Evolutionary determinants of non-seasonal breeding in wild chacma baboons

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ABSTRACT

Animal reproductive phenology varies from strongly seasonal to non-seasonal, sometimes among closely related or sympatric species. While the extent of reproductive seasonality is often attributed to environmental seasonality, this fails to explain many cases of non-seasonal breeding in seasonal environments. We investigated the evolutionary determinants of non-seasonal breeding in a wild primate, the chacma baboon (*Papio ursinus*), living in a seasonal environment with high climatic unpredictability. We tested three hypotheses proposing that non-seasonal breeding has evolved in response to (1) climatic unpredictability, (2) reproductive competition between females favoring birth asynchrony, and (3) individual, rank-dependent variations in optimal reproductive timing. We found strong support for an effect of reproductive asynchrony modulated by rank: (i) birth synchrony is costly to subordinate females, lengthening their interbirth intervals, (ii) females alter their reproductive timings (fertility periods and conceptions) in relation to previous conceptions in the group, and (iii) the reported effect of birth synchrony on interbirth intervals weakens the intensity of reproductive seasonality at the population level. This study emphasizes the importance of sociality in mediating the evolution of reproductive phenology in group-living organisms, a result of broad significance for understanding key demographic parameters driving population responses to increasing climatic fluctuations.

KEYWORDS

Primate, reproductive seasonality, reproductive phenology, reproductive suppression, paternal care, female-female competition.

INTRODUCTION

Reproduction is energetically costly, and many species therefore adjust the timing of their reproduction, referred to as reproductive phenology, to seasonal fluctuations in food availability (Boyce 1979). Reproductive seasonality, the temporal clustering of reproductive events in one period of the annual cycle (Lindburg 1987), is widespread taxonomically and geographically (Brockman and van Schaik 2005; Bronson 2009), and usually characterized by the timing and width of the birth peak. Although non-seasonal breeders can reproduce at any point in the annual cycle (unlike seasonal breeders, who experience a period without any births), non-seasonal breeding populations may still exhibit a seasonal peak in the annual distribution of births (Janson and Verdolin 2005).

Ultimate explanations for seasonal reproduction have largely assumed that variation in the intensity of reproductive seasonality reflects variation in the intensity of environmental seasonality (Rutberg 1987; Conover 1992; Di Bitetti and Janson 2000). However, numerous sympatric species exhibit a range of reproductive schedules despite sharing the same climate. For example, in the Serengeti National Park (Tanzania), the korrigum *Damascilus korrigum* is a highly seasonal breeder while the phylogenetically related hartebeest *Alcelaphus buselaphus* is not, and seasonal breeders vary widely in the timing and length of their breeding season (Sinclair et al. 2000). More generally, numerous species living in highly seasonal environments breed year round (Burthe et al. 2011; Swedell 2011; Campos et al. 2017). Overall, the intensity of environmental seasonality is not always a reliable predictor of a species' reproductive seasonality.

Several additional predictors of seasonal breeding could be considered. First, if the height and/or the timing of the annual food peak vary between years, individuals may benefit from maintaining a flexible reproductive schedule (Colwell 1974; van Schaik and van Noordwijk 1985; Loe et al. 2005). For example, across 38 ungulate species, the intensity of seasonal breeding decreases with increasing seasonal unpredictability, i.e., inter-annual variation in the timing and strength of environmental seasonality (English et al. 2012). In environments where within-year (seasonal) variations are negligible compared to between-year (non-seasonal) variations, individuals adjusting their reproductive events with relative flexibility might be favored to exploit the unpredictable food peak opportunistically (van Schaik and van Noordwijk 1985); this flexibility may cause the absence of reproductive seasonality. Yet, few studies have asked whether seasonal predictability could represent an evolutionary driver of reproductive seasonality.

Second, social factors might further affect reproductive seasonality by modulating reproductive synchrony, the 'phenomenon caused by biological interactions to produce a tighter clustering of reproductive events than environmental seasonality alone' (Ims 1990; page 135). Synchronizing births in order to satiate predators is a common anti-predator adaptation producing extreme reproductive synchrony for numerous species, including some ungulates (Rutberg 1987; Ims 1990; Sinclair et al. 2000; Canu et al. 2015) and squirrel monkeys (Boinski 1987). Sociality could also lead to the reverse pattern where reproductive events are staggered to decrease reproductive competition over access to mates, paternal care or food (Wiebe et al. 1995). For instance, estrus asynchrony has been reported in both seasonal breeding ring-tailed lemurs (*Lemur catta)* (Pereira 1990) and non-seasonal breeding chimpanzees (*Pan troglodytes)* (Matsumoto-Oda et al. 2007), apparently allowing females greater mate choice by decreasing female mating competition.

Third, individual variation in reproductive seasonality might also occur, leading to non-seasonal breeding across the population as a whole. This is especially true in hierarchical societies, where dominant females often have privileged access to resources and may subsequently exhibit earlier age at first reproduction, shorter interbirth intervals, higher offspring survival and increased longevity (Clutton-Brock and Huchard 2013; Stockley and Bro-Jørgensen 2011). The consequences of rank-related variation in foraging success and life history traits on reproductive seasonality have not been studied, but may mediate both the effects of environmental variation and group reproductive synchrony described above. If females compete mainly over food, we should detect rank-related variation in sensitivity to environmental fluctuations. If females compete mainly over mating opportunities and/or paternal care, we should detect rank-related variation in sensitivity to group synchrony.

Here, we propose three non-exclusive hypotheses that could explain the evolution of non-seasonal reproduction. (H1) The ‘non-seasonal environment hypothesis’ proposes that the absence of reproductive seasonality stems from a population-level factor, namely non-seasonal (i.e. between-year) environmental fluctuations. (H2) The ‘group asynchrony hypothesis’ proposes that the absence of reproductive seasonality results from a group-level factor, where females within a group stagger their reproductive events to minimize reproductive synchrony in response to reproductive competition. (H3) The ‘social rank hypothesis’ proposes that an individual-level factor, namely social rank, leads to the absence of reproductive seasonality at the population level because there are dominance-related differences in how females are affected by seasonal and non-seasonal environmental variation (H3a), and/or reproductive synchrony (H3b).

Our study model is a wild social primate, the chacma baboon (*Papio ursinus*). Focusing on a long-lived mammal in the tropics will bring a fresh perspective on the breeding seasonality literature, which is biased towards short-lived passerines in northern temperate climates (Verhulst and Nilsson 2008; Bronson 2009; Varpe et al. 2009). In addition, the selective pressures affecting breeding seasonality in tropical latitudes, where the environment is characterized by more unpredictable rainfall (Feng et al. 2013), have been less studied. Extensive variations in patterns of reproductive synchrony occur across primate populations (Ostner et al. 2008; Gogarten and Koenig 2013), and may reflect female reproductive competition (Beehner and Lu 2013). Finally, social primates such as baboons, which live in large multimale-multifemale groups where the female dominance hierarchy is linear and affects foraging success and reproductive performance (Pusey 2012), may provide a valuable model for understanding rank differences in sensitivity to environmental and social factors likely to lead to individual variations in seasonal breeding strategies. In our study population, a recent study showed that baboons breed year-round despite living in a seasonal environment and revealed fitness variations associated with seasonal birth timing (Dezeure et al. 2021*a*). It hence raises the question of the nature of the benefits of non-seasonal breeding.

We tested these three hypotheses according to their predicted effects on (1) females' fitness, assayed by: female interbirth interval (IBIs) and offspring survival until weaning; and (2) on reproductive timings, assayed by the monthly probabilities of cycle resumption and conception (see Table 1 below). Under the non-seasonal environment hypothesis (H1), we predicted that female reproduction should be particularly sensitive to unpredictable environmental variations (i.e. deviations from seasonal averages), such that an unusually low amount of food for a given season should lead to longer IBIs, higher infant mortality, and lower probabilities of cycling resumption and conception. This may occur on top of the effects of predictable, seasonal variations. Under the reproductive synchrony hypothesis (H2), female reproduction should be responsive to the degree of reproductive synchrony in the group, such that higher group synchrony should lead to longer IBIs, higher infant mortality, and lower probabilities of cycling resumption and conception. Under the social rank hypothesis, lower-ranking females should be more restricted in their access to food resources (H3a), or experience greater costs of reproductive synchrony (H3b), such that the respective negative effects of food scarcity and group synchrony on IBI, infant mortality, cycle resumption, and conception would be greater for subordinate females.

METHODS

Field site and population

Data were collected between 2005 and 2019 from three habituated groups of wild chacma baboons (J and L since 2005, and M, a fission group from J, since 2016) living on the edge of the Namib Desert at Tsaobis Nature Park (22°23S, 15°44’50E) in central Namibia. The Tsaobis environment is characterized by steep rocky hills descending towards alluvial plains, and crossed by the ephemeral Swakop riverbed (Cowlishaw and Davies 1997). It is a strongly seasonal environment: the desert vegetation responds quickly to the austral summer rains, which usually fall between December and April, and then dies back during the dry winter months (Dezeure et al. 2021*a*). The annual rainfall is sparse and highly variable between years. Each year, a field season of variable length (mean = 137 days, range: 57-240 days) was conducted, mainly during the dry winter season (between May and October). The groups were followed on foot from dawn to dusk on a daily basis, allowing us to collect demographic and behavioral data, as well as GPS locations.

Individual data

A female was considered adult when she reached menarche. The reproductive state of each adult female was monitored on a daily basis. A female could be assigned as: (i) lactating, for the period until the female resumed cycling after an infant birth; (ii) cycling, including both swollen females in estrus (i.e., sexually receptive with a perineal swelling) and non-swollen females (i.e. at other stages of their menstrual cycle); (iii) pregnant, with pregnancy being determined *post hoc* following an infant’s birth when field observers were absent around conception, and encompassing the six months between the conceptive cycle and the birth. Alternatively, when observers were present, a conception was determined based on the interruption of cycling combined with the subsequent reddening of female paracallosal skin following the first third of pregnancy, and was usually confirmed by a birth. Both methods may miss early abortions, which would be hard to distinguish from natural variations in menstrual cycle length. The first post-partum cycle (i.e. cycle resumption) is the first cycle following an infant's birth, when the female resumes cycling after lactation. The exact date of the cycle resumption corresponds to the first day of estrus of the first post-partum cycle, i.e. the first day when a sexual swelling is recorded. The dates of these reproductive events were known with accuracy when they were recorded by field observers, and were otherwise estimated using the methods detailed below.

For females born after 2005, their dates of births were either witnessed in the field or estimated with relative precision (see below). For females born before 2005, age was estimated through dentition, using both tooth eruption schedules and tables of molar wear (Huchard et al. 2009; Kahumbu and Eley 1991).

Females' parity was determined using long-term life history data and defined as: nulliparous (before the birth of her first infant), primiparous (between the birth of her first and second infant) and multiparous (after the birth of her second infant).

Female social rank was established annually for each group using *ad libitum* and focal observations of agonistic interactions between adult females: supplants, displacements, attacks, chases and threats (Huchard and Cowlishaw 2011). We computed a linear hierarchy using Matman 1.1.4 (Noldus Information Technology, 2013), and then converted to a relative rank to control for group size. Each female was thus assigned one rank per year, ranging from 0 (lowest ranking) to 1 (highest ranking).

Each year, we also computed the number of adult females in each group. A female was considered in the group each year if she was present for more than half of the annual field season.

Individual reproductive data

To test our hypotheses, we considered two measures of female fitness, namely the interbirth interval ('IBI') duration and offspring mortality before weaning, and two measures of the timing of female reproduction, namely the monthly probabilities of conception and of cycle resumption.

As baboons are not followed throughout the year at Tsaobis, we had to estimate dates of conceptions, births and cycle resumptions in a number of cases. The dates of those unobserved events—as well as the number of days of uncertainty around those events—were established using a combination of photographs and field observations of infant fur and skin color (ears, eye contours, hands and feet, muzzle, muzzle tip, and ischial callosities), following a protocol detailed in a recent study (Dezeure et al. 2021*b*). In all, we generated a sample of 241 conceptions, with a median uncertainty of 10 days (range: 0-164 days) (Supplement, Table S1); 215 births, with a median uncertainty of 10 days (range: 0-153 days); and 155 cycle resumptions, with a median uncertainty of 93 days (range: 0-272 days), between 2005 and 2019. The uncertainty of each reproductive event date has been considered in all analyses (see Supplement, Section S1).

We defined interbirth intervals (IBIs) as the number of days between two consecutive live births of a mother. We only considered IBIs for which the first infant reached weaning (i.e. survived until 550 days old) (Gesquiere et al. 2017), because females resumed cycling rapidly after their infant's death (median = 21 days, range = 9-51, n = 9 observed deaths), and their IBIs would have been shortened regardless of environmental or social factors. This age threshold (550 days) was estimated to be the maximum length of post-partum anestrus in our population (Dezeure et al. 2021*a*), and presumably reflected the upper threshold of weaning age, assuming that females who resumed cycling had weaned their offspring (Lee et al. 1991; Saltzman et al. 2011; Borries et al. 2014). We further removed one IBI where the infant closing the IBI was stillborn (because it might have been due to premature delivery). We computed a total of 120 IBIs from 43 adult females, ranging from 397-1132 days with a mean of 678 days (SD = 128).

For each infant born between 2005-01-01 and 2018-08-01, we investigated whether it died (yes/no) before weaning, i.e. reaching 550 days of age. Death was recorded when a corpse was observed or when the infant had been missing in the group for five consecutive days. Infants born later than August 2018 were not considered as their survival outcome at 550 days was unknown. Four infants that disappeared between two consecutive field seasons (in the absence of observers) were omitted because we could not establish whether the age of death was before or after 550 days. In our final dataset, a total of 39 of 195 infants died before reaching 550 days of age, with mortality occurring at a median age of 74 days (range 1-284 days, n = 17 known dates of death).

Characterization of environmental variation

We first considered four aspects of environmental variation at Tsaobis: the temperature, rainfall, vegetation cover (food availability) and photoperiod (daytime length) (see Supplement, Section S2). However, we found that our indicator of food availability (vegetation cover) was always selected as the best environmental variable affecting reproductive success and timings (see Supplement, Sections S2, S3 and S4, for further details on the selection of this variable). Therefore, we only present in the main text the methods and results associated with food availability.

