, L. W. Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215-223 (1977).
4 Clutton-Brock, T. & Huchard, E. Social competition and its consequences in female mammals. *Journal of Zoology* **289**, 151-171 (2013).
5 Stockley, P. & Bro-Jørgensen, J. Female competition and its evolutionary consequences in mammals. *Biological Reviews* **86**, 341-366 (2011).
6 Baniel, A., Cowlishaw, G. & Huchard, E. Jealous females? Female competition and reproductive suppression in a wild promiscuous primate. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20181332 (2018).
7 Lukas, D. & Huchard, E. The evolution of infanticide by females in mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20180075 (2019).
8 Rosvall, K. A. Intrasexual competition in females: evidence for sexual selection? *Behavioral Ecology* **22**, 1131-1140 (2011).
9 Summers, K. Sexual selection and intra-female competition in the green poison-dart frog, *Dendrobates auratus*. *Animal Behaviour* **37**, 797-805 (1989).
10 Lutnesky, M. M. F. & Kosaki, R. K. Female-female competition in a coral reef fish and a test of the temporal threshold model of polygynous mating. *The American Naturalist* **146**, 832-847 (1995).
11 Pusey, A., Williams, J. & Goodall, J. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* **277**, 828-831 (1997).
12 von Holst, D. *et al.* Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). *Behavioral Ecology and Sociobiology* **51**, 245-254 (2002).
13 Holekamp, K. E., Smale, L. & Szykman, M. Rank and reproduction in the female spotted hyaena. *Journal of Reproduction and Fertility* **108**, 229-237 (1996).
14 Altmann, J. & Alberts, S. C. in *Offspring: the biodemography of fertility and family behavior* (eds K W Wachter & R A Bulatao) 140-169 (National Academy Press, 2003).
15 Rosvall, K. A. Sexual selection on aggressiveness in females: evidence from an experimental test with tree swallows. *Animal Behaviour* **75**, 1603-1610 (2008).
16 Sinn, D. L., While, G. M. & Wapstra, E. Maternal care in a social lizard: links between female aggression and offspring fitness. *Animal Behaviour* **76**, 1249-1257 (2008).
17 Sterck, E. H. M., Watts, D. P. & Van Schaik, C. P. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology* **41**, 291-309 (1997).
18 Koenig, A. Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology* **23**, 759-783 (2002).
19 Wheeler, B. C., Scarry, C. J. & Koenig, A. Rates of agonism among female primates: a cross-taxon perspective. *Behavioral Ecology* **24**, 1369-1380 (2013).
20 Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. Competition between female relatives in a matrilocal mammal. *Nature* **300**, 178-180 (1982).
21 Blumstein, D. T., Evans, C. S. & Daniel, J. C. An experimental study of behavioural group size effects in tammar wallabies, *Macropus eugenii*. *Animal Behaviour* **58**, 351-360 (1999).

22 Goss-Custard, J. D. Competition for food and interference among waders. *Ardea* **55**, 31-52 (1980).
23 Van Schaik, C. P., Van Noordwijk, M. A., de Boer, R. J. & den Tonkelaar, I. The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology* **13**, 173-181 (1983).
24 Slotow, R. Aggression in white-crowned sparrows: effects of distance from cover and group size. *The Condor* **98**, 245-252 (1996).
25 Johnson, C. A., Grant, J. W. A. & Giraldeau, L.-A. Thhe effect of patch size and competitor number on aggression among foraging house sparrows. *Behavioral Ecology* **15**, 412-418 (2004).
26 Creel, S. & Creel, N. M. Opposing effects of group size on reproduction and survival in African wild dogs. *Behavioral Ecology* **26**, 1414-1422 (2015).
27 Markham, A. C. & Gesquiere, L. R. Costs and benefits of group living in primates: an energetic perspective. *Philosophical Transactions of the Royal Society B* **372**, 20160239 (2017).
28 Hirsch, B. T. Within-group spatial position in ring-tailed coatis: Balancing predation, feeding competition, and social competition. *Behavioral Ecology and Sociobiology* **65**, 391-399 (2011).
29 Bronson, F. H. Mammalian reproduction: an ecological perspective. *Biology of Reproduction* **32**, 1-26 (1985).
30 Möller, L. & Harcourt, R. G. Shared reproductive state enhances female associations in dolphins. *Research Letters in Ecology*, 1-5 (2008).
31 Bro-Jørgensen, J. Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences* **99**, 9290-9293 (2002).
32 Bebié, N. & McElligott, A. G. Female aggression in red deer: Does it indicate competition for mates? *Mammalian Biology* **71**, 347-355 (2006).
33 Powell, D. M. Female-female competition or male mate choice? Patterns of courtship and breeding behavior among feral horses (*Equus caballus*) on Assateague Island. *Journal of Ethology* **26**, 137-144 (2008).
34 Qi, X.-G. *et al.* Sexual interference in the golden snub-nosed monkey (*Rhinopithecus roxellana*): A test of the sexual competition hypothesis in a polygynous species. *American Journal of Primatology* **73**, 366-377 (2011).
35 Dezeure, J. *et al.* Evolutionary determinants of nonseasonal breeding in wild chacma baboons. *The American Naturalist* **201**, 106-124 (2023).
36 Sinclair, A. R. E., Mduma, S. A. R. & Arcese, P. What determines phenology and synchrony of ungulate breeding in Serengeti? *Ecology* **81**, 2100-2111 (2000).
37 Altmann, J. *Baboon mothers and infants*. (Harvard University Press, 1980).
38 Altmann, J. & Samuels, A. Costs of maternal care: infant carrying in baboons. *Behavioral Ecology and Sociobiology* **29**, 391-398 (1992).
39 Altmann, S. A. *Foraging for survival: yearling baboons in Africa*. (University of Chicago Press, 1998).
40 Palombit, R. A. in *Sexual selection and reproductive competition in primates: new perspectives and directions* (ed Clara B Jones) 3-47 (American Society of Primatologists, 2003).

