

1 **Flexible reproductive seasonality in Africa-dwelling**
2 **papionins is associated with low environmental**
3 **productivity and high climatic unpredictability**

4
5 Jules Dezeure^{1*}, Julie Dagherrette², Lugdiwine Burtschell^{2,3}, Shahrina Chowdhury^{4,7,8}, Dieter
6 Lukas⁵, Larissa Swedell^{6,7,8,9,10}, Elise Huchard²

7 ¹Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), Université de Montpellier, CNRS, IRD,
8 EPHE, Montpellier, France

9 ²Institute of Evolutionary Sciences of Montpellier (ISEM), Université de Montpellier, CNRS,
10 IRD, EPHE, Montpellier, France.

11 ³AgroParisTech, Paris, France

12 ⁴Department of Anthropology, Brooklyn College, CUNY, 2900 Bedford Ave, Brooklyn, NY
13 112

14 ⁵Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary
15 Anthropology, Leipzig, Germany

16 ⁶Department of Anthropology, Queens College, City University of New York, Flushing, NY
17 11367-1597, USA

18 ⁷New York Consortium in Evolutionary Primatology, New York, NY, USA

19 ⁸Anthropology Program, CUNY Graduate Center, 365 Fifth Avenue, New York, NY 10016,
20 USA

21 ⁹Biology and Psychology Programs, CUNY Graduate Center, 365 Fifth Avenue, New York,
22 NY 10016, USA

23 ¹⁰Department of Archaeology, University of Cape Town, Rondebosch 7701, Cape Town, South
24 Africa

25

26 * corresponding author: dezeurejules@gmail.com

27

28 **ABSTRACT**

29 At a time when seasonal cycles are increasingly disrupted, the ecology and evolution of
30 reproductive seasonality in tropical vertebrates remains poorly understood. In order to predict
31 how changes in seasonality might affect these animals, it is important to understand which
32 aspects of their diverse patterns of reproductive phenology are linked to either the equally
33 diverse patterns of rainfall seasonality (within-year variations) or instead the marked climatic
34 unpredictability (year-to-year variations) occurring across the intertropical belt. Here, we gather
35 birth and climatic seasonality data from 21 populations of 11 Africa-dwelling primate species
36 from the papionin tribe, occupying a wide range of environments, including equatorial, tropical,
37 temperate and arid climates. We investigate (1) the environmental **variations** that influence the
38 intensity of reproductive seasonality, and (2) the reproductive stage that is synchronized with
39 increased resource availability. Our results demonstrate wide variation in the intensity of birth
40 seasonality between and within species. Across multiple measures of climatic variation, we
41 found rainfall unpredictability to be the only clear predictor of the intensity of reproductive
42 seasonality across populations, i.e., greater year-to-year variation in the amount of rainfall was
43 associated with lower to no reproductive seasonality. Finally, we identified diverse patterns of
44 reproductive phenology, with the most seasonal breeders generally aligning lactation with the
45 peak in resource availability while other populations show more diverse patterns, where
46 conception, lactation or weaning can all be synchronized with maximal food availability. This
47 study sheds new light on the extent and ecological drivers of flexible reproductive phenology

48 in long-lived tropical mammals, and may even contribute to our understanding of why humans
49 give birth year-round.

50

51 INTRODUCTION

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

62 Comparative studies investigating determinants of variation in reproductive seasonality
63 across mammals have often been conducted at the level of the order (Rodents: Heldstab, 2021,
64 Lagomorphs: Heldstab, 2021, ruminants: Rutberg, 1987; Zerbe et al., 2012, Carnivora:
65 Heldstab et al., 2018, Primates: Di Bitetti & Janson, 2000; Heldstab et al., 2020; Janson &
66 Verdolin, 2005) and thus focus on broad-scale macro-evolutionary patterns. These studies have
67 typically detected a relationship between geographic latitude and birth seasonality, suggesting
68 that at higher latitudes, birth seasonality is more pronounced, with a more intense birth peak (a
69 birth peak being the temporal period in the annual cycle during which most birth occur).
70 However, important gaps remain in our understanding of the determinants of reproductive
71 seasonality. Few studies have attempted to quantify the extent of variation in reproductive
72 seasonality across multiple populations of the same species (but see in African wild dogs

73 (*Lycaon pictus*): McNutt, Groom, & Woodroffe, 2019, and in red-tailed monkeys
74 (*Cercopithecus ascanius*): Struhsaker, 1997), or across closely related species sharing relatively
75 similar diets, body sizes and life histories (but see in several ungulate species: Pereira, Dos
76 Santos Zanetti, & Furlan Polegato, 2010; Spinage, 1973; Brogi et al., 2022; macaque species:
77 Trébouet, Malaivijitnond, & Reichard, 2021). Thus, studies that control for major sources of
78 variation in life history or broad dietary categories should be particularly useful for identifying
79 the climatic drivers of variation in reproductive phenology.

80 The well-known association between latitude and reproductive seasonality fails to
81 explain the diversity of reproductive seasonality patterns observed within restricted latitudinal
82 ranges, such as in the tropics (Heldstab et al., 2020; Janson & Verdolin, 2005). In addition,
83 latitude encapsulates multiple components of climatic variation, which need to be disentangled
84 in order to identify the main climatic factors at play (Burtschell, Dezeure, Huchard, & Godelle,
85 2023). First, latitude correlates positively with the degree of environmental seasonality,
86 measured as the magnitude of within-year variation (such as the difference between maximal
87 and minimal monthly rainfall in the annual cycle) (Botero, Dor, McCain, & Safran, 2014).
88 Further, latitude covaries negatively with environmental productivity, i.e., overall food
89 availability in a given environment. Variation in productivity may alter the benefits of seasonal
90 breeding, as populations living in more productive habitats may face less pressure to breed
91 seasonally (Burtschell et al., 2023).

92 Finally, environmental predictability, independently of latitude and seasonality (Tonkin,
93 Bogan, Bonada, Rios-Touma, & Lytle, 2017), could also influence breeding schedules. In
94 locations with intense year-to-year environmental variation, a flexible reproductive phenology
95 (i.e., individual ability to start a reproductive cycle at different timings of the year, in response
96 to internal or external factors) may be more advantageous than a strictly seasonal reproduction
97 (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985). Indeed, regular delays

98 or decreases in the food peak may lead to reproductive failures in strict seasonal breeders, thus
99 reducing the fitness benefits of breeding seasonally. However, few studies have investigated
100 the effects of environmental unpredictability on the intensity of reproductive seasonality, with
101 mixed results so far. While English, Chauvenet, Safi, & Pettorelli (2012) found that higher
102 inter-annual variation in food availability decreased the intensity of birth synchrony across 38
103 ungulate species, two studies of red deer, *Cervus elaphus* L. (Loe *et al.*, 2005) and chacma
104 baboons, *Papio ursinus* (Dezeure *et al.*, 2023) found no effect of environmental unpredictability
105 on reproductive seasonality. A recent modelling study similarly detected limited effects of
106 environmental unpredictability on evolutionary transitions to nonseasonal breeding (Burtshell
107 *et al.*, 2023).

108 Aside from the selective pressures favouring a flexible reproductive phenology,
109 relatively little is known about how birth timing varies in relation to the annual resource peak
110 in long-lived species. In short-lived species, the full reproductive cycle, from conception to
111 offspring nutritional independence (such as weaning in mammals or fledging in birds), can take
112 place within a single productive season (Bronson, 2009). However, this is not the case for long-
113 lived species, in which multiple stages of a female's reproductive cycle can be aligned with the
114 annual food peak, with varying fitness consequences (Dezeure *et al.*, 2021). For example,
115 females of some species may have to reach a certain threshold of body condition for the onset
116 of reproduction and conception to take place (Brockman & van Schaik, 2005a), meaning that
117 most conceptions are expected to follow a peak of food availability (Brockman & van Schaik,
118 2005a). In some other species, females may instead synchronize the costliest part of their
119 reproductive cycle with the most productive season so as to enhance maternal condition and
120 survival (Bronson, 2009; Bronson & Heideman, 1994), such that early- or mid-lactation occurs
121 during the annual food peak, as in many primates (J. Altmann, 1980; Brockman & van Schaik,
122 2005a; Janson & Verdolin, 2005). Lastly, weaning is a critically vulnerable life stage, where

123 juveniles must begin to forage for themselves (J. Altmann, 1980; Lee, 1996). Accordingly,
124 several species have been shown to time their births so as to align weaning with the seasonal
125 food peak (Brockman & van Schaik, 2005a; Janson & Verdolin, 2005), as occurs in most lemurs
126 (Wright, 1999). Overall, the reasons underlying the observed variation in alignment of
127 reproductive stages with the food peak across species and populations remain largely unknown.