We used the Normalized Difference Vegetation Index (NDVI) as a measure of vegetation cover and therefore food availability. NDVI is computed using the near-infrared and red light reflected by the surface of an area and measured with satellite sensors; it produces a quantitative index of primary productivity with higher values corresponding to a higher degree of greenness (Didan et al. 2015). It has previously been used as an indicator of habitat quality for the Tsaobis baboons (Baniel et al. 2018*a*; Dezeure et al. 2021*b*) and other baboon populations (Zinner et al. 2001). We computed home ranges for each group using kernel density estimates and the adehabitatHR package ('kernelUD' function) (Calenge 2006) based on the daily 30-min GPS locations from 2005-2019 (in Figure 1, we plotted NDVI values for the J group home range; the two other groups' range showed identical patterns). We then extracted the mean NDVI per 16 day-period on a 500 m × 500 m resolution (these 16-days windows are imposed by the resolution of the NASA datasets) across these periods using the MODIS13A1 data provided by NASA (Didan et al. 2015) within these home ranges. Daily NDVI was computed by linear interpolation and then averaged to obtain a monthly value (see also Dezeure et al. 2021*a*).

In subsequent analyses, to test the influence of environmental unpredictability on baboon reproductive seasonality, we disentangled seasonal from non-seasonal variations of NDVI (Figure 1A). To achieve this, and for each month of the calendar year, we first computed seasonal variation using the mean monthly NDVI values across all 15 years of study, and labelled this variable 'NDVI_S'. We then computed non-seasonal variation as the differences between each actual monthly value in a given year and this mean monthly value across years, and labelled this variable 'NDVI_NS'. For example, for L group in January, NDVI_S=0.140. This refers to the NDVI value observed in January averaged across years throughout the study period (2005-2019). In January 2005, when NDVI=0.158, we calculated NDVI_NS=0.018 (i.e. 0.158 minus 0.140). This positive value of NDVI_NS indicates that the habitat in January 2005 was greener than for an average month of January. More broadly, seasonal variables reflect within-year variation only (predictable variations, consistent between years), while non-seasonal variables reflect between-year variation only (unpredictable, inconsistent between years).

Statistical analyses

We tested our three hypotheses about the causes of non-seasonal breeding in a series of four models (Table 1). Models 1 and 2 tested our hypotheses in relation to their effects on female fitness, using two measures: IBI and infant mortality, respectively. Models 3 and 4 tested our hypotheses in relation to their effects on female reproductive timings, again using two measures: the timing of cycle resumption and probability of conception, respectively.

Models 1 and 2

For Model 1, exploring the length of the IBI following the birth of an infant (in days), we ran a linear mixed model (LMM), while for Model 2, exploring the probability of infant mortality before weaning (i.e. before 550 days), we ran a generalized linear mixed model (GLMM) with a binomial error structure (see also Supplement, Section S3). The identity of the female/mother was included as a random effect to control for the non-independence of observations of the same female/mother. Both models comprised the following fixed effects.

First, to test our hypotheses, we included *: (i) non-seasonal environmental variation (NDVI_NS)*. Under the non-seasonal environment hypothesis (H1), female reproductive performance should be highly sensitive to non-seasonal environmental variations in an environment with important between-year fluctuations of rainfall and food availability. Therefore, we expected females to have longer IBIs and higher offspring mortality before weaning when monthly food availability was lower than average for those months (i.e. accounting for seasonal variation). We estimated the non-seasonal environmental variation using the NDVI_NS variable described above. We averaged NDVI_NS across the whole period spanning the IBI for Model 1, and from conception to 550 days of age (for live infants) or to death (for dead infants) for Model 2. (ii) *Reproductive synchrony.* Under the asynchrony hypothesis (H2), we expected that when reproductive synchrony increased, IBI would be longer and infant survival would be lower. In both models, we considered as a proxy of reproductive synchrony the number of infants born in the same group, in a given time window of variable length around the birth of the focal infant. We computed the number of infants born *x* months before, *x* months after, and *x* months surrounding the birth of the focal infant, where *x* = 1, 2, 4 = or 6 months for a total of 12 variables. We identified the best of these twelve variables as the one minimizing the AIC of a model including only this fixed effect (but controlling for all random effects) for each of our two response variables. We then incorporated this best-synchrony variable, which was the number of infants born in the 4 months surrounding the birth of the focal infant (i.e. 2 months before and 2 months after) for IBI, and the month after for infant mortality, into the full model (see also Supplement, Section S3). *(iii) Interactions between female rank and both seasonal (see metric below) and non-seasonal (NDVI_NS) environmental variations*. Under the social rank hypothesis (H3a), we expected lower-ranking females to suffer higher fitness costs during environmental harshness. *(iv) Interaction between female rank and reproductive synchrony*. Under the social rank hypothesis (H3b), we expected lower ranking females to suffer higher fitness costs when reproductive synchrony in the group was higher.

Second, as control variables, we included: (i) *Seasonal environmental variation*, to control for those seasonal variations that are known to affect individual fitness, even for this non-seasonal breeder (Dezeure et al. 2021*a*). Seasonal environmental variation at Tsaobis is unimodal, with one rainy season followed by one food peak per year, in a pattern that is by definition periodic with a period of one year. Because such periodic variation can be represented by sine waves (English et al. 2012*b*; Rickard et al. 2012), which allow for the introduction of a circular variable into a multivariate model (See Supplement, Section S2), we used a sine term of the birth date of the focal infant to describe the timing of that infant's birth in the annual cycle (in radians). We used only one harmonic and changed the phase value φ (to

0, π/6, π/3, π/2, 2*π/3 or 5*π/6), to account for potential phase shifts across the year (see Supplement, Sections S3 and S4) (Dezeure et al. 2021*b*). For these models, we could not average NDVI_S to capture seasonal environmental variation across extended periods such as the mean duration between two births (for IBI) and between conceptions and weaning (for mortality) because those equal two years on average (and thus an average of two years would be constant for every individual). Nonetheless, the sine wave with the best phase was highly correlated with seasonal fluctuations of NDVI (phase = 5* π/6, for J group, Pearson correlation test: R = -0.92, t = -31.5, p < 0.001) so we used only this fixed effect to capture seasonal environmental variation. (ii) *The number of adult females in the group* during the birth year of the focal infant, which is an indicator of within-group competition. A reduction in group size is often associated with an increase of primate (including baboon) female fertility, in particular by shortening IBI (Altmann and Alberts 2003; Borries et al. 2008). There may be an optimum in group size which makes living in both small and large group costly in terms of reproduction (Markham et al. 2015). Therefore, we tested both the quadratic and simple effect of the number of adult females in the group by selecting the full models (i.e. with all random and fixed effects except the reproductive synchrony variable and the rank interaction terms) with the lowest AICs. We selected the quadratic effect for Model 1 and the simple effect for Model 2. (iii) *Group identity*, to control for possible differences between social groups. (iv) *Maternal social rank* during the birth year. Lower-ranking females were expected to have longer IBIs and lower infant survival (Bulger and Hamilton 1987; Gesquiere et al. 2017; Dezeure et al. 2021a). (v) *Maternal parity.* Primiparous females have not yet achieved full body size and may lack the relevant experience to provide optimal offspring care in comparison to multiparous females. Consequently, they could have longer IBIs, and their offspring could face a higher mortality probability (Altmann and Alberts 2005; Gesquiere et al. 2017). (vi) *Infant sex.* We expected mothers of males to have longer IBIs than mothers of female infants, and possibly lower survival, in this sexually dimorphic species (Bercovitch and Berard 1993; but see Cheney et al. 2004; Gesquiere et al. 2017).

For Model 1, the IBI model, we also included a quadratic effect of female age (years). Following Gesquiere et al. (2017), we expected both younger and older females to have longer IBIs. We kept parity as fixed effect in the IBI model for consistency, and after checking for the absence of collinearity between our fixed effects (parity and female age) in our model (vif < 2).

Models 3 and 4

In the case of Models 3 and 4, because seasonal reproduction is usually characterized by a mating season (determined by the seasonality of female fertility or sexual receptivity) and/or a birth season (determined by the seasonality of conceptions), we tested our hypotheses in relation to both the monthly timing of cycle resumptions, i.e., the beginning of the mating period for each female (Model 3), and the monthly timing of conceptions (Model 4). We did not analyze births because conceptions and births were highly dependent in our dataset (most conceptions had been estimated based on the dates of birth), and because females should have more flexibility to adjust the timings of conceptions than births.

To calculate the 'cycle resumption' response variable (Model 3), we assessed the monthly probability that a female would resume cycling during those time windows in which cycle resumption was possible, i.e., following the post-partum anestrus period, which lasts between 223 to 550 days in our population (7-18 months). During the 14 years of study and for each female, we considered only those months that were included within this window of possibility (7-18 months after each birth) and coded 0 if she did not commence cycling in a given month, and 1 if she did. Similarly, to calculate the 'conception' response variable (Model 4), we considered whether a female was cycling during each month of the 14 years of study, and for each cycling month coded 0 if she did not conceive and 1 if she did. For each model, we ran a GLMM with a binomial error structure, with the identity of the female set as a random effect.

Regarding our predictors, there were several differences in our approach between Models 1 and 2 versus Models 3 and 4, reflecting their different foci on fitness and timing effects respectively. First, we used a different proxy of reproductive synchrony in Models 3 and 4: the 'monthly number of conceptions' in the same group as the focal event.

Second, the effects of environmental variations (NDVI_S and NDVI_NS) and group reproductive synchrony (number of conceptions per month) on the timing of cycle resumptions and conceptions may operate over various time periods. We thus used a moving-window approach to consider possible time period effects (van de Pol et al. 2016). For our two environmental variables, we identified the best time window testing periods covering 0 to over 12 months prior to the focal event using an AIC-based selection procedure in a univariate mixed model containing only the fixed effect of interest (see Supplement, Figure S1 and Section S4). We then added the best variable as a fixed effect in our final multivariate model. For group reproductive synchrony, we investigated the effects of the number of conceptions *x* months before (labelled 'Xb' and in blue in Figure 2), *x* months after (labelled 'Xa' and in green in Figure 2), and *x* months surrounding (labelled 'Xs' and in red in Figure 2), with x=1, 2, 4 or 6 months , resulting in 12 different models for each response variable. Details on these procedures are given in Figure 2 and in the Supplement, Section S4. Note that a female's probability of conceiving can, in theory, be related to the future conceptions of her group mates; specifically, if a subordinate female has her probability of conception reduced due to the harassment of a higher-ranking lactating female who resumes cycling shortly thereafter (Baniel et al. 2018*b*).

To test our hypotheses, the fixed effects in both models comprised: (i) *Non-seasonal environmental variations (NDVI_NS)*. Under the non-seasonal environment hypothesis (H1), we expected the probabilities of cycling resumption and conception to increase when the food availability was higher than average for this particular time of the year. (ii) *Reproductive synchrony*. Under the asynchrony hypothesis (H2), we expected the probabilities of cycling resumption and conception to increase when the group synchrony decreased. (iii) *Interactions between female rank and environmental variations (both seasonal and non-seasonal)*. Under the social rank hypothesis (H3a), we expected that higher-ranking females would be less sensitive to environmental variation than lower-ranking ones. (iv) *Interaction between reproductive synchrony and female rank*. Under the social rank hypothesis (H3b), we expected that higher-ranking females would be less sensitive to group reproductive synchrony than lower-ranking ones.

As control variables we also included: (i) *Seasonal environmental variations (NDVI_S)*. Even for non-seasonal breeders, the intensity of the seasonal environment (regardless of its non-seasonal variation) could affect both the probability to resume cycling and to conceive for females (Cheney et al. 2004). In this population, the annual conceptive peak occurs at the end of the rainy season (Dezeure et al. 2021*a*) and we therefore expect seasonal environmental variation to affect conception probabilities. (ii) *The number of adult females in the group* during the year of the reproductive event. We expected to find a negative effect of this indicator of within-group competition on the probability of conception (Bulger and Hamilton 1987; Beehner et al. 2006; Roberts and Cords 2013), and possibly on cycle resumption timings. As for Models 1 & 2, we tested both the quadratic and simple effect of the number of adult females in the group by selecting the full models (i.e. with all random and fixed effects, except the reproductive synchrony variable and the rank interaction terms) with the lowest AICs. The simple effect was selected for both Models 3 & 4. (iii)

Group identity, to control for possible differences between social groups. (iv) *Female rank*. Higher-ranking females could exhibit a higher probability of conception, even if this has not been found in previous baboon studies (Wasser et al. 1998; Beehner et al. 2006; Gesquiere et al. 2017). (v) *Female parity*. Nulliparous and primiparous females often have lower reproductive performances than multiparous females, in particular a lower probability of conception (Gesquiere et al. 2017).

Statistical tests

Statistical analyses were conducted in R version 4.0.2 (R Core Team, 2018). To test our hypotheses with our four mixed models, we used the 'lmer' (for LMM, i.e. Model 1) or 'glmer' (for binomial GLMMs, i.e Models 2, 3 and 4) function of the lme4 package (Bates et al. 2015). The distribution of residuals were checked using the 'qqPlot' function of the car package for LMMs (Fox et al. 2019) and using 'simulateResiduals' from DHARMa package for binomial GLMMs (Hartig 2020). All quantitative variables were z-transformed to have a mean of zero and a standard deviation of one in order to facilitate model convergence. When the fits obtained were singular, we double-checked the results by running the exact same models with a Bayesian approach, using the 'bglmer' function from the blme package (Dorie 2015). To diagnose the presence of multicollinearity, we calculated the variance inflation factor (VIF) for each of the predictors in each full model using the vif function of the R car package (Fox et al. 2019). These VIFs were < 2.5 across all our final models. We also removed from the models presented in the main text the non-significant interactions, in order to interpret the estimates of the simple effects (and when an interaction was significant, we also tested the significance of the simple effects without their interaction term, and present the results where necessary). During the model selection process (see Supplement, Sections S3 and S4), some variables had very close AIC values (ΔAIC < 2, see Supplement, Tables S2 and S3) suggesting that they were equally supported. In such cases, we re-ran the final model by including the variable with the second lowest AIC value (instead of the variable with the lowest AIC value) to check whether it would affect our results. We found that the results were qualitatively similar and this extra step can be found in the code uploaded into the Dryad Digital Repository https://doi.org/10.5061/dryad.dr7sqvb1n (Dezeure et al. 2022).

Uncertainty in the dates of conceptions, births, and cycle resumptions were taken into account in all models, by running 1000 models with randomized dates (Supplement, Section S1). We pooled the 1000 obtained estimates for each fixed effect of each model using Rubin's rules (Van Buuren and Groothuis-Oudshoorn 2011). Briefly, the estimates are simply averaged, but not their standard errors, as both the variation between imputations and within an imputation must be taken into account (see Supplement, Section S1 for more details on such computations). We thus extracted and presented in the Results section (Tables 2-5) the mean estimates and their pooled standard errors, along with their 95% confidence intervals and associated P-values. Only those fixed effects whose confidence intervals did not cross zero and whose P-values < 0.05 were treated as having support.

RESULTS

We tested our three non-exclusive hypotheses using four models to explain the evolution of non-seasonal breeding, focusing on two fitness parameters (IBI and infant mortality before weaning, Models 1 and 2) and two timings of reproductive events (cycle resumption and conception, Models 3 and 4). See Table 1 for a summary of predictions and results. Below we describe the support for each hypothesis based on the results across the four models.