41 Kleindorfer, S. & Wasser, S. K. Infant handling and mortality in yellow baboons (*Papio cynocephalus*): evidence for female reproductive competition? *Behavioral Ecology and Sociobiology* **56**, 328-337 (2004).
42 Patterson, S. K., Strum, S. C. & Silk, J. B. Resource competition shapes female–female aggression in olive baboons, *Papio anubis*. *Animal Behaviour* **176**, 23-41 (2021).
43 Silk, J. B. Correlates of agonistic and competitive interactions in pregnant baboons. *American Journal of Primatology* **12**, 479-495 (1987).
44 Barton, R. A. & Whiten, A. Feeding competition among female olive baboons, *Papio anubis*. *Animal Behaviour* **46**, 777-789 (1993).
45 Baniel, A., Cowlishaw, G. & Huchard, E. Context dependence of female reproductive competition in wild chacma baboons. *Animal Behaviour* **139**, 37-49 (2018).
46 Archie, E. A., Tung, J., Clark, M., Altmann, J. & Alberts, S. C. Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20141261 (2014).
47 Nguyen, N., Van Horn, R. C., Alberts, S. C. & Altmann, J. "Friendships" between new mothers and adult males: adaptive benefits and determinants in wild baboons (*Papio cynocephalus*). *Behavioral Ecology and Sociobiology* **63**, 1331-1344 (2009).
48 Palombit, R. A., Cheney, D. L. & Seyfarth, R. M. Female–female competition for male 'friends' in wild chacma baboons (*Papio cynocephalus ursinus*). *Animal Behaviour* **61**, 1159-1171 (2001).
49 Palombit, R. A., Seyfarth, R. M. & Cheney, D. L. The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Animal Behaviour* **54**, 599-614 (1997).
50 Jansen, D. J., Warutere, J. K., Tung, J., Alberts, S. C. & Archie, E. A. Early-life paternal relationships predict adult female survival in wild baboons. *Proceedings of the Royal Society B* **292**, 20250194 (2025).
51 Alberts, S. C. & Altmann, J. Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. *American Journal of Primatology* **53**, 139-154 (2001).
52 Vilgalys, T. P. *et al.* Selection against admixture and gene regulatory divergence in a long-term primate field study. *Science* **377**, 635-641 (2022).
53 Alberts, S. C. & Altmann, J. in *Long-term field studies of primates* (eds P Kappeler & DAVID P Watts) 261-287 (Springer, 2012).
54 Hausfater, G., Altmann, J. & Altmann, S. Long-term consistency of dominance relations among female baboons (*Papio cynocephalus*). *Science* **217**, 752-755 (1982).
55 Lea, A. J., Learn, N. H., Theus, M. J., Altmann, J. & Alberts, S. C. Complex sources of variance in female dominance rank in a nepotistic society. *Animal behaviour* **94**, 87-99 (2014).
56 Gesquiere, L. R. *et al.* Thyroid hormone concentrations in female baboons: metabolic consequences of living in a highly seasonal environment. *Hormones and Behavior* **161**, 105505 (2024).
57 Altmann, J., Altmann, S. & Hausfater, G. Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. *American Journal of Primatology* **1**, 389-399 (1981).
58 Roberts, S. B., Cole, T. J. & Coward, W. A. Lactational performance in relation to energy intake in the baboon. *The American Journal of Clinical Nutrition* **41**, 1270-1276 (1985).

