# The climatic determinants of flexible reproductive seasonality in Africa-dwelling papionins

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## ABSTRACT

At a time when seasonal cycles are increasingly disrupted, the ecology and evolution of reproductive seasonality in tropical vertebrates remains poorly understood. In order to predict how changes in seasonality might affect these animals, it is important to understand which aspects of their diverse patterns of reproductive phenology are linked to either the equally diverse patterns of rainfall seasonality (within-year variations) or instead the marked climatic unpredictability (year-to-year variations) occurring across the intertropical belt. Here, we gather birth and climatic seasonality data from 19 populations of ten Africa-dwelling primate species from the papionin tribe, from strict seasonal to non-seasonal breeders, occupying a wide range of environments, including equatorial, tropical, temperate and arid climates. We investigate (1) the environmental measures that influence the intensity of reproductive seasonality, and (2) the reproductive stage that is synchronized with increased resource availability. Our results demonstrate wide variation in the intensity of birth seasonality between and within species. Across multiple measures of climatic variation, we found rainfall unpredictability to be the only clear predictor of the intensity of reproductive seasonality across populations, i.e., greater year-to-year variation in the amount of rainfall was associated with lower to no reproductive seasonality. Finally, we identified diverse patterns of reproductive phenology, with the most seasonal breeders generally aligning lactation with the peak in resource availability while other populations show more diverse patterns, where conception, lactation or weaning can all be synchronized with maximal food availability. This study sheds new light on the extent and ecological drivers of flexible reproductive phenology in long-lived tropical mammals, and may even contribute to our understanding of why humans give birth year-round.


## INTRODUCTION

Most animals face variation in their environment across the year (Boyce, 1979) in the form of seasonal fluctuations in rainfall, temperature and resource availability that affect their energy balance. Reproductive seasonality, the temporal clustering of reproductive events in the annual cycle, is thought to be beneficial because it synchronizes the most energetically costly reproductive stage with the seasonal food peak, thereby enhancing the condition and survival probability of mothers and offspring (Bronson, 2009; Bronson & Heideman, 1994). Variation in birth frequencies across the annual cycle is a continuous trait, ranging from a complete absence of reproductive seasonality (i.e., random distribution of births throughout the year), as in mountain gorillas (Campos et al., 2017), to cases in which all births occur within a few weeks each year, as in many lemurs (Wright, 1999).

Comparative studies investigating determinants of variation in reproductive seasonality across mammals have often been conducted at the level of the order (rodents: Heldstab, 2021, lagomorphs: Heldstab, 2021, ruminants: Rutberg, 1987; Zerbe et al., 2012, Carnivora: Heldstab et al., 2018, primates: Di Bitetti & Janson, 2000; Heldstab et al., 2020; Janson & Verdolin, 2005) and thus focus on broad-scale macro-evolutionary patterns. These studies have typically detected a relationship between geographic latitude and birth seasonality, suggesting that at higher latitudes, birth seasonality is more pronounced, with a more intense birth peak (more births concentrated over a shorter duration of time). However, important gaps remain in our understanding of the determinants of reproductive seasonality. Few studies have attempted to quantify the extent of variation in reproductive seasonality across multiple populations of the same species (but see in African wild dogs (*Lycaon pictus*): McNutt, Groom, & Woodroffe, 2019, and in red-tailed monkeys (*Cercopithecus ascanius*): Struhsaker, 1997), or across closely related species sharing relatively similar diets, body sizes and life histories (but see in several ungulate species: Pereira, Dos Santos Zanetti, & Furlan Polegato, 2010; Spinage, 1973; Brogi et al., 2022; macaque species: Trébouet, Malaivijitnond, & Reichard, 2021). Thus, studies that

control for major sources of variation in life history or broad dietary categories should be particularly useful for identifying the climatic drivers of variation in reproductive phenology.

The well-known association between latitude and reproductive seasonality fails to explain the diversity of reproductive seasonality patterns observed within restricted latitudinal ranges, such as in the tropics (Heldstab et al., 2020; Janson & Verdolin, 2005). In addition, latitude encapsulates multiple components of climatic variation, which need to be disentangled in order to identify the main climatic factors at play (Burtschell, Dezeure, Huchard, & Godelle, 2023). First, latitude correlates positively with the degree of environmental seasonality, measured as the magnitude of within-year variation (such as the difference between maximal and minimal monthly rainfall in the annual cycle) (Botero, Dor, McCain, & Safran, 2014). Further, latitude covaries negatively with environmental productivity, i.e., overall food availability in a given environment. Variation in productivity may alter the benefits of seasonal breeding, as populations living in more productive habitats may face less pressure to breed seasonally (Burtschell et al., 2023).

Finally, environmental predictability, independently of latitude and seasonality (Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017), could also influence breeding schedules. In locations with intense year-to-year environmental variation, flexible reproduction may be more advantageous than strictly seasonal reproduction (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985). Indeed, regular delays or decreases in the food peak may lead to reproductive failures in strict seasonal breeders, thus reducing the fitness benefits of breeding seasonally. However, few studies have investigated the effects of environmental unpredictability on the intensity of reproductive seasonality, with mixed results so far. While English *et al.* (2012) found that higher inter-annual variation in food availability decreased the intensity of birth synchrony across 38 ungulate species, two studies of red deer, *Cervus elaphus* L. (Loe *et al.*, 2005) and chacma baboons, *Papio ursinus* (Dezeure *et al.*, 2023) found no effect

of environmental unpredictability on reproductive seasonality. A recent modelling study similarly detected limited effects of environmental unpredictability on evolutionary transitions to nonseasonal breeding (Burtschell et al., 2023).

Aside from the selective pressures favouring a flexible reproductive phenology, relatively little is known about how birth timing varies in relation to the annual resource peak in long-lived species. In short-lived species, the full reproductive cycle, from conception to offspring nutritional independence (weaning in mammals), can take place within a single productive season (Bronson, 2009). However, this is not the case for long-lived species, in which multiple stages of a female's reproductive cycle can be aligned with the annual food peak, with varying fitness consequences (Dezeure et al., 2021). For example, females of some species may have to reach a certain threshold of body condition for the onset of reproduction and conception to take place (Brockman & van Schaik, 2005a), meaning that most conceptions are expected to follow a peak of food availability (Brockman & van Schaik, 2005a). In some other species, females may instead synchronize the costliest part of their reproductive cycle with the most productive season so as to enhance maternal condition and survival (Bronson, 2009; Bronson & Heideman, 1994), such that early- or mid-lactation occurs during the annual food peak, as in many primates (J. Altmann, 1980; Brockman & van Schaik, 2005a; Janson & Verdolin, 2005). Lastly, weaning is a critically vulnerable life stage, where juveniles must begin to forage for themselves (J. Altmann, 1980; Lee, 1996). Accordingly, several species have been shown to time their births so as to align weaning with the seasonal food peak (Brockman & van Schaik, 2005a; Janson & Verdolin, 2005), as occurs in most lemurs (Wright, 1999). Overall, the reasons underlying the observed variation in alignment of reproductive stages with the food peak across species and populations remain largely unknown.

