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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

45

Introduction

46 Reproductive seasonality, which consists in a temporal gathering of reproductive events, is a major
47 adaptation to seasonal cycles as it allows synchronising the energetic costs of reproduction with the annual
48 food peak (van Schaik & Brockman, 2005). Because seasonal cycles are increasingly disrupted by climate
49 change (Easterling *et al.*, 2000), a better understanding of the ecology and evolution of reproductive
50 seasonality could generate important insights on how climate change may affect biodiversity (Thackeray *et al.*,
51 2016).

52 Many studies have focused on understanding the physiological regulation of reproductive seasonality
53 as well as variation in its timing (Brockman & van Schaik, 2005; Bradshaw & Holzapfel, 2007; Bronson, 2009;
54 Vatka *et al.*, 2014; Clauss *et al.*, 2021), but less work has investigated why the intensity of reproductive
55 seasonality exhibits such a broad range of variation across species (Campos *et al.*, 2017). Understanding the
56 drivers of such variation in strategies of reproductive phenology (i.e. timing and length of the annual birth
57 season) is essential to predict the resilience of species to climate change.

58 The intensity of environmental seasonality (often approximated by latitude) has traditionally been
59 used to predict reproductive seasonality (Conover, 1992; Ogotu *et al.*, 2014; Heldstab, 2021b) with tropical
60 species breeding year-round and temperate and Arctic species breeding seasonally. Yet, a great part of its
61 variation remains unexplained by this predictor alone. For instance, some tropical species reproduce
62 seasonally (Brown & Shine, 2006; Hongo *et al.*, 2016) while non-seasonal breeding has been observed in some
63 temperate (Riedman *et al.*, 1994) and Arctic (Gruyer *et al.*, 2010) species. There are also examples of sympatric
64 species which largely differ in their reproductive phenology (Sinclair *et al.*, 2000). In sum, besides
65 environmental seasonality, other determinants likely play a significant role in the evolution of reproductive
66 seasonality, such as other ecological factors, life-history traits, and their interaction (English *et al.*, 2012; Clauss
67 *et al.*, 2021)

68 Ecological factors other than environmental seasonality could include environmental productivity
69 (average level of food availability) and unpredictability (hereafter approximated by the non-seasonal variation
70 in food availability and modelled as an added noise to food availability). First, in highly productive habitats, the
71 energy requirements of reproduction could be met year-round even in seasonal environments, thus decreasing

72 the benefits of seasonal breeding. Interestingly, environmental seasonality and productivity are both highly
73 correlated with latitude (Botero *et al.*, 2014), which is a major predictor of reproductive seasonality (Heldstab,
74 2021b; Heldstab *et al.*, 2021). Yet, most studies only investigate the global effect of latitude without
75 disentangling the effects of environmental productivity, seasonality and their interaction. Second, in
76 unpredictable environments, even with some degree of environmental seasonality, a flexible reproduction
77 may be more advantageous than a strictly seasonal reproduction. Indeed, reproducing seasonally in an
78 environment where the food peak is regularly reduced or delayed may generate mismatches between a fixed
79 reproductive timing and a variable annual food peak (Vatka *et al.*, 2014; Clauss *et al.*, 2021). Such mismatches
80 could reduce the benefit of breeding seasonally and therefore lead to a decrease in the intensity of
81 reproductive seasonality. However, only a few studies have investigated this latter effect of environmental
82 unpredictability on the *intensity* (and not only on the *timing*) of reproductive seasonality, with mixed results
83 so far. While English *et al.* (2012) found that inter-annual variation in food availability had an effect on the
84 intensity of birth synchrony of wild ungulate populations from 38 species, two other studies on red deer, *Cervus*
85 *elaphus* L. (Loe *et al.*, 2005) and chacma baboons, *Papio ursinus* (Dezeure *et al.*, 2023) found no effect of
86 environmental unpredictability on reproductive seasonality.

87 Regarding the effect of life-history traits, variation across species in strategies used to finance the
88 energetic costs of reproduction has likely played a major role in shaping the evolution of their reproductive
89 schedule. In particular, the mechanism consisting in limiting the peak in energy demand for reproduction, by
90 adopting a “slower” life history, as defined by the fast-slow continuum framework (Stearns, 1989; Bielby *et al.*,
91 2007) could be critical to sustain non-seasonal reproduction. Indeed, high day-to-day reproductive energy
92 requirements, which are typical of short-lived species with large litter size and fast reproductive cycles (Bielby
93 *et al.*, 2007), likely limit the period of the year where the energetic costs of reproduction can be met. In
94 contrast, in species with slower reproductive paces, reproductive costs are spread over time and more easily
95 afforded year-round (van Noordwijk *et al.*, 2013). Additionally, and regardless of the life-history pace, the
96 length of the reproductive cycle could also be a key factor, depending on whether or not it is synchronised
97 with the annual schedule. Particularly, for long lived species, a reproductive cycle lasting more than exactly
98 one, two, three or more full years (i.e., that is not an integer number of years), could decrease the benefits of

99 seasonal breeding by introducing gaps at the end of each reproductive cycle, where females must wait the
100 next reproductive season in order to reproduce again. Lastly, slow-living species often have small litters or
101 singletons that can be lost all at once (Bielby *et al.*, 2007). In such cases, species with high external offspring
102 mortality compared to that of adults – a defining feature of slow life histories (Jones, 2011) – could face costs
103 from reproducing seasonally by experiencing gaps after losing their offspring if they have to wait the next
104 reproductive season to conceive again, similarly to species whose reproductive cycles are not integer years.

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

116 In this study, we developed an agent-based optimisation model to investigate the effects of variations
117 in ecological and life history traits on the emergence of reproductive seasonality. We chose to create a realistic
118 and detailed model based on energetics, that we parameterized using published empirical data from the yellow
119 baboon (*Papio cynocephalus*). This choice of a long-lived tropical and non-seasonally breeding (Campos *et al.*,
120 2017) model species contrasts with most studies on reproductive seasonality. First, focusing on a non-seasonal
121 breeder and on how reproductive seasonality could emerge from this point is a new approach and the *Papio*
122 genus is well suited for it because it is characterised by phenological flexibility, with one in six *Papio* species
123 breeding seasonally (Petersdorf *et al.*, 2019). Second, studying a tropical species like baboons is of major
124 interest because most studies of reproductive seasonality focus on organisms from temperate regions
125 (Bronson, 1985; Vatka *et al.*, 2014). Lastly, long-lived species such as baboons, where reproductive cycles

126 spread over multiple years, tend to be under-represented in studies of breeding seasonality, but could bring
127 important insights to understand our own reproductive phenology, namely why humans reproduce year-
128 round.

129 Yellow baboons live in tropical semi-arid savannas characterised by relatively low productivity, high
130 unpredictability and moderate seasonality (Gesquiere *et al.*, 2008). They give birth to one offspring at a time
131 with a limited growth rate during lactation (Altmann & Alberts, 1987) inducing relatively low day-to-day
132 reproductive energy requirements. Their mean interbirth interval (IBI) is 638 days, or 1.75 years (Gesquiere *et*
133 *al.*, 2018), which is not an integer number of years, and they exhibit a moderate extrinsic infant mortality (for
134 a slow-living species) (Alberts, 2019). Altogether, their non-seasonal reproductive phenology appears
135 consistent with our hypotheses regarding their habitat characteristics and life history 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 vegetation productivity, extracted from the Amboseli national Park coordinates, as a proxy of food
144 availability. By artificially reshaping the NDVI time series, we subsequently investigated the effect of variation
145 in three environmental traits (seasonality, productivity and unpredictability) on the fitness of these different
146 strategies. We further tested the influence of three life-history traits (daily reproductive expenditure, length
147 of the reproductive cycle and infant extrinsic mortality rate) on the optimal phenology strategy by modifying
148 the model parameters. By doing so, we were able to test our working hypotheses, respectively proposing that
149 the 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.