128 In this study, we attempt to address the above gap in our understanding by investigating
129 the evolutionary determinants of the intensity and timing of reproductive seasonality in Africa-
130 dwelling papionin monkeys. We focus on papionins for several reasons. First, they exhibit
131 relatively similar body sizes (large-bodied), life history traits (slow) and diet (mostly
132 omnivorous) (Kingdon et al., 2012; Swedell, 2011), allowing us to investigate environmental
133 effects on reproductive seasonality while controlling for these – potentially confounding –
134 factors. Second, this taxonomic group displays a wide diversity of patterns of reproductive
135 seasonality. Indeed, most baboon (*Papio* spp.) species are non-seasonal breeders (Bercovitch
136 & Harding, 1993; Swedell, 2011) despite exhibiting variation in monthly birth frequencies
137 (Cheney et al., 2004; Lycett, Weingrill, & Henzi, 1999), while mandrills (*Mandrillus sphinx*)
138 (Setchell, Lee, Wickings, & Dixson, 2002), Kinda baboons (*Papio kindae*) (Petersdorf,
139 Weyher, Kamilar, Dubuc, & Higham, 2019) and most mangabey species (i.e., *Cercocebus* and
140 *Lophocebus* spp.) (Swedell, 2011) are seasonal breeders. Third, this species constellation
141 exhibits great ecological flexibility, inhabiting arid areas, woodland savannahs, equatorial
142 forests, and high altitude grasslands (J. Fischer et al., 2019; Kingdon et al., 2012; Swedell,
143 2011) (see also Figure 1). Fourth, within the African members of this tribe, baboons are one of
144 the most well studied primate **taxon**, with data available from multiple populations of some
145 species within the genus *Papio* (J. Fischer et al., 2019). Lastly, species from this taxonomic
146 group, and in particular from the genus *Papio*, possess a variety of features shared with early
147 hominins (Alberts et al., 2005; Brockman, 2005; Jolly, 2001): they are large, terrestrial and

148 eclectic omnivorous primates (Alberts et al., 2005; Rhine, Norton, Wynn, & Wynn, 1989) that,
149 unlike the great apes, have colonized African savannahs (Bobe, Martínez, & Carvalho, 2020)
150 and give birth to a single offspring every one to three years (J. Altmann & Alberts, 2005;
151 Swedell, 2011). Investigating the environmental determinants of their reproductive seasonality
152 may thus shed new light on the evolution and maintenance of non-seasonal breeding in early
153 hominins (King, 2022).

154 Here we ask three main questions regarding reproductive seasonality in the papionins
155 in our sample:

156 (i) What is the extent of inter- and intra-specific variation in patterns of reproductive
157 seasonality, specifically regarding the height and width of the birth peak, as well as its timing
158 in the annual cycle?

159 (ii) What are the main environmental factors responsible for variation in the intensity of
160 reproductive seasonality? We isolated eight components of environmental variation: latitude,
161 environmental productivity, magnitude of seasonal variation in rainfall, number of rainy
162 seasons, breadth of the rainy season, amount of between-year (unpredictable) variation in
163 rainfall, between-year variation in the timing of the rainfall season, and the type of habitat. We
164 tested the eight corresponding hypotheses (H1.1-1.8) and their associated predictions, which
165 are listed in Table 1.

166 (iii) In seasonally breeding populations, which stage of the reproductive cycle is synchronized
167 with the food peak? We tested whether females match the seasonal food peak with conceptions
168 (H2.1 - the ‘conception hypothesis’), lactation (H2.2 - the ‘lactation hypothesis’), or weaning
169 (H2.3 - the ‘weaning hypothesis’).

170

171 **Table 1:** Hypotheses and predictions proposed on the effects of various environmental components on the intensity of reproductive seasonality

Predictor	Description	Hypothesis	Prediction	Results	
Latitude	Latitude, in degrees	H1.1	When latitude increases, r_{birth} increases	No	
Environmental productivity	Mean annual rainfall ($12 \times K_{\text{rain}}^1$)	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 those living in tropical forests	No	

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

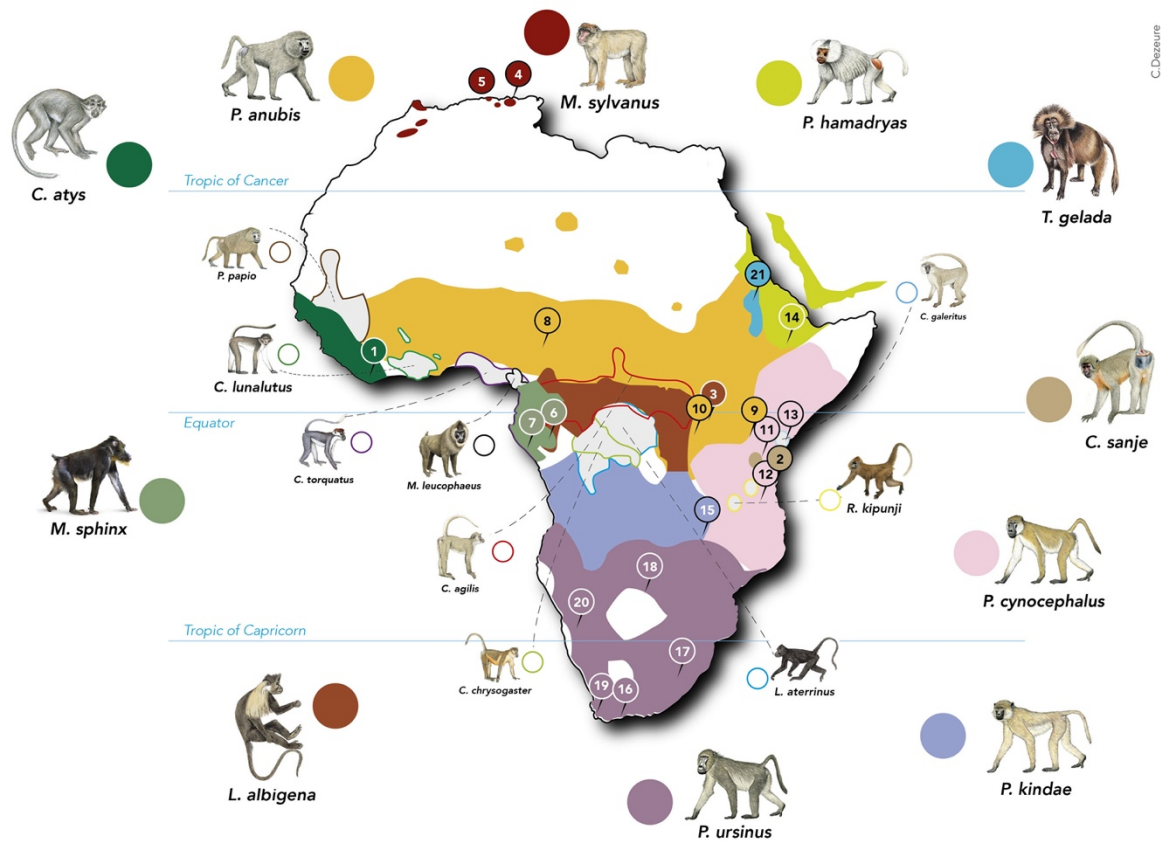
173 K_{rain} is a constant and refers to the mean monthly rainfall

174 **METHODS**

175 *1- Sample and data selection*

176 Our data set includes published reports on reproductive seasonality in natural populations of
177 Africa-dwelling papionins from the genera *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*,
178 *Papio*, *Rungwecebus* and *Theropithecus* (Figure 1). We selected papers that reported the
179 number of births per month (except for yellow baboons, *Papio cynocephalus*, from Mikumi
180 National Park, where births were provided in three month-periods). We obtained birth
181 seasonality data from 21 wild populations representing 11 species: see Table S1 for references
182 associated with each population, and Figure 1 for their locations. We did not find any monthly
183 birth data for nine species of interest for which only data from captivity were available (Kingdon
184 et al., 2012; Swedell, 2011): five species of *Cercocebus* (*agilis*, *chrysogaster*, *galeritus*,
185 *lumulatus*, *torquatus*), as well as *Lophocebus aterrimus*, *Mandrillus leucophaeus*, *Papio papio*
186 and *Rungwecebus kipunji* (Figure 1).

187



C. Decourse

188
189
190
191
192
193
194
195
196
197
198
199
200

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, as well as empty circles. 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.