In this study, we attempt to address the above gap in our understanding by investigating the evolutionary determinants of the intensity and timing of reproductive seasonality in Africa-

124 dwelling papionin monkeys. We focus on papionins for several reasons. First, they exhibit
125 relatively similar body sizes (large-bodied), life history traits (slow) and diet (omnivorous)
126 (Kingdon et al., 2012; Swedell, 2011), allowing us to investigate environmental effects on
127 reproductive seasonality while controlling for these – potentially confounding – factors.
128 Second, this taxonomic group displays a wide diversity of patterns of reproductive seasonality.
129 Indeed, most baboon (*Papio* spp.) species are non-seasonal breeders (Bercovitch & Harding,
130 1993; Swedell, 2011) despite exhibiting variation in monthly birth frequencies (Cheney et al.,
131 2004; Lycett, Weingrill, & Henzi, 1999), while mandrills (*Mandrillus sphinx*) (Setchell, Lee,
132 Wickings, & Dixson, 2002), Kinda baboons (*Papio kindae*) (Petersdorf, Weyher, Kamilar,
133 Dubuc, & Higham, 2019) and most mangabey species (i.e., *Cercocebus* and *Lophocebus* spp.)
134 (Swedell, 2011) are seasonal breeders. Third, this species constellation exhibits great ecological
135 flexibility, inhabiting arid areas, woodland savannahs, equatorial forests, and high altitude
136 grasslands (J. Fischer et al., 2019; Kingdon et al., 2012; Swedell, 2011) (see also Figure 1).
137 Fourth, within the African members of this tribe, baboons are one of the most well studied
138 primates, with data available from multiple populations of each species within the genus *Papio*
139 (J. Fischer et al., 2019).

140 Lastly, species from this taxonomic group, and in particular from the genus *Papio*,
141 possess a variety of features shared with early hominins (Alberts et al., 2005; Brockman, 2005;
142 Jolly, 2001): they are large, terrestrial and eclectic omnivorous primates (Alberts et al., 2005;
143 Rhine, Norton, Wynn, & Wynn, 1989) that, unlike the great apes, have colonized African
144 savannahs (Bobe, Martínez, & Carvalho, 2020) and give birth to a single offspring every one
145 to three years (J. Altmann & Alberts, 2005; Swedell, 2011). Investigating the environmental
146 determinants of their reproductive seasonality may thus shed new light on the evolution and
147 maintenance of non-seasonal breeding in early hominins (King, 2022).

148 Here we ask three main questions regarding reproductive seasonality in the papionins
149 in our sample:
150 (i) What is the extent of inter- and intra-specific variation in patterns of reproductive
151 seasonality, specifically regarding the height and width of the birth peak, as well as its timing
152 in the annual cycle?
153 (ii) What are the main environmental factors responsible for variation in the intensity of
154 reproductive seasonality? We isolated eight components of environmental variation: latitude,
155 environmental productivity, magnitude of seasonal variation in rainfall, number of rainy
156 seasons, breadth of the rainy season, amount of between-year (unpredictable) variation in
157 rainfall, between-year variation in the timing of the rainfall season, and the type of habitat. We
158 tested the eight corresponding hypotheses (H1.1-1.8) and their associated predictions, which
159 are listed in Table 1.
160 (iii) In seasonally breeding populations, which stage of the reproductive cycle is synchronized
161 with the food peak? We tested whether females match the seasonal food peak with conceptions
162 (H2.1 - the 'conception hypothesis'), lactation (H2.2 - the 'lactation hypothesis'), or weaning
163 (H2.3 - the 'weaning hypothesis').
164

165 # METHODS

166 ## *1- Sample and data selection*

167 Our data set includes published reports on reproductive seasonality in natural populations of
168 Africa-dwelling papionins from the genera *Cercocebus*, *Lophocebus*, *Macaca, Mandrillus*,
169 *Papio*, *Rungwecebus* and *Theropithecus* (Figure 1). We selected papers that reported the
170 number of births per month (except for yellow baboons, *Papio cynocephalus*, from Mikumi
171 National Park, where births were provided in three month-periods). We obtained birth
172 seasonality data from 21 wild populations representing 11 species: see Table S1 for references

associated with each population, and Figure 1 for their locations. We did not find any monthly birth data for nine species of interest for which only data from captivity were available (Kingdon et al., 2012; Swedell, 2011): five species of *Cercocebus* (*agilis*, *chrysogaster*, *galeritus*, *lunulatus*, *torquatus*), as well as *Lophocebus aterrimus*, *Mandrillus leucophaeus*, *Papio papio* and *Rungwecebus kipunji* (Figure 1).

### *2- Birth seasonality data*

We were interested in quantifying two components of reproductive seasonality: the timing of the birth peak and the intensity of birth seasonality. For our analysis of the monthly distribution of births, we considered each birth to have occurred in the middle of the month (i.e., the 15$^{th}$ of each month, except for February where births were considered to occur on the 14$^{th}$). For the Mikumi population, we considered that births occurred in the middle of each 3 month-period. We then used a circular statistic and represented each birth on the annual circle by a vector of length 1 and of angle θ representing its date ($15\times2\times\pi/365.25$ for January, $(14+31)\times2\times\pi/365.25$ for February, etc.). We computed the mean vector (r-vector) per population, whose angle (converted in a date: $\mu_{birth}$) indicates the mean day of the year in which births occur (see Table S1) and is thus a measure of birth seasonality. We computed $\mu_{birth}$ using the function 'circ.summary' from the 'CircStats' package (Agostinelli & Lund, 2018). The length ($r_{birth}$) of the r-vector measures the intensity of birth seasonality, i.e., the degree of uniformity of the birth distribution across the annual cycle, varying from 0 to 1 (Di Bitetti & Janson, 2000; Janson & Verdolin, 2005; Thompson & McCabe, 2013). When $r_{birth}=0$, births are evenly spread across months (i.e., non-seasonal), while when $r_{birth}=1$, births all occur during the same month of the year (extremely seasonal). After comparing several classical measures of reproductive seasonality (Supplementary Materials, Appendix S1), we used only $r_{birth}$ to measure the intensity of reproductive seasonality, as this measure is more robust to differences in sample

size than other metrics, facilitating the comparison of seasonality measures between populations (Janson & Verdolin, 2005; Thel, Chamaillé-Jammes, & Bonenfant, 2022).

## *3- Environmental data*

### *i. Two indicators of environmental variation: rainfall and NDVI*

In order to test our set of hypotheses, we considered environmental variation through two components: rainfall and the Normalized Difference Vegetation Index (NDVI). NDVI produces a quantitative index of vegetation productivity, where higher values indicate a higher degree of vegetation cover (Didan, Barreto Munoz, Solano, & Huete, 2015). Climatic seasonality in Africa (and in most tropical habitats) is mainly characterized by within-year variation in rainfall (Alberts et al., 2005; Feng, Porporato, & Rodriguez-Iturbe, 2013; Van Schaik, Terborgh, & Wright, 1993), which has been successfully used as an indicator of food availability for several of our studied populations (Alberts et al., 2005; Hill, Lycett, & Dunbar, 2000; Petersdorf et al., 2019; Tinsley Johnson, Snyder-Mackler, Lu, Bergman, & Beehner, 2018). In addition, NDVI values have to be used with caution when comparing productivity across environments (Pettorelli et al., 2005), which is why we opted to use rainfall to test hypotheses H1.1-H1-8. For example, the mean annual NDVI value at De Hoop, one of our driest habitats, was almost equal to that of Gashaka, one of our wettest habitats. We thus used variation in rainfall, rather than in NDVI, to disentangle the various components of climatic variation that may affect the intensity of reproductive seasonality (such as environmental productivity, predictability and seasonality) when testing hypotheses H1.1-H1.8.