153

Methods

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A. Model description

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The programme 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).

158

1. Purpose

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The purpose of this study is to investigate the determinants of reproductive seasonality in a mammalian species. To do so, we simulate the life cycle of a female yellow baboon (*Papio cynocephalus*) with an energetic approach to evaluate the optimal strategy of reproductive phenology. We parameterized the model using published empirical data (Table S1), but we developed its structure to be as general as possible so that it could be adapted to other mammalian species.

164

2. Entities, state variables, and scales

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Agents/individuals:

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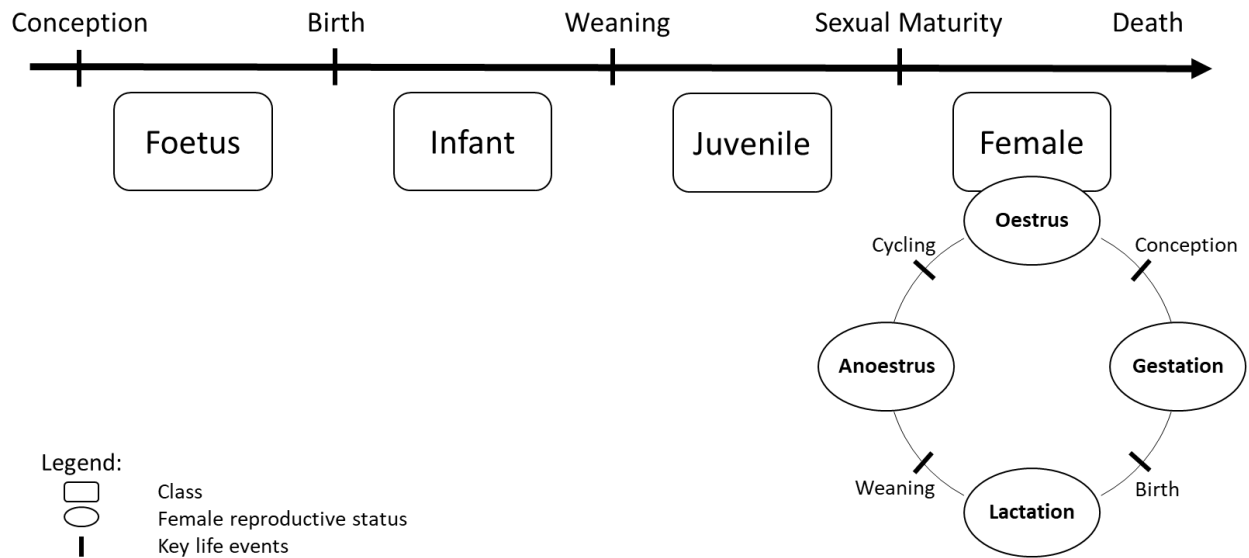
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The model simulates the life cycle of a female adult baboon and her offspring. We do not discriminate the offspring by sex and only include adult females. We consider here that males are non-limiting for female reproductive success, and do not affect 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 inherit (acquire properties and behaviour) from one another (Fig. 1). Each individual is characterised by some attributes or state variables, according to his life stage (Appendix A, Table S2) which accounts for the changes occurring during the simulation.

177



178

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

179

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.

183

184 *Temporal scales:*

185

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.

186

187 *Environment:*

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Each simulation occurs in an environment characterised by its food availability, approximated by the Normalized Difference Vegetation Index (NDVI). NDVI is an indicator of vegetation productivity (Pettorelli *et al.*, 2005) and is therefore relevant to predict food availability for yellow baboons whose diet, although omnivorous, consists mainly in plants (Post, 1982). NDVI has indeed previously been used in several baboon populations to estimate food availability (Baniel *et al.*, 2018; Dezeure *et al.*, 2021; Walton *et al.*, 2021; Dezeure *et al.*, 2023) and has also proved relevant to predict reproductive seasonality in humans (Macfarlan *et al.*, 2021). When vegetation productivity is weak (low NDVI), the model also allows the use of alternative sources of food, called 'fallback food', as described in wild yellow baboons (Altmann, 1998) (see Appendix B - Section 3 "Energy intake" and Figure S1 in the Supplementary Material for details).

196

197 To account for realistic seasonal changes in NDVI, we used real values from the Amboseli population
198 of yellow baboons. We used a GPS tracking study (Amboseli Baboon Research Project, 2015 - see Markham *et*
199 *al.*, 2013 for methods) to assess the coordinates of a quadrat where the majority of the baboon movements
200 occurred (South/West: -2.75, 37.04 ; North/East: -2.70, 37.11). This quadrat covers a surface of about 42 km²,
201 which is consistent with the annual home range size observed in wild baboons (Altmann & Muruthi, 1988). We
202 extracted NDVI within this quadrat using the 250-m resolution NDVI 16-day composite data from the
203 MOD13Q1 product (Didan, 2015) which we linearly interpolated to have a daily time series from February 18,
204 2000 to May 09, 2022. Because our simulations can run for more than 27 years, we needed to extend the NDVI
205 dataset. To do so, we chose to simply repeat the entire NDVI time series. To minimise discontinuity, we
206 compared the first and last years of the time series and selected the day of year with the least variable NDVI
207 that we therefore used as the transition point for concatenation of the NDVI time series.

208 **3. Process overview and scheduling**

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

- 210 1. Potential death of the female and/or offspring (if any)
- 211 2. Potential change of the female reproductive status (cycling, conception, birth or weaning)
- 212 3. Evaluation of daily energy intake extracted from the environment
- 213 4. Evaluation of daily energy needs based on reproductive status
- 214 5. Energy allocation:
 - 215 5.1. If positive energy balance: storage of energy for the female and offspring (if any)
 - 216 5.2. If negative energy balance: release of energy and/or energy restrictions (slowdown of growth,
217 miscarriage, infant abandon) for the female and offspring (if any)
- 218 6. Growth of the female and/or dependent offspring (if any)

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

222 These six submodels (Death, Change of reproductive status, Energy intake, Energy needs, Energy
223 allocation and Growth) are described in Appendix B of the supplementary material (Fig S1-3).

