Evolutionary determinants of reproductive seasonality: a theoretical approach

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ABSTRACT

Reproductive seasonality is a major adaptation to seasonal cycles and varies substantially among organisms. This variation, which was long thought to reflect a simple latitudinal gradient, remains poorly understood for many species, in part due to a lacunary theoretical framework. Because seasonal cycles are increasingly disrupted by climate change, a better understanding of the ecology of reproductive seasonality could generate important insights on how climate change may affect biodiversity. The goal of this study was to investigate the drivers of evolutionary transitions towards reproductive seasonality using a realistic agent-based optimisation model simulating the life cycle of a female yellow baboon, who typically breeds year-round. Specifically, we tested the influence of three ecological traits (environmental seasonality, productivity and unpredictability) and three life-history traits (daily reproductive energy expenditure, reproductive cycle length and infant extrinsic mortality) on the intensity of reproductive seasonality. To do so, we simulated diverse reproductive phenology strategies (from non-seasonal to highly seasonal), assessed which were optimal and computed, for the set of optimal strategies, the intensity of reproductive seasonality. We then induced variation in each trait of interest and examined how it affected the intensity of reproductive seasonality. We found significant effects of all three environmental traits: high reproductive seasonality was favoured by high environmental seasonality, low environmental productivity and low unpredictability. It was further, and most strongly, favoured by high daily reproductive energy expenditure. In contrast, there was no significant effect of reproductive cycle length and infant extrinsic mortality. Our modelling approach successfully disentangled the effects of environmental seasonality, productivity and unpredictability on the intensity of reproductive seasonality, which likely all contribute to generate the well-known association between latitude and reproductive seasonality. Our results further highlight the critical importance of life history pace on the evolution of reproductive seasonality. Overall, this study contributes a powerful theoretical framework and modelling tool that may apply across the life-history space, as well as sheds new light on the emergence and maintenance of non-seasonal breeding in slow-living species, including humans.

Keywords: Baboon, ecology, life history, modelling, phenology, reproduction, seasonality, unpredictability

Introduction

Reproductive seasonality, which consists in a temporal gathering of reproductive events, is a major adaptation to seasonal cycles as it allows to synchronize the energetic costs of reproduction with the annual food peak (van Schaik & Brockman, 2005). Because seasonal cycles are increasingly disrupted by climate change (Easterling *et al.*, 2000), a better understanding of the ecology and evolution of reproductive seasonality could generate important insights on how climate change may affect biodiversity (Thackeray *et al.*, 2016).

Many studies have focused on understanding the physiological regulation of reproductive seasonality as well as variation in its timing (Brockman & van Schaik, 2005; Bradshaw & Holzapfel, 2007; Bronson, 2009; Vatka *et al.*, 2014; Clauss *et al.*, 2021), but less work has investigated why the intensity of reproductive seasonality exhibits such a broad range of variation across species. For example, Alaskan caribous (*Rangifer tarandus*) give birth during only one month every year (Adams & Dale, 1998) whereas mountain gorillas (*Gorilla beringei beringei*) give birth year round (Campos *et al.*, 2017). Understanding the drivers of such variation in strategies of reproductive phenology (i.e. timing and length of the annual birth season) is essential to predict the resilience of species to climate change.

The intensity of environmental seasonality (often approximated by latitude) has traditionally been used to predict reproductive seasonality (Conover, 1992; Ogutu *et al.*, 2014; Heldstab, 2021b) but a great part of its variation remains unexplained by this predictor alone. For instance, some tropical species reproduce seasonally (Brown & Shine, 2006; Hongo *et al.*, 2016) while some temperate species breed year-round (Riedman *et al.*, 1994). There are also examples of sympatric species which largely differ in their reproductive phenology (Sinclair *et al.*, 2000). In sum, besides environmental seasonality, other determinants likely play a significant role in the evolution of reproductive seasonality, such as other ecological factors, life-history traits, and their interaction (English *et al.*, 2012; Clauss *et al.*, 2021)

Ecological factors other than environmental seasonality could include environmental productivity (average level of food availability) and unpredictability (year-to-year variation in food availability). First, in highly productive habitats, the energy requirements of reproduction could be met year-round even in seasonal environments, thus decreasing the benefits of seasonal breeding. Interestingly, environmental seasonality and

productivity are both highly correlated with latitude (Botero *et al.*, 2014), which is a major predictor of reproductive seasonality (Heldstab *et al.*, 2021; Heldstab, 2021b). Yet, most studies only investigate the global effect of latitude without disentangling environmental productivity, seasonality and their interaction. Second, in unpredictable environments, even with some degree of environmental seasonality, a flexible reproduction may be more advantageous than a strictly seasonal reproduction. Indeed, reproducing seasonally in an environment where the food peak is regularly reduced or delayed may generate mismatches between a fixed reproductive timing and a variable annual food peak (Vatka *et al.*, 2014; Clauss *et al.*, 2021). However, only a few studies have investigated the effect of environmental unpredictability on reproductive seasonality (Dezeure *et al.*, in press; English *et al.*, 2012), with mixed results so far.

Regarding the effect of life-history traits, variation across species in strategies used to finance the energetic costs of reproduction have likely played a major role in shaping the evolution of their reproductive schedule. In particular, the "capital" versus "income" breeding dichotomy (Drent & Daan, 2002) (Jönsson, 1997) has proven useful to predict the timing and cues (exogenous or endogenous) used to onset reproduction in mammals (Brockman & van Schaik, 2005 but see Clauss *et al.*, 2021 for discussion). While a "capital breeder" stores energy for a subsequent reproduction, an "income breeder" re-invests it immediately into reproduction (Stearns, 1989). In fact, capacity to store energy may promote both seasonal and non-seasonal breeding (Williams *et al.*, 2017), by helping seasonal breeders to survive the lean season (Varpe, 2017) sometimes coupled with other physiological mechanisms such as delayed implantation (Langvatn *et al.*, 2004) or hibernation (Hellgren, 1998), or alternatively by allowing non-seasonal breeders to reproduce year round by extending the benefits of the food peak (Kerby & Post, 2013; Williams *et al.*, 2017). As a result, a species capacity to store energy may not be essential to predict the emergence of non-seasonal reproduction (Sun *et al.*, 2020).

Other mechanisms could be critical to sustain non-seasonal reproduction. One consists in limiting the peak in energy demand for reproduction, by adopting a "slower" life history, as defined by the fast-slow continuum framework (Stearns, 1989; Bielby *et al.*, 2007). Indeed, high day-to-day reproductive energy requirements, which are typical of short-lived species with large litter size and fast reproductive cycles (Bielby *et al.*, 2007), likely limit the period of the year where the energetic costs of reproduction can be met. In

contrast, in species with slower reproductive paces, reproductive costs are spread over time and more easily afforded year-round (van Noordwijk *et al.*, 2013). Additionally, and regardless of the life-history pace, the length of the reproductive cycle could also be a key factor, depending on whether or not it is close to an integer number of years. A reproductive cycle that is far from an integer number of years could indeed decrease the benefits of seasonal breeding by introducing gaps at the end of each reproductive cycle, where females must wait the next reproductive season in order to reproduce again. Lastly, slow living species often have small litters or singletons that can be lost all at once (Bielby *et al.*, 2007). In such cases, species with high external offspring mortality compared to that of adults – a defining feature of slow life histories (Jones, 2011) – could face costs from reproducing seasonally by experiencing gaps after losing their offspring if they have to wait the next reproductive season to conceive again, similarly to species whose reproductive cycles are not integer years.