Minimal support for the non-seasonal environment hypothesis (H1)

Non-seasonal NDVI variation (NDVI_NS), despite being substantial at Tsaobis (Figure 1A), had no effect on our first indicator of reproductive performance: IBI (Table 2). However, survival to weaning was lower for infants who were raised in relatively bad periods in terms of food availability (Table 3, Figure 1C), in support of H1. Non-seasonal variation of NDVI did not affect the timing of cycle resumption (Table 4), or probability of conception (Table 5), and thus failed to support H1 in these models. In contrast, we found various effects of seasonal environmental variation, either expressed by the sine term derived from the infant date of birth (for IBI and infant mortality, Tables 2 and 3) or by seasonal NDVI variation (for conception, Table 5 and Supplement, Figure S2). However, we did not detect any effect of seasonal environment variation on cycle resumption timings (Table 4). In all, we found more effects of seasonal than non-seasonal environmental variation on baboon reproduction.

Minimal support for the reproductive asynchrony hypothesis (H2)

We found no effect of reproductive synchrony on IBI (Table 2), infant mortality (Table 3), or the timing of cycle resumption (Tables 4 and S2), contrary to H2. Moreover, the influence of reproductive synchrony on the probability of conception was positive, contrary to H2 (Table 5; without the interaction between rank and reproductive synchrony, estimate = 0.28, SE = 0.08, 95% CI = [0.11, 0.44], P-value = 0.001). Additional analyses were run to characterize female's temporal sensitivity to others' conceptions. First, we found that conception likelihood is better explained by the mean number of conceptions occurring before, rather than around or after, the focal event (Figure 2C). Second, conception likelihood is better explained by the mean number of conceptions occurring 4 or 6 than 1 or 2 months before (Figure 2C). Taken together, our results indicate that female conceptive probability responds more to past than current or future numbers of conceptions in the group.

Social rank hypothesis: strong support for rank-related variation in response to reproductive synchrony (H3b), but not in response to environmental fluctuations (H3a)

We did not detect any rank-related variation of reproductive seasonality in relation to non-seasonal environmental fluctuations (H3a), tested by our interactions between rank and environmental variation for each of our four measures of reproduction: IBI (Table 2), infant survival (Table 3), the timing of cycle resumption (Tables 4), and the probability of conceptions (Table 5). However, we did find support for rank-related variation in reproductive seasonality in relation to reproductive synchrony (H3b), tested by interactions between rank and synchrony, in three of our four measures: IBI (Table 2), the timing of cycle resumption (Table 4) and the probability of conception (Table 5); but such effects were not seen on infant survival (Table 3). We will consider each of these three observed effects in turn. Firstly, subordinate females experienced longer IBIs when more infants were born in the group in the four months surrounding their parturition; this effect was not detectable for high-ranking females (Table 2, Figure 3A). Secondly, lower-ranking females were less likely to resume cycling when there had been more conceptions over the past 6 months, whereas higher-ranking females were unaffected (Table 4, Figure 3B). More precisely, and as for conceptions, we found that conceptions occurring before (over the past 2, 4 or 6 months) better explain cycle resumption probabilities than conceptions occurring soon before (1 month), around or after the focal cycle resumption (Figure 2B). Thirdly, subordinate females were more likely to conceive when there had been more conceptions in the group over the past 4 months, and this pattern was less pronounced in dominant females (Table 5, Figure 3C).

Finally, we designed a set of simple simulations in order to link observed patterns of behavior to demography, by examining how the results of our models, and specifically the rank-related influence of reproductive synchrony on IBI, affects emerging patterns of reproductive seasonality at the population-level (Supplement, Section S5, Figure S3). We did not examine separately the contrasting effects of reproductive synchrony on individual cycling resumption and probability of conception, because variation in IBI length is generated by variation in both the timing to cycling resumption post-birth and the number of cycles to conception (Gesquiere et al. 2017), and is thus not independent from these effects. We found that the negative, rank-related effect of reproductive synchrony on IBI length translates into a weakened intensity of reproductive seasonality at the population level, although the magnitude of the effect remains modest for populations exhibiting low reproductive seasonality as in Tsaobis (Supplement, Figure S3). Nevertheless, the effect size increases when the intensity of reproductive seasonality increases (Supplement, Figure S4).

DISCUSSION

Our study emphasizes the importance of the social environment, and more precisely of group reproductive synchrony, on reproductive phenology in a wild social primate. Female reproductive competition may alter reproductive timings, regardless of the season. Below we speculate about the potential drivers of such intrasexual reproductive competition, with limited access to paternal care as a primary candidate. We further shed light on individual variation in strategies over reproductive phenology dependent on female rank, and on the possible significance of our findings to understand the evolution of vertebrate breeding seasonality.

The rank-related asynchrony hypothesis may help to explain non-seasonal breeding (H3b)

Several results converged to indicate that non-seasonal breeding may be an emergent consequence of individual strategies facing reproductive competition, leading to breeding asynchrony and a decreased intensity of reproductive seasonality. **First**, our results showed a fitness cost of birth synchrony for subordinate females only, who experienced a longer interval to the next birth when more infants were born in the same group in the two months surrounding the birth of their own infant. Such an effect may reflect the influence of reproductive synchrony on cycle resumption experienced by subordinate females when breeding soon after other females of the group. It could also reflect the costs suffered by subordinate females with lower phenotypic quality who miss the optimal conception peak and thus breed after dominants in a given year. **Second**, the more conceptions that occurred during the previous six months within the group, the less likely it was that a lower-ranking female would resume cycling. In addition, there was no effect of seasonal or non-seasonal environmental variation on the probability of cycling resumption, indicating that reproductive competition may be an important factor causing the extension of a mating season in chacma baboons, and thus decreasing the strength of reproductive seasonality. **Third**, the likelihood to conceive increased after conceptions had peaked in a female's group in the previous four months, but was less affected by the number of conceptions occurring during the same month or the following months. Subordinate females were more strongly affected by this positive effect. A positive effect of others' conceptions on a female's conceptive probability was unexpected, and is thus hard to interpret in the context of our hypotheses and predictions, although perhaps not incompatible (see below). **Fourth**, we used a simple set of simulations informed by the output of our multivariate GLMMs in order to examine the link between individual competitive strategies and group-level reproductive phenology. Variations in the probability of conception and in the timing of cycling resumption are the two key components of variation in the length of interbirth interval (Gesquiere et al. 2017). As such, it is critical to understand how the effects of reproductive synchrony on the length of interbirth interval may affect the group-level reproductive seasonality. The results of such simulations indicate that the cost of reproductive synchrony observed on the length of IBI translates into a decreased intensity of reproductive seasonality.

At the proximate level, the alteration of subordinates' reproductive timings dependent on other females' reproductive phenology may be explained by female-female competition at different stages of the reproductive cycles. Indeed, both the longer IBIs and later cycling resumption experienced by subordinate females after periods of high reproductive synchrony most likely reflect late weaning and/or a delay to cycling resumption after weaning in these females. An increase in the number of cycles to conception could also theoretically lead to longer IBIs, but this seems unlikely given that the probability of conception increases with reproductive synchrony. Both late weaning and a delay to cycling resumption may be caused by poor female condition, which reflects reduced access to food resources in periods of high reproductive synchrony. We know that this is not related to food availability in the environment as we controlled for such signals in our models, and male-mediated access to the best food patches may thus be the critical factor explaining this pattern. In our baboon population, higher-ranking pregnant and lactating females monopolize access to the dominant males at the expense of subordinate females (Baniel et al. 2016, 2018*a*): when more females are pregnant or lactating, subordinate females will be increasingly excluded from sharing the best food patches with the dominant males. This mechanism may underpin the negative effects of reproductive synchrony on IBI length and cycling resumption. Additionally, this same mechanism of male access may also explain the positive effect of reproductive synchrony on the probability of conception. Once females are in sufficient condition to resume cycling, their probability of conception will be contingent on competition for access to males from other cycling females (Tsaobis: Huchard and Cowlishaw 2011; Baniel et al. 2018*a*; other baboons: Zinner et al. 1994). As such, following a period of high synchrony in conceptions, there will be relatively fewer cycling females to compete for access to males, thus leading to an increase in conception probability for subordinate females, as observed. Crucially, pregnant and lactating females may be less able to keep fertile females away from their male partners, because males are strongly motivated to mate with such females (Baniel et al. 2017). At the ultimate level, females likely adopt competitive tactics to minimize the number of other females with whom they will have to share paternal care in a polygynous mating system, where the alpha male sires nearly 70% of offspring born in the group (Tsaobis: Huchard et al. 2010; other baboons: Alberts 2012). Such an interpretation is strengthened by recent evidence that pregnant and lactating females aggressively target cycling females who mate with the father of their offspring, presumably in an attempt to delay the birth of a paternal half-sibling (Baniel et al. 2018*b*). Paternal care in baboon societies increases offspring survival and growth (Charpentier et al. 2008) through several mechanisms, including protection against infanticide (Huchard et al. 2010; Palombit 2012; Palombit 2003; Palombit et al. 1997), aggression from conspecifics (Lemasson et al. 2008; Nguyen et al. 2009), and increased access to food during weaning (Huchard et al. 2012).

More generally, although fitness costs of synchronous births have been reported in several species, including social primates like yellow baboons (Wasser and Starling 1988) and bonnet macaques (Silk 1989), cooperative breeders such as meerkats and banded mongooses (Clutton-Brock et al. 2001; Nichols et al. 2012), and polygynous birds where females compete over paternal care (Yasukawa et al. 1990, 1993; Slagsvold and Lifjeldt 1994), their consequences for patterns of seasonal reproduction have never been established at the population level. Our study provides the first empirical evidence that reproductive competition at the individual level may alter reproductive phenology at the population level.

Weak support for the non-seasonal environment hypothesis (H1) and no support for a rank-mediated response to seasonal and non-seasonal environmental variations (H3a)

Periods of unusual food scarcity (beyond the seasonal norm) increased offspring mortality before weaning. Food scarcity is known to negatively impact offspring survival before weaning in baboon and other primate populations (Altmann et al. 1977; Cheney et al. 2004; Kleindorfer and Wasser 2004; Gogarten et al. 2012; Campos et al. 2020). Nonetheless, these studies did not disentangle predictable/seasonal from unpredictable/non-seasonal environmental variation, whereas our results show that when infants face harsher periods in early life than usual (i.e. lower than the yearly average), they are less likely to survive. Extreme climatic conditions, including severe droughts, become more frequent with climate change (Easterling et al. 2000; Dai 2013), and our results confirm, in addition to other studies (Wiederholt and Post 2011; Korstjens and Hillyer 2016; Campos et al. 2020), that extreme climatic conditions negatively affect the demography of wild primates – and probably many other taxa.

We failed to detect any additional evidence in support of the non-seasonal environment hypothesis. Females did not adjust their cycle resumptions or conceptions in relation to between-year variation of rainfall or food availability, but only adjusted their conceptions in line with seasonal variation in food availability (Table 5). Despite important year-to-year variation in cumulative rainfall and thus food availability in Southern Africa, rainfall nearly always occurs during the rainy season (Figure 1A; Alberts et al. 2005). In other words, the timing of rains, when they occur (and the associated food peak), remains relatively predictable, which may explain why female reproductive phenology is more responsive to seasonal than non-seasonal environmental variations. In addition, our 15-year sample in this study may limit our ability to detect the impact of year-to-year environmental variation in such long-lived species. Two aspects of baboons' biology may also help them to cope with non-seasonal environmental variation and thus explain the absence of strong support for the non-seasonal environment hypothesis in this study. First, baboons are generalist, eclectic omnivores and as such, they are well-equipped to face periods of food scarcity by extracting and exploiting various fallback food resources (Altmann 2009; Swedell 2011). Second, in the context of the income-capital breeder continuum, a common framework for the study of alternative strategies to finance offspring production, capital breeders such as baboons are able to store energy for later use and are often better adapted to such between-year variable environments than income breeders (which rely on current energy available to breed) (Drent and Daan 1980; Brockman and van Schaik 2005; Stephens et al. 2014). In all, our results suggest that females may have their reproduction timed according to predictable food peaks rather than relying on the energetic stores accumulated from past unpredictable food availability.

Females show similar reproductive responses to variation in food availability irrespective of their social rank. A large fraction of baboon resources at Tsaobis is non-monopolizable, and it is possible that subordinate females use fallback foods during food scarcity, or negotiate the tolerance of dominant females to access monopolizable food patches (Sick et al. 2014; Marshall et al. 2015). This ability of subordinates to develop counter-strategies to limit the costs of contest feeding competition has been found in a wide range of animal species (Bugnyar and Kotrschal 2004; Hewitson et al. 2007; Held et al. 2010). Nevertheless, although subordinate females might have been able to minimize competition for food, it appears they were less able to minimize competition over access to mates, given the observed rank-dependent effects of reproductive synchrony on female reproduction. This may reflect the fact that males are more monopolizable than food, e..g, subordinate females can spread out and forage away from dominant females to minimize feeding competition, but cannot do the same for mating competition because dominant females tend to be closely associated with males.

Other perspectives to explain the evolution of non-seasonal breeding

On top of reproductive asynchrony, several additional ecological or evolutionary mechanisms can help to explain non-seasonal breeding in social primates, and probably beyond. First, a previous study in this population showed the existence of two optimal birth timings in the annual cycle, because the timing that minimizes the mother's IBI occurs four months before the timing that minimizes offspring mortality (Dezeure et al. 2021*a*). Maternal trade-offs over birth timing may be widespread, and help to explain extended birth seasons between these optima due to individual variation in trade-off resolution. Second, offspring mortality occurs year-round for a variety of reasons including disease, predation, and infanticide; the latter cause can affect up to 30% of offspring in some baboon populations (Palombit 2012). Females typically resume reproduction quickly after losing an infant in social primates (Palombit et al. 2000; Palombit 2003, 2012, 2015) and this may occur even outside the reproductive season. For example, in geladas (*Theropithecus gelada*), females who lose an infant from infanticide following male takeovers can conceive outside the main mating season, resulting in a second annual peak of births, as male takeovers are seasonal (Tinsley Johnson et al. 2018). Such ability to conceive/resume reproduction year-round, which may have evolved in response to high levels of infanticide or more broadly extrinsic infant mortality (infanticide is the cause of 19 to 28 % of infant death in our population: Baniel et al. in prep.), may contribute to the absence of seasonal breeding at the population level. Future studies could usefully explore the interplay between ecology, life-history and sociality that may influence variation in the intensity of reproductive seasonality across mammals, a field that has been largely understudied.