59 Wasser, S. K. & Starling, A. K. Proximate and ultimate causes of reproductive suppression among female yellow baboons at Mikumi National Park, Tanzania. *American Journal of Primatology* **16**, 97-121 (1988).
60 Rhine, R. J., Wasser, S. K. & Norton, G. W. Eight-year study of social and ecological correlates of mortality among immature baboons of Mikumi National Park, Tanzania. *American Journal of Primatology* **16**, 199-212 (1988).
61 Baniel, A., Cowlishaw, G. & Huchard, E. Stability and strength of male-female associations in a promiscuous primate society. *Behavioral Ecology and Sociobiology* **70**, 761-775 (2016).
62 Pusey, A. E. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution* **2**, 295-299 (1987).
63 Mattison, S. M., Shenk, M. K., Emery Thompson, M., Mulder, M. B. & Fortunato, L. The evolution of female-biased kinship in humans and other mammals. *Philosophical Transactions of the Royal Society B* **374**, 20190007 (2019).
64 Brown, A. K., Pioon, M. O., Holekamp, K. E. & Strauss, E. D. Infanticide by females is a leading source of juvenile mortality in a large social carnivore. *The American Naturalist* **198**, 642-652 (2021).
65 Alberts, S. C. *et al.* in *Primate seasonality: Implications for human evolution* (eds D K Brockman & C P van Schaik) 157-196 (Cambridge University Press, 2005).
66 Gesquiere, L. R., Altmann, J., Archie, E. A. & Alberts, S. C. Interbirth intervals in wild baboons: Environmental predictors and hormonal correlates. *American Journal of Physical Anthropology* **166**, 107-126 (2018).
67 Gesquiere, L. R., Wango, E. O., Alberts, S. C. & Altmann, J. Mechanisms of sexual selection: sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons. *Hormones and Behavior* **51**, 114-125 (2007).
68 R Core Team. *R: A language and environment for statistical computing*, <http://www.r-project.org/index.html> (2020).
69 Package 'MuMIn' (2018).
70 Burnham, K. P. & Anderson, D. R. *Model selection and multimodel inference: A practical information-theoretic approach.*, (Springer-Verlag, 1998).
71 Burnham, K. P., Anderson, D. R. & Huyvaert, K. P. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* **65**, 23-35 (2011).
72 A package for survival analysis in R v. R package version 3.3-1 (2022).
73 Brooks, M. E. *et al. glmmTMB* balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9**, 378-400 (2017).
74 Markham, A. C., Gesquiere, L. R., Alberts, S. C. & Altmann, J. Optimal group size in a highly social mammal. *Proceedings of the National Academy of Sciences* **112**, 14882-14887 (2015).
75 Bronikowski, A. M. & Altmann, J. Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behavioral ecology and Sociobiology* **39**, 11-25 (1996).
76 Alberts, S. C. & Altmann, J. Preparation and activation: determinants of age at reproductive maturity in male baboons. *Behavioral Ecology and Sociobiology* **36**, 397-406 (1995).

77 Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P. & Makowski, D. performance: An R Package for Assessment, Comparison, and Testing of Statistical Models. *Journal of Open Source Software* **6**, 3139 (2021).

78 Levy, E. J. *et al.* A comparison of dominance rank metrics reveals multiple competitive landscapes in an animal society. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20201013 (2020).

79 Digby, L. in *Infanticide by males and its implications* (eds C P van Schaik & Charles H Janson) 178-197 (Cambridge University Press, 2000).

Tables & Figures

Table 1. GLMM results for the models predicting per-dyad agonistic interaction rates between adult females (n = 8,655 group-days), the proportion of time that early lactating females spent in close proximity to adult males (n = 7,640 focal samples), and the proportion of time that pregnant females spent in close proximity to adult males (n = 16,991 focal samples). The results for 'Proportion of time spent close to an adult male (early lactating females)' reflect model averaging of candidate models that were within 2 AIC_c units of the top candidate model. For the other two analyses (agonistic interaction rates and time spent with adult males by pregnant females), no other candidate models were within 2 AIC_c units of the top models (see Tables S3-5 for the top candidate models for all three response variables). Bold effects are those where the 95% CI does not overlap zero. Model predictions are presented to aid interpretation of estimates and were calculated for the extreme values of each significant fixed effect, while holding values for other fixed effects constant at their observed median value.

Response variable	Fixed effect	Estimate	Std. Error	95 % CI	Model predictions
Per-dyad agonistic interaction rate	(intercept)	-5.92	0.30	[-6.50, -5.34]	–
	Group size	**-0.064**	**0.009**	**[-0.081, -0.047]**	–
	Group size^2	**0.00046**	**0.00006**	**[0.00034, 0.00059]**	Group size (min) = 11 individuals, agonistic interaction rate = 0.0015 interactions per minute per dyad; Group size (median) = 53 individuals, agonistic interaction rate = 0.00035 interactions per minute per dyad; Group size (max) = 118 individuals, agonistic interaction rate = 0.00092 interactions per minute per dyad
	Early lactational synchrony (ELS)	**0.61**	**0.23**	**[0.16, 1.07]**	ELS (min) = 0.00, agonistic interaction rate = 0.00033 interactions per minute per dyad; ELS (max) = 0.54, agonistic interaction rate = 0.00046 interactions per minute per dyad
	Cumulative rainfall	**0.00107**	**0.00005**	**[0.00004, 0.00210]**	Rainfall (min) = 0.0 mm, agonistic interaction rate = 0.00035 interactions per minute per dyad; Rainfall (max) = 326.9 mm, agonistic interaction rate = 0.00050 interactions per minute per dyad
	(intercept)	-1.00	0.10	[-1.19, -0.80]	–