224 **4. Design concepts**

225 *Emergence, Adaptation:*

226 In this statistic optimisation model, we compute the female fitness associated with each phenology
227 strategy. The fitness of an individual does not depend on the strategy of others. In particular, male function is
228 supposed to be non-limiting, and we do not consider density-dependence interactions. The phenology strategy
229 (i.e. the beginning and length of the time window during which a female can conceive) is constant throughout
230 each simulation (i.e. throughout her lifetime), but different phenology strategies are tested in a given set of
231 simulations. To account for both different reproductive timings (the date in the annual cycle of the mating
232 season) and different intensities of the reproductive seasonality (i.e. the length of the mating season), we
233 tested various phenology strategies, with reproductive windows starting each first day of each month (12
234 different timings) and lasting from 1 to 11 months (11 different intensities of reproductive seasonality). We
235 also tested the non-seasonal phenology strategy (females can conceive year-round), resulting in 133
236 phenology strategies tested for each set of simulation. We ran 2000 simulations for each phenology strategy
237 and extracted the resulting mean fitness values. The optimal strategies of reproductive seasonality emerged
238 from the set of simulations as the strategies associated with the highest fitness values. Because differences
239 between some phenology strategies can be small (one-month difference in start or length of reproductive
240 window), in most cases there is not a single phenology strategy that emerges but rather a group of optimal
241 phenology strategies associated with the highest fitness values. More precisely, we assessed the difference
242 between the mean fitness value of the “best” phenology strategy (i.e. highest one) and the mean fitness values
243 associated with each other phenology strategy and allowed a 5% decrease in fitness as a confidence margin.
244 Optimal phenology strategies were therefore defined as strategies whose mean fitness value ranged above
245 95% of the highest mean fitness value.

246 *Fitness:*

247 Individual fitness (λ_{ind}) is calculated at the end of each simulation as described in McGraw and Caswell
248 (1996) and represents the “population growth rate of an individual”. Previously used in empirical studies

249 (McLean *et al.*, 2019), this value takes into account not only the number of offspring born to a female but also
250 the timing at which they are produced: the earlier in life a female has offspring, the higher her individual growth
251 rate. Specifically, λ_{ind} is the dominant eigenvalue of Leslie matrices built on individual females, which indicates
252 the number of offspring produced each year. It should be noted that λ_{ind} does not represent an individual's
253 contribution to the demographic growth of the population. In particular, the mean of several individual fitness
254 values cannot be used to estimate a population growth rate (McGraw & Caswell, 1996). Because our
255 simulations begin when the female has just reached sexual maturity, we decided to consider in the calculation
256 of the individual fitness only offspring having reached the same point (i.e. sexual maturity). This method
257 prevents us from overestimating or underestimating any life stage in the calculation of fitness, and it especially
258 allows to take into account the post-weaning period which is known to be critical for juveniles (McLean *et al.*,
259 2019). Even if sexual maturity seems to appear around 10 months later for male offspring than for female
260 offspring in yellow baboons (Charpentier *et al.*, 2008), early maturation has been observed in male hamadryas
261 baboons (Zinner *et al.*, 2006). Because of the uncertainty on male sexual maturity age and for simplicity, we
262 chose to use the female age at sexual maturity as a unique milestone for offspring of both sexes.

263

264 *Stochasticity:*

265 There are two stochastic processes in this model: conception and extrinsic mortality. Variation in the
266 probability of conception is accounted for by randomly picking a cycling duration from observed data in the
267 Amboseli yellow baboons (Gesquiere *et al.*, 2018) before each cycling phase of the reproductive cycle. Extrinsic
268 mortality (external causes of death) is accounted for by assigning a maximal lifespan to each individual, also
269 randomly picked from empirical data (McLean *et al.*, 2019) and independent of environmental variations.
270 Individuals die if they reach their maximal lifespan, independently of their current energy resources. Yet,
271 individuals can also die before their assigned lifespan is reached, if the environmental conditions do not
272 provide them with enough energy to survive (“intrinsic” mortality). Overall, individuals in the model can either
273 die from a stochastic external mortality or from an environmentally-dependent intrinsic mortality (see the
274 submodels “Death” and “Cycling” in supplementary for details). Finally, the first day of the simulation is also
275 randomly picked in the annual cycle, in order not to favour one time of the year over another. We ran each

276 simulation 2000 times to account for such stochasticity. We assessed this number by increasing the number of
277 simulation runs until reaching stability in the results.

278

279 *Observation:*

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

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

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

289 **5. Initialisation**

290 At time $t=0$, only one individual of class Female is created. It represents a female yellow baboon that
291 has just reached sexual maturity and its state variables are initialised using parameters from the literature
292 (Appendix A, Table S3). Initial attributes for offspring are presented in Appendix A, Table S4.

293 **6. Input data**

294 We use some species-specific parameters in the model that remain constant throughout each
295 simulation. We compiled and calculated them from the literature (Table S1). Most of them come from
296 published empirical data from wild populations of yellow baboons. When such data were unavailable, we used
297 available values from phylogenetically close species or captive populations.

298 **B. Test of hypotheses**

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

301 **1. Computation of simulated birth seasonality**

302 To compute the birth seasonality associated with specific environmental and life history conditions,
303 we first evaluated all 133 possible phenology strategies (from highly seasonal to non-seasonal) to identify
304 which were optimal (i.e. associated with the highest fitness values, see the section “*Emergence, Adaptation*”
305 section above). We then pooled all births coming from the pool of optimal phenology strategies, and
306 calculated, from these births dates, the mean vector length (r) and direction (μ), using the functions
307 ‘rho.circular’ and ‘mean.circular’ from the ‘circular’ package (Lund *et al.*, 2017) as a measure of birth
308 seasonality.

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

310 In order to disentangle the effects of environment and life history, we chose to modify only the three
311 environmental traits first. By doing so, we drew an environmental landscape composed of three axes
312 (productivity, seasonality and unpredictability) in order to explore their whole range of (co)-variation. We
313 expected one or more interactions, and specifically that the effect of environmental seasonality on
314 reproductive seasonality would be modulated across a gradient of environmental productivity, with higher
315 productivity extending the annual time window where reproduction is sustainable in seasonal environments.
316 For example, abnormally extended birth seasons were observed in a population of North American elk that
317 punctually experienced a higher habitat quality (Keller *et al.*, 2015). Because a 3D representation of the
318 environmental parameter space (productivity, seasonality and unpredictability) can be difficult to apprehend
319 and increases computing time, we chose to systematically simulate and represent only a two-dimensional
320 environmental landscape covering the full range of variation of both environmental seasonality and
321 productivity – and later represented through heatmaps. Variation in those two parameters can indeed reflect
322 a variation in latitude with the top-right to bottom-left diagonal of the heatmaps representing a gradient from
323 low latitudes (high productivity and low seasonality) to high latitude (low productivity and high seasonality).
324 We then tested for the effect of unpredictability, the third environmental dimension, by simulating this same
325 heatmap for four levels of unpredictability (i.e. sectional views of the 3D environmental landscape). We
326 subsequently tested the effect of each life history trait on reproductive seasonality across this two-dimensional

327 landscape in order to cover a broad range of viable environments, but kept unpredictability unchanged for
328 simplicity.

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

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

$$333 \quad NDVI(t) = K + NDVI_S(t) + NDVI_{NS}(t)$$

334 K is the mean NDVI over the entire time series and is therefore a constant that represents the overall
335 productivity of the environment. NDVI_S represents the seasonal part of the variation in NDVI and is obtained
336 by calculating, for each day of the calendar year, the mean daily offset of NDVI from its mean over the 22 years
337 of data (i.e. the mean daily NDVI, minus K). NDVI_S captures the within-year variation of NDVI and is completely
338 identical between years. Lastly, NDVI_NS captures the rest of the NDVI variation and is computed by removing
339 to the overall NDVI its mean K and its seasonal component NDVI_S. NDVI_NS can be seen as the noise, where
340 a positive value indicates that the NDVI is higher than expected for a given calendar day, i.e. for the season. In
341 other words, NDVI_NS essentially captures the non-seasonal variation in NDVI, later used as a proxy for
342 environmental unpredictability. It should be noted that NDVI_NS also encompasses the noise due to
343 measurement errors, that cannot be disentangled from the biological noise but that is likely negligible
344 compared to non-seasonal environmental variation. In addition, unpredictability is a multidimensional entity
345 that cannot be restricted to the NDVI_NS component alone: for example, one additional dimension is the
346 unpredictability in the timing of the food peak. In other words, this decomposition describes the changes in
347 NDVI magnitude for the same calendar date, but does not directly capture the changes in timing of the NDVI
348 time series.