Conclusion

We detected fitness costs associated with birth synchrony, and showed that the reproductive phenology of females, in particular subordinates, may be influenced by the phenology of other females in the group, in a way that decreases the intensity of reproductive seasonality. Such results likely reflect the occurrence of intrasexual competition over access to paternal care. In contrast, female reproductive events were poorly predicted by unpredictable variations in resource availability, such as droughts or peaks of primary productivity, suggesting that females have their reproduction timed according to future, predictable food peaks, rather than relying on the energetic stores accumulated from past unpredictable food availability. This study highlights the importance of female reproductive competition as one driver of the evolution of reproductive seasonality in social mammals, opening new avenues for future research. It further points to the necessity of understanding the causes and mechanisms of competition at the behavioral level to gain insights on key demographic parameters of a population, including its responses to environmental change.

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Authors’ contribution statement

JD, LB, GC and EH conceived the ideas and designed the methodology; JD, AB, AJC, GC, EH collected the data; JD analyzed the data; LB created the simulation model, JD led the writing of the manuscript. EH funded the study. All authors contributed critically to the drafts and gave final approval for publication.

DATA, CODE AND SUPPORTING MATERIAL

Data and codes used in this study are provided in the following Dryad repository: https://doi.org/10.5061/dryad.dr7sqvb1n

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Tables

Table 1: Models and predictions of each fixed effect depending on the hypothesis tested.

We indicated with a black and bold writing the predictions supported by our results, and with a grey writing the predictions not supported by our results. We used a darker grey and added an asterisk in cases where we found mixed support for the corresponding prediction, which depends on the proposed interpretation (see Discussion).

		Fitness effects		**Timing effects**	
	Hypothesis	**Model 1** **IBI**	**Model 2** **Infant survival**	**Model 3** **Cycling resumption**	**Model 4** **Conception**
H1	**Non-seasonal environmental variation:** Unpredictable environmental variation leads females to retain a flexible reproductive schedule that responds opportunistically to better environmental conditions	Longer when food is scarce	**Lower when food is scarce**	Less likely when food is scarce	Less likely when food is scarce
H2	**Reproductive synchrony:** Females avoid simultaneous reproduction to reduce competition for mates, paternal care or ecological resources	Longer when female synchrony is higher	Lower when female synchrony is higher	Less likely when synchrony is higher	Less likely when synchrony is higher *
H3a	**Rank*environment effects:** Subordinate females experience more restricted resource access during the lean season	Negative effects of food scarcity on IBI greater for subordinate females	Negative effects of food scarcity on infant survival greater for subordinate females	Negative effects of food scarcity on cycling resumption greater for subordinate females	Negative effects of food scarcity on conception greater for subordinate females

H3b	**Rank*synchrony effects:** Costs of reproductive synchrony fall more heavily on subordinate females	**Negative effects of synchrony on IBI greater for subordinate females**	Negative effects of synchrony on infant survival greater for subordinate females	**Negative effects of synchrony on cycling resumption greater for subordinate females**	Negative effects of synchrony on conception greater for subordinate females *

Table 2: Environmental and social determinants of interbirth interval (IBI) duration (Model 1).

We ran 1000 models with simulated birth date, in order to consider the uncertainty of birth dates. The table shows the pooled estimates along with their standard errors (SE), their associated 95% confidence intervals and p-values of the predictors computed following Rubin's rules and provided by these 1000 linear mixed models including female identity as random effect, based on 120 observations from 43 females. Significant effects are indicated in bold. The best fit for seasonal environmental variation is the sine term of the infant date of birth with a phase of π/6. The best fit for non-seasonal environmental variation is the mean 'NDVI_NS' between the two births. The best fit for reproductive synchrony is the number of infants born in the group in the four months surrounding the focal birth. For categorical predictors, the tested category is indicated in parentheses. The interactions between female rank and seasonal environmental variation (Estimates=-0.099, SE Estimates=14.505, p=0.995), and between female rank and non-seasonal environmental variation (Estimates=10.164, SE Estimates=10.484, p=0.333), were not significant and were thus excluded from the full model.

Hypothesis tested	Fixed effects	Estimates	SE Estimates	Confidence intervals (95%)		P-values
				Lower	Upper	
H1	Non-seasonal environmental variation	6.637	11.203	-15.322	28.595	0.554
H2	Reproductive synchrony	3.976	10.544	-16.691	24.643	0.706
H3b	**Reproductive synchrony : Rank**	**-31.927**	**10.334**	**-52.182**	**-11.673**	**0.002**
Control	**Seasonal environmental variation**	**54.462**	**18.378**	**18.441**	**90.483**	**0.003**
	Number of adult females	**-268.508**	**65.694**	**-397.269**	**-139.748**	**$<10^{-3}$**
	Number of adult females ^{2}	**263.447**	**62.119**	**141.694**	**385.201**	**$<10^{-3}$**
	Group (L)	-55.794	30.339	-115.258	3.671	0.066
	Group (M)	**-213.936**	**85.912**	**-382.324**	**-45.549**	**0.013**
	Rank	**-37.955**	**13.671**	**-64.751**	**-11.160**	**0.006**
	Parity (primiparous)	5.982	33.812	-60.289	72.253	0.860
	Sex (Male)	**45.512**	**19.565**	**7.164**	**83.859**	**0.020**
	Age	**-169.302**	**67.286**	**-301.183**	**-37.421**	**0.012**
	Age ^{2}	**146.302**	**63.912**	**21.033**	**271.570**	**0.022**

Table 3: Environmental and social determinants of infant mortality before weaning (0/1: survived until / died before weaning) (Model 2).

We ran 1000 models with simulated birth date, in order to consider the uncertainty of birth dates. The table shows the pooled estimates along with their standard errors (SE), their associated 95% confidence intervals and p-values of the predictors computed following Rubin's rules and provided by these 1000 binomial generalized mixed models including female identity as a random effect, based on 19 dead infants out of 195 from 57 females. Significant effects are indicated in bold. The best fit for seasonal environmental variation is the sine term of the infant date of birth with a phase of π/2. The best fit for non-seasonal environmental variation is the mean 'NDVI_NS' from infant conception to weaning or death. The best fit for reproductive synchrony is the number of infants born in the group in the four months surrounding the focal birth. For categorical predictors, the tested category is indicated in parentheses. The interactions between female rank and seasonal environmental variation (Estimates=-0.584, SE Estimates=0.435, p=0.180), between female rank and non-seasonal environmental variation (Estimates=-0.249, SE Estimates=0.330, p=0.451) and between female rank and group reproductive synchrony (Estimates=0.028, SE Estimates=0.242, p=0.907) were not significant and were thus excluded from the full model.

Hypothesis tested	Fixed effects	Estimates	SE Estimates	Confidence intervals (95%)		P-values
				Lower	Upper	
H1	**Non-seasonal environmental variation**	**-0.617**	**0.292**	**-1.189**	**-0.045**	**0.035**
H2	Reproductive synchrony	0.315	0.266	-0.206	0.837	0.236
Control	**Seasonal environmental variation**	**-1.338**	**0.413**	**-2.147**	**-0.529**	**0.001**
	Number of adult females	-0.054	0.284	-0.611	0.502	0.849
	Group (L)	**-1.214**	**0.559**	**-2.309**	**-0.118**	**0.030**
	Group (M)	0.736	1.824	-2.839	4.312	0.687
	Rank	**-0.532**	**0.265**	**-1.052**	**-0.013**	**0.045**
	Parity (primiparous)	-0.476	0.757	-1.961	1.008	0.530
	Sex (Male)	0.197	0.477	-0.738	1.132	0.680

Table 4: Environmental and social determinants on the timing of cycle resumption in a given month (Model 3).

We ran 1000 models with simulated cycle resumption date in order to take into account their uncertainty. The table shows the pooled estimates along with their standard errors (SE), their associated 95% confidence intervals and p-values of the predictors computed following Rubin's rules and provided by these 1000 binomial generalized linear mixed model including female identity as a random effect, based on 155 cycle resumptions out of 1768 observations from 56 females. Significant effects are indicated in bold. The best fit for seasonal environmental variation is the 'NDVI_S' over the past four months. The best fit for non-seasonal environmental variation is the 'NDVI_NS' over the past three months. The best fit reproductive synchrony is the mean number of conceptions in the group over the past six months. For categorical predictors, the tested category is indicated in parentheses. The interactions between female rank and seasonal environmental variation (Estimates=0.013, SE Estimates=0.099, p=0.897), and between female rank and non-seasonal environmental variation (Estimates=-0.050, SE Estimates=0.078, p=0.524), were not significant and were thus excluded from the full model.

Hypothesis tested	Fixed effects	Estimates	SE Estimates	Confidence intervals (95%)		P-values
				Lower	Upper	
H1	Non-seasonal environmental variation	0.135	0.089	-0.040	0.309	0.131
H2	Reproductive synchrony	-0.200	0.115	-0.424	0.025	0.082
H3b	**Reproductive synchrony : Rank**	**0.218**	**0.104**	**0.014**	**0.423**	**0.037**
Control	Seasonal environmental variation	-0.135	0.106	-0.342	0.073	0.205
	Number of adult females	-0.028	0.156	-0.334	0.277	0.857
	Group (L)	0.136	0.183	-0.224	0.495	0.460
	Group (M)	-0.615	0.707	-2.001	0.771	0.385
	Rank	0.038	0.090	-0.137	0.214	0.669
	Parity (primiparous)	-0.226	0.232	-0.680	0.228	0.330

Table 5: Environmental and social determinants on the probability of conception in a given month (Model 4).

We ran 1000 models with simulated conception date in order to take into account their uncertainty. The table shows the pooled estimates along with their standard errors (SE), their associated 95% confidence intervals and p-values of the predictors computed following Rubin's rules and provided by these 1000 binomial generalized linear mixed model including female identity as a random effect, based on 241 conceptions out of 1484 observations from 68 females. Significant effects are indicated in bold. The best fit for seasonal environmental variation is the 'NDVI_S' over the past two months. The best fit for non-seasonal environmental variation is the 'NDVI_NS' over the past 12 months. The best fit reproductive synchrony is the mean number of conceptions in the group over the past four months. For categorical predictors, the tested category is indicated in parentheses. The interactions between female rank and seasonal environmental variation (Estimates=-0.004, SE Estimates=0.081, p=0.957), and between female rank and non-seasonal environmental variation (Estimates=-0.017, SE Estimates=0.078, p=0.825), were not significant and were thus excluded from the full model.

Hypothesis tested	Fixed effects	Estimates	SE Estimates	Confidence intervals (95%)		P-values
				Lower	Upper	
H1	Non-seasonal environmental variation	-0.120	0.082	-0.281	0.041	0.146
H2	**Reproductive synchrony**	**0.302**	**0.085**	0.134	0.469	**$<10^{-3}$**
H3b	**Reproductive synchrony : Rank**	**-0.185**	**0.079**	-0.339	-0.030	**0.019**
Control	**Seasonal environmental variation**	**0.191**	**0.082**	0.031	0.352	**0.020**
	Number of adult females	**-0.489**	**0.143**	-0.770	-0.209	**0.001**
	Group (L)	-0.103	0.179	-0.455	0.248	0.564
	Group (M)	-1.143	0.632	-2.381	0.096	0.071
	Rank	0.107	0.088	-0.066	0.280	0.226
	Parity (nulliparous)	**-1.006**	**0.212**	-1.421	-0.591	**$<10^{-3}$**
	Parity (primiparous)	0.160	0.236	-0.301	0.622	0.496

Figures

Figure 1: Non-seasonal environmental variation in Tsaobis and its influence on infant mortality.

In Panel A, we plot variation in Tsaobis food availability (i.e. NDVI, in green) over the study period, and its seasonal (in dashed blue) versus non-seasonal (in dashed red) components. In panel B, the black points are the fitted values of our full model (Table 3) focusing on infant survival before weaning in relation to the mean value of non-seasonal NDVI between infant conception and infant death or the end of weaning (550 days). The blue curve represents the logistic fit, and the shaded area displays the 95% confidence interval around it.

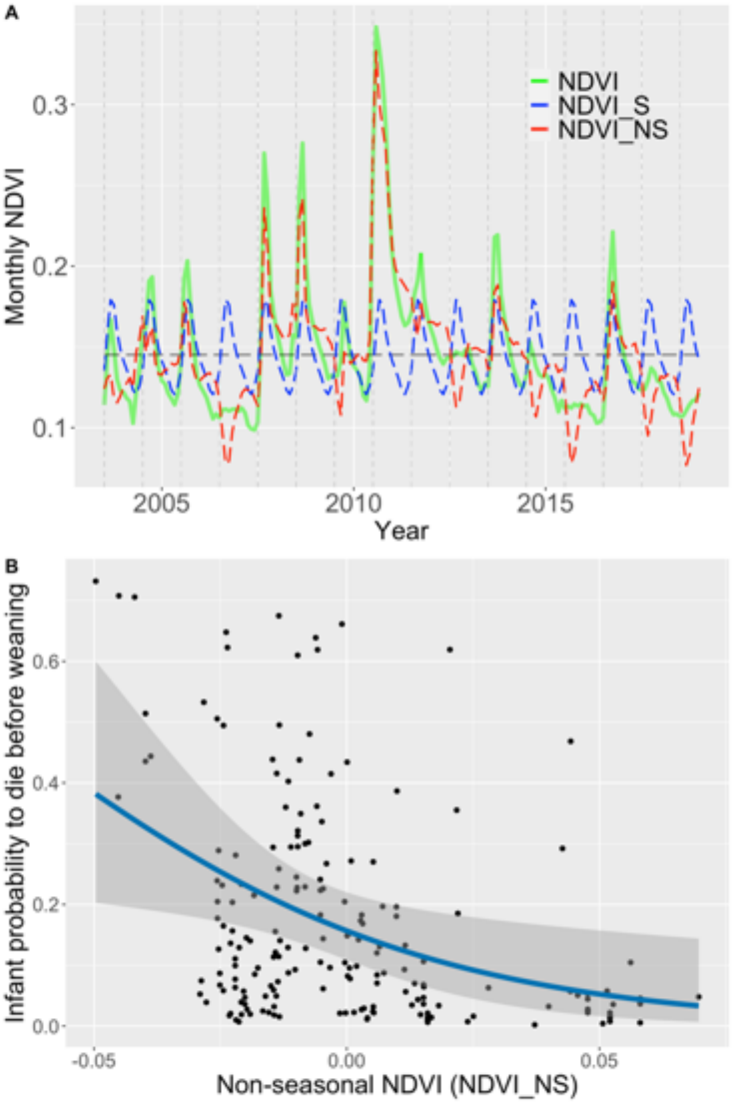


Figure 2: Effects of group reproductive synchrony over various time windows on cycle resumption and conception probabilities.