Proportion of time spent close to an adult male (early lactating females)	**Dominance rank**	**-0.029**	**0.005**	**[-0.039, -0.019]**	–
	Early lactational synchrony	**0.41**	**0.16**	**[0.09, 0.72]**	–
	Dominance rank*Early lactational synchrony	**-0.04**	**0.02**	**[-0.07, -0.01]**	Rank (max) = 1, ELS (min) = 0.03, proportion of time spent with male = 0.27; Rank (min) = 29; ELS (min) = 0.03, proportion of time spent with male = 0.13; Rank (max) = 1, ELS (max) = 0.54, proportion of time spent with male = 0.30; Rank (min) = 29, ELS (max) = 0.54, proportion of time spent with male = 0.09
	Group size	0.00005	0.00053	[-0.00099, 0.00109]	–
Proportion of time spent close to an adult male (pregnant females)	(intercept)	-1.97	0.08	[-2,13, -1.81]	–
	Dominance rank	**-0.017**	**0.004**	**[-0.025, -0.010]**	–
	Early lactational synchrony	**0.66**	**0.11**	**[0.43, 0.88]**	–
	Dominance rank*Early lactational synchrony	**-0.07**	**0.01**	**[-0.08, -0.04]**	Rank (max) = 1, ELS (min) = 0.00, proportion of time spent with male = 0.15; Rank (min) = 29, ELS (min) = 0.00, proportion of time spent with male = 0.10; Rank (max) = 1, ELS (max) = 0.54, proportion of time spent with male = 0.20; Rank (min) = 29, ELS (max) = 0.54, proportion of time spent with male = 0.05
	Group size	**0.0056**	**0.0007**	**[0.0041, 0.0071]**	Group size (min) = 11 individuals, proportion of time spent with male = 0.12; Group size (max) = 118 individuals, proportion of time spent with male = 0.20

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Table 2. Model-averaged estimates for the best-fitting models ($\Delta AIC_c < 2$) predicting the daily risk of all-cause infant mortality in the first 90 days after birth (Cox proportional hazards model, total infants = 1,304; died = 140, censored = 33; top 20 candidate models are shown in Table S10). Effects where the 95% CI does not overlap zero are in bold. Model predictions are presented to aid interpretation of estimates and were calculated for the extreme observed values 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	Std. Error	95 % CI	Hazard ratio[1]	Model predictions
Maternal death	**6.4**	**0.3**	**[5.8, 7.0]**	**611.3**	Mother alive, probability of death = 0.0004; Mother dead, probability of death = 0.2452
Early lactational synchrony	**2.7**	**0.8**	**[1.2, 4.2]**	**14.6**	ELS (min) = 0.00, probability of death = 0.0002; ELS (max) = 0.71, probability of death = 0.0017
Maternal age	**-0.29**	**0.10**	**[-0.50, -0.08]**	**0.7**	–
Maternal age^2	**0.011**	**0.004**	**[0.003, 0.019]**	**1.0**	Maternal age (min) = 4.8 years, probability of death = 0.0008; Maternal age (median) = 10.2 years, probability of death = 0.0004; Maternal age (max) = 24.2, years probability of death = 0.0015
Maternal rank	0.005	0.012	[-0.018, 0.028]	1.0	–
Group size	-0.003	0.005	[-0.013, 0.006]	1.0	–
Cumulative rainfall	-0.0008	0.0011	[-0.0030, 0.0013]	1.0	–

[1]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 associated with lower mortality hazard (higher infant survival).