349 We then artificially modified these different components of the NDVI time series by introducing three
350 parameters, s , p and u . This allowed us to modulate the contribution of each component of NDVI as follow:

$$351 \quad NDVI_{modified}(t) = p \times K + s \times NDVI_S(t) + u \times NDVI_{NS}(t)$$

352 The higher p , s and u , the higher the environmental productivity, seasonality and unpredictability
353 (respectively). The parameter p varied from 0.85 to 1.4 while s and u varied from 0 to 3, with the real NDVI

354 given by $p = s = u = 1$. NDVI being a normalised index whose values range between 0 and 1, we truncated
355 accordingly the modified NDVI time series, replacing any negative values with zero, and any value superior to
356 one with one. The ranges of variation for the three parameters p , s and u were chosen in order to explore
357 substantial variation in environmental productivity, seasonality and unpredictability while still simulating
358 viable environments for baboons (i.e., with a sufficiently high productivity). Non-viable environments are
359 characterised by a fitness of zero and appear as grey cells on heatmaps.

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

361 To investigate the effect of an increase in daily reproductive energy expenditure (H4), we modified the
362 daily growth rate at 7.5 g/day instead of the original 5g/day, which is a highly variable parameter between
363 species with different life-history paces (Bielby *et al.*, 2007). This represents an increase of 50% in the energy
364 expenditure associated with growth. Gestation was accordingly reduced from 178 days to 118 to ensure a
365 constant birth mass.

366 To test the effect of a reproductive cycle being an integer number of years (H5), we chose to artificially
367 modify the year length, instead of the reproductive cycle length. With this approach, the biological timing (and
368 especially the daily reproductive energy expenditure) remains unchanged, but the temporal synchronisation
369 between reproductive cycle and year length can change, thus disentangling the two effects predicted by H4
370 and H5. Reducing or extending the reproductive cycle length (for example by modifying gestation length,
371 growth rate, weaning mass...) would indeed be an alternative approach to synchronise the reproductive
372 schedule with the annual cycle. Yet, by also modifying the energetical aspects of the reproductive cycle, this
373 approach could influence reproductive seasonality indirectly, for example via an effect of daily reproductive
374 energy expenditure (H4). On the contrary, modifying the year length alone allows us to isolate the effect of
375 synchronising the reproductive cycle with the annual cycle without altering the energetic transfers between
376 mother and offspring. To do so, we interpolated the 16-days NDVI time series from the raw data assuming a
377 year length of 637 days (equal to the interbirth interval), 425 days (so the IBI would be of exactly 1.5 year) and
378 365 days (normal conditions, IBI = 1.75 year). In other words, we “stretched” the NDVI time series so its
379 seasonal variations would be perfectly synchronised with the reproductive cycle (year length = interbirth
380 interval) or desynchronised (year length = 1.5 interbirth interval). For example, in the synchronised

381 configuration, with a year length of 637 days, the annual good season would always fall during the same phase
382 of the reproductive cycle. In this particular case, each month lasts 53 days and the raw NDVI values, originally
383 spaced of 16 days, are spaced of 28 days.

384 Lastly, to investigate the influence of infant mortality (H6), we modified the proportion of infants dying
385 from external causes by a coefficient m (see submodels “Death” in supplementary for details). The coefficient
386 m took three different values, 0, 1 and 4, corresponding respectively to 0, 11.61 and 46.44% of infants dying
387 from external deaths and representing the range observed in baboon species (Palombit, 2003).

388 **Results**

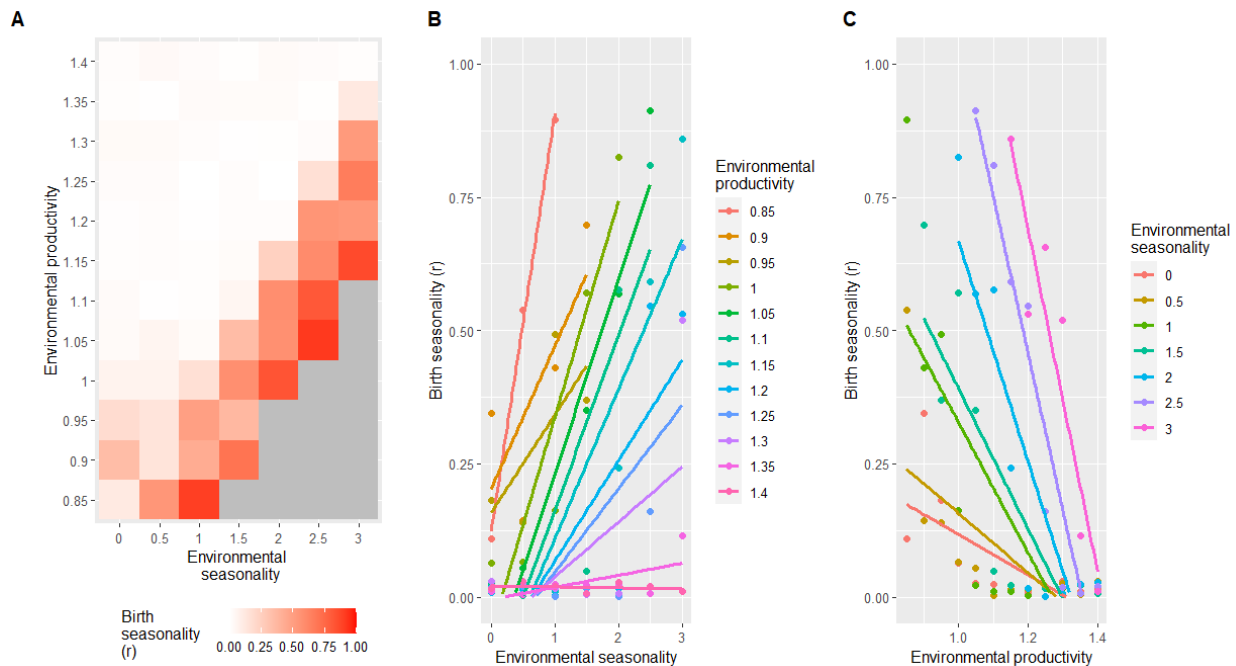
389 We created a model simulating the life cycle of a female yellow baboon. Under realistic conditions, we
390 found as output of our model comparable key life-history traits and reproductive seasonality (non-seasonal
391 reproduction) to the ones observed in the wild, thus confirming its validity (Appendix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

393

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

395 An increasing gradient of birth seasonality was observed for increasing values of environmental
396 seasonality and decreasing values of environmental productivity (Fig. 2a, top-left to bottom-right diagonal).
397 High birth seasonality was therefore observed for environments characterised by both a high seasonality and
398 a low productivity that still sustained a viable reproduction (non-grey cells in Fig. 2a). In very seasonal and very
399 unproductive environments (bottom right corner of the heatmap), baboons’ fitness was indeed of zero,
400 regardless of the phenology strategy followed (Fig. S6). Birth seasonality increased with environmental
401 seasonality but this effect almost disappeared when environmental productivity was high (Fig. 2b). Similarly,
402 birth seasonality decreased when environmental productivity increased, and this effect was modulated by
403 environmental seasonality: the higher the environmental seasonality, the higher the effect of environmental
404 productivity on birth seasonality (Fig. 2c). More precisely, high birth seasonality was observed only for the
405 lowest values of environmental productivity.