In Panel A, we illustrate the different time windows investigated when looking at the effects of past, current and future conceptions in the group, our proxy of group reproductive synchrony, on probabilities of cycle resumption and conception (Models 3 & 4). In Panels B & C, we present ΔAIC of each model compared to the best model for respectively the probabilities of cycle resumption (Panel B, model 6b) and of conception (Panel C, model 4b).

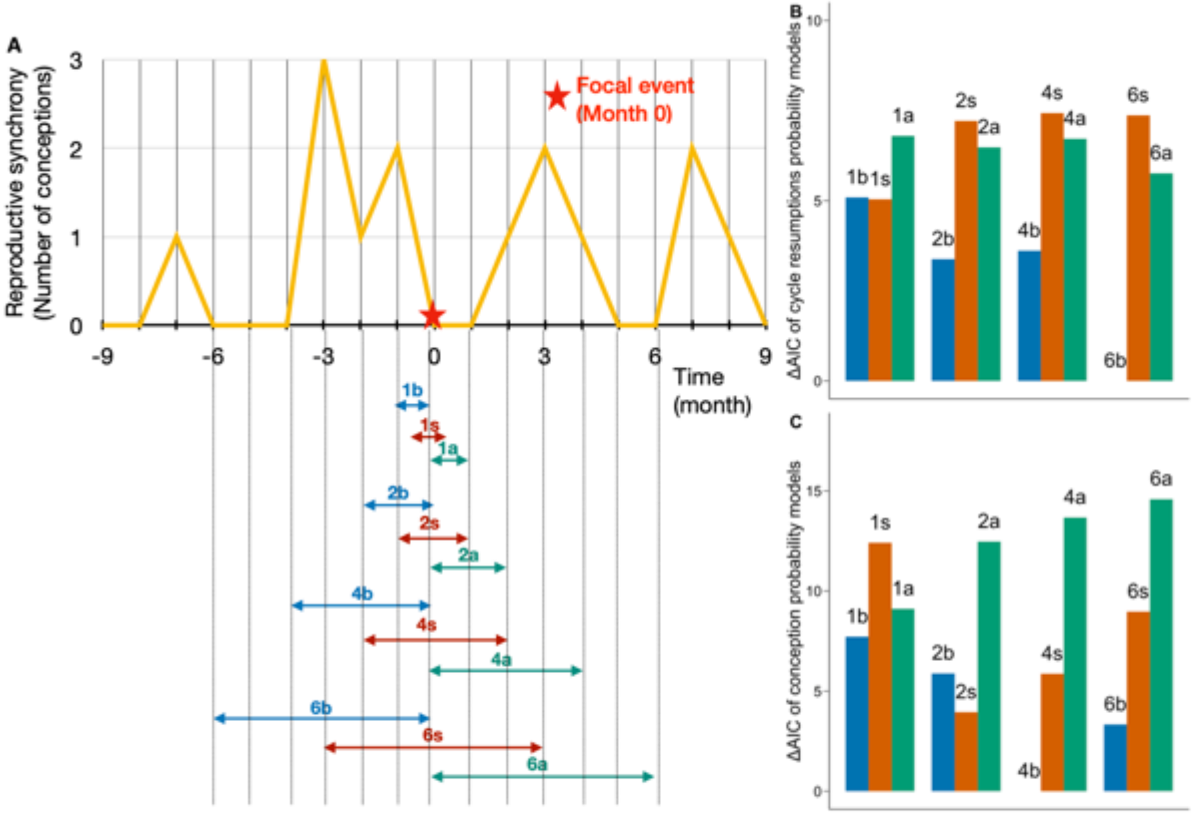
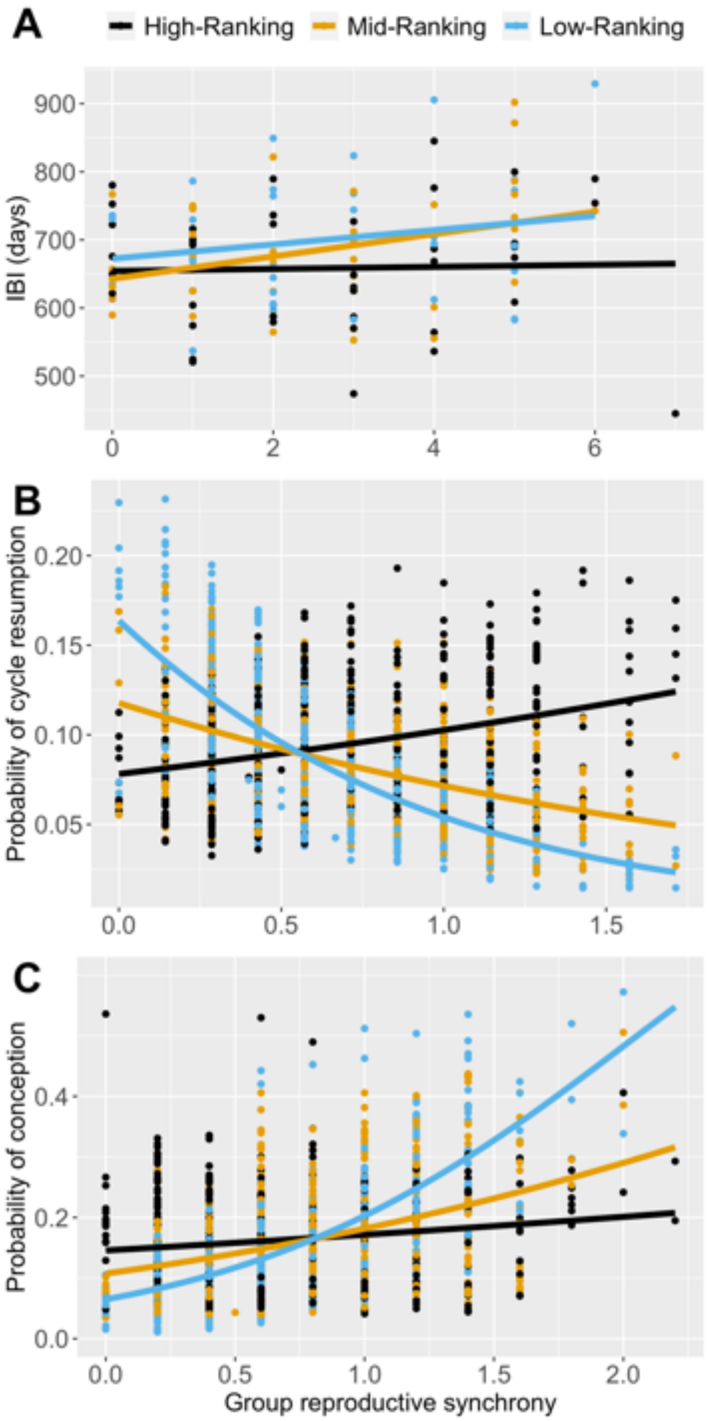


Figure 3: Group reproductive synchrony affects interbirth intervals and probabilities of cycle resumption and conception.

For each panel, each dot represents a fitted value of our full models depending on our proxy of group reproductive synchrony (see Table 2 for Panel A, Table 4 for Panel B and Table 5 for Panel C). For illustrative purposes, female social rank has been converted into a categorical variable, with females being low-ranking when their rank value is below 0.34 (blue points), high-ranking when it is above 0.67 (black points), and mid-ranking otherwise (orange points). The curves represent the linear (Panel A) or logistic (Panels B & C) fits for each social rank.



SUPPLEMENT FOR:

Evolutionary determinants of non-seasonal breeding in wild chacma baboons

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The American Naturalist

Contents

SECTIONS

Section S1. Uncertainty of the dates of conceptions, births and cycle resumptions in our models

Dates of conceptions, births and cycle resumptions were estimated in many cases, because the Tsaobis baboons were not followed all year long. Uncertainty in these estimations varied with the time of year, as we generally followed baboons during the cold and dry months, which introduced a systematic bias in our dataset that was important to account for in these analyses. We ran a set of randomizations to evaluate the robustness of the significant effects (see also Dezeure et al. 2021*a* following the same procedure). For each estimated value of our variables (date of cycle resumptions, conceptions and births), we created an artificial set of 1000 simulated dates covering the full range of potential dates for a given reproductive event. A random date was drawn between the minimal and maximal estimate for each value of a given reproductive parameter, and this procedure was repeated 1000 times. For example, for a birth estimated to occur between the 13th of January and the 2nd of February, we randomly chose a date between Jan 13th and Feb 2nd in one given iteration of our 1000 simulations.

For models 1 and 2, the randomization affected the sine term of the focal infant's date of birth, introduced as a fixed effect in the full model, as these dates of birth could be uncertain. We ran 1000 models, and from these computed manually the pooled estimates of fixed effects along with their standard errors, 95% confidence intervals and p-values based on Rubin's rules, following the same formulae as those used in the package 'mice' (Van Buuren and Groothuis-Oudshoorn 2011). For models 3 and 4, the randomization affected the response variables (probability to resume cycling and to conceive, respectively). Similarly, we ran 1000 models using each of these 1000 simulated datasets, and extracted pooled estimates of the fixed effects, along with their standard errors, 95% confidence intervals and p-values using Rubin's rules (Van Buuren and Groothuis-Oudshoorn 2011). All tables of results presented in the main text

(Tables 2-5) report the parameters obtained through this randomization process controlling for uncertainties in the estimates of reproductive events.

Section S2. Characterization of Tsaobis environmental variation

We considered four environmental aspects to characterize environmental variation at Tsaobis: the photoperiod (daytime length), temperature, rainfall and vegetation cover (food availability). First, we extracted these four environmental factors as follows:

(i) Daily daytime length at Karibib (situated 60km north of Tsaobis) was computed using sunset and sunrise time in this town from a website (‘https://dateandtime.info’), then converted into minutes and averaged per month.

(ii) Mean daily daytime land surface temperatures over an 8-day period per pixel of 1km*1km resolution were obtained using MODIS data (product MOD11A2) provided by NASA (Wan et al. 2015). These data were extracted from a rectangular geographic area encompassing the global ranging area of the Tsaobis baboons, computed using GPS locations collected by observers every 30 minutes when following the study groups. We used the minimal and maximal latitude and longitude recorded between 2005 and 2019, producing a rectangular area of 14km*19km. We extracted the mean pixel value for every 8-period in this area, and further compute the monthly means of the daily temperatures (mean pixel values) across 2004-2019.

(iii) Daily rainfall was obtained at 0.25*0.25 degree resolution (corresponding to 28*28km at this latitude) from satellite data sensors (product TRMM 3B42) (Huffman et al. 2016) available on the Giovanni NASA website, using the same geographical area as for temperatures. Monthly accumulated rainfalls (summed across daily values) were subsequently averaged between 2004 and 2019.

(iv) The method of extraction of NDVI, our proxy of food availability, reflecting vegetation cover, is provided in the main text and in a recently published paper (Dezeure et al. 2021*a*).

Once extracted, we were interested to disentangle seasonal from non-seasonal variations of our four environmental variables, allowing us to test in subsequent analyses the influence of environmental unpredictability on baboon reproduction. These environmental conditions might show either strong seasonality, varying in a consistent predictable pattern across years, or weak seasonality, varying in less predictable way between years. We identified which of these four conditions showed strong versus weak seasonality by assessing how well they were predicted by a sine wave. Sine waves provide a good representation of seasonal variation (English et al. 2012; Rickard et al. 2012). At Tsaobis where environmental variation is unimodal, with one rainy season followed by one food peak per year, these variations are by definition periodic (with a period of one year). Importantly, sine waves allow the introduction of a circular variable into a multivariate model: the possible effects of the month or date of birth are circular with a period of one year, and not linear, as the 31st of December is the day before the 1st of January, and should be considered as close as the 31st of October and the 1st of November are, for example. In addition, a sinusoidal term can be used to detect any seasonal effects, i.e. any effect of month or date of birth on reproductive parameters, which may not be captured by our other environmental variables. For example, the phenology of some baboon foods may depend on particular combinations of climatic and photoperiodic cues that very between plant species, and would therefore be difficult to detect using a single environmental predictor. To assess the strength of seasonal variations of each of our environmental factors, we ran four linear models in which each of our four environmental variables was the response variable and a sinusoidal term was the only fixed effect. This sinusoidal term was as follows (as all our environmental variables were monthly values):

$$sin(Month + \varphi)$$

The month of the year in the formula above was converted in a radian measure, so that the period, i.e. one year, equaled to 2*π, ranging from π/6 for January to 2*π for December. We tested different phase values (0, π/6, π/3, π/2, 2*π/3 or 5*π/6), to account for potential phase shifts across the year. For example, a phase of 0 could maximize the months of March or September, a phase of π/6 could maximize the months of February or August (depending on the sign of the fitted coefficient), etc. We then selected the best phase as the one minimizing the AIC in our model. We found that the sine term of phase π/2, maximizing December (the solstice), explains 88% of temperature variation and 99% of photoperiod variation between 2004 and 2019. Thus, in the following analyses, temperature and photoperiod are represented with the sine term only, as we show that between-year variations of temperature and photoperiod are negligible compared to within-year variations. On the contrary, and as expected (see Figure 1A, which shows substantial between-year variations of NDVI), the sinusoidal term with the best phase only explained 18% of NDVI variation and 20% of rainfall variation. For NDVI and rainfall, we thus decomposed their seasonal and non-seasonal variation. We first computed the mean monthly values across all 15 years, and labelled these variables as 'NDVI_S' and 'Rain_S'. We then computed the difference between each actual monthly value in a given year and this averaged monthly value across years. We labelled these differences as 'NDVI_NS' and 'Rain_NS'. Here, seasonal variables (with the suffix 'S') reflect within-year variation only, i.e., predictable variation, consistent between years; while non-seasonal variables (with the suffix 'NS') reflect between-year variation only, i.e., unpredictable variation, inconsistent between years (see Figure 1A for a graphical representation of this decomposition).