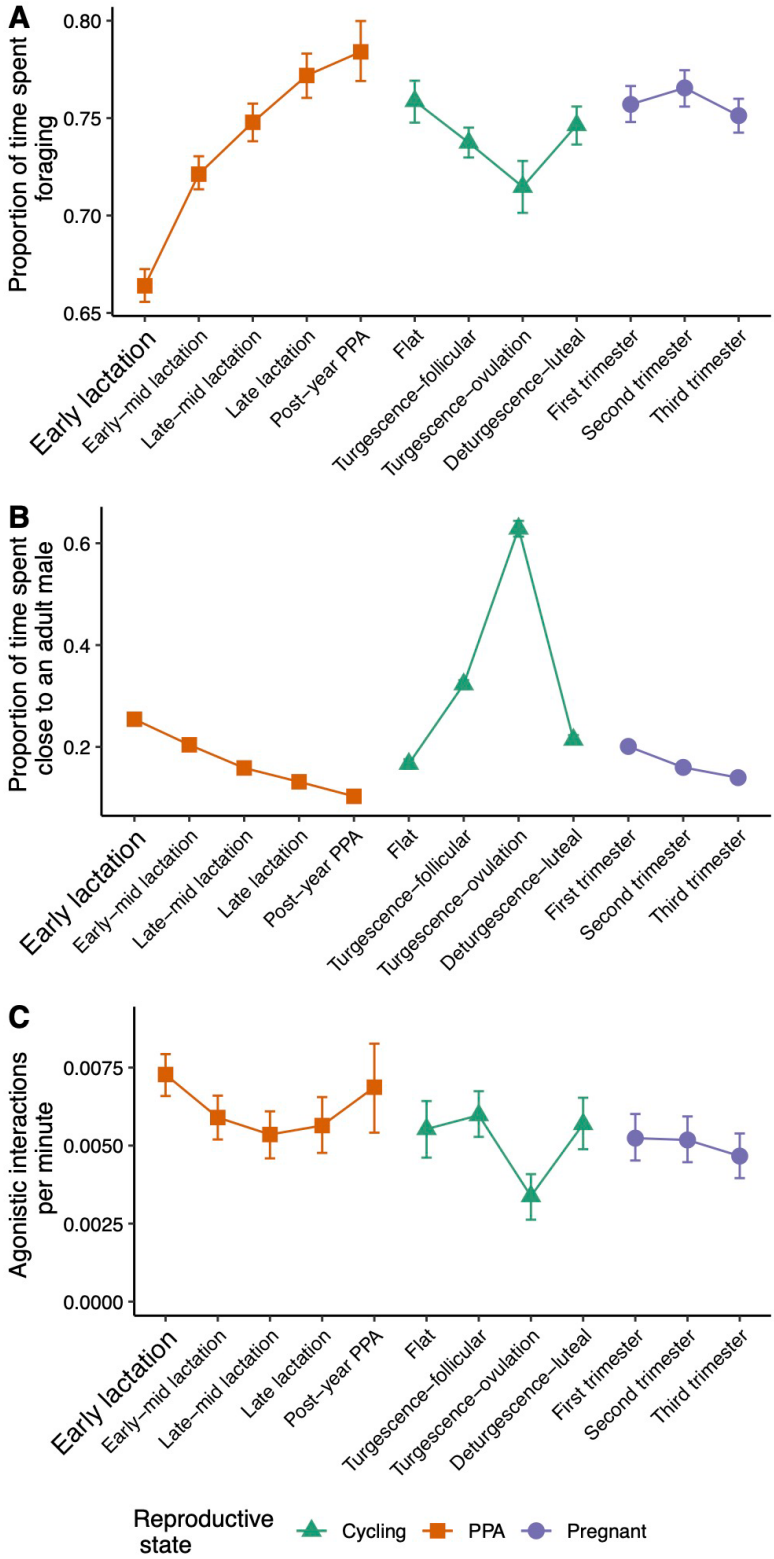

Figure 1. Changes in competition-related behavior across the interbirth interval. Among adult females, (A) the mean proportion of time spent foraging, (B) the mean proportion of time spent within 5 m of an adult male, and (C) the mean rate of agonistic interactions with other adult