201

202 2- Birth seasonality data

203 We were interested in quantifying two components of reproductive seasonality in each
204 population: (1) the mean population birth date, i.e. describing when most births mainly occur
205 during the year, and (2) the intensity of population birth seasonality, i.e. describing how
206 seasonal the births are. For our analysis, given the heterogeneity of the data (in some datasets,
207 precise birth dates were available, but in most datasets, we could only obtain a count of births
208 per month), we considered each birth to have occurred in the middle of the month (i.e., the 15th
209 of each month, except for February where births were considered to occur on the 14th). For the
210 Mikumi population, we considered that births occurred in the middle of each 3 month-period.
211 We then used a circular statistic and represented each birth event on the annual circle by a vector
212 of length 1 and of angle θ representing its date ($15 \times 2 \times \pi / 365.25$ for January, $(14+31)$
213 $\times 2 \times \pi / 365.25$ for February, etc.). We computed the mean vector (r-vector) per population,
214 whose angle (converted in a date: μ_{birth}) indicates the mean day of the year in which births occur
215 (see Table S1) and is thus a measure of birth seasonality. We computed μ_{birth} using the function
216 ‘circ.summary’ from the ‘CircStats’ package (Agostinelli & Lund, 2018). For populations with
217 a significant birth peak, μ_{birth} represents the date of the population birth peak, i.e. when births
218 are the most likely to occur in the annual cycle. The length (r_{birth}) of the r-vector measures the
219 intensity of birth seasonality, i.e., the degree of uniformity of the birth distribution across the
220 annual cycle, varying from 0 to 1 (Di Bitetti & Janson, 2000; Janson & Verdolin, 2005;
221 Thompson & McCabe, 2013). When $r_{\text{birth}}=0$, births are evenly spread across months (i.e., non-
222 seasonal), while when $r_{\text{birth}}=1$, births all occur during the same month of the year (extremely
223 seasonal). After comparing several classical measures of reproductive seasonality
224 (Supplementary Materials, Appendix S1), we used only r_{birth} to measure the intensity of
225 reproductive seasonality, as this measure is more robust to differences in sample size than other

226 metrics, facilitating the comparison of seasonality measures between populations (Janson &
227 Verdolin, 2005; Thel, Chamaille-Jammes, & Bonenfant, 2022).

228

229 3- *Environmental data*

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

231 In order to test our set of hypotheses, we considered environmental variation through
232 two components: rainfall and the Normalized Difference Vegetation Index (NDVI). NDVI
233 produces a quantitative index of vegetation productivity, where higher values indicate a higher
234 degree of vegetation cover (Didan, Barreto Munoz, Solano, & Huete, 2015). Climatic
235 seasonality in Africa (and in most tropical habitats) is mainly characterized by within-year
236 variation in rainfall (Alberts et al., 2005; Feng, Porporato, & Rodriguez-Iturbe, 2013; Van
237 Schaik, Terborgh, & Wright, 1993), which has been successfully used as an indicator of food
238 availability for several of our studied populations (Alberts et al., 2005; Hill, Lycett, & Dunbar,
239 2000; Petersdorf et al., 2019; Tinsley Johnson, Snyder-Mackler, Lu, Bergman, & Beehner,
240 2018). Yet, NDVI values have to be used with caution when comparing productivity across
241 environments (Pettorelli et al., 2005), which is why we opted to use rainfall to test hypotheses
242 H1.1-H1.8. For example, the mean annual NDVI value at De Hoop, one of our driest habitats,
243 was almost equal to that of Gashaka, one of our wettest habitats. We thus used variation in
244 rainfall, rather than in NDVI, to disentangle the various components of climatic variation that
245 may affect the intensity of reproductive seasonality (such as environmental productivity,
246 predictability and seasonality) when testing hypotheses H1.1-H1.8.

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

251 may vary depending on local climatic or environmental conditions (Bercovitch & Harding,
252 1993; Dezeure et al., 2021; Jarvey, Low, Pappano, Bergman, & Beehner, 2018). Consequently,
253 we thought that using NDVI would be preferable than rainfall to assess the timing of the annual
254 food peak, and test hypotheses regarding its match to the birth peak in each population.
255 Nevertheless, the use of NDVI as an index of food productivity in papinions, which are not
256 herbivorous (except for *Theropithecus gelada*), could be arguable, and results of this analysis
257 would be discussed accordingly.

258

259 *ii. Data extraction*

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

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

275

276 *iii. Components of environmental variation*

277 In order to test our hypotheses, we identified multiple components of rainfall variation within
278 and across years. First, we decomposed for a given site the observed rainfall value into three
279 components as follows: $\text{Rainfall}_{m,i} = K_{\text{rain}} + \text{Rainfall } S_m + \text{Rainfall NS}_{m,i}$, where m is the month
280 of the year (going from January to December) and i is the year (from 1998 to 2019). K_{rain} is a
281 constant, equalling the mean monthly rainfall across 22 years of records (Figure S1). Rainfall
282 S_m is the seasonal component of rainfall, i.e., the rainfall value, averaged across 22 years, for
283 each month of the year, minus K_{rain} (Figure S1). For example, for a given site, $\text{Rainfall } S_1$ ($m=1$)
284 is the mean of all January rainfall values. The term $\text{Rainfall } S$ thus captures the seasonal
285 component of rainfall variation in the annual cycle, i.e., its within-year variation. Finally,
286 $\text{Rainfall NS}_{m,i}$ is the non-seasonal component of rainfall, i.e., the difference between the
287 observed rainfall value in any month at a given site ($\text{Rainfall}_{m,i}$) and the predictable component
288 of rainfall variation for that particular site in that particular month ($K_{\text{rain}} + \text{Rainfall } S_m$) (Figure
289 S1). This captures the unpredictable, i.e., between-year, rainfall variation. Using these
290 measures, we assessed the following for each population (see Table S2 for the values associated
291 with each population):

- 292 - Environmental productivity, or mean annual rainfall, equal to $12 \times K_{\text{rain}}$.
- 293 - Magnitude of environmental seasonality. We computed the magnitude of within-year
294 rainfall variation, as the relative standard deviation (SD) of $\text{Rainfall } S$ standardized for
295 environmental productivity, given by the formula: $\frac{100 \times \text{SD}(\text{Rainfall } S)}{12 \times K_{\text{rain}}}$. The higher the
296 value, the more seasonal is rainfall variation.
- 297 - The number of rainy seasons per year. Using predictable rainfall variation ($K_{\text{rain}} +$
298 $\text{Rainfall } S$), we assessed graphically, for each population, the number of rainy seasons
299 per year.

- 300 - The length of the rainy season. For environments with only one rainy season, we further
301 calculated the rainfall peak breadth (RPB), which is the minimum number of
302 consecutive months of the year during which 80% of the annual rainfall ($12 \times K_{\text{rain}}$)
303 occurs. This measure is meaningless for environments with more than one rainy season,
304 and we thus excluded the populations living in such environments from this analysis.
- 305 - Magnitude of environmental unpredictability. We computed the magnitude of between-
306 year rainfall variation, as the relative standard deviation of Rainfall NS, standardized by
307 environmental productivity, given by the formula: $\frac{100 \times SD(\text{Rainfall NS})}{12 \times K_{\text{rain}}}$. The higher the
308 value, the more unpredictable rainfall variation is.

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

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

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

323

324 *iv – Phylogenetic tree*

325 We used the branch length of Version 3 of the 10kTreesPrimates consensus tree (Arnold,
326 Matthews, & Nunn, 2010). Two species of interest were absent from this tree: *Cercocebus*
327 *sanjei* and *Papio kindae*. For the former, we substituted *Cercocebus galeritus*, its closest
328 relative. For the latter, following recent genetic studies (Jordan et al., 2018; Rogers et al., 2019),
329 we added *Papio kindae* in the same branch as *Papio ursinus*, using the function ‘bind.tip’ from
330 the package ‘phytools’ (Revell, 2012).

331

332 4- Statistical analysis

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

334 i. Factors affecting the intensity of reproductive seasonality

335 We considered eight potential environmental parameters associated with reproductive
336 seasonality, which are listed along each corresponding prediction in Table 1.

337 For each hypothesis, we plotted r_{birth} (the r-vector length measuring the intensity of
338 reproductive seasonality in a given population) versus the tested predictor. We then checked
339 the significance of the relationship between each predictor and r_{birth} while controlling for
340 phylogeny using Bayesian phylogenetic generalized linear mixed models, with a Beta
341 regression and a logit link function, with the package ‘brms’ (Bürkner, 2017). We included the
342 phylogenetic relationship between species as a covariance matrix, which was derived from the
343 phylogenetic tree.

344 Given the low number of populations in this study, and the collinearity between some
345 of our environmental parameters (multivariate models had variance inflated factors >3), we
346 were not able to run stable multivariate models. For example, the magnitude of environmental
347 seasonality was negatively associated with the duration of the rainy season (cor=-0.94, t=-9.15,
348 $p < 10^{-4}$), and environmental productivity was negatively associated with both latitude (cor=-

349 0.55, $t=-2.69$, $p=0.016$) and the magnitude of environmental unpredictability ($\text{cor}=-0.80$, $t=-$
350 5.48 , $p<10^{-4}$).