406

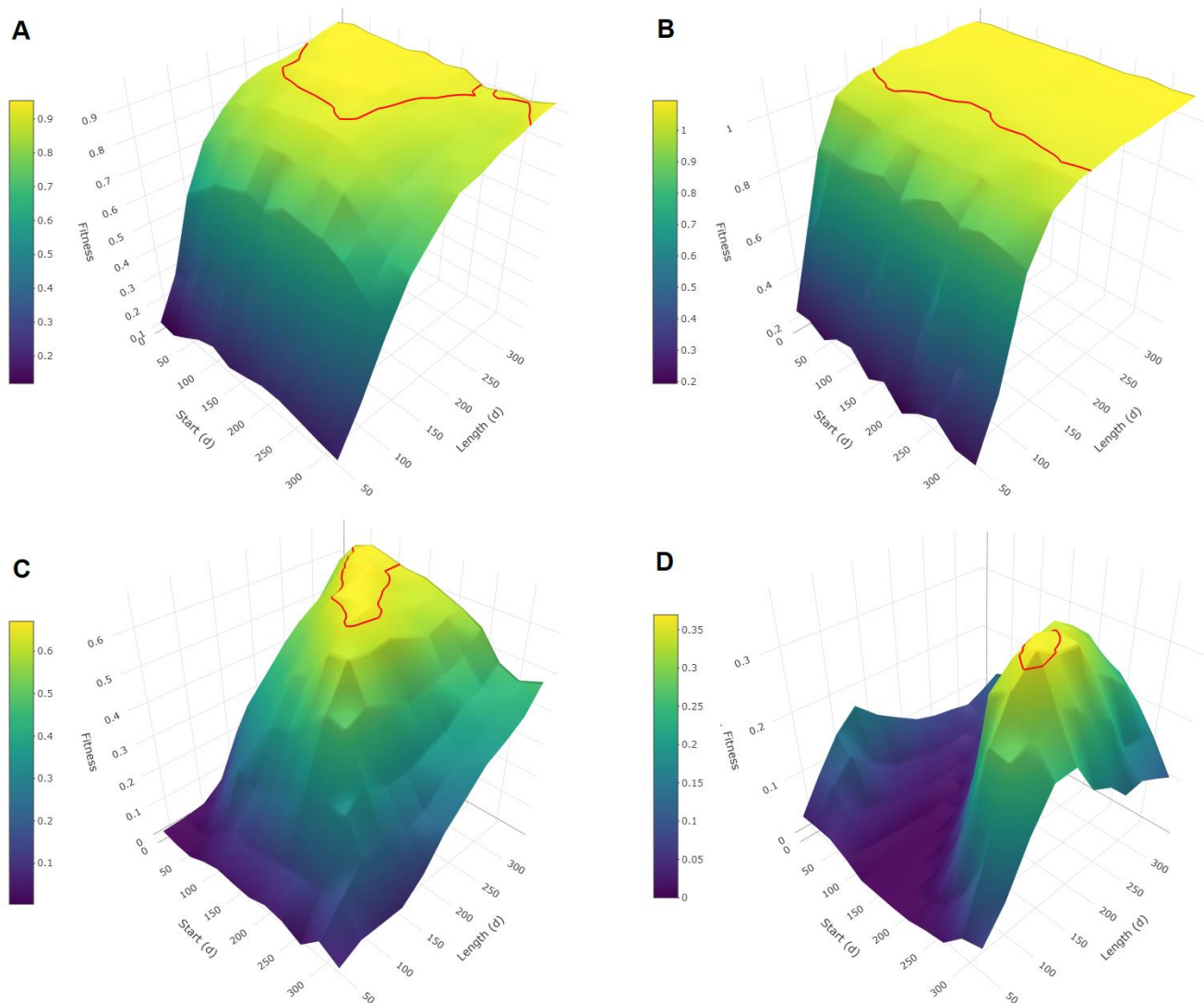


407 **Figure 2:** Effect of environmental seasonality and productivity on birth seasonality (H1-2)

408 Panel A shows a heatmap of birth seasonality along gradients of environmental seasonality and
409 productivity (normal conditions are represented by a seasonality and a productivity of 1). The other
410 parameters remain unchanged (unpredictability of 1, growth rate of 5g/day, IBI of 1.7 years, infant mortality
411 of 11.61%). Birth seasonality is represented by r , going from 0 (births are equally distributed) to 1 (all births
412 occur on the same day). Grey cells represent non-viable environments characterised by a fitness of zero
413 (regardless of the phenology strategy followed), where r cannot be computed and generates missing values.
414 Panel B and C represent the same data, focusing on the effect of environmental seasonality for panel B and
415 productivity for panel C, in interaction with the other.

416 The variation of birth seasonality observed throughout this environmental landscape results from
417 various levels of selection pressure (Fig. 3a-c), with a steeper selection in seasonal environments leading to
418 highest birth seasonality (Fig. 3c).

419



420

Figure 3: Mean fitness as a function of phenology strategies

421

Each 3D surface plot represents mean fitness (individual population growth rate, λ_{ind}) as a function of the phenology strategy followed, for different sets of parameters. For each phenology strategy, mean fitness is obtained from 2000 simulations of the life cycle of a female following this strategy. Phenology strategies are described by a time window with a specific start (day of year) and a specific length (in days) when the female is allowed to conceive. The red line delineates the optimal phenology strategies, defined as strategies whose mean fitness value ranges above 95% of the highest mean fitness value. The steepness of the slope around these strategies reflects the intensity of the selection pressure towards them, with a flat curve corresponding to a weak selection pressure. In panel A, environment and life history correspond to the realistic conditions in Amboseli. In each of the other panels, only one simulation parameter is altered from the realistic conditions. Panel B shows a more productive environment (productivity = 1.1) and panel C shows a more seasonal environment (seasonality = 1.5), while environmental unpredictability and life history remain unchanged. Panel D shows an increased daily reproductive energy expenditure (growth rate = 7.5 g/day) while the environmental parameters and the other life-history parameters remain unchanged.