857 females varied both between and within the three ‘major’ reproductive states (postpartum
858 amenorrhea, or PPA, in orange, ovarian cycling in green, and pregnancy in purple). ‘Minor’
859 reproductive states are indicated on the x-axis, where early lactation is indicated with enlarged
860 text. Within PPA, early lactation shows a marked trough in time spent foraging (panel A) and
861 marked peaks in time spent in proximity to males (panel B) and rate of agonistic interactions
862 (panel C). Points represent mean values and vertical lines represent 95% confidence intervals
863 calculated via nonparametric bootstrapping (the confidence intervals for mean time spent within
864 5 m of an adult male in panel B were narrow relative to the ranges of within- and between-state
865 variation in mean values, limiting their visibility here, see Table S1). See Methods for definitions
866 of the reproductive states.
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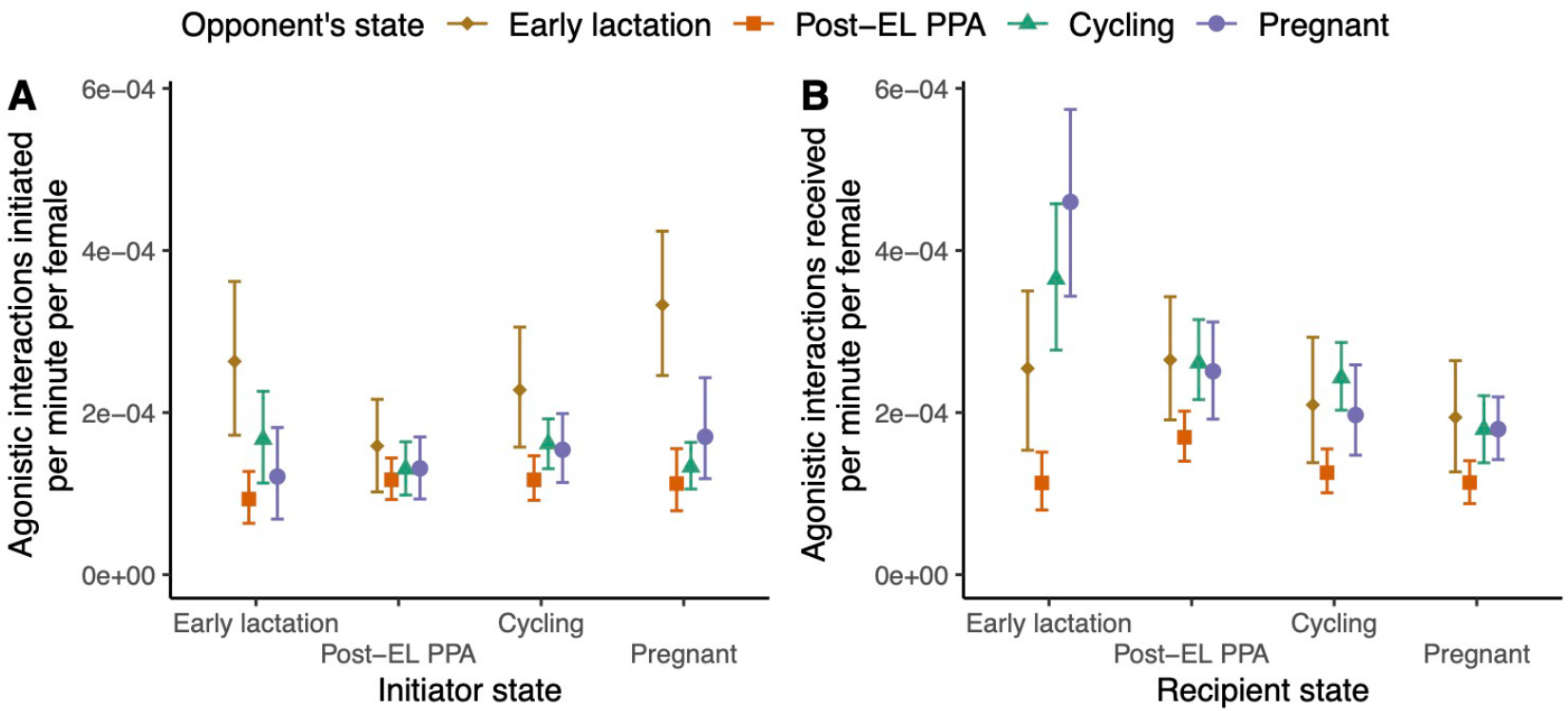

Figure 2. Mean rates of dyadic agonistic interactions as a function of the reproductive states of the interacting females. (A) depicts the mean rates at which focal females initiated agonistic behavior, and (B) depicts the mean rates at which focal females received agonistic behavior. In each case the reproductive state of the focal female is on the x-axis and the reproductive state of her opponent is indicated by color (brown = early lactation, orange = post-early lactation postpartum amenorrhea, green = cycling, purple = pregnant). In panel A, females in early lactation initiated aggression towards other females in early lactation at a higher rate than all but pregnant females, who tended to target females in early lactation. In panel B, females in early lactation received aggression at higher rates from females in almost all other reproductive states. Mean rates were calculated per minute, per potential interaction partner, to allow us to control for group- and time-dependent variation in the availability of potential interaction partners of different reproductive states (see Methods). Error bars indicate 95% confidence intervals.