Section S3. Models focusing on interbirth intervals and infant mortality

In these two models, we investigated the costs of environmental variation, group synchrony and rank-related variation of these costs on the fitness of both mothers and offspring, looking at two response variables: interbirth intervals (IBI) and infant mortality before weaning. We tested our three non-exclusive hypotheses, and expected to find fitness costs associated with non-seasonal environmental variations under the non-seasonal environment hypothesis (H1), with reproductive synchrony under the asynchrony hypothesis (H2), and with rank-related fitness costs, possibly linked with environmental fluctuations or synchrony, under the social rank hypothesis (H3). The different fixed effects considered are listed in the main text: non-seasonal environmental variation (‘NDVI_NS’), reproductive synchrony (‘Number_of_Infants’ born before, around or after the focal birth), an interaction term between female rank and environmental variation (both seasonal and non-seasonal: ‘sin(Date of Birth + φ):Rank’ and ‘NDVI_NS:Rank’), an interaction term between female rank and reproductive synchrony, seasonal environmental variation (sine term of juvenile birth date), the number of adult females in the group (‘Number_Adult_Females’) (we also tested its quadratic effect, see main text and below), group identity (‘Group’), female rank (‘Rank’), female parity (‘Parity’), and infant sex (‘Sex’). We also included female identity (‘Identity_female’) as a random effect. We further included female age (‘Age’) along with its quadratic effect for the IBI models only as a fixed effect (see main text).The two final global models we ran to test our hypothesis are shown in equations (1) and (2) below:

$$(1)\ IBI \sim NDVI\_NS + Number\_of\_Infants(Window\_IBI\ ) + \\ (\sin\,(Date\ of\ Birth + \varphi){:}\,Rank) + (NDVI\_NS{:}\,Rank) + \\ (Number\_of\_Infants(Window\_IBI\ ){:}\,Rank) + \sin\,(Date\ of\ Birth + \varphi) + \\ Number\_Adult\_Females\ + \text{Number\_Adult\_Females}^2 + Group + Rank +$$

$Parity + Age + Age^2 + Sex,\ random =$

$Identity\_female,\ family = 'gaussian'$

(2) $Infant\ mortality\ before\ weaning \sim NDVI\_NS +$

$Number\_of\_Infants(Window\_Mortality) + (\sin(Date\ of\ Birth +$

$\varphi): Rank) + (NDVI\_NS: Rank) +$

$(Number\_of\_Infants(Window\_IBI): Rank) + \sin(Date\ of\ Birth + \varphi) +$

$Number\_Adult\_Females + Group + Rank + Parity + Sex,\ random =$

$Identity\_female,\ family = 'binomial'$

In order to run these global models, we first had to identify, among the fixed effects (i) the best sine phase to capture seasonal environmental variation (of six possible phases), (ii) the best measure of non-seasonal environmental variation (of two measures, NDVI_NS or rainfall_NS), and (iii) the best time window to capture reproductive synchrony (of 12 possible time windows), where the best were defined as those which minimized AIC in the corresponding univariate models. We took as example the IBI models, and we followed the exact same steps for the infant mortality models. We selected the best environmental variables in univariate models whereas we selected the best social variables in multivariate models (i) as the effects of environmental variables on the reproductive parameters are less likely to be modulated by social variables than the reverse; and (ii) as reproductive events may be clustered (and/or spaced) due to both environmental (i.e. ecological seasonality) and social (i.e. reproductive competition) variables, we needed to control for the effect of environmental seasonality when assessing social effects on observed patterns of reproductive synchrony in our hypotheses tests.

First, we ran the six following univariate models (3), (4), (5), (6), (7) and (8), considering only the seasonal environmental variations, i.e. the offspring dates of births with a sine term:

(3) $IBI \sim \sin(Date\ of\ Birth), random = Identity\_female, family = 'gaussian'$

(4) $IBI \sim \sin(Date\ of\ Birth + \pi/6), random = Identity\_female, family = 'gaussian'$

(5) $IBI \sim \sin(Date\ of\ Birth + \pi/3), random = Identity\_female, family = 'gaussian'$

(6) $IBI \sim \sin(Date\ of\ Birth + \pi/2), random = Identity\_female, family = 'gaussian'$

(7) $IBI \sim \sin(Date\ of\ Birth + 2 * \pi/3), random = Identity\_female, family = 'gaussian'$

(8) $IBI \sim \sin(Date\ of\ Birth + 5 * \pi/6), random = Identity\_female, family = 'gaussian'$

The only differences between these six models are the value of the phase. For the IBI model, the best phase equaled to π/6 while for infant mortality model it equaled π/2 (Table S2). By doing so, we characterized the best seasonal environment fluctuations likely to affect our two response variables.

Secondly, we estimated the non-seasonal environmental variation using the NDVI_NS and Rainfall _NS variables described above. We averaged NDVI_NS and Rainfall_NS across the whole period spanning the IBI for Model 1, and from conception to 550 days of age (for live infants) or to death (for dead infants) for Model 2. The two non-seasonal fixed effects: (i) NDVI_NS and (ii) Rain_NS were introduced in separate models given that they reflect the same effect and are well correlated (Pearson correlation test: R=0.51, t=8.10, $p<10^{-4}$). We ran the following models, (9) and (10), to determine which non-seasonal environmental variation was the best in each model:

(9) $IBI \sim \sin\left(Date\ of\ Birth + \frac{\pi}{6}\right) + NDVI\_NS, random = Identity\_female, family = 'gaussian'$

(10) $IBI \sim \sin\left(Date\ of\ Birth + \frac{\pi}{6}\right) + Rainfall\_NS, random = Identity\_female, family = 'gaussian'$

For both IBI and infant mortality, the models containing NDVI_NS had lower AIC values (Table S2). NDVI_NS was subsequently used as our metric to represent non-seasonal environmental variation.

Thirdly, we tested both the quadratic and simple effect of the number of adult females in the group by selecting the full models (i.e. with all random and fixed effects except the reproductive synchrony variable and the rank interaction terms) with the lowest AICs, with the structure of the following models (11) and (12):

(11) $IBI \sim NDVI\_NS + \sin(Date\ of\ Birth + \varphi) + Number\_Adult\_Females + Group + Rank + Parity + Age + Age^2 + Sex,\ random = Identity\_female,\ family = 'gaussian'$

(12) $IBI \sim NDVI\_NS + \sin(Date\ of\ Birth + \varphi) + Number\_Adult\_Females + Number\_Adult\_Females^2 + Group + Rank + Parity + Age + Age^2 + Sex,\ random = Identity\_female,\ family = 'gaussian'$

We selected the quadratic effect for Model 1 and the simple effect for Model 2 (Table S2).

Fourthly, we selected the best time window for our reproductive synchrony variable, i.e. the number of infants born before, around or after the focal infant (written 'Number_of_Infants' in models (1) and (2)). 'Window_IBI' and 'Window_Mortality' could be: X months before, surrounding or following the focal birth with X being equal to 1, 2, 4 or 6 months. Therefore, we ran 12 models for each response variable, with these different time windows, with the structure of the following models (13) and (14):

(13) $IBI \sim NDVI\_NS + Number\_of\_Infants(Window\_IBI) + \sin(Date\ of\ Birth + \varphi) + Number\_Adult\_Females + Group + Rank + Parity + Age + Age^2 + Sex + (NDVI\_NS{:}Rank) + (\sin(Date\ of\ birth + \varphi){:}Rank) + (Number\_of\_infants(Window\_IBI){:}Rank),\ random = Identity\_female,\ family = 'gaussian'$

(14) $Infant\ mortality\ before\ weaning \sim NDVI\_NS + Number\_of\_Infants(Window\_Mortality) + \sin(Date\ of\ Birth + \varphi) + Number\_Adult\_Females + Group + Rank + Parity + Sex + (NDVI\_NS{:}Rank) + (\sin(Date\ of\ birth + \varphi){:}Rank) + (Number\_of\_infants(Window\_Mortality){:}Rank),\ random = Identity\_female,\ family = 'binomial'$

We identified the best time window, 'Window_IBI' and 'Window_Mortality': 'Window_IBI' and 'Window_Mortality' were both the number of infants born in the four months surrounding the focal birth (Table S2). We finally ran our global models (1) and (2) with these best synchrony time windows and best phase of seasonal variation, along with all other predictors.

During this model selection process, some variables had very close AIC values ($\Delta AIC < 2$, see Table S2) suggesting that they were equally supported. In such cases, we re-ran the final model by including the variable with the second lowest AIC value (instead of the variable with the lowest AIC value) to check whether it would affect our results. We found that the results were qualitatively similar and this extra step can be found in the code uploaded into the Dryad repository).

Section S4. Models focusing on timing of cycle resumption and probability of conception

In these two models, we investigated if females adjusted or delayed their reproductive timings, focusing on their onset of cycle resumption and conception, according to (H1) non-seasonal environmental fluctuations under the non-seasonal environment hypothesis, or (H2) reproductive synchrony under the asynchrony hypothesis. In (H3), we tested whether female reproductive timings showed rank-related adjustments in response to environmental variations or group synchrony. The different fixed effects considered are listed in the main text: non-seasonal environmental variation ('NDVI_NS'), reproductive synchrony ('Mean_Number_of_Conception' before, around or after the reproductive focal event), an interaction term between female rank and environmental variation (both seasonal and non-seasonal: 'NDVI_S:Rank' and 'NDVI_NS:Rank'), an interaction term between female rank and reproductive synchrony ('Mean_Number_of_Conception:Rank'), seasonal environmental variation ('NDVI_S'), the number of adult females in the group ('Number_Adult_Females'), group identity ('Group'), female rank ('Rank') and female parity ('Parity'). We also included female identity ('Identity_female') as a random effect. The two final global models we ran to test our hypothesis are shown in the equations (1) and (2) below:

$$(1)\, Conception \sim NDVI\_NS(Window\_NS\_Conception)\ +$$

$$Mean\_Number\_of\_Conceptions(Window\_Conception) +$$

$$+(NDVI\_S(Window\_S\_Conception){:}\, Rank) +$$

$$(NDVI\_NS(Window\_NS\_Conception) : Rank) +$$

$$(Mean\_Number\_of\_Conceptions(Window\_Conception): Rank) +$$

$$NDVI\_S(Window\_S\_Conception\ ) \ + Number\_Adult\_Females + \ Group +$$

$$Parity + Rank,\ random = Identity\_female, family = binomial$$

$$(2)\ Cycle\ resumption \sim NDVI\_NS(Window\_NS\_Cycle\_resumption) \ +$$

$$Mean\_Number\_of\_Conceptions(Window\_Cycle\_resumption) +$$

$$+(NDVI\_S(Window\_S\_Cycle\_resumption): Rank) +$$

$$(NDVI\_NS(Window\_NS\_Cycle\_resumption) : Rank) +$$

$$(Mean\_Number\_of\_Conceptions(Window\_Cycle\_resumption): Rank) +$$

$$NDVI\_S(Window\_S\_Cycle\_resumption) \ + Number\_Adult\_Females +$$

$$Group + Parity + Rank,\ random = Identity\_female, family = binomial$$

In order to run these global models, we first had to identify, among the fixed effects (i) the best sine phase to capture seasonal environmental variation (of six possible phases), (ii) the best time window to capture NDVI (NDVI_S and NDVI_NS) and rainfall (Rain_S and Rain_NS) variation, where the best were defined as those which minimized AIC in the corresponding univariate models, (iii) the best measure of both seasonal and non-seasonal environmental variation (of three measures of seasonal variations: the sine term, NDVI_S and Rain_S ; and of two measures of non-seasonal variations: NDVI_NS or Rain_NS), and (iv) the best time window to capture reproductive synchrony, where the best were defined as those which minimized AIC in the corresponding multivariate models. The main differences from the steps explained in Section S3 are that we considered other aspects of environmental seasonality, and a different metric of group reproductive synchrony. We took as examples the conception models, and we followed the exact same steps for the cycle resumption models. Following the same reasoning as for Models (1) and (2) (Section S3), we selected the best environmental variables in univariate models and the best social variables in multivariate models.

We first investigated which were the best ecological factors to consider between sinusoidal parameters (seasonal environmental fluctuations only, reflecting temperatures, day time length, or any other seasonal parameter), rainfall and the normalized difference vegetation index (NDVI). The three seasonal effects: (i) the sine wave, (ii) NDVI_S, and (iii) Rain_S were introduced in separate models given that they reflect seasonal environmental variations and were highly correlated (Pearson correlation test: $R>0.84$ and $p<10^{-4}$ for each pair). Similarly, the two non-seasonal fixed effects: (i) NDVI_NS and (ii) Rain_NS were introduced in separate models given that they reflect the same effect and are well correlated (Pearson correlation test: $R=0.51$, $t=8.10$, $p<10^{-4}$). We therefore introduced each of our seasonal environmental parameters (sine wave of the month, Rain_S, NDVI_S), and likewise each of our non-seasonal parameters (Rain_NS, NDVI_NS), in separate models. Although we could have simply tested one representative of each, the timing of cycle resumptions and conceptions could be affected by different environmental factors, so we considered the best of all possible environmental predictors for each model.

First of all, we estimated the best phase of the sine fixed effects (with the months in radian), by running the six univariate following models (3), (4), (5), (6), (7), (8):

(3) $Conception \sim \sin(Month)\,,\ random = Identity\_female, family = binomial$

(4) $Conception \sim \sin(Month + \pi/6)\,,\ random = Identity\_female, family = binomial$

(5) $Conception \sim \sin(Month + \pi/3)\,,\ random = Identity\_female, family = binomial$

(6) $Conception \sim \sin(Month + \pi/2)\,,\ random = Identity\_female, family = binomial$

(7) $Conception \sim \sin(Month + 2 * \pi/3)\,,\ random = Identity\_female, family = binomial$

(8) $Conception \sim \sin(Month + 5 * \pi/6)\,,\ random = Identity\_female, family = binomial$

The only differences between these three models are the value of the phase. It was the phase 2*π/3 which was selected. We followed the same method for the timings of cycle resumption as response variables, and we selected π/2 as the best phase (Table S3).

For rainfall and NDVI fixed effects, we investigated a time window of 0-12 months because (i) other studies found lagged effects of similar length when studying the effect of weather variability on the demography and reproduction of primates (Wiederholt and Post 2011; Campos et al. 2017), and (ii) a lag of more than 12 months (i.e. one annual cycle) would presumably not influence reproductive seasonality. See also Figure S1 for a graphical representation of the 13 time windows tested (taking the example of NDVI_S). We ran sets of univariate models to select the best time window for each rainfall and NDVI predictors (see models (9), (10), (11), (12)). A time window of N months meant that we averaged the value of the fixed effect over the past N months. Therefore, each time window indicated below ('Rainfall_Window_S_Conception', 'Rainfall_Window_NS_Conception', 'NDVI_Window_S_Conception', 'NDVI_Window_NS_Conception') reflects the average value of the environmental effect considered over the past N months, N going from 0 to 12.

(9) $Conception \sim Rain\_S(Rainfall\_Window\_S\_Conception),\ random = Identity\_Female, family = binomial$

(10) $Conception \sim NDVI\_S(NDVI\_Window\_S\_Conception),\ random = Identity\_Female, family = binomial$

(11) $Conception \sim Rain\_NS(Rainfall\_Window\_NS\_Conception),\ random = Identity\_Female, family = binomial$

(12) $Conception \sim NDVI\_NS(NDVI\_Window\_NSConception),\ random = Identity\_Female, family = binomial$

We selected Rain_S over the past 4 months, Rain_NS over the past 12 months, NDVI_S over the past 2 months, and NDVI_NS over the past 12 months, respectively (Table S3). We similarly ran the same models ((9), (10), (11), (12)) with the timings of cycle resumption as the response variable. We selected for the cycle resumption Rain_S over the past 5 months, Rain_NS over the past 4 months, NDVI_S over the past 4 months and NDVI_NS over the past 3 months (Table S3).