434

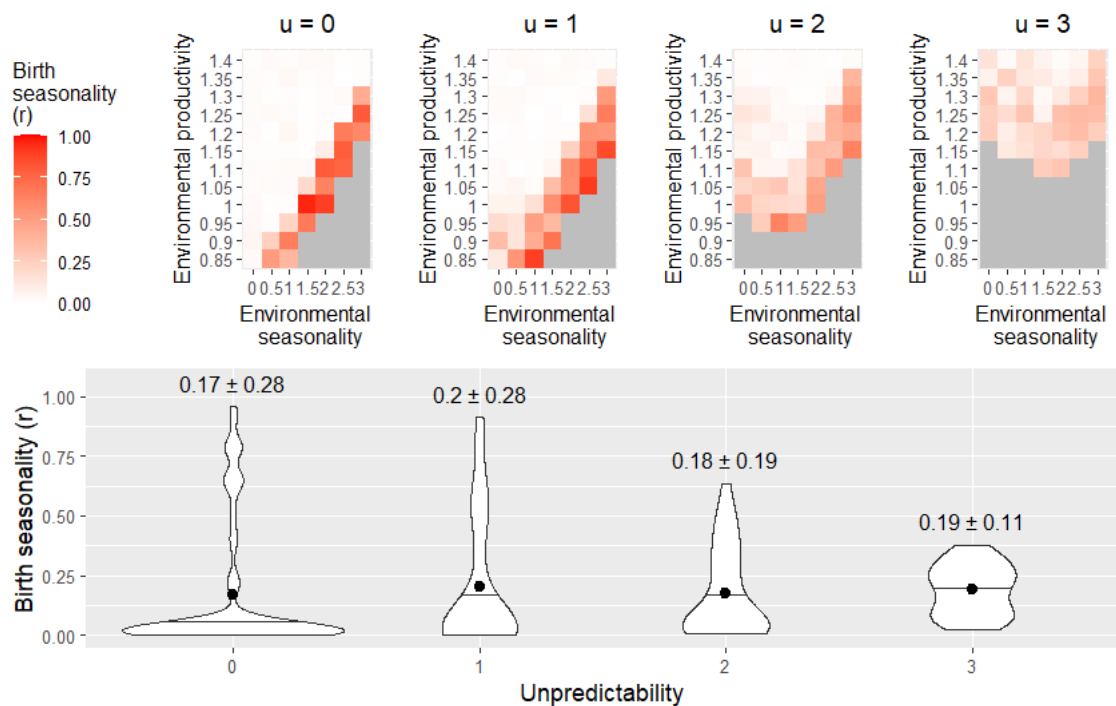
435

Modifying environmental unpredictability (Fig. 4) did not have an effect on mean birth seasonality

436

($r_{mean} = 0.17, 0.20, 0.18$ and 0.19 for $u = 0, 1, 2$ and 3 respectively). However, it had an effect on the variance

437 of birth seasonality values observed within each heatmap ($sd = 0.28, 0.28, 0.19$ and 0.11 for $u = 0, 1, 2$ and 3
 438 respectively) with a strong decrease in maximal values ($r_{max} = 0.96, 0.91, 0.64$ and 0.38 for $u = 0, 1, 2$ and 3
 439 respectively). Yet, this effect was observed only for high values of unpredictability ($u = 2$ or 3), and we did not
 440 observe any effect on birth seasonality when completely removing the unpredictability of the environment (u
 441 $= 0$). Finally, here again, the effects of environmental traits on reproductive seasonality were modulated by
 442 each other: the higher the environmental unpredictability, the weaker the effects of environmental
 443 productivity and seasonality on birth seasonality.



444

445

Figure 4: Effect of environmental unpredictability on birth seasonality (H3)

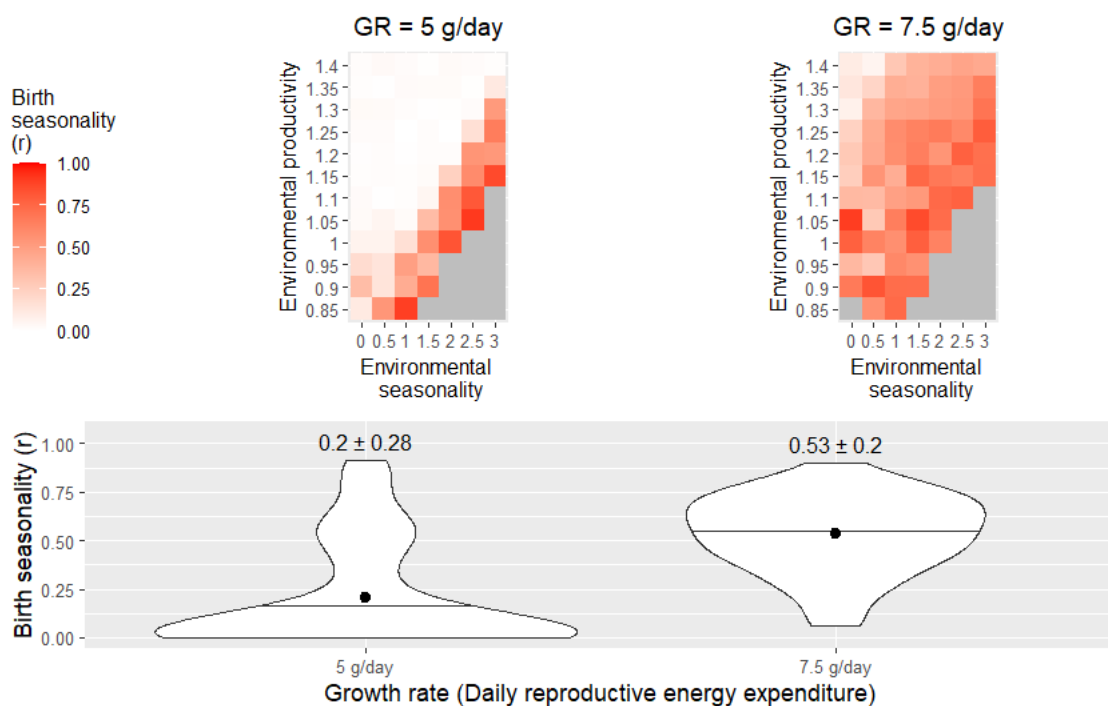
446 The top panel shows heatmaps of birth seasonality along gradients of environmental seasonality and
 447 productivity in four different conditions of environmental unpredictability: no unpredictability ($u = 0$), normal
 448 unpredictability ($u = 1$) and increased unpredictability ($u = 2$ and 3 , respectively). The other parameters remain
 449 unchanged (growth rate of 5g/day, IBI of 1.7 years, infant mortality of 11.61%). Birth seasonality is represented
 450 by r , going from 0 (births are equally distributed) to 1 (all births occur on the same day). Grey cells represent
 451 non-viable environments characterised by a fitness of zero (regardless of the phenology strategy followed),
 452 where r cannot be computed and generates missing values. The panel below shows the distribution of birth
 453 seasonality values observed in each heatmap. Black dots indicate mean values while black horizontal lines
 454 indicate median values. Means and standard deviations are given above each distribution (mean \pm sd).'
 455

455

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

457 Increasing the daily energy expenditure during reproduction by increasing the daily growth rate from
458 5 g/day to 7.5 g/day (+50%) dramatically increased the birth seasonality (+165%) even in environments
459 characterised by high environmental productivity or low environmental seasonality (Fig. 5, $r_{mean} = 0.20$ and
460 0.53 for growth rates of 5 g/day and 7.5 g/day, respectively). This increase in birth seasonality with daily energy
461 expenditure was associated with a steeper selection pressure (Fig. 3d). Individual fitness simultaneously
462 decreased for practically all environmental conditions (Fig. S6).

463



464 **Figure 5:** Effect of daily reproductive energy expenditure on birth seasonality (H4)

465 The top panel shows heatmaps of birth seasonality along gradients of environmental seasonality and
466 productivity in two different conditions of daily reproductive energy expenditure: regular (growth rate = 5
467 g/day) and increased (growth rate = 7.5 g/day). The other parameters remain unchanged (unpredictability of
468 1, IBI of 1.7 years, infant mortality of 11.61%). Birth seasonality is represented by r , going from 0 (births are
469 equally distributed) to 1 (all births occur on the same day). Grey cells represent non-viable environments
470 characterised by a fitness of zero (regardless of the phenology strategy followed), where r cannot be computed
471 and generates missing values. The panel below shows the distributions of birth seasonality values observed in
472 each heatmap. Black dots indicate mean values while black horizontal lines indicate median values. Means and
473 standard deviations are given above each distribution (mean \pm sd).