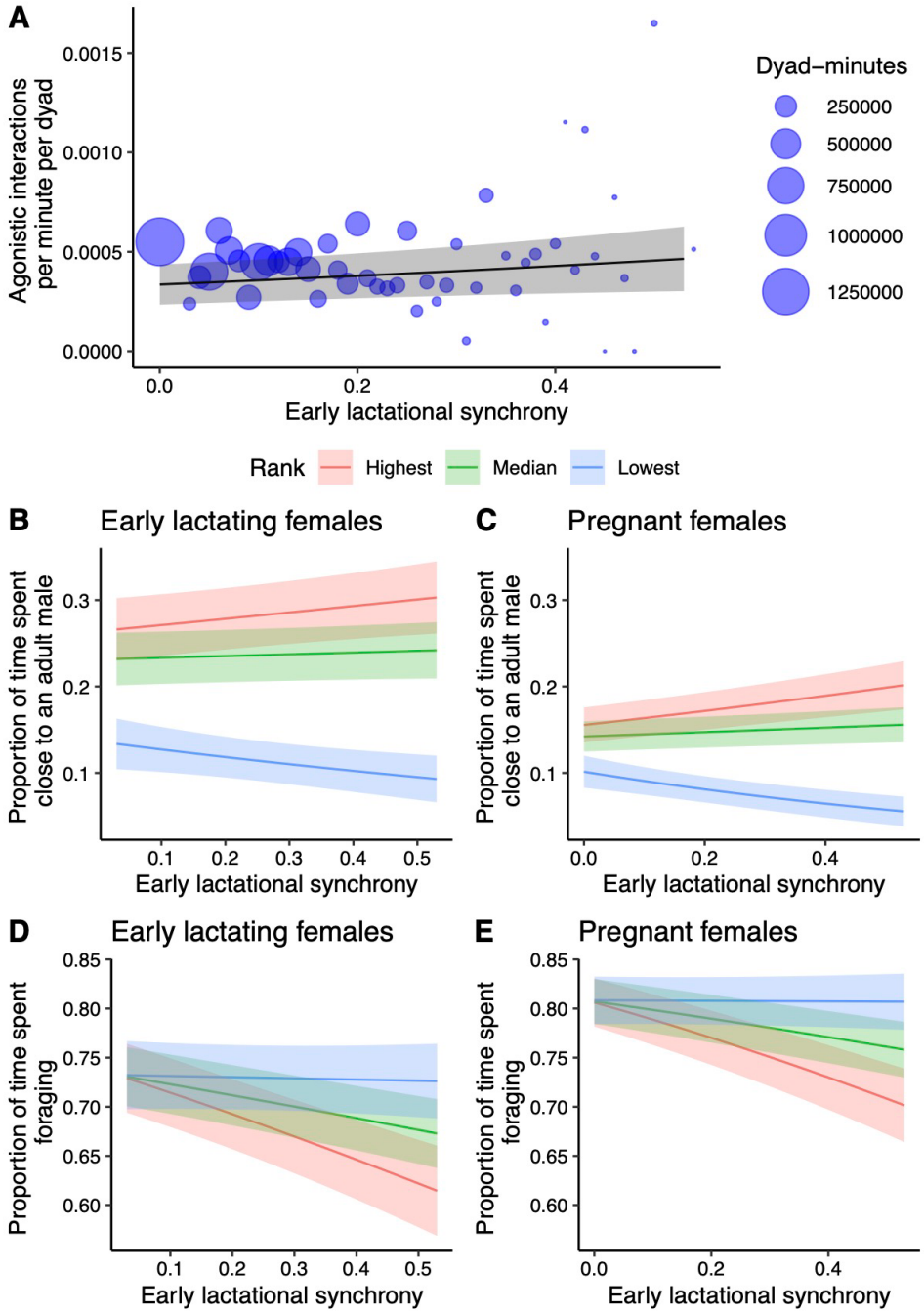

Figure 3. High early lactational synchrony predicted increased female-female competition. (A) Per-dyad agonistic interaction rates were higher on group-days with higher early lactational synchrony. The black line and shaded region depict the model-predicted values and their 95% confidence intervals. The blue circles depict the underlying data, binned at hundredths intervals (0.00, 0.01, …) and presented as means. Circles are sized to reflect the number of dyad-minutes of observation at each bin (see Methods). (B-C) Higher-ranking females spent more time in proximity to adult males both in early lactation (B) and pregnancy (C), and this effect was strongest when early lactational synchrony was high. The colored lines and shaded regions depict the model-predicted values for females of the highest dominance rank (red, ordinal rank = 1), of

the median rank observed in our dataset (green, ordinal rank = 7), and of the lowest dominance rank observed in our dataset (blue, ordinal rank = 29). (D-E) High-ranking females spent less time foraging as early lactational synchrony increased, both during early lactation (D) and during pregnancy (E) but no such relationship existed for low-ranking females. The colored lines and shaded regions depict the model-predicted values for females at the top of the dominance hierarchy (red, proportional rank = 1.0), in the middle of the dominance hierarchy (green, proportional rank = 0.5), and at the bottom of the dominance hierarchy (blue, proportional rank = 0.0). Decisions to model these relationships using ordinal or proportional dominance ranks were informed by biological considerations and goodness of fit evaluations (see Methods).