However, we opted to use NDVI as an index of food availability to calculate the timing of the food peak when testing hypotheses H2.1-H2-3, as Africa-dwelling papionins rely mainly on plants for their diet (Swedell, 2011). Specifically, the annual peak in NDVI – and presumably in food availability - is likely to lag behind that of rainfall by a few weeks, and this lag duration

may vary depending on local climatic or environmental conditions (Bercovitch & Harding, 1993; Dezeure et al., 2021; Jarvey, Low, Pappano, Bergman, & Beehner, 2018). Consequently, we thought that using NDVI would be preferable than rainfall to assess the timing of the annual food peak, and test hypotheses regarding its match to the birth peak in each population.

### *ii. Data extraction*

Daily rainfall was extracted from satellite data sensors with the Giovanni NASA website (product TRMM 3B42) (Huffman, Bolvin, Nelkin, & Adler, 2016) using a 0.25×0.25 degree resolution (corresponding to between 28×28km at the equator and 23×23km at 35° latitude). The GPS coordinates used for this extraction are indicated per population in Table S2, and were assessed either from indications about the home ranges of the habituated groups per population when available in the literature, or alternatively from the geographical location (Park, Reserve or nearby city) of the population (see also Figure 1). Monthly cumulative rainfall (summed across daily values) was subsequently computed between January 1998 and December 2019. We therefore gathered 22 years of rainfall data per population over the same period of time.

We then extracted the mean NDVI per 16 day-period on a 500m × 500m resolution within the same geographical areas used for rainfall extraction (see GPS coordinates in Table S2) between March 2000 and March 2017 (data before and after these dates were not available at the time of data extraction) using MODIS data (MODIS13A1 product) provided by NASA (Didan et al., 2015). Daily NDVI was computed by linear interpolation and then averaged to obtain a monthly value across 18 years.

### *iii. Components of environmental variation*

In order to test our hypotheses, we identified multiple components of rainfall variation within and across years. First, we decomposed for a given site the observed rainfall value into three

248 components as follows: $Rainfall_{m,i} = K_{rain} + Rainfall\ S_m + Rainfall\ NS_{m,i}$ , where m is the month
249 of the year (going from January to December) and i is the year (from 1998 to 2019). $K_{rain}$ is a
250 constant, equalling the mean monthly rainfall across 22 years of records (Figure S1). Rainfall
251 $S_m$ is the seasonal component of rainfall, i.e., the rainfall value, averaged across 22 years, for
252 each month of the year, minus $K_{rain}$ (Figure S1). For example, for a given site, Rainfall $S_1$ (m=1)
253 is the mean of all January rainfall values. The term Rainfall S thus captures the seasonal
254 component of rainfall variation in the annual cycle, i.e., its within-year variation. Finally,
255 Rainfall $NS_{m,i}$ is the non-seasonal component of rainfall, i.e., the difference between the
256 observed rainfall value in any month at a given site ($Rainfall_{m,i}$) and the predictable component
257 of rainfall variation for that particular site in that particular month ($K_{rain}$ + Rainfall $S_m$) (Figure
258 S1). This captures the unpredictable, i.e., between-year, rainfall variation. Using these
259 measures, we assessed the following for each population (see Table S2 for the values associated
260 with each population):

261 - Environmental productivity, or mean annual rainfall, equal to $12 \times K_{rain}$.
262 - Magnitude of environmental seasonality. We computed the magnitude of within-year
263 rainfall variation, as the relative standard deviation (SD) of Rainfall S standardized for
264 environmental productivity, given by the formula: $\frac{100 \times SD(Rainfall\ S)}{12 \times K\mathrm{rain}}$. The higher the
265 value, the more seasonal is rainfall variation.
266 - The number of rainy seasons per year. Using predictable rainfall variation ($K_{rain}$ +
267 Rainfall S), we assessed graphically, for each population, the number of rainy seasons
268 per year.
269 - The length of the rainy season. For environments with only one rainy season, we further
270 calculated the rainfall peak breadth (RPB), which is the minimum number of
271 consecutive months of the year during which 80% of the annual rainfall ($12 * K_{rain}$)

occurs. This measure is meaningless for environments with more than one rainy season, and we thus excluded the populations living in such environments from this analysis.

- Magnitude of environmental unpredictability. We computed the magnitude of between-year rainfall variation, as the relative standard deviation of Rainfall NS, standardized by environmental productivity, given by the formula: $\frac{100 \times SD(Rainfall\ NS)}{12 \times K\mathrm{rain}}$. The higher the value, the more unpredictable rainfall variation is.

Using the literature, we categorized the habitat of each population into three types: tropical forest, open savannah, and mosaic forest-grassland (Table S2).

In addition to the magnitude of environmental unpredictability, we were interested in quantifying unpredictability in the timing of the annual rainfall peak, i.e., quantifying how much the timing of rainfall varied between years. Details on the procedure can be found in Appendix S2, but briefly, using circular statistics, we computed standard deviations of the mean dates of the annual rainfall peak over the 20 years sampled. Values close to zero mean that rainfall peak occurs the same month every year, and the higher the value, the more variation in rainfall peak's timing between years.

Lastly, we computed the mean monthly NDVI across 18 years (i.e., $K_{NDVI}$) and the seasonal component of NDVI variation for each month of the year (i.e., NDVI S), following the same notation used to disentangle the components of rainfall variation. To characterise the timing of the seasonal food peak, we used circular statistics to compute the mean annual NDVI date, $\mu_{NDVI}$ (see Appendix S2 for methodology and Table S2 for values of $\mu_{NDVI}$).

*iv – Phylogenetic tree*

We used the branch length of Version 3 of the 10kTreesPrimates consensus tree (Arnold, Matthews, & Nunn, 2010). Two species of interest were absent from this tree: *Cercocebus sanjei* and *Papio kindae*. For the former, we substituted *Cercocebus galeritus*, its closest

297 relative. For the latter, following recent genetic studies (Jordan et al., 2018; Rogers et al., 2019),
298 we added *Papio kindae* in the same branch as *Papio ursinus*, using the function 'bind.tip' from
299 the package 'phytools' (Revell, 2012).
300

301 ## *4- Statistical analysis*

302 All statistical analyses were conducted in R version 3.5.0 (R Core Team, 2019).

303 ### *i. Factors affecting the intensity of reproductive seasonality*

304 We considered eight potential environmental determinants of reproductive seasonality,
305 which are listed along each corresponding prediction in Table 1.

306 For each hypothesis, we plotted $r_{birth}$ (the r-vector length measuring the intensity of
307 reproductive seasonality in a given population) versus the tested predictor. We then checked
308 the significance of the relationship between each predictor and $r_{birth}$ while controlling for
309 phylogeny using Bayesian phylogenetic generalized linear mixed models with the package
310 'MCMCglmm' (Hadfield, 2010). We included the phylogenetic relationship between species
311 as a covariance matrix, which was derived from the phylogenetic tree. We transformed $r_{birth}$
312 (which could vary from 0 to 1) by multiplying it by 10000 and taking its integer values, and
313 thereafter used a Poisson distribution.

314 Given the low number of populations in this study, and the collinearity between some
315 of our environmental parameters (multivariate models had variance inflated factors >3), we
316 were not able to run stable multivariate models. For example, the magnitude of environmental
317 seasonality was negatively associated with the duration of the rainy season (cor=-0.94, t=-9.15,
318 $p<10^{-4}$), and environmental productivity was negatively associated with both latitude (cor=-
319 0.55, t=-2.69, p=0.016) and the magnitude of environmental unpredictability (cor=-0.80, t=-
320 5.48, $p<10^{-4}$).