Finally, despite an abundant empirical literature on reproductive seasonality, few models have been developed to explain the variation of reproductive strategies in seasonal environments (Tökölyi *et al.*, 2012; Stephens *et al.*, 2014; Kristensen *et al.*, 2015), with only one, to our knowledge, studying the emergence of reproductive seasonality (Sun *et al.*, 2020). Yet, this last model focuses on the evolution of income versus capital breeding and considers environmental seasonality as the only determinant of the emergence of seasonal breeding. This highlights a general lack of theory regarding the drivers of the intensity of reproductive seasonality, and a specific need to develop a predictive framework integrating the combined effects of various ecological and life-history traits across ecological and evolutionary timescales. In addition, because several potential determinants of the intensity of reproductive seasonality typically co-vary in natural environments, modelling approaches appear essential to disentangle their effects by introducing variation in some traits while keeping others constant.

In this study, we developed an agent-based optimisation model to investigate the effects of variations in ecological and life history traits on the emergence of reproductive seasonality. We chose to create a realistic and detailed model based on energetics, that we parameterized using published empirical data from the yellow baboon (*Papio cynocephalus*). This species was chosen here because it belongs to a genus characterised by phenological flexibility with one in six *Papio* species breeding seasonally (Petersdorf *et al.*, 2019). Additionally,

126 long-lived, tropical organisms such as baboons tend to be under-represented in studies of reproductive
127 seasonality, mostly focused on short-lived seasonal breeders from temperate regions (Bronson, 1985; Vatka
128 *et al.*, 2014). Yellow baboons are non-seasonal breeders (Campos *et al.*, 2017) living in tropical savannas
129 characterized by relatively low productivity, high unpredictability and moderate seasonality (Gesquiere *et al.*,
130 2008). Yellow baboons give birth to one offspring at a time with a limited growth rate during lactation (Altmann
131 & Alberts, 1987) inducing relatively low day-to-day reproductive energy requirements. Their mean interbirth
132 interval (IBI) is 638 days (Gesquiere *et al.*, 2018), which is not an integer number of years (1.75 years). They
133 also exhibit a moderate extrinsic infant mortality (for a slow-living species) (Alberts, 2019). Altogether, their
134 non-seasonal reproductive phenology appears consistent with their habitat characteristics and life history
135 traits.

136 We therefore simulated variable strategies of reproductive phenology, from non-seasonal breeding to
137 a highly seasonal reproduction, together with their energy budget, in order to calculate their associated fitness
138 outcome. The phenology strategies that maximized individual fitness, here calculated as λ_{ind}, the individual-
139 level equivalent of the population growth rate (McGraw & Caswell, 1996), were interpreted as the optimal
140 reproductive phenology strategies. We first identified the optimal reproductive phenology strategies in the
141 natural environment of yellow baboons, the Amboseli National Park, source of most empirical data used here.
142 To do so, we used the Normalized Difference Vegetation Index (NDVI), a satellite-derived quantitative measure
143 of primary productivity, extracted from the Amboseli national Park coordinates, as a proxy of food availability.
144 By artificially reshaping the NDVI time series, we subsequently investigated the effect of variation in three
145 environmental traits (seasonality, productivity and unpredictability) on the fitness of these different strategies.
146 We further tested the influence of three life-history traits (daily reproductive expenditure, length of the
147 reproductive cycle and infant extrinsic mortality rate) on the optimal phenology strategy by modifying the
148 model parameters. By doing so, we were able to test our working hypotheses, respectively proposing that the
149 emergence of reproductive seasonality is favoured by (H1) high environmental seasonality, (H2) low
150 environmental productivity, (H3) low environmental unpredictability, (H4) high daily energetic expenditure of
151 reproduction, (H5) a reproductive cycle that is an integer number of years and (H6) low infant extrinsic
152 mortality rate.

Methods

A. Model description

The program code uses a combination of R (R Core Team, 2020) and C++ functions through the Rcpp package (Eddelbuettel & François, 2011). The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual and agent-based models (Grimm *et al.*, 2010).

1. Purpose

The aim of this study is to investigate the determinants of reproductive seasonality in a mammalian species. To do so, we simulated the life cycle of a female yellow baboon (*Papio cynocephalus*) with an energetic approach in order to evaluate the optimal strategy of reproductive phenology. We developed the structure of this model to be as general as possible so it could be adapted to another mammalian species.

2. Entities, state variables, and scales

Agents/individuals:

The model simulates the life cycle of a female adult baboon and her offspring. We do not discriminate the offspring by sex and only include adult females. We consider here that males are non-limiting for female reproductive success, and do not affect the outcome of reproduction, which sounds reasonable in a species where paternal care is optional (Buchan *et al.*, 2003). Therefore, each individual in the model belongs to one of four possible life stages: foetus, infant, juvenile and (adult) female. A foetus is created when a female conceives and switches to the next life stages through defined events: birth, weaning and sexual maturity. As individuals grow, they acquire new abilities (e.g. foraging or reproducing). Technically, we simulated these individuals using object-oriented programming where the four life stages are represented by four classes that inherits (acquires properties and behaviour) from one another (Fig. 1). Each individual is characterized by some attributes or state variables, according to his life stage (Appendix A, Table S1) that accounts for the changes occurring during the simulation.