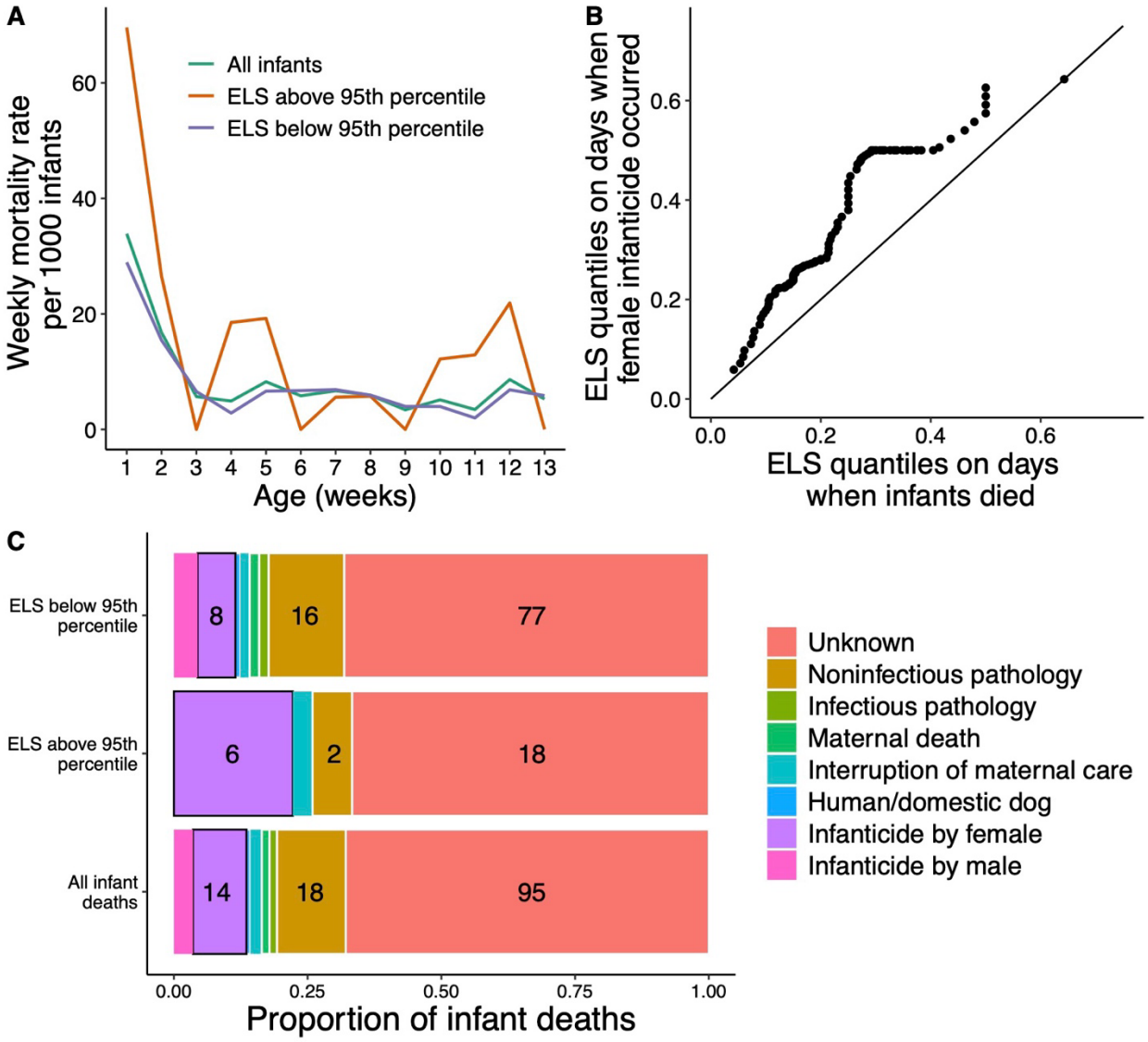

Figure 4. The relationship between early lactational synchrony (ELS), infant mortality, and infanticide. (A) Early lactational synchrony predicted infant mortality risk. Weekly mortality rates per 1000 infants are depicted with values calculated across all infants (green line), for infants in weeks in which the mean early lactational synchrony in their group was less than the 95th percentile value of early lactational synchrony (purple line; <32.0% of females were in early lactation), and for infants in weeks in which the mean early lactational synchrony in their group exceeded the 95th percentile value of early lactational synchrony (orange line; >32.0% of females were in early lactation). Early lactational synchrony was modeled as a continuous, daily, time-varying variable in our survival analysis; weekly mean values are used for visualization purposes. (B) Quantile-quantile plot showing that the distribution of early lactational synchrony is shifted higher on days when infants are killed by females (y-axis) than on days when infants die by any cause (x-axis). The solid, black line depicts the expected relationship if infanticide by females 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. (C) Assigned causes of infant

death. Bar graphs depict proportion of infant death causes for all infants included in the survival analysis (n = 140). The bottom bar includes all infants who died in their first 90 days of life during the study period (n = 140), the center bar only includes infants who died on days that were above the 95th percentile value of early lactational synchrony (>32.0% of females in early lactation, n = 27), and the top bar only includes infants who died on days that were below the 95th percentile value of early lactational synchrony (<32.0% of females in early lactation, n = 113). In all, infanticide deaths caused by females are highlighted with a black border. Numbers on the bar graphs indicate the sample sizes for the three most prevalent death causes (unknown, noninfectious pathology, and infanticide by females). Sample sizes for all death causes are given in Table S29.