321 Therefore, our Poisson regressions included as a response variable the transformed $r_{birth}$
322 values, one fixed effect (each environmental predictor in turn listed in Table 1, standardised if
323 continuous) and the phylogenetic matrix as a random effect. For each model, we set an
324 informative prior and used 500 000 iterations, a burn-in of 100 000 and a thinning interval of
325 100. We visually inspected for convergence and checked the absence of autocorrelations for the
326 posterior distributions of fixed and random effects. A Bonferroni correction was applied due to
327 the number of tests, so that predictors were considered statistically significant when their
328 associated pMCMC values were less than 0.05/n, with n being the number of tests run for a
329 given research question.
330
331 *ii. Timings of conceptions and births in relation with NDVI seasonality*

332 We assessed whether populations were seasonal breeders using the Rayleigh test for circular
333 statistic, more precisely the 'r.test' function from 'CircStats' package (Agostinelli & Lund,
334 2018). Populations were categorized as seasonal breeders when P-values associated with the
335 Rayleigh test were <0.05, meaning that the null hypothesis of a uniform birth distribution could
336 be rejected. Among these seasonally breeding populations (listed in Table S1), we investigated
337 which reproductive stage (H2.1, 'conception'; H2.2, 'lactation'; or H2.3, 'weaning') was
338 synchronized with the annual NDVI peak, i.e. $\mu_{NDVI}$. Additional details are given in
339 Supplementary Materials, Appendix 3 & Table S3. We employed exact two-sample Fisher-
340 Pitman permutation tests, using the 'oneway_test' function from the 'coin' package (Hothorn,
341 Hornik, Van De Wiel, & Zeileis, 2006). This function tests if the observed monthly value of
342 NDVI during a target period, which depends on the hypothesis tested, is significantly higher
343 than monthly values of NDVI randomized across the entire year. For example, using mean
344 gestation length to infer the annual distribution of conception dates, we tested H2.1 by asking
345 if females tended to conceive during, soon before, or soon after the annual food peak, looking

346 at seasonal NDVI values respectively in (i) the six months surrounding $\mu_{conc}$, (ii) the three
347 months before $\mu_{conc}$ and (iii) the three months after $\mu_{conc}$.
348

349 **RESULTS**

350 *1) How variable are patterns of reproductive seasonality?*

351 The annual distribution of births for each population is shown in Figure 2, alongside seasonal
352 variation in rainfall and NDVI. The intensity of reproductive seasonality varies widely across
353 species: hamadryas baboons (Filoha population: $r_{birth}$ =0.02) and most olive baboon populations
354 ($r_{birth}$ <0.22) show non-seasonal births while mandrills (Lékédi: $r_{birth}$ =0.67 and Moukalaba-
355 Doudou: $r_{birth}$ =0.80 resp.) and Kinda baboons (Kasanka: $r_{birth}$ =0.50) exhibit pronounced birth
356 seasonality (Figure 3). The phylogenetic signal associated with the intensity of reproductive
357 seasonality is substantial (Lambda=0.61, 95% Highest Posterior Density Intervals = [0.002 ;
358 0.923]), indicating that more closely related species have more similar patterns of reproductive
359 seasonality. However, such a value is also compatible with some phylogenetic flexibility.
360 Among papionins, the genera *Mandrillus*, *Cercocebus* and *Macaca* show strong reproductive
361 seasonality, whereas the genera *Lophocebus*, *Papio* and *Theropithecus* show an overall lower
362 intensity of birth seasonality, which may be associated with greater flexibility within species
363 (Figure 3). Such flexibility is particularly pronounced in chacma baboons, extending from low
364 (de Hoop: $r_{birth}$ =0.10; Tokai: $r_{birth}$ =0.22, and Tsaobis: $r_{birth}$ =0.10) to moderate birth seasonality
365 (Drakensberg: $r_{birth}$ =0.42; Moremi: $r_{birth}$ =0.37) (Figure 3), while intra-specific variation is less
366 marked for the other species in our sample.

367 The timing of birth seasonality can also be surprisingly variable, even between species
368 that live in adjacent geographical ranges: for instance, Kinda baboons from Kasanka give birth
369 mainly around July, whereas chacma baboons from Moremi give birth primarily between July
370 and November (Figure 2).

371

372 *2) What are the ecological factors affecting the intensity of reproductive seasonality?*

373 We detected an effect of the magnitude of environmental unpredictability on the intensity of
374 reproductive seasonality, while controlling for species relatedness, which supported our
375 prediction H1.6 (Table 2): the higher the magnitude of between-year variation in rainfall, the
376 lower the intensity of reproductive seasonality (Figure 4F). We also found an effect of habitat
377 productivity that contradicted our prediction H1.2 (Table 2): the lower the mean annual rainfall,
378 the lower the intensity of reproductive seasonality (Figure 4B). Note that these two effects lost
379 significance when applying a Bonferroni correction for multiple tests, which was expected
380 given our modest sample size. Lastly, we did not find any support for the other five hypotheses:
381 there was no effect of latitude, magnitude of rainfall seasonality, number of rainy seasons,
382 breadth of the rainfall peak, unpredictability in the timing of the annual peak of rainfall, or
383 habitat on the intensity of reproductive seasonality (Table 2, Figure 4).

384

385 *3) Which stage of the reproductive cycle is timed with the annual food peak?*

386 When considering all taxa in our sample as a whole, none of our three hypotheses were clearly
387 supported (H2.1, H2.2, H2.3). However, in five of the six populations with the strongest
388 reproductive seasonality ($r_{birth}$ >0.5), females appeared to synchronize lactation with the annual
389 NDVI peak, and overall lactation was generally aligned with the NDVI peak in 8 of the 14
390 populations with significant birth seasonality (P-value of the Rayleigh test <0.05) (Table 3,
391 Table S4). In less seasonally breeding populations, females were more variable in the
392 reproductive stages that were timed with the annual NDVI peak, ranging from conception (6 of
393 14 populations, and mainly before than after conception: e.g. Amboseli or Kibale) to weaning
394 (3 of 8 populations: e.g., Moremi or Gilgil) to none (e.g., Simien) or all of these stages (e.g.,
395 Udzungwa) (Table 3, Table S4). Moreover, the timing of the annual NDVI peak compared to

396 the mean conception, birth or weaning dates was highly variable between populations (Table
397 S4).
398

399 # DISCUSSION

400 We revealed strong inter- and intra-specific variation in the intensity of reproductive seasonality
401 as well as in the annual timing of births in Africa-dwelling papionins. Our study further
402 emphasizes the importance of environmental unpredictability for the evolution of flexible
403 reproductive seasonality. Lastly, we found that females from different populations of Africa-
404 dwelling papionins match different reproductive stages with the annual food peak.
405

406 **Papionins exhibit flexible reproductive seasonality**

407 Of the sampled Papio populations, most showed very little seasonality, about a third showed
408 moderate seasonality, and Kinda baboons departed from the overall baboon pattern in being
409 highly seasonal breeders. Such diverse patterns of reproductive seasonality within a single
410 genus have rarely been reported outside primates (see for example *Cervus*: English et al., 2012;
411 Loe et al., 2005; Rutberg, 1987, *Damaliscus*: Rutberg, 1987, *Ovis*: Rutberg, 1987, *Ursus*:
412 Spady, Lindburg, & Durrant, 2007, *Mustela*: Heldstab et al., 2018, *Vulpes*: Heldstab et al.,
413 2018), but apparently occur in some other primate genera with large distribution ranges, such
414 as *Alouatta* (Di Bitetti & Janson, 2000; Janson & Verdolin, 2005), *Cercopithecus* (Heldstab et
415 al., 2020; Janson & Verdolin, 2005), *Cebus* (Janson & Verdolin, 2005) and *Macaca* (Heldstab
416 et al., 2020; Janson & Verdolin, 2005; Trébouet et al., 2021). Given the limited taxonomic scale
417 of our study, it is impossible to establish whether seasonal breeding was the ancestral state in
418 papionins, but it seems possible that the loss of seasonal reproduction is a derived state affecting
419 the *Papio* genus (Fig 3).