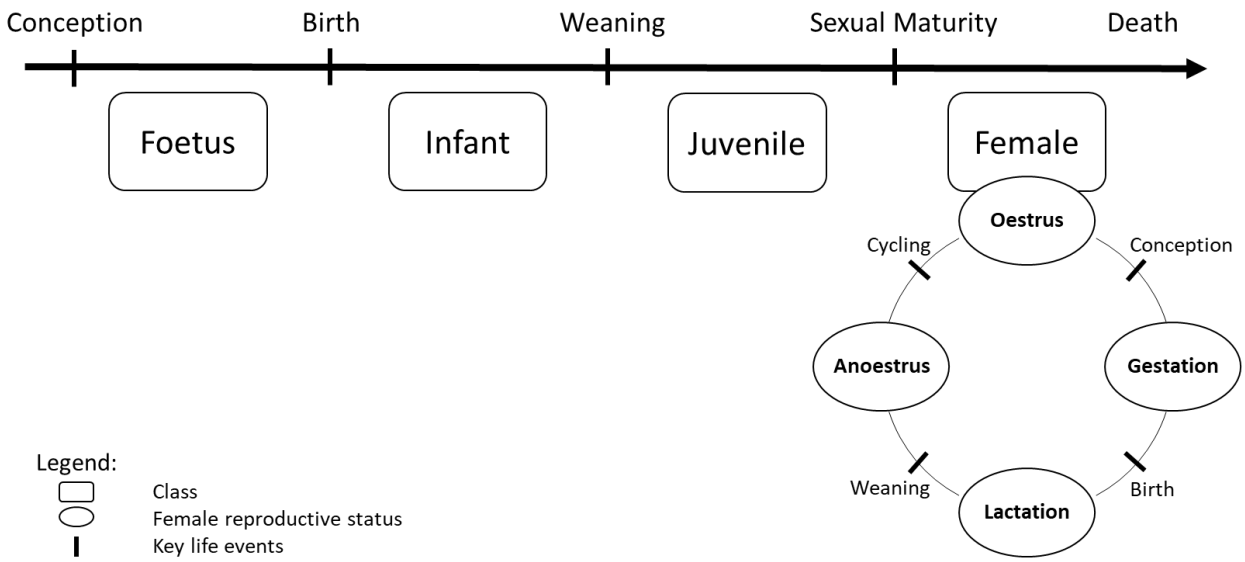


Figure 1: Schematic representation of the class-structure used in the model

Each rounded rectangle represents a class. The Foetus class is the base-class while the Female class is the class with the most advanced properties, including reproduction. Class Female individuals can therefore produce offspring that will appear as an individual of class Foetus and evolve to the other classes through key life events associated with changes in the female reproductive status.

Temporal scales:

One time step represents one day and simulations end with the female death or her last offspring reaching sexual maturity, depending on which event occurs last.

Environment:

Each simulation occurs in an environment characterized by its food availability, approximated by the Normalized Difference Vegetation Index (NDVI). NDVI is an indicator of the greenness of an area and has been largely used to estimate plant biomass (Carlson & Ripley, 1997). NDVI has previously been used to estimate food availability (Dezeure *et al.*, in press; Baniel *et al.*, 2018; Dezeure *et al.*, 2021; Walton *et al.*, 2021) in several baboons populations and has also proved relevant to predict reproductive seasonality in humans (Macfarlan *et al.*, 2021).

To account for realistic seasonal changes in NDVI, we used real values from the Amboseli population of yellow baboons. We used a GPS tracking study (Amboseli Baboon Research Project, 2015 - see Markham *et al.*, 2013 for methods) to assess the coordinates of a quadrat where the majority of the baboon movements occurred (South/West: -2.75, 37.04 ; North/East: -2.70, 37.11). This quadrat covers a surface of about 42 km²,

which is consistent with the annual home range size observed in wild baboons (Altmann & Muruthi, 1988). We extracted NDVI within this quadrat using the 250-m resolution NDVI 16-day composite data from the MOD13Q1 product (Didan, 2015) which we linearly interpolated to have a daily time series from Feb 18, 2000 until May 09, 2022. Because our simulations can run for more than 27 years, we needed to extend the NDVI dataset. To do so, we chose to simply repeat the whole NDVI time series. To minimize discontinuity, we compared the first and last years of the time series and selected the day of year with the least variable NDVI that we therefore used as the transition point for concatenation of the NDVI time series.

3. Process overview and scheduling

The same following sequence happens at every time step (day) of the simulation

1. Potential death of the female and/or offspring (if any)
2. Potential change of the female reproductive status (cycling, conception, birth or weaning)
3. Evaluation of daily energy intake extracted from the environment
4. Evaluation of daily energy needs based on reproductive status
5. Energy allocation:
    - 5.1. If positive energy balance: storage of energy for the female and offspring (if any)
    - 5.2. If negative energy balance: release of energy and/or energy restrictions (slowdown of growth, miscarriage, infant abandon) for the female and offspring (if any)
6. Growth of the female and/or dependent offspring (if any)

Following the death of a female, the same sequence (without reproduction) is repeated for each independent offspring (juvenile) until they die or reach sexual maturity. Dependent offspring (foetus or infant) do not survive after their mother's death.

These six submodels (Death, Change of reproductive status, Energy intake, Energy needs, Energy allocation and Growth) are described in the appendix A of the supplementary material.

4. Design concepts

Emergence, Adaptation:

In this optimisation model, we compute the female fitness associated with each phenology strategy. The fitness of an individual does not depend on the strategy of others. In particular, male function is supposed to be non-limiting, and we do not consider density-dependence interactions. Phenology strategy (i.e. the beginning and length of the time window during which a female can conceive) is constant throughout each simulation, but different phenology strategies are tested in a given set of simulations. To account for both different reproductive timings (the date in the annual cycle of the mating season) and different intensities of the reproductive seasonality (i.e. the length of the mating season), we tested various phenology strategies, with reproductive windows starting each first day of each month (12 different timings) and lasting from 1 to 11 months (11 different intensities of reproductive seasonality). We also tested the non-seasonal phenology strategy (females can conceive year-round), resulting in 133 phenology strategies tested for each set of simulation. From each phenology strategy tested, we calculated a fitness value. The optimal strategy of reproductive seasonality emerged from the set of simulations as the strategy associated with the highest fitness values. Because differences between some phenology strategies can be small, in most cases there is not a single phenology strategy that emerges but rather a group of optimal phenology strategies associated with the highest fitness values.

Fitness:

Individual fitness (λ_{ind}) is calculated at the end of each simulation as described in McGraw and Caswell (1996) and represents the "population growth rate of an individual". Previously used in empirical studies (McLean *et al.*, 2019), this value takes into account not only the number of offspring born to a female but also the timing at which they are produced: the earlier in life a female has offspring, the higher her individual growth rate. Specifically, λ_{ind} is the dominant eigenvalue of Leslie matrices built on individual females, which indicates the number of offspring produced each year. It should be noted that λ_{ind} does not represent an individual's contribution to the demographic growth of the population. In particular, the mean of several individual fitness values cannot be used to estimate a population growth rate (McGraw & Caswell, 1996). Because our simulations begin when the female has just reached sexual maturity, we decided to consider in the calculation

of the individual fitness only offspring having reached the same point (i.e. sexual maturity). This method prevents us from overestimating or underestimating any life stage in the calculation of fitness, and especially to take into account the post-weaning period which is known to be critical for juveniles (McLean *et al.*, 2019). Even if sexual maturity seems to appear around 10 months later for male than for female offspring in yellow baboon (Charpentier *et al.*, 2008), early maturation has been observed in male hamadryas baboons (Zinner *et al.*, 2006). Because of the uncertainty on male sexual maturity age and for simplicity, we chose to use the female age at sexual maturity as a unique milestone for offspring of both sexes.

Stochasticity:

There are two stochastic processes in this model: conception and mortality. Female cycling durations at each cycling phase (which accounts for conception probability) and female maximal lifespans (which account for external causes of death) are therefore randomly picked from observed data in the Amboseli yellow baboons (Gesquiere *et al.*, 2018; McLean *et al.*, 2019). Some of the offspring lifespans are also randomly picked from observed data, in order to account for extrinsic mortality (see submodels "Death" and "Cycling" in supplementary for details). Finally, the first day of the simulation is also randomly picked in the annual cycle, in order not to favour a time of the year over another. We ran each simulation 2000 times to account for such stochasticity.