351 Therefore, our Beta regressions included as a response variable r_{birth} values, one fixed effect
352 (each environmental predictor in turn listed in Table 1, standardised if continuous) and the
353 phylogenetic matrix as a random effect. Given the high variation in sample size (i.e., number
354 of births recorded) between populations, we used a weighed regression, where the weight given
355 to each data point equals to $\log(N) / \text{minimum}(\log(N))$ so that the population with the lowest
356 sample size counts for 1 observation, and the other populations count for more observations
357 depending on their sample size, following a logarithmic scale ; the logarithmic scale was chosen
358 to account for the diminishing return of increasing the sample size of samples that are already
359 large. Beyond a given sample size, further increases in sample size do not affect much r_{birth}
360 estimates, which are already stable and precise. For each model, we set an informative prior
361 and used 3 000 iterations, a burn-in of 1 000 and 3 chains. We visually inspected for
362 convergence and checked the absence of autocorrelations for the posterior distributions of fixed
363 and random effects. The predictors were considered statistically significant when their
364 associated 95% confidence intervals did not cross 0.

365 Finally, we extracted the phylogenetic signal in our dataset with the metric of Blomberg's
366 K , allowing us to compare it with other signals from other traits. To do so, we computed the
367 mean r_{birth} per species, and use the 'phylosig' function with 1000 simulations from the
368 'phytools' package (Revell, 2024).

369

370 *ii. Timings of conceptions, births and weaning in relation with NDVI seasonality*

371 We tested H2 only for those populations for which a significant birth peak can be detected, as
372 it does not make sense to test which period of the reproductive cycle is matched with the annual
373 food peak if there is not a clear seasonal pattern of births in one population. We therefore

374 assessed whether each population had a significant birth peak using the Rayleigh test for
375 circular statistics, more precisely the 'r.test' function from 'CircStats' package (Agostinelli &
376 Lund, 2018). For each population, when the P-value associated with the Rayleigh test was
377 <0.05 , meaning that the null hypothesis of a uniform birth distribution could be rejected, the
378 birth peak was considered significant. With this approach, some populations with relatively low
379 reproductive seasonality (low r_{birth}) but with a large number of births are included, which should
380 be taken into account when interpreting the results. Among these populations with a significant
381 birth peak (see Table S1), we investigated which reproductive stage (H2.1, 'conception'; H2.2,
382 'lactation'; or H2.3, 'weaning') was synchronized with the annual NDVI peak, i.e. μ_{NDVI} .
383 Additional details are given in Supplementary Materials, Appendix 3 & Table S3. We employed
384 exact two-sample Fisher-Pitman permutation tests, using the 'oneway_test' function from the
385 'coin' package (Hothorn, Hornik, Van De Wiel, & Zeileis, 2006). This function tests if the
386 observed monthly value of NDVI during a target period, which depends on the hypothesis
387 tested, is significantly higher than monthly values of NDVI randomized across the entire year.
388 For example, using mean gestation length to infer the annual distribution of conception dates,
389 we tested H2.1 by asking if females tended to conceive during, soon before, or soon after the
390 annual food peak, looking at seasonal NDVI values respectively in (i) the six months
391 surrounding μ_{conc} , (ii) the three months before μ_{conc} and (iii) the three months after μ_{conc} .

392

393 RESULTS

394 1) How variable are patterns of reproductive seasonality?

395 The annual distribution of births for each population is shown in Figure 2, alongside seasonal
396 variation in rainfall and NDVI. The intensity of reproductive seasonality varies widely across
397 species: *Papio hamadryas* (Filoha population: $r_{\text{birth}}=0.02$) and most *Papio anubis* populations
398 ($r_{\text{birth}} <0.22$) show non-seasonal births while *Mandrillus sphinx* (Lékédi: $r_{\text{birth}}=0.67$ and

399 Moukalaba-Doudou: $r_{\text{birth}} = 0.80$ resp.) and *Papio kindae* (Kasanka: $r_{\text{birth}} = 0.50$) exhibit
400 pronounced birth seasonality (Figure 3). The phylogenetic signal associated with the intensity
401 of reproductive seasonality is substantial (Blomberg's $K=1.83$, $p\text{value} < 0.01$), indicating that
402 more closely related species have more similar patterns of reproductive seasonality. Among
403 papionins, the genera *Mandrillus*, *Cercocebus* and *Macaca* show strong reproductive
404 seasonality, whereas the genera *Lophocebus*, *Papio* and *Theropithecus* show an overall lower
405 intensity of birth seasonality, which may be associated with greater flexibility within species
406 (Figure 3). Such flexibility is particularly pronounced in *Papio ursinus* populations, extending
407 from low (de Hoop: $r_{\text{birth}} = 0.10$; Tokai: $r_{\text{birth}} = 0.22$, and Tsaobis: $r_{\text{birth}} = 0.10$) to moderate birth
408 seasonality (Drakensberg: $r_{\text{birth}} = 0.42$; Moremi: $r_{\text{birth}} = 0.37$) (Figure 3), while intra-specific
409 variation seems less marked for the other species represented by multiple populations in our
410 sample.

411 The timing of birth seasonality can also be surprisingly variable, even between species
412 that live in adjacent geographical ranges: for instance, *Papio kindae* from Kasanka give birth
413 mainly around July, whereas *Papio ursinus* from Moremi give birth primarily between July and
414 November (Figure 2).

415



416

417

418

419

420

421

422

423

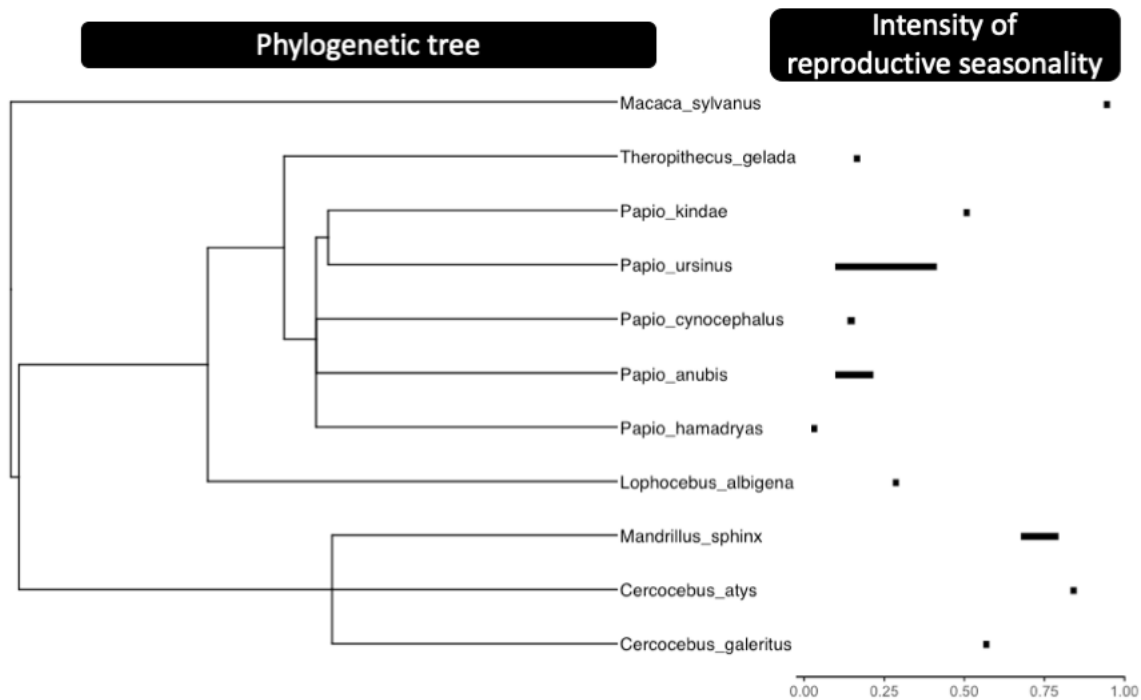
424

425

426

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 (μ_{birth}) for seasonal breeding populations. We indicate 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 $K_{\text{rain}} + \text{Rainfall } S$, in mm) in blue (right side of the y-axis), and the mean monthly NDVI (equal to $K_{\text{NDVI}} + \text{NDVI } S$ and 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).