420 Importantly, the key adaptive trait that evolved in the *Papio* genus may not be simply
421 the loss of breeding seasonality *per se*, but the evolution of a flexible reproductive phenology.
422 Such flexibility would imply that each population, or even each individual (Dezeure et al., 2021,
423 2023; Dezeure, Charpentier, & Huchard, 2022), may be able to adjust phenology to current
424 environmental conditions. In line with this, intraspecific variation is particularly pronounced in
425 chacma baboons, the only species in our sample represented by more than three populations
426 with a reasonable number of births. In addition, chacma baboons exhibit a large distributional
427 range characterized by exceptional ecological diversity, which includes cold and temperate
428 climates, oceanic and mountainous ecosystems, and tropical and arid savannahs.

429 Flexibility in reproductive phenology may be facilitated by several mechanisms. First,
430 a slower life history may allow papionin species to spread the energetic costs of reproduction
431 over a prolonged period, such that pregnant or lactating females face only a small daily extra
432 energetic expenditure that can be afforded at any time, as suggested by a recent modelling study
433 (Burtschell et al., 2023). In addition, unlike many other mammals, cercopithecids do not use
434 strict photoperiodic cues to trigger their reproduction (Heldstab et al., 2020) but may instead
435 exhibit condition-induced reproduction, whereby conceptions (and/or cycle resumption after
436 lactation) are more likely to occur when females are in better condition (Alberts et al., 2005;
437 Beehner, Onderdonk, Alberts, & Altmann, 2006). Such reproductive flexibility may have
438 contributed to their historical ecological success via their ability to colonize diverse
439 environments, and may become a critical asset to facilitate their resilience to climate change,
440 associated with increasing environmental unpredictability (Feng et al., 2013).

441

442 **Environmental unpredictability may drive flexible reproductive seasonality**

443 We examined several possible climatic drivers of the intensity of reproductive seasonality
444 across our sample, and found that environmental unpredictability was a significant predictor,

445 with higher between-year rainfall variation being associated with lower reproductive
446 seasonality. So far, most studies investigating climatic effects on reproductive phenology have
447 focused on environmental seasonality, i.e., the magnitude of within-year environmental
448 variation. In primates, the effect of environmental unpredictability on reproductive seasonality,
449 e.g., through climatic events such as el Niño or fruit mast years in South-East Asia, has been
450 suggested (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985; Wiederholt
451 & Post, 2011) but had never been tested. In line with our results, a previous study across 70
452 ungulate populations showed that the birth peak is more spread out in environments with more
453 year-to-year environmental variation (English et al., 2012).

454 Unpredictable climates may considerably reduce the fitness benefits associated with
455 seasonal breeding, such as enhancing maternal condition and offspring survival. In southern
456 Africa, year-to-year climatic variation frequently takes the shape of an absence of rain during
457 the rainy season (Alberts et al., 2005), which could cause severe reproductive costs in seasonal
458 breeders who often synchronize lactation or weaning with the rainy season, subsequently
459 forcing females to wait until the next breeding season to initiate a new reproductive event. In
460 such conditions, other adaptive traits may be more advantageous than seasonal breeding to face
461 the energetic costs of reproduction, such as a better ability to store energy (Brockman & van
462 Schaik, 2005a; van Schaik & van Noordwijk, 1985), to expand the dietary repertoire via a
463 generalist diet or foraging innovations (Grueter, 2017), to increase daily foraging time (Alberts
464 et al., 2005; Grueter, 2017), to flexibly adjust lactation duration (Dezeure et al., 2021; van
465 Noordwijk, 2012), or to reproduce cooperatively (Cornwallis et al., 2017; Lukas & Clutton-
466 Brock, 2017). Papionin species show many such traits: they can store energy, they have an
467 eclectic omnivorous diet, and they are flexible foragers that typically rely on fallback foods
468 during the dry season (J. Altmann, Schoeller, Altmann, Muruthi, & Sapolsky, 1993; S. A.
469 Altmann, 2009; Swedell, 2011).

Two recent studies found no or little effect of climatic unpredictability on the intensity of reproductive seasonality at the population level, one in chacma baboons (Dezeure et al., 2023) and one on yellow baboons using a modelling approach (Burtschell et al., 2023), questioning the robustness of the effect found in this study. This discrepancy may come from the fact that unpredictable climates select for reproductive flexibility, rather than nonseasonal breeding. In fact, the study by Burtschell et al., 2023 revealed that increasing climatic unpredictability was associated with a lower variance, but not a lower mean, in the intensity of reproductive seasonality. In addition, the effect of climatic unpredictability may be better detected across space than time, i.e., by comparing different populations living in distinct climates and environments, as is the case here, than by comparing the same population across time, as was the case for Dezeure et al., 2023. Different study designs should be combined, across time, taxonomic or spatial scales, to reveal the full complexity of selective pressures at play.

The numerous pressures affecting the intensity of reproductive seasonality are often hard to disentangle, meaning that the effects uncovered by correlational studies like ours may sometimes reflect other co-varying pressures, and should thus be interpreted cautiously. Specifically, environmental productivity, which is negatively correlated with climatic unpredictability at our study sites (cor=-0.80, t=-5.48, $p<10^{-4}$), was also a significant predictor of the intensity of reproductive seasonality, but in a direction opposed to our prediction, as well as to previous results (Burtschell et al., 2023). In our sample, the least productive climates are also the most unpredictable, and environmental productivity may thus represent a confounding factor in the relationship between climatic unpredictability and seasonal breeding. In species with a flexible phenology, females can start a new reproductive event rapidly after a reproductive failure, without having to wait the next mating season. Such failures are likely to be particularly frequent where environmental productivity is low, contributing to spread

495 reproductive events across the year cycle, and explaining how environmental productivity may
496 contribute to decrease reproductive seasonality.

497 Lastly, our decomposition of rainfall components further calls for a more rigorous
498 definition of the term seasonality, especially when it is used in a quantitative way. Indeed, a
499 'more seasonal' environment can either be an environment with higher within-year variation
500 (i.e. the amplitude of variation between the 'best' and the 'worst' month of the year), with
501 higher within-year over between-year variation (i.e. the amplitude of within-year variation
502 controlling for the intensity of unpredictable variations), with a shorter productive season (i.e.
503 the rainfall peak breadth), or with only a unimodal season (i.e. one rainy, or one warm season
504 per year). Similarly, climatic unpredictability can be broken into two components: (1) the
505 amount/magnitude of year-to-year variation (i.e., if the rainy season brings more or less rainfall
506 than usual), and (2) year-to-year variation in the timing of the rainy season (i.e., if the rainy
507 season occurs earlier or later than usual) (Clauss, Zerbe, Bingaman Lackey, Codron, & Müller,
508 2020). These various components have rarely been disentangled in empirical studies so far, and
509 this study opens new methodological avenues to investigate various environmental components
510 that are likely to affect reproductive seasonality.