Observation:

The model outputs recorded at the end of a simulation are:

- The fitness of the female with respect to the phenology strategy she has followed
- The seasonality of births that took place during the simulation

We used circular statistics to characterize the seasonality of births, according to recent recommendations (Thel *et al.*, 2022). In circular statistics, days of the year are represented as angles on a circle and each birth event is characterized by a vector of length 1 pointing to the day of year when it occurred. By computing the mean vector of all birth events, we can characterize their seasonality: the direction (μ) of the mean vector gives the mean date of birth, while its length (r) defines the intensity of seasonality ($r = 0$ when births are evenly distributed and $r = 1$ when they all occur on the same day).

5. Initialization

At time t=0, only one individual of class Female is created. It represents a female yellow baboon that has just reached sexual maturity. Its state variables are initialized using parameters from the literature (Table S2).

6. Input data

We use some species-specific parameters in the model that remain constant throughout each simulation. We compiled and calculated them from the literature (Table S3). Most of them come from published empirical data from wild populations of yellow baboons. When such data were unavailable, we used available values from phylogenetically close species or captive populations.

B. Test of hypotheses

To test our hypotheses (H1-6), we artificially modified in the model the value of each of the six environmental or life history traits investigated and computed the associated birth seasonality.

1. Computation of simulated birth seasonality

To compute the birth seasonality associated with specific environmental and life history conditions, we first evaluated all 133 possible phenology strategies (from highly seasonal to non-seasonal) to identify which were optimal. To do so, we ran 2000 simulations for each phenology strategy and extracted the resulting 2000 fitness values (λ_{ind}). We sorted them by descending mean and conducted a Student's t-test to assess the significance of the difference between the mean fitness value of the “best” phenology strategy (i.e. highest one) and the mean fitness values associated with each other phenology strategy. We then pooled all births coming from simulations of phenology strategies that were non-significantly different from the “best” one (p-values > 0.05). From these births dates, we calculated the mean vector length (r) and direction (μ), using the functions ‘rho.circular’ and ‘mean.circular’ from the ‘circular’ package (Lund *et al.*, 2017) as a measure of birth seasonality.

296 **2. Artificial variation of environmental and life history effects**

297 In order to disentangle the effects of environment and life history, we chose to modify only the three
298 environmental traits first. By doing so, we drew an environmental landscape composed of three axes
299 (productivity, seasonality and unpredictability) in order to explore their whole range of (co)-variation. We
300 expected one or more interactions, and specifically that the effect of environmental seasonality on
301 reproductive seasonality would be modulated across a gradient of environmental productivity, with higher
302 productivity extending the time window where reproduction is sustainable in seasonal environments. For
303 example, abnormally extended birth season were observed in a population of North American elk that
304 punctually experienced a higher habitat quality (Keller *et al.*, 2015). Because 3D representation can be difficult
305 to apprehend and increases computing time, we chose to represent a two-dimensional environmental
306 landscape covering the full range of variation of both environmental seasonality and productivity – and later
307 represented through heatmaps. We then examined this same heatmap for different levels of unpredictability
308 (i.e. sectional views of the 3D environmental landscape). We subsequently tested for the effect of each life
309 history trait on reproductive seasonality across this two-dimensional landscape in order to cover a broad range
310 of viable environments, but keeping unpredictability unchanged for simplicity. Finally, the significance of the
311 effect of environmental unpredictability and of our three life history traits on birth seasonality was tested using
312 Student's t-tests comparing the mean values of birth seasonality across two-dimensional landscapes that were
313 obtained for different values of each trait.

314 **3. Modification of environmental traits: test of hypotheses H1-3**

315 In order to test for the influence of environmental seasonality, productivity and unpredictability (H1-
316 3), we first decomposed the NDVI time series in three components, therefore disentangling seasonal from non-
317 seasonal variation (Fig. S4):

318 $$NDVI(t) = K + NDVI_S(t) + NDVI_NS(t)$$

319 K is the mean NDVI over the entire time series and is therefore a constant that represents the overall
320 productivity of the environment. NDVI_S represents the seasonal part of the variation in NDVI and is obtained
321 by calculating, for each day of the calendar year, the mean daily NDVI value over the 22 years of data. NDVI_S
322 captures the within-year variation of NDVI and is completely identical between years. Lastly, NDVI_NS captures

the rest of the NDVI variation and is computed by removing to the overall NDVI its mean K and its seasonal component NDVI_S. NDVI_NS can be seen as the noise, where a positive value indicates that the NDVI is higher than expected for a given calendar day, i.e. for the season. In other words, NDVI_NS captures the unpredictable between-year variation in NDVI. We then artificially modified these different components of the NDVI time series by introducing three parameters, *s*, *p* and *u*. This allowed us to modulate the contribution of each component of NDVI as follow:

$$NDVI_{modified}(t) = p \times K + s \times NDVI_S(t) + u \times NDVI_NS(t)$$

The higher p, s and u, the higher the environmental productivity, seasonality and unpredictability (respectively). The parameter *p* varied from 0.85 to 1.4 while *s* and *u* varied from 0 to 3, with the real NDVI given by $p = s = u = 1$.

4. Modification of life history traits: test of hypotheses H4-6

To investigate the effect of an increase in daily energy expenditure (H4), we modified the daily growth rate at 7.5 g/day instead of the original 5g/day. This represents an increase of 50% in the energy expenditure associated with growth. Gestation was accordingly reduced from 178 days to 118 to ensure a constant birth mass. To test for the effect of a reproductive cycle being and integer number of years (H5), we chose to artificially modify the year length, instead of the reproductive cycle length. With this approach, the biological timing (and especially the daily energy expenditure) remains unchanged, but the temporal synchronization between reproductive cycle and year length can change, thus disentangling the two effects. To do so, we interpolated the 16-days NDVI time series from the MODIS data assuming a year length of 637 days (equal to the interbirth interval), 425 days (so the IBI would be of exactly 1.5 year) and 365 days (normal conditions, IBI = 1.75 year). For example, with a year length of 637 days months last 53 day and the raw NDVI values, originally spaced of 16 days, are spaced of 28 days. Lastly, to test for the influence of infant mortality (H6), we modified the proportion of infants dying from external causes by a coefficient *m* (see submodels "Death" in supplementary for details). The coefficient *m* took three different values, 0, 1 and 4, corresponding respectively to 0, 11.61 and 46.44% of infants dying from external deaths and representing the range observed in baboon species (Palombit, 2003).