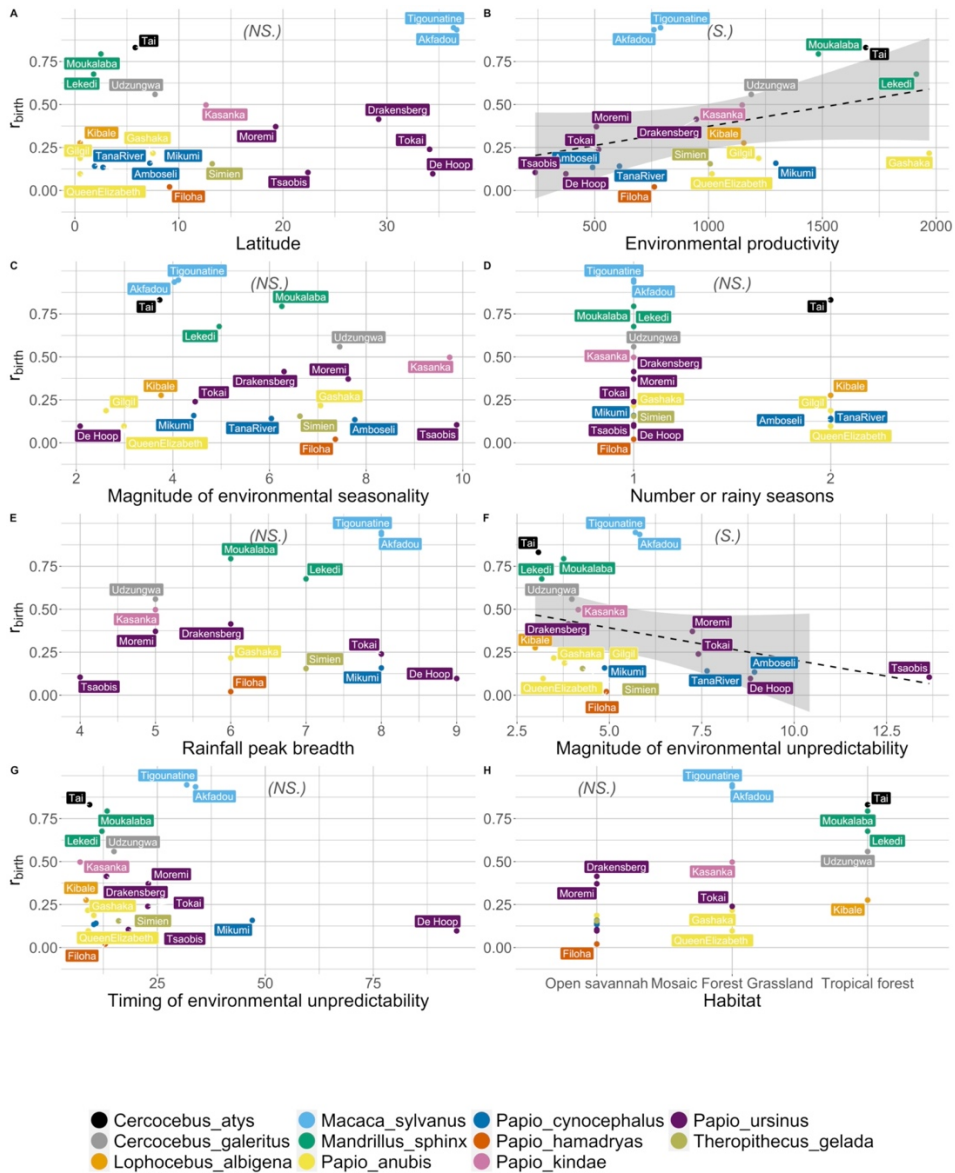
428
429
430
431
432
433
434

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 the intensity of birth seasonality among populations.

435 2) What are the ecological parameters correlated with the intensity of reproductive
436 seasonality?

437 We detected a significant correlation between the magnitude of environmental unpredictability
438 and the intensity of reproductive seasonality, while controlling for species relatedness, which
439 supported our prediction H1.6 (Table 2): the higher the magnitude of between-year variation in
440 rainfall, the lower the intensity of reproductive seasonality (Figure 4F). We also found an effect
441 of habitat productivity that contradicted our prediction H1.2 (Table 2): the lower the mean
442 annual rainfall, the lower the intensity of reproductive seasonality (Figure 4B). Lastly, we did
443 not find any support for the other six hypotheses: there was no effect of latitude, magnitude of
444 rainfall seasonality, number of rainy seasons, breadth of the rainfall peak, unpredictability in
445 the timing of the annual peak of rainfall, or habitat on the intensity of reproductive seasonality
446 (Table 2, Figure 4).



447

448

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

449

450

451

452

453

454

455

456

457

458

459

460

We plotted the intensity of reproductive seasonality (T_{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, S for significant).

461 **Table 2:** Influence of several components of rainfall variation on the reproductive seasonality of Africa-dwelling papionin
 462 populations

463 The table shows the posterior mean, the estimate error and the 95% (marginal) confidence intervals (CI) associated for each posterior distribution of the predictors of the Beta
 464 regression brms models including species' relatedness as random effect, I_{birth} as response variable, weighted by the log-transformed number of observations, and each
 465 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	estimate error	CI	
			lower	upper
Latitude	0.11	0.34	-0.56	0.77
Habitat productivity	0.38	0.18	0.01	0.73
Magnitude of environmental seasonality	0.03	0.13	-0.23	0.28
Number of rainy seasons (2) [†]	-0.22	0.40	-0.98	0.58
Rainfall peak breadth	-0.06	0.17	-0.40	0.27
Magnitude of environmental unpredictability	-0.44	0.13	-0.70	-0.20
Timing of environmental unpredictability	-0.21	0.14	-0.52	0.05
Habitat type	(Mosaic forest-savannah) [§]	0.41	-1.05	0.59
	(Tropical forest) [§]	0.56	1.45	3.45

466 [†] The reference category is 1 rainy season

467 [§] The reference category is open savannah habitat

468

469 3) Which stage of the reproductive cycle is timed with the annual food peak?
 470 When considering all taxa in our sample as a whole, none of our three hypotheses were clearly
 471 supported (H2.1, H2.2, H2.3). However, in five of the six populations with the strongest
 472 reproductive seasonality ($r_{\text{birth}} > 0.5$), females appeared to synchronize lactation with the annual
 473 NDVI peak, and overall lactation was generally aligned with the NDVI peak in 8 of the 14
 474 populations with a significant birth peak (P-value of the Rayleigh test < 0.05) (Table 3, Table
 475 S4). In less seasonally breeding populations ($r_{\text{birth}} < 0.5$), females were more variable in the
 476 reproductive stages that were timed with the annual NDVI peak, ranging from conception (6 of
 477 14 populations, and mainly before than after conception: e.g. Amboseli or Kibale) to weaning
 478 (3 of 8 populations: e.g., Moremi or Gilgil) to none (e.g., Simien) or all of these stages (e.g.,
 479 Udzungwa) (Table 3, Table S4). Moreover, the timing of the annual NDVI peak compared to
 480 the mean conception, birth or weaning dates was highly variable between populations (Table
 481 S4).

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

484 Cells are filled with NAs when the alignment of the food peak with this reproductive stage
 485 was not tested (either because the data on weaning age in this population was missing, or
 486 because the birth peak of the population is non-significant, i.e., with P-value of the
 487 Rayleigh test > 0.05). Cells are filled with X when there is no alignment, and shaded when
 488 there is an alignment of the given reproductive stage with the food peak.

Species	Population	r_{birth}	Reproductive stages match with food peak		
			Conception (H2.1)	Lactation (H2.2)	Weaning (H2.3)
<i>Cercocebus atys</i>	Taï	0.8312	X	Early	X
<i>Cercocebus sanjei</i>	Udzungwu Mountains	0.5588	Before	Mid	Before
<i>Lophocebus albigena</i>	Kibale	0.2762	Before	Mid	X

<i>Macaca sylvanus</i>	Akfadou	0.9350	X	Early	NA
	Tigounatine	0.9467	X	X	NA
<i>Mandrillus sphinx</i>	Lekedi	0.6766	Before	Mid	X
	Moukalaba-Doudou	0.7940	X	Whole	NA
<i>Papio anubis</i>	Gashaka-Gumti	0.2167	NA	NA	NA
	Gilgil	0.1873	X	X	After
	Queen Elizabeth	0.0971	NA	NA	NA
<i>Papio cynocephalus</i>	Amboseli	0.1344	Before	X	X
	Mikumi	0.1584	X	X	NA
	Tana River	0.1413	NA	NA	NA
<i>Papio hamadryas</i>	Filoha	0.0208	NA	NA	NA
<i>Papio kindae</i>	Kasanka	0.4971	After	X	NA
<i>Papio ursinus</i>	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
<i>Theropithecus gelada</i>	Simien	0.1550	X	X	X