511

512 **Females can match different reproductive stages with the food peak**

513 The main pattern emerging from our investigations suggests that females from species with
514 high breeding seasonality match lactation with the peak in vegetation productivity (Table 3).
515 For species and populations with a more flexible reproductive phenology, females can match
516 different reproductive stages with the annual vegetation peak, with a possible preference
517 towards conception. This trend may reflect the condition-dependence of conception – a
518 proximate mechanism – rather than an adaptive, optimal strategy aimed at synchronizing the
519 vegetation peak with a particular reproductive stage. These results, obtained from (mostly)

520 tropical primates, echo the broader mammalian literature showing that most mammals from
521 temperate regions match lactation with the best season of the year (Bronson, 2009; Bronson &
522 Heideman, 1994), while patterns are more variable in tropical and long-lived mammals,
523 depending on body size, energy storage capacities and environmental predictability (Brockman
524 & van Schaik, 2005a; Janson & Verdolin, 2005; van Schaik & van Noordwijk, 1985). Finally,
525 even though weaning is a vulnerable life-history stage in young primates, which can be buffered
526 when matched with the vegetation peak in wild chacma baboons (Dezeure et al., 2021), few
527 populations seemed to adopt this strategy. Our estimations of lactation peak and weaning might
528 lack accuracy, due to strong between-populations and between-individuals variation. Data
529 quantifying maternal energy expenditure during lactation (Rosetta, Lee, & Garcia, 2011), or
530 isotopic measures of trophic levels between mother and infants (Reitsema, 2012; Reitsema,
531 Partrick, & Muir, 2016) would be necessary, for each population, to determine the dynamics of
532 lactation and weaning. Second, additional unexplored factors can potentially affect
533 reproductive timing and further limit our ability to detect a clear pattern. For example, for
534 populations living at high altitudes like the geladas from Simien and the chacma baboons from
535 Drakensberg, seasonal variation in temperatures also constrain reproductive phenology (Lycett
536 et al., 1999; Tinsley Johnson et al., 2018).
537

538 **The evolution of reproductive flexibility in Anthropoid primates may inform our**
539 **understanding of the reproductive phenology in early humans**

540 Baboons and relatives represent an interesting model for understanding the evolution of
541 behavioural and reproductive plasticity of early humans (J. Fischer et al., 2019; King, 2022).
542 Although most great apes are nonseasonal breeders (Brockman & van Schaik, 2005b; Campos
543 et al., 2017), suggesting that their common ancestor also bred year-round, humans are distinct
544 from other apes by exhibiting much faster reproductive paces (which are similar to most Africa-

545 dwelling papionins: Swedell, 2011), and by living in a wider variety of environments, rather
546 than being restricted to tropical forests (Wells & Stock, 2007). The selective pressures that have
547 shaped reproductive phenology in the human lineage versus in other apes may therefore differ,
548 and the papionins, who have similarly left forested habitats to colonize savannahs may provide
549 valuable insights to understand the adaptation of early humans to such diverse and
550 unpredictable environments. Our results suggest that baboons have acquired a low and flexible
551 reproductive seasonality, as well as several other adaptive traits, when facing more arid and
552 unpredictable environments, such as a generalist omnivorous diet and the frequent use of
553 fallback foods, frequent foraging innovations, an increased ability to store fat and to switch
554 home ranges to more suitable areas. Similar reproductive, physiological and behavioural
555 adaptations to environmental unpredictability may have allowed early humans to thrive and
556 maintain fast reproductive paces during their colonization of a wide variety of environments.
557

558 **Conclusion**

559 Our work revealed substantial variation in patterns of reproductive seasonality within and
560 across species of Africa-dwelling papionins, highlighting an exceptional flexibility in their
561 reproductive phenology. Among multiple dimensions of climatic variation, rainfall
562 unpredictability and productivity were the main predictors of the intensity of reproductive
563 seasonality, with arid and unpredictable climates being associated with less seasonal
564 reproduction. Among populations with a pronounced breeding seasonality, females often match
565 lactation with the annual vegetation peak, while phenology patterns are very diverse in other
566 populations. This study sheds new light on the selective pressures shaping reproductive
567 seasonality in long-lived tropical mammals, as well as on potential adaptations to environmental
568 unpredictability. It may further provide an original contribution to understand why humans

breed year-round, given their phylogenetic ties and convergences in life-history and ecology with our taxonomic group.

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## DATA AVAILABILITY

The raw data and scripts used for this paper will be made available online upon submission, on a Dryad repository.

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# FIGURES

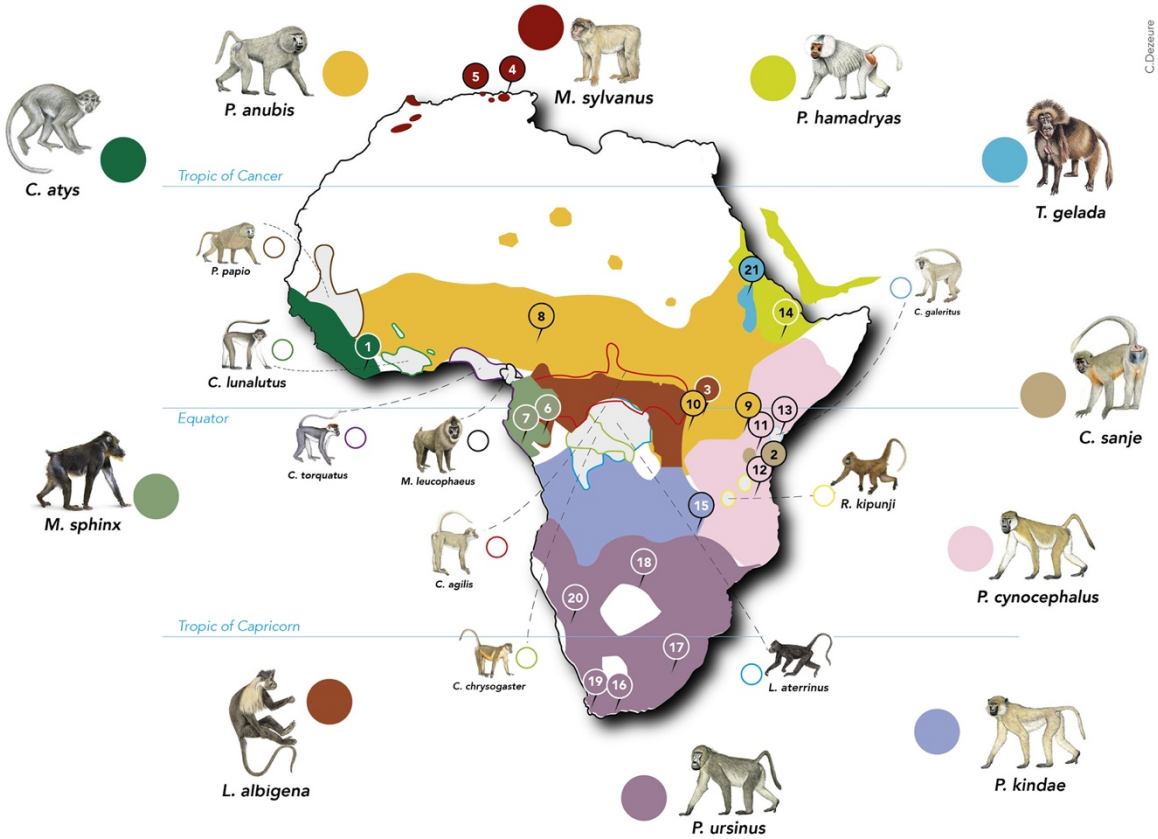


**Figure 1:** Distribution of the sampled species in Africa, and locations of the populations considered in this study.

The species sampled in this study are depicted with relatively larger icons and species names, as well as full coloured circles. Species for which we could not find birth seasonality data are represented with smaller icons and names. The coloured areas on the map, corresponding to each species as indicated by the coloured circles, show the geographical distribution of each species. Within each range, small circled numbers show the location of the populations included in this study. 1: Taï, 2: Udzungwa Mountains, 3: Kibale, 4: Akfadou, 5: Tigounatine, 6: Lékédi. 7: Moukalaba-Doudou. 8: Gashaka-Gumti. 9: Gilgil. 10: Queen Elizabeth. 11: Amboseli. 12: Mikumi. 13: Tana River. 14: Filoha. 15: Kasanka. 16: De Hoop. 17: Drakensberg. 18: Moremi. 19: Tokai. 20: Tsaobis. 21: Simien. The species distribution ranges and icons come from Julia Fischer et al., 2017; Kingdon et al., 2012.