Results

1. Substantial support for the ecological hypotheses (H1-3)

High birth seasonality was observed only for environments characterized by both a high seasonality and a low productivity (Fig. 2a). Birth seasonality increased with environmental seasonality but this effect almost disappeared when environmental productivity was high (Fig. 2b). Similarly, birth seasonality decreased when environmental productivity increased, and this effect was modulated by environmental seasonality: the higher the environmental seasonality, the higher the effect of environmental productivity on birth seasonality (Fig. 2c). More precisely, high birth seasonality was observed only for the lowest values of environmental productivity that still sustained a viable reproduction ($\lambda_{ind} \neq 0$) (Fig. S7).

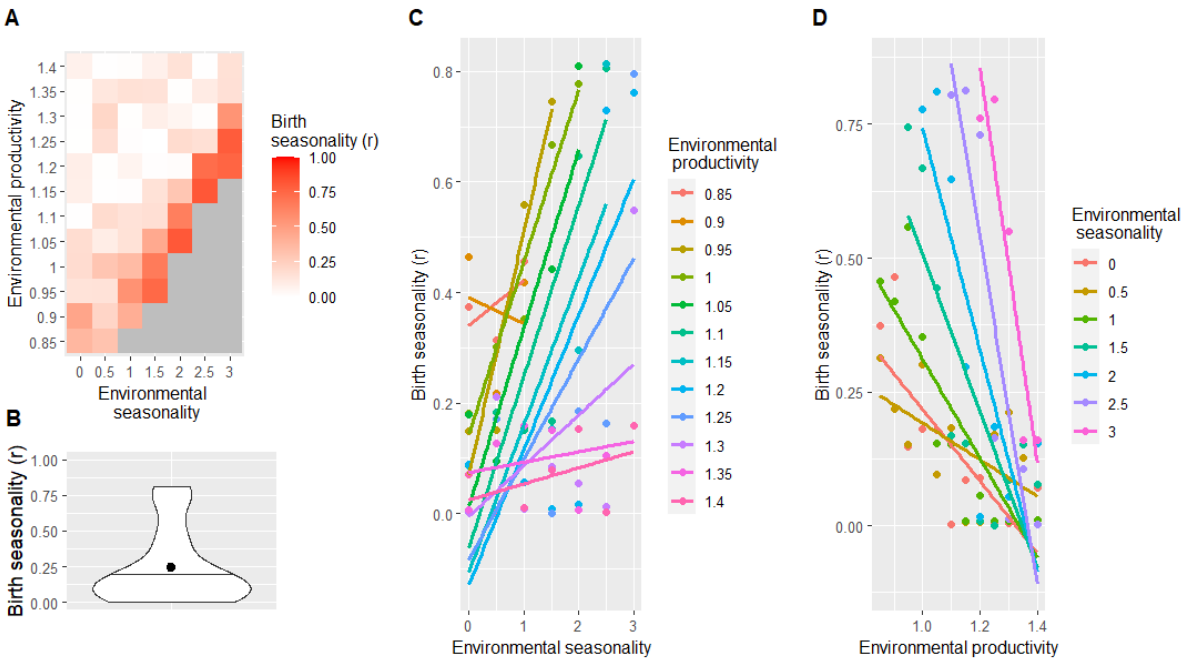


Figure 2: Effect of environmental seasonality and productivity on birth seasonality (H1-2)

In panel A, we plotted a heatmap of birth seasonality along gradients of environmental seasonality and productivity. Birth seasonality is represented by *r*, going from 0 (births are equally distributed) to 1 (all births occur on the same day). Panel B represents the distribution of birth seasonality values observed in the heatmap. The black dot indicates the mean value while the black horizontal line indicates the median value. In panels C and D, we represented the same data, focusing on the effect of environmental seasonality for panel C and productivity for panel D, in interaction with the other.

Modifying environmental unpredictability did not have an effect on mean birth seasonality (Fig. 3, t-test: p-value>0.05). However, it had a significant effect on variance of birth seasonality values observed within

each heatmap (Fig. 3, F-test: p-value<0.05), with a decrease in maximal values (r_{max} = 0.83, 0.81, 0.66 and 0.51 for u = 0, 1, 2 and 3 respectively). Yet, this significant effect was observed only for high values of unpredictability, and we did not observe any effect on birth seasonality when removing completely the unpredictability of the environment (u=0). Finally, here again, the effect of environmental traits on reproductive seasonality were modulated by each other: the higher the environmental unpredictability, the weaker the effects of environmental productivity and seasonality on birth seasonality.

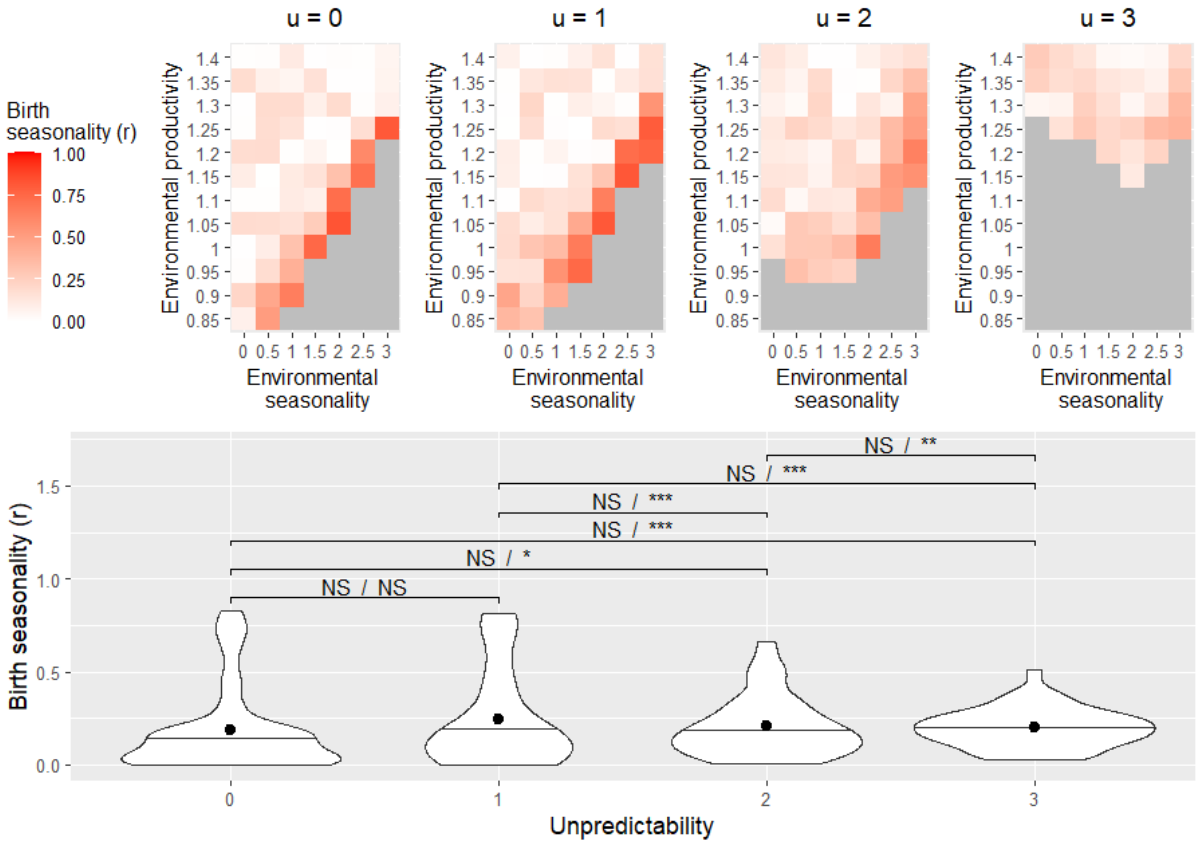
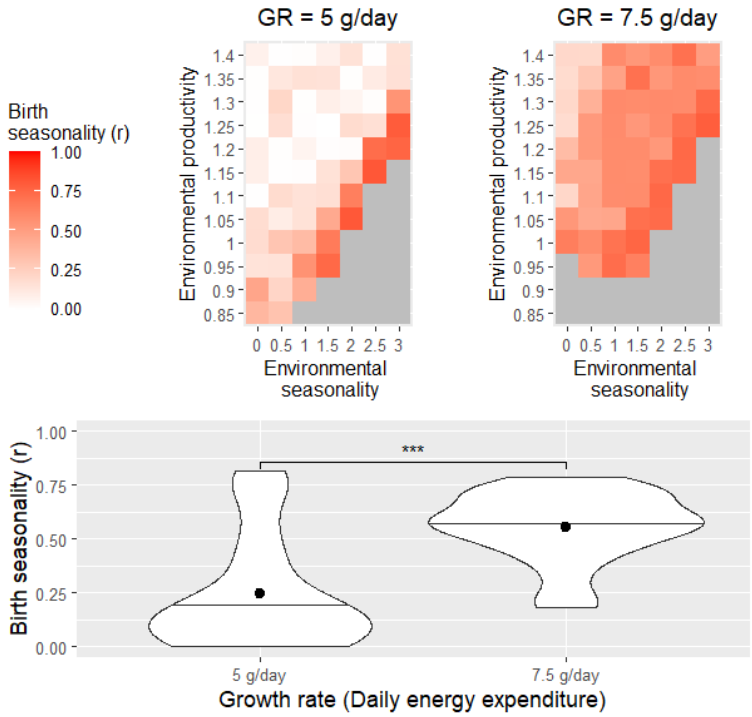