489

490

491 **DISCUSSION**

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

497

498 **Papionins exhibit flexible reproductive seasonality**

499 Of the sampled *Papio* populations, most showed very little seasonality and *Papio kindae*
500 departed from the overall baboon pattern in being relatively highly seasonal breeders. Such
501 diverse patterns of reproductive seasonality within a single genus have rarely been reported
502 outside primates (see for example *Cervus*: English et al., 2012; Loe et al., 2005; Rutberg, 1987,
503 *Damaliscus*: Rutberg, 1987, *Ovis*: Rutberg, 1987, *Ursus*: Spady, Lindburg, & Durrant, 2007,
504 *Mustela*: Heldstab et al., 2018, *Vulpes*: Heldstab et al., 2018), but apparently occur in some
505 other primate genera with large distribution ranges, such as *Alouatta* (Di Bitetti & Janson, 2000;
506 Janson & Verdolin, 2005), *Cercopithecus* (Heldstab et al., 2020; Janson & Verdolin, 2005),
507 *Cebus* (Janson & Verdolin, 2005) and *Macaca* (Heldstab et al., 2020; Janson & Verdolin, 2005;
508 Trébouet et al., 2021). Given the limited taxonomic scale of our study, it is impossible to
509 establish whether seasonal breeding was the ancestral state in papionins, but it seems possible
510 that the loss of seasonal reproduction is a derived state affecting the *Papio* genus (Fig 3). The
511 estimated phylogenetic signal is significant and shows that among the 11 sampled papionin
512 species, the intensity of birth seasonality is more similar among two closely related species.
513 The value of this phylogenetic signal (Blomberg's $K=1.83$) is relatively high, among the highest
514 of many life history traits (such as age at maturity, adult mortality, clutch size in birds, sexual
515 dimorphism, etc.), and higher than behavioural traits (such as daily movement distance, prey
516 size, preferred body temperature, etc.), that are more labile (Blomberg, Garland, & Ives, 2003).
517 Despite this strong impact of phylogeny on the intensity of reproductive seasonality, our study
518 emphasizes the importance of the variations in birth seasonality between two closely-related
519 species, or even within a single species.

520 Importantly, the key adaptive trait that evolved in the *Papio* genus may not be simply
521 the loss of breeding seasonality *per se*, but the evolution of a flexible reproductive phenology.
522 A same papionin female can give birth at different timings for successive birth events,
523 depending on her own individual traits or physiological constraints, or alternatively depending

524 on the strategies of other females in the same social group, as shown in *Papio ursinus* (Dezeure
525 et al., 2021, 2023). This reproductive flexibility at the individual level necessarily shapes
526 population patterns of reproductive seasonality, leading to lower reproductive seasonality.
527 Reproductive flexibility at the population level could be defined as the ability for different
528 populations of a same species to exhibit diverse patterns of reproductive seasonality, depending
529 on the environmental conditions. Such flexibility is observed at the population level in *Papio*
530 *ursinus*, living in a large distributional range characterized by exceptional ecological diversity,
531 which includes cold and temperate climates, oceanic and mountainous ecosystems, and tropical
532 and arid savannahs. Indeed, populations of this species exhibit a wide range of intensity of
533 reproductive seasonality ($r_{\text{birth}}=[0.10-0.41]$), with significant (Moremi) or non-significant
534 (Tsaobis) birth peaks, and to some extent, various timings in their birth peaks (Moremi: around
535 November, versus Drakensberg: around September). However, such population-level flexibility
536 is often difficult to assess in many species, given the datasets available (*Papio ursinus* is indeed
537 the only species in our sample represented by more than three populations with a reasonable
538 number of births).

539 Flexibility in reproductive phenology may be facilitated by several mechanisms. First,
540 a slower life history may allow papionin species to spread the energetic costs of reproduction
541 over a prolonged period, such that pregnant or lactating females face only a small daily extra
542 energetic expenditure that can be afforded at any time, as suggested by a recent modelling study
543 (Burtshell et al., 2023). In addition, unlike many other mammals, cercopithecids do not use
544 strict photoperiodic cues to trigger their reproduction (Heldstab et al., 2020) but may instead
545 exhibit condition-induced reproduction, whereby conceptions (and/or cycle resumption after
546 lactation) are more likely to occur when females are in better condition (Alberts et al., 2005;
547 Beehner, Onderdonk, Alberts, & Altmann, 2006). Such reproductive flexibility may have
548 contributed to their historical ecological success via their ability to colonize diverse

549 environments, and may become a critical asset to facilitate their resilience to climate change,
550 associated with increasing environmental unpredictability (Feng et al., 2013).

551

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

553 We examined several climatic **correlates** of the intensity of reproductive seasonality across our
554 sample, and found that environmental unpredictability was a significant predictor, with higher
555 between-year rainfall variation being associated with lower reproductive seasonality. So far,
556 most studies investigating climatic effects on reproductive phenology have focused on
557 environmental seasonality, i.e., the magnitude of within-year environmental variation. In
558 primates, the effect of environmental unpredictability on reproductive seasonality, e.g., through
559 climatic events such as el Niño or fruit mast years in South-East Asia, has been suggested
560 (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985; Wiederholt & Post,
561 2011) but had never been tested. In line with our results, a previous study across 70 ungulate
562 populations showed that the birth peak is more spread out in environments with more year-to-
563 year environmental variation (English et al., 2012).

564 Unpredictable climates may considerably reduce the fitness benefits associated with
565 seasonal breeding, such as enhancing maternal condition and offspring survival. In Africa, year-
566 to-year climatic variation frequently takes the shape of an absence of rain during the rainy
567 season (Alberts et al., 2005), which could cause severe reproductive costs in seasonal breeders
568 who often synchronize lactation or weaning with the rainy season, subsequently forcing females
569 to wait until the next breeding season to initiate a new reproductive event. In such conditions,
570 other adaptive traits may be more advantageous than seasonal breeding to face the energetic
571 costs of reproduction, such as the capacity to store energy (Brockman & van Schaik, 2005a;
572 van Schaik & van Noordwijk, 1985), to expand the dietary repertoire via a generalist diet or
573 foraging innovations (Grueter, 2017), to increase daily foraging time (Alberts et al., 2005;

574 Grueter, 2017), to flexibly adjust lactation duration (Dezeure et al., 2021; van Noordwijk,
575 2012), or to reproduce cooperatively (Cornwallis et al., 2017; Lukas & Clutton-Brock, 2017).
576 Papionin species show many such traits: they can store energy, they have an eclectic
577 omnivorous diet, and they are flexible foragers that typically rely on fallback foods during the
578 dry season (J. Altmann, Schoeller, Altmann, Muruthi, & Sapolsky, 1993; S. A. Altmann, 2009;
579 Swedell, 2011). As such, it is likely that rainfall unpredictability selected these traits in papionin
580 species (energy storage, omnivorous diet, slow life histories, etc.), which in turn contributed to
581 shape their flexible reproductive seasonality.

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

595 The numerous pressures affecting the intensity of reproductive seasonality are often
596 hard to disentangle, meaning that the effects uncovered by correlational studies like ours may
597 sometimes reflect other co-varying pressures, and should thus be interpreted cautiously.
598 Specifically, environmental productivity, which is negatively correlated with climatic

599 unpredictability at our study sites ($\text{cor}=-0.80$, $t=-5.48$, $p<10^{-4}$), was also a significant predictor
600 of the intensity of reproductive seasonality, but in a direction opposed to our prediction, as well
601 as to previous results (Burtshell et al., 2023). In our sample, the least productive climates are
602 also the most unpredictable, and environmental productivity may thus represent a confounding
603 factor in the relationship between climatic unpredictability and seasonal breeding. In species
604 with a flexible phenology, females can start a new reproductive event rapidly after a
605 reproductive failure, without having to wait the next mating season. Such failures are likely to
606 be particularly frequent where environmental productivity is low, contributing to spread
607 reproductive events across the year cycle, and explaining how low environmental productivity
608 may contribute to decrease reproductive seasonality. In addition, this study is based on datasets
609 with heterogenous resolutions, including diverse numbers of births and years of study (e.g.
610 Amboseli: $N=496$, $N_{\text{years}}=33$, versus Queen Elizabeth: $N=35$, $N_{\text{years}}=2$). Additional birth
611 records in small datasets may change r_{birth} , and could thus alter some of the results in our study.

612 Lastly, our decomposition of rainfall components further calls for a more rigorous
613 definition of the term seasonality, especially when it is used in a quantitative way. Indeed, a
614 ‘more seasonal’ environment can either be an environment with higher within-year variation
615 (i.e. the amplitude of variation between the ‘best’ and the ‘worst’ month of the year), with
616 higher within-year over between-year variation (i.e. the amplitude of within-year variation
617 controlling for the intensity of unpredictable variations), with a shorter productive season (i.e.
618 the rainfall peak breadth), or with only a unimodal season (i.e. one rainy, or one warm season
619 per year). Similarly, climatic unpredictability can be broken into two components: (1) the
620 amount/magnitude of year-to-year variation (i.e., if the rainy season brings more or less rainfall
621 than usual), and (2) year-to-year variation in the timing of the rainy season (i.e., if the rainy
622 season occurs earlier or later than usual) (Clauss, Zerbe, Bingaman Lackey, Codron, & Müller,
623 2020). These various components have rarely been disentangled in empirical studies so far, and

624 this study opens new methodological avenues to investigate various environmental components
625 that are likely to affect reproductive seasonality.