After this first step of identifying the best time window and best phase, we ran other models to estimate which ecological factors, between the sine term, rainfall (Rain_S and Rain_NS), and NDVI (NDVI_S and NDVI_NS) effects, were the best to predict our response variables. To do so, we ran the three following models ((13), (14), and (15)):

(13) $Conception \sim \sin(Month + 2 * pi/3) + (1|ID)$

(14) $Conception \sim Rain\_S(4) + Rain\_NS(12) + (1|ID)$

(15) $Conception \sim NDVI\_S(2) + NDVI\_NS(12) + (1|ID)$

We similarly ran models (13), (14) and (15) for cycle resumptions as response variable. For both our response variables, the NDVI model was the best one (Table S3), and we consequently only kept the NDVI fixed effects in our global model looking at reproductive synchrony effects too (and only presented the models with NDVI fixed effects in the main text of this study).

As for Models 1 and 2 (Section S3), we tested both the quadratic and simple effect of the number of adult females in the group by selecting the full models (i.e. with all random and fixed effects, except the reproductive synchrony variable and the rank interaction terms, see the following models (16) & (17)) with the lowest AICs:

$$(16)\quad Conception \sim NDVI\_NS(Window\_NS\_Conception) + NDVI\_S(Window\_S\_Conception) + Number\_Adult\_Females + Group + Parity + Rank,\ random = Identity\_Female, family = binomial$$

$$(17)\quad Conception \sim NDVI\_NS(Window\_NS\_Conception) + NDVI\_S(Window\_S\_Conception) + Number\_Adult\_Females + Number\_Adult\_Females^2 + Group + Parity + Rank,\ random = Identity\_Female, family = binomial$$

The simple effect was selected for both Models 3 & 4 (Table S3).

After selecting the best time windows for ecological factors, and selecting the best ecological factors, we wanted to run a global model considering reproductive synchrony as a fixed effect, taking the number of conceptions occurring in the same group as indicator. We arbitrarily restricted our exploration to a possible lag of 6 months prior to and after the focal event, on the basis that females were unlikely to react to conceptions occurring more than 6 months away from their reproductive events. In addition, females in this species were expected to compete over paternal care, which is especially important in the first 6 months of life, the age window in which vulnerability to infanticide is greatest (Palombit 2003), meaning that female reproductive competition may decrease when the age gap between their offspring is greater than 6 months. We therefore investigated the effects of reproductive synchrony by considering the number of conceptions in the group occurring before, around and after the focal reproductive event, with varying time windows going from 0 to 6 months. Our fixed effect is thus respectively the mean number of conceptions in the group occurring in the past X months, in the X months surrounding the focal, or in the X months after the focal event, with X being equal to 1, 2, 4 or 6 months. See also Figure 2A for a graphical representation of the various past and future time windows that were tested. We thus ran 12 multivariate models for each response variable with the structure of the following models (18) in order to select the best 'Window_Conception' to include in our full final model.

$$(18)\quad Conception \sim NDVI\_NS(Window\_NS\_Conception) + Mean\_Number\_of\_Conceptions(Window\_Conception) + NDVI\_S(Window\_S\_Conception\ ) + Number\_Adult\_Females + Group + Parity + Rank) + (NDVI\_S(Window\_S\_Conception){:}\,Rank) + (NDVI\_NS(Window\_NS\_Conception) : Rank) + (Mean\_Number\_of\_Conceptions(Window\_Conception){:}\,Rank)\ ,\ random = Identity\_Female, family = binomial$$

We ran the exact same models, with different best time windows for the NDVI and reproductive synchrony effects, for the cycle resumption response variable. The results shown in the tables of the main text include variables that minimized AIC in this selection process (Figure 2, Table S2), i.e. with the mean number of conceptions over the past four months for the probability of conception (Table 5), and with the mean number of conceptions over the past six months for the timing of cycling resumption (Table 4). Figure 2 shows a graphical representation of ΔAIC for each time window of group reproductive synchrony investigated for Models 3 (Figure 2B) and 4 (Figure 2C). Note that the models shown in Figure 2 were ran without the interactions between rank and seasonal or non-seasonal environmental variations as these interactions were non-significant, whereas the results of the models showed in Table S2 include these interactions (we do not observe any qualitative differences between those results).

As for Models (1) and (2) (see Section S3), some variables had very close AIC values (ΔAIC < 2, see Table S2) during this model selection process, suggesting that they were equally supported. In such cases, we re-ran the final model by including the variable with the second lowest AIC value (instead of the variable with the lowest AIC value) to check whether it would affect our results. We found that the results were qualitatively similar and this extra step can be found in the code uploaded into the Dryad repository).

Section S5. Simulations investigating how the effect of group reproductive synchrony on interbirth intervals affects the intensity of population-level reproductive seasonality

We modeled the consequences of the effect of group reproductive synchrony detected on IBI for population-level reproductive seasonality (Table 2). We investigated the consequences of these social effects using IBI only, and omitted their effects on the probability of cycle resumption and of conception, because variation in IBI is generated by variation in both the timing of cycle resumption and the probability of conception.

In a first step, we used the simplest possible model, only considering the social effect of interest (female rank and interaction between female rank and group reproductive synchrony) in a simulated population showing the same level of reproductive seasonality as our study population (Dezeure et al., 2021a). We simulated a group of females during 15 years (the length of our study period). Females were divided equally between 3 rank categories: high, medium and low. We used a constant group size of 18 females (the closest multiple of three to the median number of females in our groups: 17). We used a time step of one day. In each group, we assumed that all females would have conceived within the first 24 month-period (initiation phase) and sampled the initial birth dates randomly using births observed in our population, in order to account for their seasonality. We used the distribution of birth months in our population and assumed that births occurred on the 15th day of each month (given the uncertainty of our birth dataset, see also Section S1). Such a process resulted in an overall level of reproductive seasonality that matched the observed level. For a given female, each subsequent birth date was assessed by adding the simulated IBI to the previous one. We computed the IBI following each birth depending on the mother's rank and the group reproductive synchrony in the 3 months preceding the birth opening the IBI, according to the estimate extracted from the results of Model 1 (Table 2). To do so, we simply used the three regression functions (Figure 3A) corresponding to each rank category. In order to compare the reproductive seasonality of the population in the presence versus absence of this effect of group reproductive synchrony on IBI, we designed a second model, called thereafter 'random' model, where IBIs were only influenced by female rank and not by reproductive synchrony. We therefore used for each female a fixed value of IBI corresponding to the mean IBI value for each category of rank (High-rank=654 days, mid-rank=691 days, low-rank=696 days).

All simulations were run in R version 4.0.2 (R Core Team, 2018). We recorded all births, for both 'synchrony' and 'random' models and converted their dates in radians. We then computed the Rayleigh statistic R, using the function 'r.test' from the R package 'CircStats' (Agostinelli and Lund 2018), which measures their degree of seasonality, i.e. the strength of birth seasonality, going from 0 (births randomly distributed, i.e. completely non-seasonal) to 1 (all births occur at the same date in the annual cycle, i.e. completely seasonal) (Batschelet 1981). We repeated these simulations 1000 times for each model and compared the distributions of the

Rayleigh statistics with a Welch two sample t-test (function ‘t.test’ in R). The results of these simulations are presented in Figure S3.

In a second phase, and in order to test the robustness of these results for different levels of reproductive seasonality, we introduced an extra seasonal effect. We added a seasonality parameter called s, ranging from 0 (no seasonality) to 1 (complete seasonality). Technically, for each birth date computed, we estimated its deviation to the mean birth date in the population, i.e. the shortest number of days between the birth date and the next (or previous) 18th of November (Dezeure et al. 2021*a*). We then added (or removed) to this birth date a proportion s of the deviation (when s equals zero, all birth dates are unchanged, and when s equals 1, all births occur at the mean birth date). By modifying the value of s from 0 to 1, we were able to test the effect of group reproductive synchrony on birth seasonality on an increasing range of population-level reproductive seasonality. The results of these simulations are presented in Figure S4.

The code used for this simulation is available in the following Dryad repository: https://doi.org/10.5061/dryad.dr7sqvb1n

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TABLES

Table S1: Different methods used to estimate the dates of 241 conceptions of baboons in Tsaobis between 2005 and 2019.

Criteria used for estimation	Number of conceptions estimated	Median of the number of days of uncertainty	Range of the number of days of uncertainty
Conceptions observed in the field	68	0	0
Conceptions occurred during a field break	13	10	3 - 30
Birth date observed (in the field or during a field break)	65	10	10 - 40
Infant coloration & mother's reproductive state (Dezeure et al. 2021*b*)	56	61	0 - 151
Mother's reproductive state only (with birth observed)	23	65	21 - 153
Mother's reproductive state only (with no birth observed)	16	90	24 - 164
Total	241	10	0 - 164

Table S2: Selection of variables to include in the final models for models 1 (IBI) and 2 (infant mortality)

The model numbers correspond to the ones presented in the Section S3. For each model type, we present ΔAIC of each model compared to the best model (in bold writing). The models with ΔAIC < 2 are showed in italic writing.

Model number (Section S3)	**Model type**	**Variable**	**ΔAIC Model 1 IBI**	**ΔAIC Model 2 Infant mortality**
3	Environmental seasonality	sin(dob + 0*pi/6)	3.47	9.85
4		sin(dob + 1*pi/6)	**0.00**	11.10
5		sin(dob + 2*pi/6)	*1.47*	5.95
6		sin(dob + 3*pi/6)	6.42	0.00
7		sin(dob + 4*pi/6)	9.13	*0.04*
8		sin(dob + 5*pi/6)	7.67	4.72
9	Non-seasonal environmental variation	Rainfall_NS	9.28	3.15
10		NDVI_NS	**0.00**	**0.00**
11	Number of adult females in the group	Simple effect	22.44	**0.00**
12		Square effect	**0.00**	*1.73*
13 or 14	Group reproductive synchrony (number of births in the group)	1 months around	2.25	2.41
		1 month before	2.12	*1.75*
		1 month after	3.42	2.69
		2 months around	2.59	2.83
		2 months before	3.25	2.28
		2 months after	3.55	*1.70*
		4 months around	**0.00**	**0.00**
		4 months before	2.63	2.62
		4 months after	6.18	*1.51*
		6 months around	2.09	3.51
		6 months before	2.46	3.73

6 months after	6.54	3.36

Table S3: Selection of variables to include in the final models for models 3 (cycle resumption) and 4 (conception)

The model numbers correspond to the ones presented in the Section S4. For each model type, we present ΔAIC of each model compared to the best model (in bold writing). The models with ΔAIC < 2 are showed in italic writing.

Model number (Section S4)	**Model type**	**Variable**	**ΔAIC Model 3 Cycle resumption probability**	**ΔAIC Model 4 Conception probability**
3	Environmental seasonality (sine term)	sin(month + 0*pi/6)	*1.88*	5.62
4		sin(month + 1*pi/6)	*1.71*	8.50
5		sin(month + 2*pi/6)	*0.77*	7.13
6		sin(month + 3*pi/6)	**0.00**	2.82
7		sin(month + 4*pi/6)	*0.16*	**0.00**
8		sin(month + 5*pi/6)	*1.10*	*1.43*
9	Environmental seasonality (rainfall)	Rainfall_S 0	*0.39*	8.10
		Rainfall_S 1	*0.10*	7.68
		Rainfall_S 2	*0.77*	4.22
		Rainfall_S 3	*1.56*	*1.35*
		Rainfall_S 4	*0.70*	**0.00**
		Rainfall_S 5	**0.00**	*0.31*
		Rainfall_S 6	*0.90*	2.22
		Rainfall_S 7	*1.28*	*1.71*
		Rainfall_S 8	*1.30*	*1.67*
		Rainfall_S 9	*1.08*	2.52
		Rainfall_S 10	*1.18*	4.26
		Rainfall_S 11	*1.83*	4.02
		Rainfall_S 12	*0.39*	8.10
10	Environmental seasonality (NDVI)	NDVI_S 0	*1.87*	3.96
		NDVI_S 1	2.10	*0.61*
		NDVI_S 2	*1.43*	**0.00**
		NDVI_S 3	*0.07*	*1.70*
		NDVI_S 4	**0.00**	4.39
		NDVI_S 5	*1.21*	7.15
		NDVI_S 6	2.18	8.97
		NDVI_S 7	2.45	10.06

		NDVI_S 8	2.48	10.66
		NDVI_S 9	2.43	10.95
		NDVI_S 10	2.45	11.02
		NDVI_S 11	2.35	10.81
		NDVI_S 12	2.10	8.77
11	Non-seasonal environmental variation (rainfall)	Rainfall_NS 0	*1.10*	2.74
		Rainfall_NS 1	*1.85*	2.62
		Rainfall_NS 2	*1.69*	2.42
		Rainfall_NS 3	*0.73*	2.67
		Rainfall_NS 4	**0.00**	2.48
		Rainfall_NS 5	*1.62*	3.01
		Rainfall_NS 6	2.66	2.64
		Rainfall_NS 7	3.69	2.17
		Rainfall_NS 8	2.72	*1.73*
		Rainfall_NS 9	2.68	*1.15*
		Rainfall_NS 10	2.34	2.15
		Rainfall_NS 11	2.05	*1.02*
		Rainfall_NS 12	2.09	**0.00**
12	Non-seasonal environmental variation (NDVI)	NDVI_NS 0	*0.65*	5.11
		NDVI_NS 1	*0.59*	5.11
		NDVI_NS 2	*0.32*	5.14
		NDVI_NS 3	**0.00**	5.11
		NDVI_NS 4	*0.15*	4.74
		NDVI_NS 5	*0.73*	3.90
		NDVI_NS 6	*1.38*	3.12
		NDVI_NS 7	*1.98*	2.59
		NDVI_NS 8	2.41	*1.98*
		NDVI_NS 9	2.61	*1.67*
		NDVI_NS 10	2.68	*1.30*
		NDVI_NS 11	2.72	*0.60*
		NDVI_NS 12	2.76	**0.00**
13	Environmental variation	Sine term	2.42	5.51
14		Rainfall	*0.92*	5.48
15		NDVI	**0.00**	**0.00**
16	Number of adult females in the group	Simple effect	**0.00**	**0.00**
17		Square effect	*1.81*	*1.52*
18	Group reproductive synchrony (number of conceptions in the group)	1 months around	4.74	12.44
		1 month before	4.85	7.74
		1 month after	6.60	9.17
		2 months around	6.97	3.99
		2 months before	3.17	5.90
		2 months after	6.09	12.53

	4 months around	7.18	5.92
	4 months before	3.49	**0.00**
	4 months after	6.26	13.74
	6 months around	7.04	9.02
	6 months before	**0.00**	3.32
	6 months after	5.38	14.65