Figure 3: Effect of environmental unpredictability on birth seasonality (H3)

In the top panel, we plotted heatmaps of birth seasonality along gradients of environmental seasonality and productivity in four different conditions of environmental unpredictability: no unpredictability (u = 0), normal unpredictability (u = 1) and increased unpredictability (u = 3 and 4, respectively). Birth seasonality is represented by r, going from 0 (births are equally distributed) to 1 (all births occur on the same day). The panel below shows the distribution of birth seasonality values observed in each heatmap. Black dots indicate mean values while black horizontal lines indicate median values. We tested for differences in mean and variance between those distributions by conducting Student's t-tests and F tests. Both significance levels are presented with t-test on the left and F-test on the right (NS: non-significant; *: p-value<0.05; **: p-value<0.01; ***: p-value<0.001).

386 **2. Strong support for the daily energy expenditure hypothesis (H4)**

387 Increasing the daily energy expenditure during reproduction by increasing the daily growth rate from
388 5 g/day to 7.5 g/day (+50%) dramatically increased the birth seasonality even in environments characterized
389 by high environmental productivity or low environmental seasonality (Fig. 4, t.test: p-value < 0.001, r_{mean} = 0.24
390 and 0.55 for growth rate of 5 g/day and 7.5 g/day, respectively). The individual fitness simultaneously
391 decreased for practically all environmental conditions (Fig S7).



392 **Figure 4:** Effect of daily energy expenditure on birth seasonality (H4)

393 In the top panel, we plotted heatmaps of birth seasonality along gradients of environmental
394 seasonality and productivity in two different conditions of daily energy expenditure: regular (growth rate = 5
395 g/day) and increased (growth rate = 7.5 g/day). Birth seasonality is represented by *r*, going from 0 (births are
396 equally distributed) to 1 (all births occur on the same day). The panel below shows the distributions of birth
397 seasonality values observed in each heatmap. Black dots indicate mean values while black horizontal lines
398 indicate median values. We tested for differences in mean between those distributions by conducting
399 Student's t-tests (NS: non-significant; *: p-value<0.05; **: p-value<0.01; ***: p-value<0.001).
400

401 **3. Minimal support for the length of reproductive cycle and the infant mortality hypotheses (H5-6)**

402 We found no significant effect of reproductive cycle length on birth seasonality (Fig. 5A and S8A, t-
403 test: p-value>0.05), although we detected a tendency suggesting that birth seasonality was higher when
404 interbirth intervals lasted exactly one year (r_{mean} = 0.33, 0.26 and 0.24 when IBI lasted 1, 1.5 and 1.7 years,
405 respectively). Birth seasonality did not increase after cancelling infant extrinsic mortality but slightly decreased

(non-significant trend) when infant mortality increased (Fig. 5B and S8B, r_{mean} = 0.25, 0.24 and 0.21 for m=0%, 11.61% and 46.44%, respectively). Nevertheless, and despite the substantial effect sizes that we explored regarding mortality rates (four-fold increase), we did not detect any significant effect on birth seasonality (Fig. 5B and S8B, t-test: p-value>0.05).

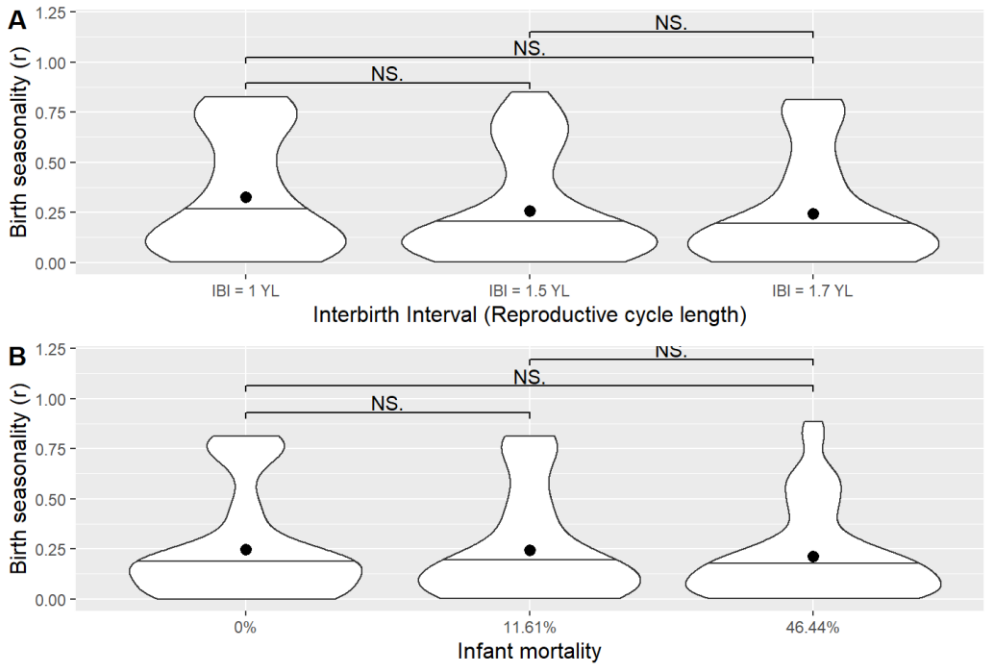


Figure 5: Effect of reproductive cycle length and infant extrinsic mortality on birth seasonality (H5-6)