626

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

628 The main pattern emerging from our investigations suggests that females from species with
629 high breeding seasonality match lactation with the peak in vegetation productivity (Table 3).
630 For species and populations with a more flexible reproductive phenology, females can match
631 different reproductive stages with the annual vegetation peak, with a possible preference
632 towards conception. This trend may reflect the condition-dependence of conception – a
633 proximate mechanism – rather than an adaptive, optimal strategy aimed at synchronizing the
634 vegetation peak with a particular reproductive stage. These results, obtained from (mostly)
635 tropical primates, echo the broader mammalian literature showing that most mammals from
636 temperate regions match lactation with the best season of the year (Bronson, 2009; Bronson &
637 Heideman, 1994), while patterns are more variable in tropical and long-lived mammals,
638 depending on body size, energy storage capacities and environmental predictability (Brockman
639 & van Schaik, 2005a; Janson & Verdolin, 2005; van Schaik & van Noordwijk, 1985). In
640 addition, even though weaning is a vulnerable life-history stage in young primates, which can
641 be buffered when matched with the vegetation peak in a wild *Papio ursinus* population
642 (Dezeure et al., 2021), few populations seemed to adopt this strategy.

643 **Several caveats apply to the test of H2. First, although NDVI is a relatively good**
644 **measure of plant productivity, highest values of NDVI do not necessarily coincide with the**
645 **annual food peak, especially when focusing on omnivorous/frugivorous species. Precise**
646 **phenological data from each population would be more accurate to quantify the annual food**
647 **peak.** Second, our estimations of lactation peak and weaning might lack accuracy, due to strong
648 between-populations and between-individuals variation. Data quantifying maternal energy

649 expenditure during lactation (Rosetta, Lee, & Garcia, 2011), or isotopic measures of trophic
650 levels between mothers and infants (Carboni, Dezeure, Cowlshaw, Huchard, & Marshall,
651 2022; Reitsema, 2012) would be necessary, for each population, to determine the dynamics of
652 lactation and weaning. Finally, additional unexplored factors can potentially affect reproductive
653 timing and further limit our ability to detect a clear pattern. For example, for populations living
654 at high altitudes like *Theropithecus gelada* from Simien and the *Papio ursinus* from
655 Drakensberg, seasonal variation in temperatures also constrain reproductive phenology (Lycett
656 et al., 1999; Tinsley Johnson et al., 2018).

657

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

660 Baboons and relatives represent an interesting model for understanding the evolution of
661 behavioural and reproductive plasticity of early humans (J. Fischer et al., 2019; King, 2022).
662 Although most great apes are nonseasonal breeders (Brockman & van Schaik, 2005b; Campos
663 et al., 2017), suggesting that their common ancestor also bred year-round, humans are distinct
664 from other apes by exhibiting much faster reproductive paces (which are similar to most Africa-
665 dwelling papionins: Swedell, 2011), and by living in a wider variety of environments, rather
666 than being restricted to tropical forests (Wells & Stock, 2007). The selective pressures that have
667 shaped reproductive phenology in the human lineage versus in other apes may therefore differ,
668 and the papionins, who have similarly left forested habitats to colonize savannahs may provide
669 valuable insights to understand the adaptation of early humans to such diverse and
670 unpredictable environments. Our results suggest that baboons have acquired a low and flexible
671 reproductive seasonality, as well as several other adaptive traits, when facing more arid and
672 unpredictable environments, such as a generalist omnivorous diet and the frequent use of
673 fallback foods, frequent foraging innovations, an increased ability to store fat and to switch

674 home ranges to more suitable areas. Similar reproductive, physiological and behavioural
675 adaptations to environmental unpredictability may have allowed early humans to thrive and
676 maintain fast reproductive paces during their colonization of a wide variety of environments.

677

678 **Conclusion**

679 Our work revealed substantial variation in patterns of reproductive seasonality within and
680 across species of Africa-dwelling papionins, highlighting an exceptional flexibility in their
681 reproductive phenology. Among multiple dimensions of climatic variation, rainfall
682 unpredictability and productivity were the main predictors of the intensity of reproductive
683 seasonality, with arid and unpredictable climates being associated with less seasonal
684 reproduction. Among populations with a pronounced breeding seasonality, females often match
685 lactation with the annual vegetation peak, while phenology patterns are very diverse in other
686 populations. This study sheds new light on the selective pressures shaping reproductive
687 seasonality in long-lived tropical mammals, as well as on potential adaptations to environmental
688 unpredictability. It may further provide an original contribution to understand why humans
689 breed year-round, given their phylogenetic ties and convergences in life-history and ecology
690 with our taxonomic group.

691

692 **ACKNOWLEDGMENTS**

693 We thank Cassandra Raby for her kind help on extracting NDVI data, and Christophe Dezeure
694 for making the Figure 1 of this paper (and more generally for his paternal care). This project
695 was funded by a grant from the Agence Nationale de la Recherche (ANR ERS-17-CE02-0008,
696 2018-2021) awarded to E. H.

697

698 **DATA AVAILABILITY**

699 The raw data and scripts used for this paper are available in the following Zenodo repository:
700 [10.5281/zenodo.13312416](https://doi.org/10.5281/zenodo.13312416).

701

702 REFERENCES

703 Agostinelli, C., & Lund, U. (2018). *Package “CircStats”: Circular Statistics, from “Topics in*
704 *Circular Statistics.”*

705 Alberts, S. C., Hollister-smith, J. A., Mututua, R. S., Sayialel, S. N., Muruthi, P. M., Warutere, K. J.,
706 & Altmann, J. (2005). Seasonality and long-term change in a savanna environment. In D. K.
707 Brockman & C. P. van Schaik (Eds.), *Seasonality in Primates: Studies of living and extinct*
708 *human and non-human primates* (pp. 157–195). Cambridge: Cambridge Univ. Press.

709 Altmann, J. (1980). *Baboon Mothers and Infants*. The University of Chicago Press.

710 Altmann, J., & Alberts, S. C. (2005). Growth rates in a wild primate population: ecological influences
711 and maternal effects. *Behavioral Ecology and Sociobiology*, *57*, 490–501. doi: 10.1007/s00265-
712 004-0870-x

713 Altmann, J., Schoeller, D., Altmann, S. A., Muruthi, P., & Sapolsky, R. M. (1993). Body size and
714 fatness of free-living baboons reflect food availability and activity levels. *American Journal of*
715 *Primatology*. doi: 10.1002/ajp.1350300207

716 Altmann, S. A. (2009). Fallback foods, eclectic omnivores, and the packaging problem. *American*
717 *Journal of Physical Anthropology*, *140*(4), 615–629. doi: 10.1002/ajpa.21097

718 Arnold, C., Matthews, L. J., & Nunn, C. L. (2010). The 10kTrees website: A new online resource for
719 primate phylogeny. *Evolutionary Anthropology*, *19*(3), 114–118. doi: 10.1002/evan.20251

720 Beehner, J. C., Onderdonk, D. A., Alberts, S. C., & Altmann, J. (2006). The ecology of conception and
721 pregnancy failure in wild baboons. *Behavioral Ecology*, *17*(5), 741–750. doi:
722 10.1093/beheco/arl006

- 723 Bercovitch, F. B., & Harding, R. S. O. (1993). Annual Birth Patterns of Savanna Baboons (*Papio*
724 *cynocephalus anubis*) over a Ten-Year Period at Gilgil, Kenya. *Folia Primatologica*, *61*, 115–
725 122.
- 726 Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative
727 data: Behavioral traits are more labile. *Evolution*, *57*(4), 717–745. doi: 10.1111/j.0014-
728 3820.2003.tb00285.x
- 729 Bobe, R., Martínez, F. I., & Carvalho, S. (2020). Primate adaptations and evolution in the Southern
730 African Rift Valley. *Evolutionary Anthropology*, *29*(3), 94–101. doi: 10.1002/evan.21826
- 731 Botero, C. A., Dor, R., McCain, C. M., & Safran, R. J. (2014). Environmental harshness is positively
732 correlated with intraspecific divergence in mammals and birds. *Molecular Ecology*, *23*(2), 259–
733 268. doi: 10.1111/mec.12572
- 734 Boyce, M. S. (1979). Seasonality and Patterns of Natural Selection for Life Histories. *The American*
735 *Naturalist*, *114*(4), 569–583. doi: 10.1086/283503
- 736 Brockman, D. K. (2005). What do studies of seasonality in primates tell us about human evolution? In
737 *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates* (pp.
738 543–570). Cambridge: Cambridge University Press. Retrieved from
739 <https://www.researchgate.net/publication/230778889>
- 740 Brockman, D. K., & van Schaik, C. (2005a). Seasonality and reproductive function. In D. K.
741 Brockman & C. P. van Schaik (Eds.), *Seasonality in Primates: Studies of Living and Extinct*
742 *Human and Non-Human Primates* (pp. 269–305). Cambridge University Press.
- 743 Brockman, D. K., & van Schaik, C. P. (2005b). *Seasonality in Primates: Studies of Living and Extinct*
744 *Human and Non-Human Primates* (D. K. Brockman & C. P. van Schaik, Eds.). Cambridge:
745 Cambridge University Press.
- 746 Brogi, R., Merli, E., Grignolio, S., Chirichella, R., Bottero, E., & Apollonio, M. (2022). It is time to
747 mate: population-level plasticity of wild boar reproductive timing and synchrony in a changing