**Figure 2**: Monthly distribution of births in relation to rainfall and NDVI seasonality

The proportion of births per month (left side of the y-axis) is represented with red bars. In addition, the darker red bar indicates the month of the mean birth date ($\mu_{birth}$) for seasonal breeding populations. We indicated in darker red the value of the r-vector length ($r_{birth}$) for each population (top-right corner of each panel). We represent the mean monthly rainfall (equalled to $K_{rain}$ + Rainfall S, in mm) in blue (right side of the y-axis), and the mean monthly NDVI (equalled to $K_{NDVI}$ + NDVI S divided by 2 for graphical purposes) in green (left-side of the y-axis). The species and population names are indicated on top of each panel, along with the number of births observed (N).

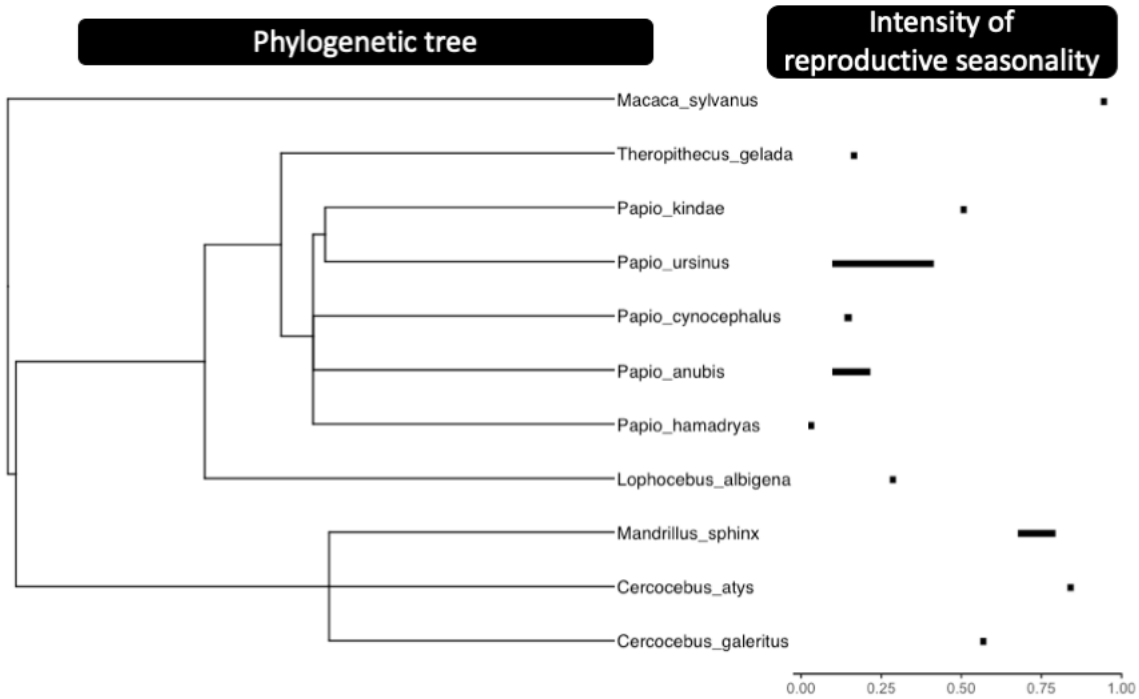


**Figure** 3: Phylogenetic tree of the studied species including the variation in the intensity of reproductive seasonality for each species.

The intensity of birth seasonality is here quantified using the $r_{birth}$ value. For those species represented by more than one population, the length of the black segment displays the variation in intensity of birth seasonality among populations.

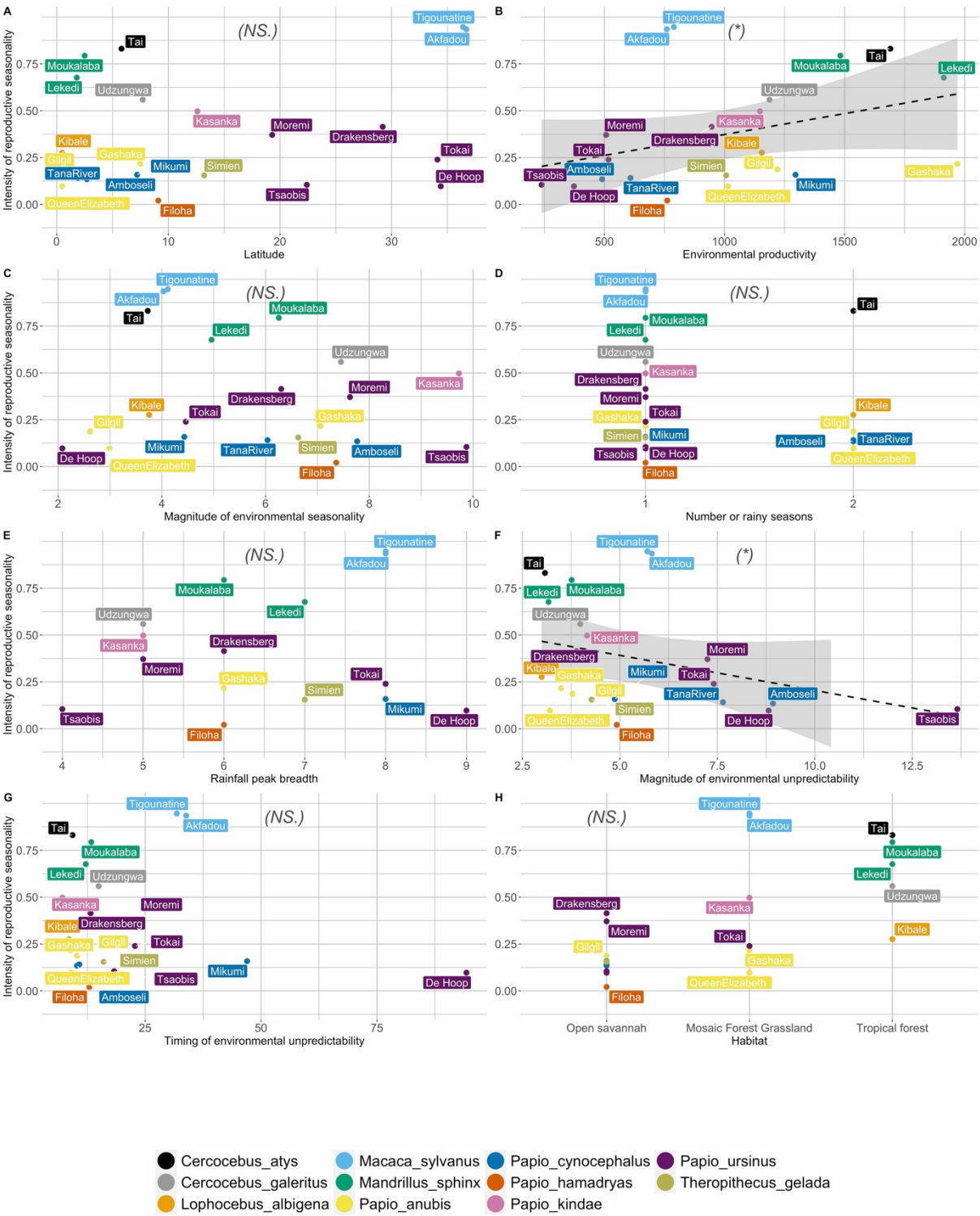


**Figure 4:** Effect of multiple environmental factors on the intensity of reproductive seasonality.

We plotted the intensity of reproductive seasonality ($r_{birth}$) depending on latitude (Panel A), environmental productivity (indexed by mean annual rainfall in mm, Panel B), the magnitude of environmental seasonality (i.e. of the rainfall peak, Panel C), the number of rainy seasons (Panel D), the rainfall peak breadth (RPB, Panel E), the