In panel A, we plotted distributions of birth seasonality along gradients of environmental seasonality and productivity in three different conditions of reproductive cycle length: when the interbirth interval (IBI) is exactly one year long (YL), when its length is 1.5 years, and in normal conditions, when it is 1.7 years long. In panel B, we plotted distributions of birth seasonality along gradients of environmental seasonality and productivity in three different conditions of infant extrinsic mortality rate (M), respectively of 0%, 11.61% (observed rate) and 46.44%. The associated heatmaps (where the plotted distributions come from) are presented in supplementary materials (Fig. S8). Birth seasonality is represented by *r*, the length of the mean vector, going from 0 (births are equally distributed) to 1 (all births occur on the same day). Black dots indicate mean values while black horizontal lines indicate median values. We tested for differences in mean between those distributions by conducting Student's t-tests (NS: non-significant; *: p-value<0.05; **: p-value<0.01; ***: p-value<0.001).

Discussion

We created a model simulating the life cycle of a female yellow baboon. Under realistic conditions, we found as output of our model comparable key life-history traits and reproductive seasonality (non-seasonal reproduction) to the ones observed in the wild, thus confirming its validity (Appendix C, Table S5). We then modified environmental and life history parameters to test our hypotheses (H1-6) and discussed thereafter their effects on the evolution of reproductive seasonality.

428 **1. Effect of ecology on reproductive seasonality**

429 Unsurprisingly, ecology appears to play a key role in shaping reproductive seasonality. As expected,
430 high environmental seasonality was associated with high levels of birth seasonality (H1). Yet, this effect gets
431 weaker when the level of environmental productivity increases (H2). These two effects are in line with many
432 studies showing a positive correlation between latitude and reproductive seasonality in most mammalian
433 orders (Di Bitetti & Janson, 2000; Janson & Verdolin, 2005; English *et al.*, 2012; Zerbe *et al.*, 2012; Heldstab *et*
434 *al.*, 2018; Heldstab, 2021a, 2021b; Heldstab *et al.*, 2021). While this association is often interpreted as the
435 effect of environmental seasonality alone, increasing latitude reflects both increasing environmental
436 seasonality and decreasing environmental productivity. Yet, the effect of environmental productivity has been
437 overlooked in previous studies, with mean temperature being the closest proxy found to have a negative effect
438 on reproductive seasonality, even when corrected for latitude (Heldstab *et al.*, 2021; Heldstab, 2021a, 2021b).

439 In addition, our results support H3, by showing that high environmental unpredictability promotes
440 non-seasonal breeding strategies while controlling for environmental seasonality and productivity; this
441 hypothesis has often been proposed but rarely tested. These results are of major interest in the context of
442 climate change, which increases the frequency and severity of extreme events (Easterling *et al.*, 2000).
443 Environmental unpredictability could even be a third overlooked factor encapsulated in the latitude effect,
444 even if its relationship with latitude is not straightforward (English *et al.*, 2012; Botero *et al.*, 2014). In line with
445 this, English *et al.* (2012) showed that birth seasonality in ungulates was better explained by the interaction
446 between NDVI constancy and contingency – two components of predictability (Colwell, 1974) – than by latitude
447 alone. However, another recent study investigating the hypothesis that non-seasonal breeding in chacma
448 baboons was linked to environmental unpredictability found no support for it (Dezeure *et al.*, in press). These
449 mixed results call for more studies, which should disentangle environmental productivity, seasonality and
450 unpredictability in order to reach firm conclusions.

451 Here, we focused on within-year and between-year variation in the *magnitude* of NDVI, while variation
452 in the *timing* of the annual peak of NDVI could also be important and contribute to explain the mixed results
453 observed for the effect of unpredictability. For example, environmental conditions characterized by a food
454 peak whose timing differs between years – while still occurring within the same annual period of 3-4 months -

would be captured by the non-seasonal component of NDVI, even though the majority of higher-than-average values occur around the same time of the year, during the (variable) seasonal food peak. This implies that this non-seasonal component of NDVI encapsulates, in fact, some part of seasonality in its timing and may explain why, in our model, removing environmental seasonality ($s = 0$) is not enough to observe complete non-seasonal reproduction. To do so, we further need to remove environmental unpredictability ($u = 0$). In this context, our methodological approach relying on the NDVI decomposition to disentangle the effect of environmental seasonality and unpredictability may therefore not be sufficient, and future studies would usefully find a way to distinguish unpredictability in the magnitude and in the timing of the annual food peak, which may influence the ecology and evolution of seasonal breeding in different ways.

2. Effect of life-history on reproductive seasonality

Low day-to-day reproductive energy requirements proved critical in enabling non-seasonal reproduction (H4). Even a rather moderate increase in growth rate (×1.5), for a constant body mass, was sufficient to increase significantly birth seasonality regardless of environmental seasonality and productivity. This acceleration of reproductive pace has two distinct, and important consequences: (1) maximal daily energy needs increase for the mother, and (2) the most demanding stages of the reproductive cycle are circumscribed in a shorter period of time - which may only represent one fragment of the year cycle. These two changes, in combination, can lead to a situation where females can only sustain reproduction during the good season. Such an increase in reproductive pace – and daily reproductive costs – corresponds to a slight move on the slow-fast continuum (Bielby *et al.*, 2007) that could be observed within phylogenetically close (and potentially sympatric) species and partly explain the diversity of reproductive seasonality observed among them. This could for example explain why mandrills (*Mandrillus sphinx*), despite being closely related to yellow baboons and living in the equatorial forests of the Congo basin, reproduce seasonally (Hongo *et al.*, 2016; Dezeure *et al.*, 2022). Growth rate in young mandrills is indeed higher (×1.34), and lactation periods are accordingly shorter than in yellow baboons (about half as long), even though gestation length, birth mass and weaning mass are comparable and adult female mandrills body mass is much lower than for female baboons (Setchell *et al.*, 2001; Dezeure *et al.*, 2022), meaning an even larger difference in daily energetic expenditure when controlled by maternal size for these two species. At the extreme end of life-history paces, are Bornean

482 orangutans (*Pongo pygmaeus wurmbii*) which flattened their reproductive energy requirements so much that
483 they reached a low and constant level of maternal effort (van Noordwijk *et al.*, 2013), with nearly six years of
484 lactation (compared to about one year in yellow baboons), which makes it easy to understand why birth timing
485 does not matter much.