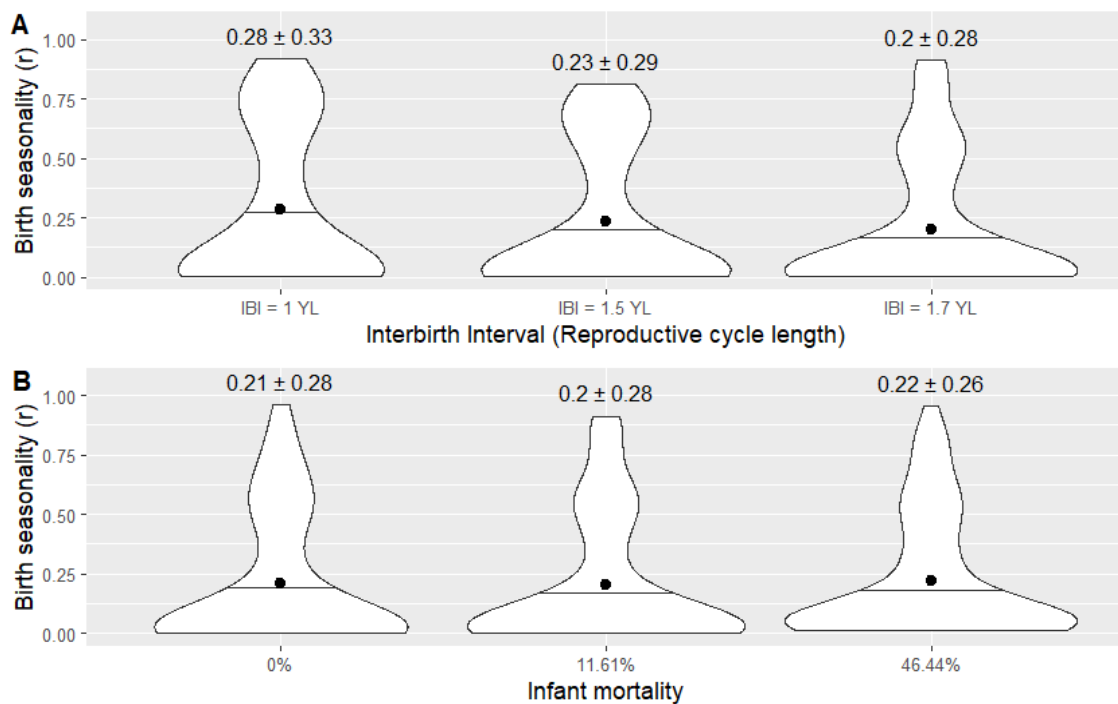
474

475 **3. Minimal support for the length of reproductive cycle hypothesis and no support for the infant**
476 **mortality hypothesis (H5-6)**

477 No strong effect of reproductive cycle length on birth seasonality was observed (Fig. 6a and S7a),
478 although we detected a tendency suggesting that birth seasonality was higher when interbirth intervals lasted
479 exactly one year ($r_{mean} = 0.28, 0.23$ and 0.20 when IBI lasted 1, 1.5 and 1.7 years, respectively).

480 Birth seasonality did not increase after cancelling infant extrinsic mortality nor decreased when infant
481 mortality increased, despite the substantial effect sizes that we explored regarding mortality rates (four-fold
482 increase) (Fig. 6B and S7B, $r_{mean} = 0.21, 0.20$ and 0.22 for $m=0\%, 11.61\%$ and 46.44% , respectively).

483



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

485 Panel A shows distributions of birth seasonality along gradients of environmental seasonality and
486 productivity in three different conditions of reproductive cycle length: when the interbirth interval (IBI) is
487 exactly one year long (YL), when its length is 1.5 years, and in normal conditions, when it is 1.7 years long. The
488 other parameters remain unchanged (unpredictability of 1, growth rate of 5g/day, infant mortality of 11.61%).
489 In panel B, we plotted distributions of birth seasonality along gradients of environmental seasonality and
490 productivity in three different conditions of infant extrinsic mortality rate (M), respectively of 0%, 11.61%
491 (observed rate) and 46.44%. The other parameters remain unchanged (unpredictability of 1, growth rate of
492 5g/day, IBI of 1.7 years). The associated heatmaps (where the plotted distributions come from) are presented
493 in supplementary materials (Fig. S7). Birth seasonality is represented by r , the length of the mean vector, going
494 from 0 (births are equally distributed) to 1 (all births occur on the same day). Black dots indicate mean values
495 while black horizontal lines indicate median values. Means and standard deviations are given above each
496 distribution (mean \pm sd).

497

Discussion

498 1. Effect of ecology on reproductive seasonality

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

509 In addition, our results support H3, by showing that high environmental unpredictability promotes
510 non-seasonal breeding strategies while controlling for environmental seasonality and productivity; this
511 hypothesis has often been proposed but rarely tested. These results are of major interest in the context of
512 climate change, which increases the frequency and severity of extreme events (Easterling *et al.*, 2000).
513 Environmental unpredictability could even be a third overlooked factor encapsulated in the latitude effect,
514 even if its relationship with latitude is not straightforward (English *et al.*, 2012; Botero *et al.*, 2014). In line with
515 this, English *et al.* (2012) showed that birth seasonality in ungulates was better explained by the interaction
516 between NDVI constancy and contingency – two components of predictability (Colwell, 1974) – than by latitude
517 alone. However, another recent study investigating the hypothesis that non-seasonal breeding in chacma
518 baboons was linked to environmental unpredictability found no support for it (Dezeure *et al.*, 2023). These
519 mixed results call for more empirical studies, which should disentangle environmental productivity, seasonality
520 and unpredictability in order to reach firm conclusions.

521 The choice of proxy used to describe environmental unpredictability is most likely critical to explain the
522 mixed results observed for the effect of unpredictability. Here, we use between-year variation as a proxy for

523 environmental unpredictability, while this component of environmental variation could be at least in part
524 predictable (e.g. El Niño climate events, Chen *et al.*, 2004). Additionally, in this study we focused on NDVI
525 variation in *magnitude*, while variation in the *timing* of the annual peak of NDVI could also be critical. For
526 example, environmental conditions characterised by a food peak whose timing differs between years – while
527 still occurring within the same annual period of 3-4 months - would be captured by the non-seasonal
528 component of NDVI, even though the majority of higher-than-average values occur around the same time of
529 the year, during the (variable) seasonal food peak. This implies that this non-seasonal component of NDVI
530 encapsulates, in fact, some part of seasonality in its timing and may explain why, in our model, removing
531 environmental seasonality ($s = 0$) is not enough to observe complete non-seasonal reproduction. To do so, we
532 further need to remove environmental unpredictability ($u = 0$). In this context, our methodological approach
533 relying on the NDVI decomposition to disentangle the effect of environmental seasonality and unpredictability
534 may therefore not be sufficient, and future studies would usefully find a way to distinguish unpredictability in
535 the magnitude and in the timing of the annual food peak, which may influence the ecology and evolution of
536 seasonal breeding in different ways.