FIGURES

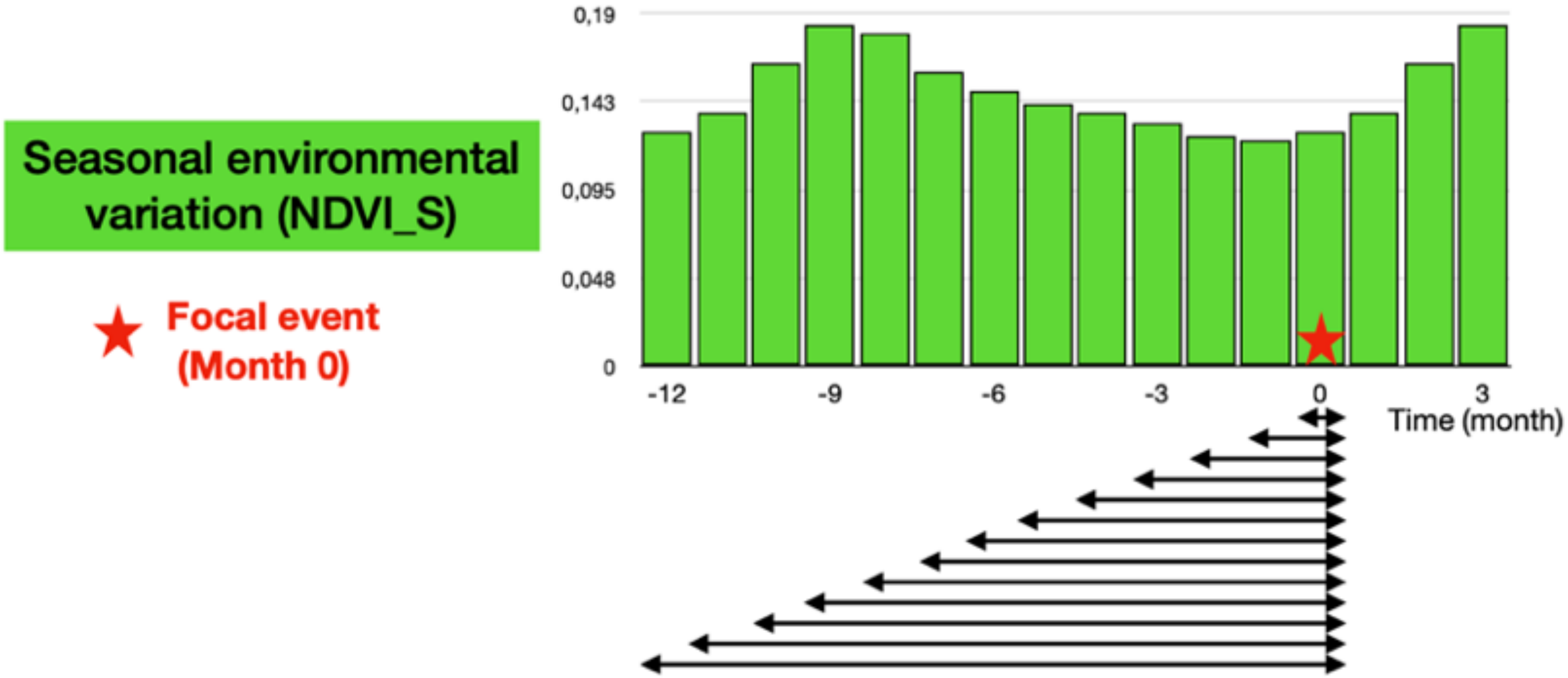

Figure S1: Examples of the different time windows considered when investigating the effects of past environmental variation on female cycle resumption and conception probabilities.

We plotted the seasonal NDVI ('NDVI_S') per month in green considering December 2018 as time 0 (and so, for example, December 2017 is indicated with -12). We tested the effect of the mean NDVI_S over the X past months, X going from 0 to 12, on female cycle resumption (Model 3) and conception (Model 4) probabilities.

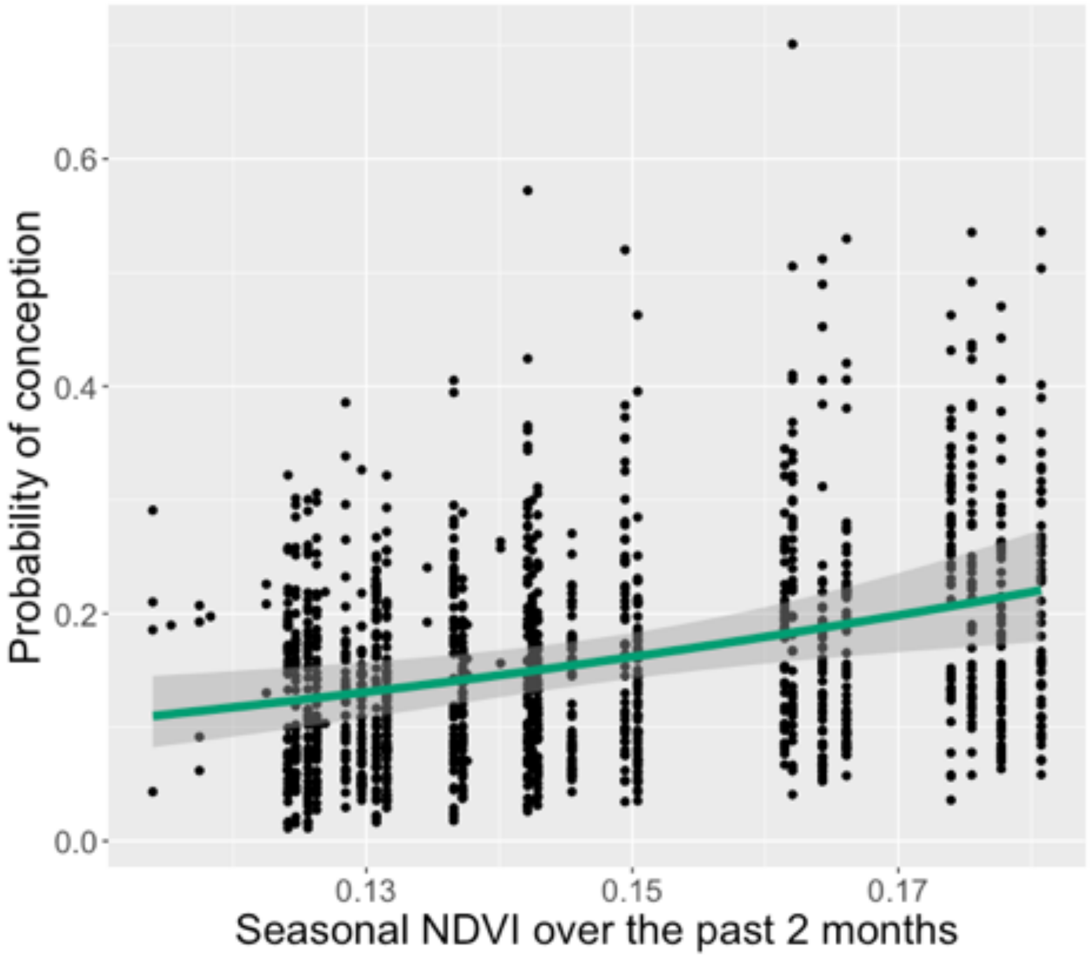

Figure S2: The probability of conception increases with higher seasonal variation of NDVI over the past two months.

Each black dot represents a fitted value of the full model (Table 5) focusing on the probability of conception according to the mean seasonal NDVI over the past 2 months. The green curve shows the logistic fit, and the shaded area displays 95% confidence intervals around it.

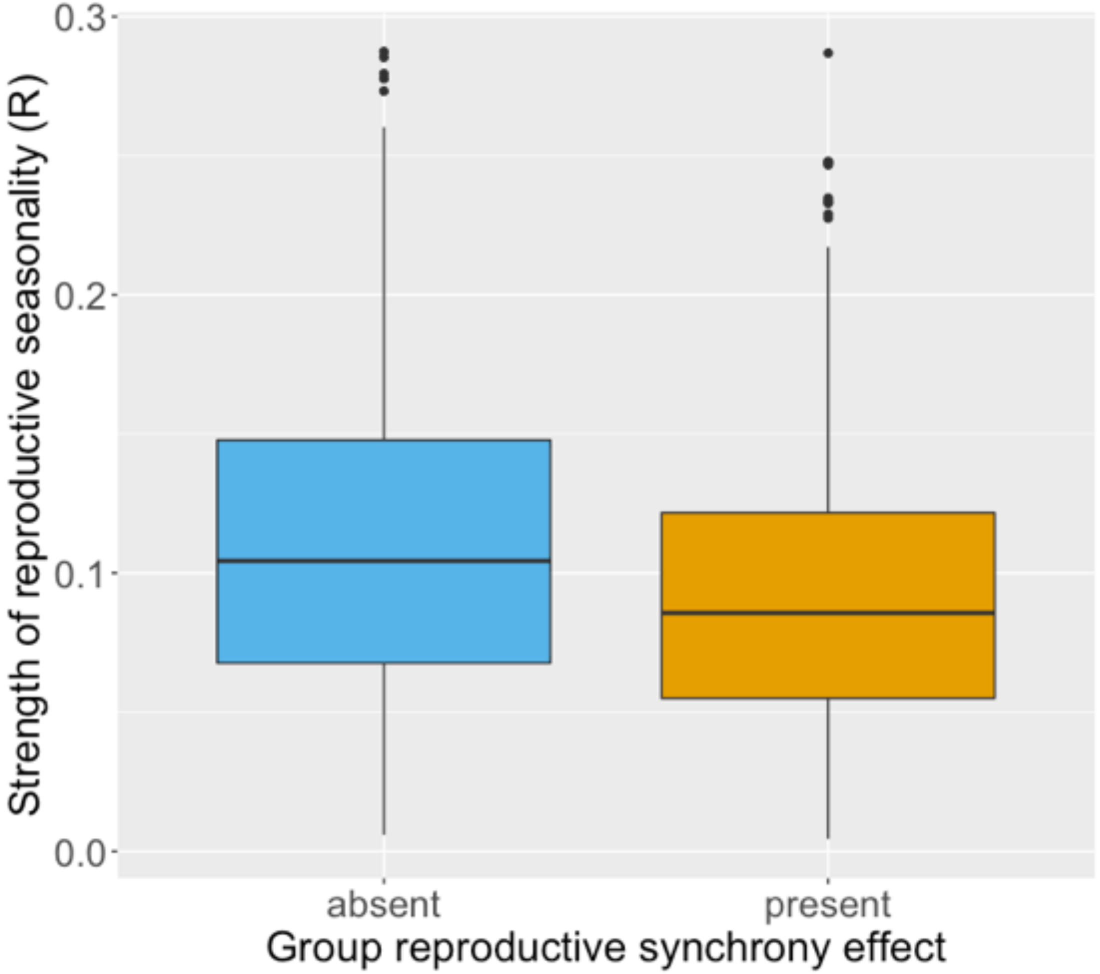

Figure S3: The effect of the group reproductive synchrony found on IBIs (Table 2) leads to lower reproductive seasonality.

The boxplots represent the strength of reproductive seasonality (R, from the Rayleigh test) according to whether or not the effect of group reproductive synchrony was incorporated in our simulated IBIs. See Section S5 for more details: ‘absent’ refers to the ‘random’ models (in blue), whereas ‘present’ refers to the ‘synchrony’ models (in orange). These two R distributions are significantly different (Welch two-sample t-test: $t=9.616$, $p<10^{-3}$).

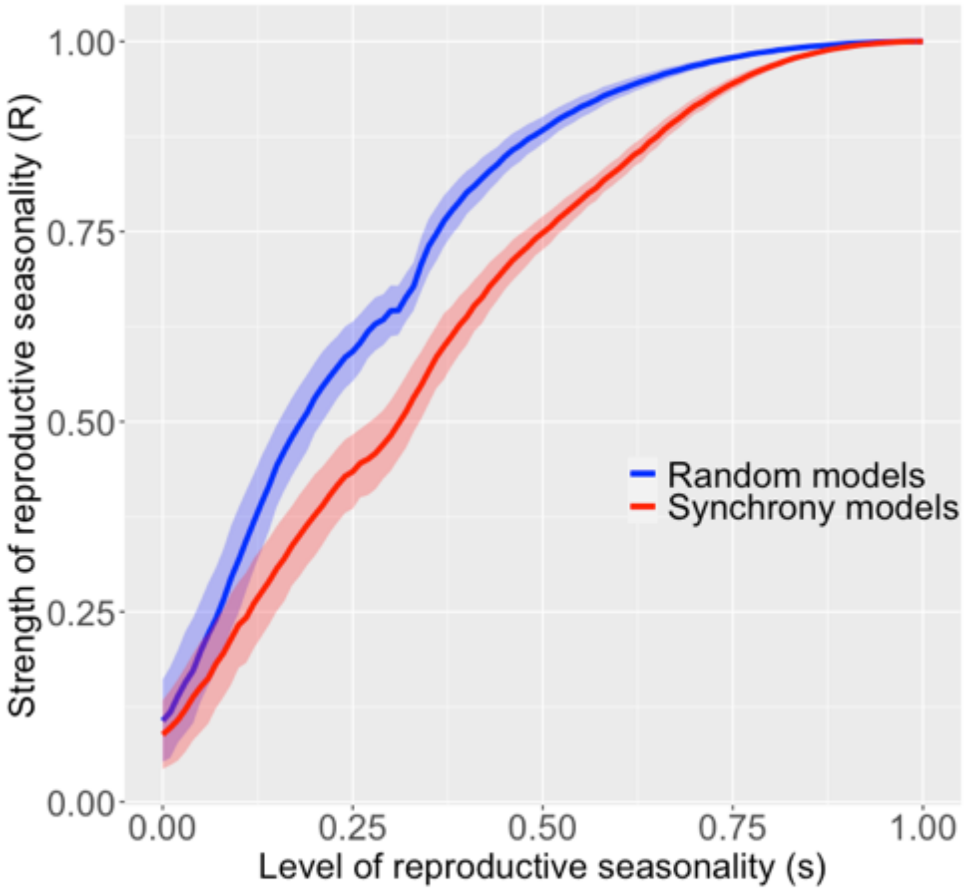

Figure S4: The effect of group reproductive synchrony on reproductive seasonality increases with the intensity of reproductive seasonality.

We represented the strength of reproductive seasonality (R) for the ‘random’ models in blue (i.e. absence of group reproductive synchrony effect) and the ‘synchrony’ models in red (i.e. presence of group reproductive synchrony effect) according to the intensity of environmental seasonality (s). See also Section S5. The colored lines represent the mean R values of the 1000 simulations for each model, and their shaded areas display their standard errors.