486 Notably, in our study model, an increase in growth rate, with a constant body mass and especially with
487 a constant weaning body mass threshold, translates into an acceleration of the reproductive cycle, which could
488 favour the evolution of seasonal breeding through another mechanism tested by hypothesis H5, namely that
489 the reproductive cycle is closer to exactly one year, leading to the reduction of gaps between the successive
490 reproductive cycles of a female, who must wait for the next reproductive season to start a new cycle after
491 weaning an infant. However, when manipulating the duration of the reproductive cycle relatively to the annual
492 seasonal cycle, we did not find any significant effect, confirming that the observed effect of growth rate is not
493 caused by a change in the length of the mother's reproductive cycle as expected under H5, but indeed by the
494 increase of her daily energy expenditure as expected under H4.

495 Even though this effect of daily energy expenditure on the evolution of reproductive seasonality has,
496 to our knowledge, never been formally tested, our results are corroborated by some empirical studies. For
497 example, a shorter gestation was found to be associated (when controlling for body mass) with a higher
498 reproductive seasonality in several mammalian orders (Zerbe *et al.*, 2012; Heldstab *et al.*, 2018; Heldstab *et*
499 *al.*, 2021) ; such a result could, in fact, reflect the increase in daily reproductive energy requirements due to a
500 shortened gestation. This interpretation is strengthened by the case of lagomorphs and rodents, where the
501 intensity of reproductive seasonality was not associated with gestation length but rather with the size and
502 number of litters per year (Heldstab, 2021a, 2021b). There, species with larger and more frequent litters, which
503 faced increased daily reproductive energy requirements, bred more seasonally. Overall, these comparative
504 studies that reported associations between reproductive seasonality and various aspects of reproductive pace
505 are consistent with our results supporting a single life-history hypothesis, namely that daily reproductive
506 energy intake is a major determinant of the evolution of (non)seasonal breeding.

507 Our last hypothesis stated that non-seasonal reproduction would emerge from a high mortality rate
508 of infants compared to adults (H6), but we could only detect a weak, non-significant tendency in support of

509 H6. It was already known that high rates of infanticide (leading to a high mortality rate of infants relatively to
510 adults) are associated with non-seasonal breeding (Lukas & Huchard, 2014). It is commonly admitted that this
511 is because infanticide is only beneficial for male killers when it accelerates female's return to cycle
512 substantially, which rarely be true in seasonal breeders where females only re-cycle in the next mating season.
513 Even if our results do not support the alternative interpretation where infanticide could instead select for non-
514 seasonal breeding, the tendency we detected could suggest a co-evolutionary pattern where both traits
515 reinforce each other.

516 **3. Insights on the emergence of reproductive seasonality**

517 High reproductive seasonality (over 0.75) was almost systematically associated with low individual
518 fitness values (under 0.25) in our simulations. Even though such simulated measures of individual fitness
519 cannot accurately inform about demographic dynamics, very low mean values of individual fitness may
520 represent ecological situations with declining populations, where reproductive seasonality is unlikely to evolve
521 successfully, at least in theory. Yet, such theoretical considerations are mitigated when confronted to empirical
522 figures: in our simulations, moderate reproductive seasonality (around 0.5, which corresponds to the highest
523 value observed within the genus *Papio*, Petersdorf *et al.*, 2019) is often associated with mean values of
524 individual fitness that are comparable to those calculated from the Amboseli baboons (λ_{ind} = 0.9, Fig.S7, tile
525 *s*=1 and *p*=1 in the top left heatmap), where the long-term demographic trend seems stable (Samuels &
526 Altmann, 1991), so that we cannot rule out the possibility for seasonal reproduction to emerge on the basis of
527 low values of individual fitness.

528 In addition, it's important to underline some limitations of our modelling strategy. In particular,
529 sociality could play an additional role and modulate the effects of environment and life history examined here.
530 For example, in some prey species, giving birth synchronously may decrease predation risk via predator
531 satiation (Ims, 1990). In other cases, synchronous births may instead enhance reproductive competition (over
532 food, access to mates or paternal care), and increase the costs of seasonal reproduction. In line with this, it
533 has recently been showed, in a wild chacma baboon population (*Papio ursinus*), that the reproductive timings
534 of subordinate females were influenced by the reproductive state of other females of the group, leading to a

lower reproductive synchrony in the group, thus decreasing breeding seasonality at the population level (Dezeure *et al.*, in press).

4. Generalisation potential

The general theoretical framework developed in this study and in particular most of our working hypotheses could apply to most species experiencing substantial reproductive costs, except perhaps for H6, the hypothesis on infant mortality rates, which is restricted to species with small litters or singletons that can be lost all at once. As such, the ecological and life-history factors that were identified as influential in our model could, potentially, have a wide predictive power. Nevertheless, because our model was deemed realistic, we only tested our hypotheses in local conditions, meaning that our results may not be valid across all environmental conditions, or across the entire life-history space. In particular, adapting our model to a faster-living species, or running a comparative analysis testing these hypotheses across a large taxonomic group encompassing variable environments and life-histories, could bring valuable insights on the generalisability of our results.

Meanwhile, these results can reasonably be extended to other slow-living species, especially slow-living primates. As such, they shed new light on the emergence and maintenance of non-seasonal breeding in apes and humans (Bronson, 1995). As other slow-living primates, humans experience low daily maternal energy costs spread over multiple years (Dufour & Sauther, 2002), and this trait may itself be sufficient to explain why they breed non-seasonally, as they otherwise live in an exceptional range of environmental conditions. Other characteristics that have often been evoked in this context, and are sometimes seen as human-specifics, such as cumulative culture and associated niche construction, agriculture and technology, or extreme behavioural flexibility may, in fact, not be required to explain why humans breed year-round. However, these traits likely provide humans with additional capacity to extract energy from harsh and fluctuating ecological conditions, possibly allowing them to sustain faster reproductive pace, and strive in a wider variety of environments, than other large primates (Wells & Stock, 2007).

Conclusion

This study contributes to the development of a broad theoretical framework on the evolution of reproductive seasonality, which, despite being a classical topic in evolutionary sciences, remains lacunary. We tested this framework through a set of hypotheses, by constructing an original and realistic agent-based model parameterized on a slow-living primate. We could show that ecology and life history interact to shape the emergence of reproductive seasonality. Specifically, this study disentangles the effect of three main components of environmental variation, namely seasonality, productivity and unpredictability, which probably all contribute to generate the well-known association between latitude and reproductive seasonality. We further highlighted how high daily reproductive energy requirements - which typically translate into a fast life history pace – strengthen the intensity of reproductive seasonality, independently of environmental variations. Overall, this study contributes a powerful theoretical framework and modelling tool that may apply across the life-history space, as well as sheds new light on the unexplained variance in the reproductive phenology of long-lived species including humans.

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Data, scripts and codes availability

Program code used in this study are freely available in the GitHub repository https://github.com/lburtschell/RepSeason

Supplementary material

Supplementary material of this study is available in the GitHub repository https://github.com/lburtschell/RepSeason

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