537 **2. Effect of life-history on reproductive seasonality**

538 Low day-to-day reproductive energy requirements proved critical in enabling non-seasonal
539 reproduction (H4). Even a rather moderate increase in growth rate ($\times 1.5$), for a constant body mass, was
540 sufficient to increase significantly birth seasonality regardless of environmental seasonality and productivity.
541 This acceleration of reproductive pace has two distinct, and important consequences: (1) maximal daily
542 reproductive energy needs increase for the mother, and (2) the most demanding stages of the reproductive
543 cycle are circumscribed in a shorter period of time - which may only represent one fragment of the year cycle.
544 These two changes, in combination, can lead to a situation where females can only sustain reproduction during
545 the good season. Such an increase in reproductive pace – and daily reproductive costs – corresponds to a slight
546 move on the slow-fast continuum (Bielby *et al.*, 2007) that could be observed within phylogenetically close
547 (and potentially sympatric) species and partly explain the diversity of reproductive seasonality observed among
548 them. This could for example explain why mandrills (*Mandrillus sphinx*), despite being closely related to yellow
549 baboons and living in the equatorial forests of the Congo basin, reproduce seasonally (Hongo *et al.*, 2016;

550 Dezeure *et al.*, 2022). Growth rate in young mandrills is indeed higher ($\times 1.34$), and lactation periods are
551 accordingly shorter than in yellow baboons (about half as long), even though gestation length, birth mass and
552 weaning mass are comparable and adult female mandrills body mass is much lower than for female baboons
553 (Setchell *et al.*, 2001; Dezeure *et al.*, 2022), meaning an even larger difference in daily reproductive energetic
554 expenditure when controlled by maternal size for these two species. At the extreme end of life-history paces,
555 are Bornean orangutans (*Pongo pygmaeus wurmbii*) which flattened their reproductive energy requirements
556 so much that they reached a low and constant level of maternal effort (van Noordwijk *et al.*, 2013), with nearly
557 six years of lactation (compared to about one year in yellow baboons), which makes it easy to understand why
558 birth timing does not matter much.

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

568 Even though this effect of daily reproductive energy expenditure on the evolution of reproductive
569 seasonality has, to our knowledge, never been formally tested, our results are corroborated by some empirical
570 studies. For example, a shorter gestation was found to be associated (when controlling for body mass) with a
571 higher reproductive seasonality in several mammalian orders (Zerbe *et al.*, 2012; Heldstab *et al.*, 2018;
572 Heldstab *et al.*, 2021) ; such a result could, in fact, reflect the increase in daily reproductive energy
573 requirements due to a shortened gestation. This interpretation is strengthened by the case of lagomorphs
574 where the intensity of reproductive seasonality was not associated with gestation length but with litter size
575 (Heldstab, 2021a), with an increased breeding seasonality for species with larger litters, facing increased daily
576 reproductive energy requirements. Overall, these comparative studies that reported associations between

577 reproductive seasonality and various aspects of reproductive pace are consistent with our results supporting
578 a single life-history hypothesis, namely that daily reproductive energy intake is a major determinant of the
579 evolution of (non)seasonal breeding.

580 Our last hypothesis stated that non-seasonal reproduction would emerge from a high mortality rate
581 of infants compared to adults (H6), but we could only detect a weak, tendency in support of H6. It was already
582 known that high rates of infanticide (leading to a high mortality rate of infants relatively to adults) are
583 associated with non-seasonal breeding (Lukas & Huchard, 2014). It is commonly admitted that this is because
584 infanticide is only beneficial for male killers when it accelerates female's return to cycle substantially, which
585 may rarely occur in seasonal breeders where females only re-cycle in the next mating season. Even if our results
586 do not support the alternative interpretation where infanticide could instead select for non-seasonal breeding,
587 the tendency we detected could suggest a co-evolutionary pattern where both traits reinforce each other.

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

589 High reproductive seasonality (over 0.75) was almost systematically associated with low individual
590 fitness values (under 0.25) in our simulations. Even though such simulated measures of individual fitness
591 cannot accurately inform about demographic dynamics, very low mean values of individual fitness may
592 represent ecological situations with declining populations, where reproductive seasonality is unlikely to evolve
593 successfully, at least in theory. Yet, such theoretical considerations are mitigated when confronted to empirical
594 figures: in our simulations, moderate reproductive seasonality (around 0.5, which corresponds to the highest
595 value observed within the genus *Papio*, Petersdorf *et al.*, 2019) is often associated with mean values of
596 individual fitness that are comparable to those calculated from the Amboseli baboons ($\lambda_{ind} = 0.9$, Fig. S6, tile
597 $s=1$ and $p=1$ in the top left heatmap), where the long-term demographic trend seems stable (Samuels &
598 Altmann, 1991), so that we cannot rule out the possibility for seasonal reproduction to emerge on the basis of
599 low values of individual fitness.

600 In addition, it's important to underline some limitations of our modelling strategy. In particular,
601 sociality could play an additional role and modulate the effects of environment and life history examined here.
602 For example, in some prey species, giving birth synchronously may decrease predation risk via predator
603 satiation (Ims, 1990). In other cases, synchronous births may instead enhance reproductive competition (over

604 food, access to mates or paternal care), and increase the costs of seasonal reproduction. In line with this, it
605 has recently been showed, in a wild chacma baboon population (*Papio ursinus*), that the reproductive timings
606 of subordinate females were influenced by the reproductive state of other females of the group, leading to a
607 lower reproductive synchrony in the group, thus decreasing breeding seasonality at the population level
608 (Dezeure *et al.*, 2023). Such a polymorphism of strategies, where some females may choose to delay their
609 reproduction or move it forward to minimize competition over limited resources, could not emerge from our
610 model that only optimises the strategy of an isolated female in the absence of competitors. In order to
611 integrate such frequency-dependent effects, other models, such as game theoretic models, should be
612 developed. Additionally, and on top of sociality, dynamic individual strategies are not considered in this study:
613 a female's investment does not vary dynamically as a function of her age and the model does not allow for
614 terminal investment or increase in reproductive investment toward the end of life. Such variation could be
615 best modelled with dynamic state modelling (dynamic programming).

616 **4. Generalisation potential**

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

627 Meanwhile, these results can reasonably be extended to other slow-living species, especially slow-
628 living primates. As such, they shed new light on the emergence and maintenance of non-seasonal breeding in
629 apes and humans (Bronson, 1995). As other slow-living primates, humans experience low daily maternal
630 energy costs spread over multiple years (Dufour & Sauther, 2002), and this trait may itself be sufficient to

631 explain why they breed non-seasonally, as they otherwise live in an exceptionally wide range of environmental
632 conditions. Other characteristics that have often been evoked in this context, and are sometimes seen as
633 human-specifics, such as cumulative culture and associated niche construction, agriculture and technology,
634 communal breeding or extreme behavioural flexibility (Bronson, 1995) may, in fact, not be required to explain
635 why humans breed year-round. However, these traits likely provide humans with additional capacity to extract
636 energy from harsh and fluctuating ecological conditions, possibly allowing them to sustain faster reproductive
637 pace, and thrive in a wider variety of environments, than other large primates (Wells & Stock, 2007).

638 **Conclusion**

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

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653 Biodiversity MBB platform. We would like to thank Jimmy Lopez and Khalid Belkhir for their assistance in
654 structuring the model and using the MBB platform.

655

Data, scripts and codes availability

656 Program code used in this study are freely available in the GitHub repository

657 <https://github.com/lburtschell/RepSeason>

658

Supplementary material

659 Supplementary material of this study is available in the GitHub repository

660 <https://github.com/lburtschell/RepSeason>

661

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664

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