magnitude of environmental unpredictability (i.e. of variation in the non-seasonal component of rainfall (Panel F), the timing of environmental unpredictability (i.e. between-year variation in rainfall timings, Panel G), and habitat type (Panel H). For each panel, each dot represents a population (with the population name annotated), and the colour indicates the species (see legend at the bottom). The dashed black line represents the linear regression, and the shaded area displays 95% confidence intervals. On top of each panel, we indicated in italic and between parentheses the significance of each predictor (NS for non-significant, * for P-values<0.05, ** for P-values<0.01).

## TABLES

**Table 1:** Hypotheses and predictions proposed on the effects of various environmental components on the intensity of reproductive seasonality ($r_{birth}$)

| Predictor | | Description | Hypothesis | Prediction | Results |
|---|---|---|---|---|---|
| Latitude | | Latitude, in degrees | H1.1 | When latitude increases, $r_{birth}$ increases | No |
| Environmental productivity | | Mean annual rainfall ($12 \times K_{rain}$) | H1.2 | When environmental productivity increases, $r_{birth}$ decreases | No (opposite effect) |
| Environmental seasonality | Magnitude of rainfall peak | Relative standard deviation of the seasonal component of rainfall (Rainfall S) | H1.3 | When the amount of within-year rainfall variation increases, $r_{birth}$ increases | No |
| | Modality of annual rainfall distribution | Number of rainy seasons (1 or 2) | H1.4 | When there is more than one rainy season, $r_{birth}$ decreases | No |
| | Breadth of the annual rainy season (broadness) | Rainfall peak breadth (RPB): minimum number of consecutive months with >80% of annual rainfall | H1.5 | When RPB increases, $r_{birth}$ decreases | No |
| Environmental unpredictability | Magnitude | Relative standard deviation of the non-seasonal component of rainfall (Rainfall NS) | H1.6 | When the amount of rainfall unpredictability (between-year variation) increases, $r_{birth}$ decreases | Yes |
| | Timing | Standard deviation of the yearly mean rainfall dates | H1.7 | When the level of rainfall unpredictability in terms of timing increases, $r_{birth}$ decreases | No |
| Habitat | | Type of habitat: tropical forest, open savannah, or mosaic forest-savannah | H1.8 | Populations living in open savannahs have lower $r_{birth}$ than the ones living in tropical forest | No |

$r_{birth}$ refers here to the r-vector length, i.e. to the intensity of reproductive seasonality

**Table 2**: Influence of several components of rainfall variation on the reproductive seasonality of African papionin populations

The table shows the posterior mean, the 95% HPD confidence intervals (CI) and the MCMC p-values (pMCMC) associated for each posterior distribution of the predictors of the Poisson MCMCglmm including species' relatedness as random effect, $r_{birth}$ as response variable (the r-vector length, transformed to be an integer value), and each predictor as the only fixed effect of a univariate model. Significant effects are indicated in bold. For categorical predictor, the tested category is indicated between parentheses.

| Predictor | | posterior mean | CI | | pMCMC |
|---|---|---|---|---|---|
| | | | lower | upper | |
| Latitude | | 0.11 | -0.49 | 0.67 | 0.686 |
| **Habitat productivity** | | **0.38** | **0.02** | **0.74** | **0.039** [+] |
| Magnitude of environmental seasonality | | 0.05 | -0.28 | 0.37 | 0.724 |
| Number or rainy seasons | (2)[†] | -0.19 | -0.96 | 0.60 | 0.617 |
| Rainfall peak breadth | | -0.06 | -0,52 | 0.45 | 0.741 |
| **Magnitude of environmental unpredictability** | | **-0.34** | **-0.62** | **-0.06** | **0.024** [+] |
| Timing of environmental unpredictability | | -0.18 | -0.46 | 0,09 | 0.184 |
| Habitat type | (Mosaic forest-savannah)[š] | 0.55 | -0.39 | 1.52 | 0.250 |
| | (Tropical forest) [š] | 1.11 | -0.63 | 2.47 | 0.152 |

[†] The reference category is 1 rainy season

[š] The reference category is open savannah habitat

[+] Note that when applying Bonferroni corrections for multiple tests, pMCMC>0.06 and is thus non-significant

**Table 3**: Reproductive stage matched with the food peak in sampled populations.

NAs are written when the alignment of the food peak with this reproductive stage was not tested (either because the data on weaning age in this population was missing, or because it is a non-seasonally breeding population, i.e. with P-value of the Rayleigh test >0.05). Xs are written when there is no alignment, while cells are shaded when there is an alignment of the given reproductive stage with the food peak.

| Species | Population | $r_{birth}$ | Reproductive stages match with food peak | | |
|---|---|---|---|---|---|
| | | | Conception | Lactation | Weaning |
| *Cercocebus atys* | Taï | 0.8312 | X | **Early** | X |
| *Cercocebus sanjei* | Udzungwu Mountains | 0.5588 | **Before** | **Mid** | **Before** |
| *Lophocebus albigena* | Kibale | 0.2762 | **Before** | **Mid** | X |
| *Macaca sylvanus* | Akfadou | 0.9350 | X | **Early** | NA |
| | Tigounatine | 0.9467 | X | X | NA |
| *Mandrillus sphinx* | Lekedi | 0.6766 | **Before** | **Mid** | X |
| | Moukalaba-Doudou | 0.7940 | X | **Whole** | NA |
| *Papio anubis* | Gashaka-Gumti | 0.2167 | NA | NA | NA |
| | Gilgil | 0.1873 | X | X | **After** |
| | Queen Elizabeth | 0.0971 | NA | NA | NA |
| *Papio cynocephalus* | Amboseli | 0.1344 | **Before** | X | X |
| | Mikumi | 0.1584 | X | X | NA |

| | | | | | |
|---|---|---|---|---|---|
| | Tana River | 0.1413 | NA | NA | NA |
| *Papio hamadryas* | Filoha | 0.0208 | NA | NA | NA |
| *Papio kindae* | Kasanka | 0.4971 | **After** | X | NA |
| *Papio ursinus* | De Hoop | 0.0969 | NA | NA | NA |
| | Drakensberg | 0.4143 | X | **Early** | NA |
| | Moremi | 0.3710 | **Before** | **Mid** | **After** |
| | Tokai | 0.2394 | NA | NA | NA |
| | Tsaobis | 0.1046 | NA | NA | NA |
| *Theropithecus gelada* | Simien | 0.1550 | X | X | X |