748 environment. *Current Zoology*, 68(4), 371–380. doi: 10.1093/cz/zoab077

749 Bronson, F. H. (2009). Climate change and seasonal reproduction in mammals. *Philosophical*
750 *Transactions of the Royal Society B: Biological Sciences*, 364(1534), 3331–3340. doi:
751 10.1098/rstb.2009.0140

752 Bronson, F. H., & Heideman, P. D. (1994). Seasonal regulation of reproduction in mammals. In E.
753 Knobil & J. D. Neill (Eds.), *The physiology of reproduction* (Vol. 2, pp. 541–583). New York:
754 New York Raven Press. Retrieved from <https://www.researchgate.net/publication/313495409>

755 Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of*
756 *Statistical Software*, 80. doi: 10.18637/jss.v080.i01

757 Burtshell, L., Dezeure, J., Huchard, E., & Godelle, B. (2023). Evolutionary determinants of
758 reproductive seasonality: A theoretical approach. *Peer Community Journal*, 3(e56). doi:
759 10.24072/pci

760 Campos, F. A., Morris, W. F., Alberts, S. C., Altmann, J., Brockman, D. K., Cords, M., ... Fedigan, L.
761 M. (2017). Does climate variability influence the demography of wild primates? Evidence from
762 long-term life-history data in seven species. *Global Change Biology*, 23(3), 1–15. doi:
763 10.1111/gcb.13754

764 Carboni, S., Dezeure, J., Cowlshaw, G., Huchard, E., & Marshall, H. H. (2022). Stable isotopes reveal
765 the effects of maternal rank and infant age on weaning dynamics in wild chacma baboons.
766 *Animal Behaviour*, 193, 21–32. doi: 10.1016/j.anbehav.2022.08.010

767 Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J., Bergman, T., Johnson, S. E., ... Silk, J. B.
768 (2004). Factors affecting reproduction and mortality among baboons in the Okavango Delta,
769 Botswana. *International Journal of Primatology*, 25(2), 401–428. doi: 0164-0291/04/0400-
770 0401/0

771 Clauss, M., Zerbe, P., Bingaman Lackey, L., Codron, D., & Müller, D. W. H. (2020). Basic
772 considerations on seasonal breeding in mammals including their testing by comparing natural

773 habitats and zoos. *Mammalian Biology*. doi: 10.1007/s42991-020-00078-y

774 Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West, S. A., & Griffin, A. S.
775 (2017). Cooperation facilitates the colonization of harsh environments. *Nature Ecology and*
776 *Evolution*, 1(3). doi: 10.1038/s41559-016-0057

777 Dezeure, J., Baniel, A., Carter, A., Cowlshaw, G., Godelle, B., & Huchard, E. (2021). Birth timing
778 generates reproductive trade-offs in a non-seasonal breeding primate. *Proceedings of the Royal*
779 *Society B*, 288, 1–9. doi: 10.1098/rspb.2021.0286

780 Dezeure, J., Burtschell, L., Baniel, A., Carter, A. J., Godelle, B., Cowlshaw, G., & Huchard, E.
781 (2023). Evolutionary Determinants of Nonseasonal Breeding in Wild Chacma Baboons.
782 *American Naturalist*, 201(1), 106–124. doi: 10.1086/722082

783 Di Bitetti, M. S., & Janson, C. H. (2000). When will the stork arrive? Patterns of birth seasonality in
784 neotropical primates. *American Journal of Primatology*, 50(2), 109–130. doi:
785 10.1002/(SICI)1098-2345(200002)50:2<109::AID-AJP2>3.0.CO;2-W

786 Didan, K., Barreto Munoz, A., Solano, R., & Huete, A. (2015). *MOD13A1 MODIS/Terra Vegetation*
787 *Indices 16-Day L3 Global 500m SIN Grid V006 [Data set]*. doi:
788 <https://doi.org/10.5067/MODIS/MOD13A1.006>

789 English, A. K., Chauvenet, L., Safi, K., & Pettorelli, N. (2012). Reassessing the Determinants of
790 Breeding Synchrony in Ungulates. *PLoS ONE*, 7(7), 1–7. doi: 10.1371/journal.pone.0041444

791 Feng, X., Porporato, A., & Rodriguez-Iturbe, I. (2013). Changes in rainfall seasonality in the tropics.
792 *Nature Climate Change*, 3(9), 811–815. doi: 10.1038/nclimate1907

793 Fischer, J., Higham, J. P., Alberts, S. C., Barrett, L., Beehner, J. C., Bergman, T. J., ... Zinner, D.
794 (2019). The Natural History of Model Organisms: Insights into the evolution of social systems
795 and species from baboon studies. *ELife*, 1960, 1–16.

796 Fischer, Julia, Kopp, G. H., Dal Pesco, F., Goffe, A., Hammerschmidt, K., Kalbitzer, U., ... Zinner, D.
797 (2017). Charting the neglected West: The social system of Guinea baboons. *American Journal of*

- 798 *Physical Anthropology*, 162, 15–31. doi: 10.1002/ajpa.23144
- 799 Grueter, C. C. (2017). Environmental Seasonality. In *The International Encyclopedia of Primatology*
800 (pp. 1–2). John Wiley & Sons, Inc. doi: 10.1002/9781119179313.wbprim0048
- 801 Heldstab, S. A. (2021a). Latitude, life history and sexual size dimorphism correlate with reproductive
802 seasonality in rodents. *Mammal Review*, 51, 256–271.
- 803 Heldstab, S. A. (2021b, December 1). Habitat characteristics and life history explain reproductive
804 seasonality in lagomorphs. *Mammalian Biology*, Vol. 101, pp. 739–757. Springer Science and
805 Business Media Deutschland GmbH. doi: 10.1007/s42991-021-00127-0
- 806 Heldstab, S. A., Müller, D. W. H., Graber, S. M., Bingaman Lackey, L., Rensch, E., Hatt, J. M., ...
807 Clauss, M. (2018). Geographical Origin, Delayed Implantation, and Induced Ovulation Explain
808 Reproductive Seasonality in the Carnivora. *Journal of Biological Rhythms*, 33(4), 402–419. doi:
809 10.1177/0748730418773620
- 810 Heldstab, S. A., van Schaik, C. P., Müller, D. W. H., Rensch, E., Lackey, L. B., Zerbe, P., ... Matsuda,
811 I. (2020). Reproductive seasonality in primates: patterns, concepts and unsolved questions.
812 *Biological Reviews*. doi: 10.1111/brv.12646
- 813 Hill, R. A., Lycett, J. E., & Dunbar, R. I. M. (2000). Ecological and social determinants of birth
814 intervals in baboons. *Behavioral Ecology*, 11(5), 560–564. doi: 10.1093/beheco/11.5.560
- 815 Hothorn, T., Hornik, K., Van De Wiel, M. A., & Zeileis, A. (2006). A lego system for conditional
816 inference. *American Statistician*, 60(3), 257–263. doi: 10.1198/000313006X118430
- 817 Huffman, G. J., Bolvin, D. T., Nelkin, E. J., & Adler, R. F. (2016). *TRMM (TMPA) Precipitation L3 1*
818 *day 0.25 degree x 0.25 degree V7*. Retrieved from 10.5067/TRMM/TMPA/DAY/7
- 819 Janson, C., & Verdolin, J. (2005). Seasonality of primate births in relation to climate. In D. K.
820 Brockman & C. P. van Schaik (Eds.), *Seasonality in Primates: Studies of Living and Extinct*
821 *Human and Non-Human Primates* (pp. 307–350). Cambridge: Cambridge University Press. doi:
822 10.1017/cbo9780511542343.012

- 823 Jarvey, J. C., Low, B. S., Pappano, D. J., Bergman, T. J., & Beehner, J. C. (2018). Graminivory and
824 Fallback Foods: Annual Diet Profile of Geladas (*Theropithecus gelada*) Living in the Simien
825 Mountains National Park, Ethiopia. *International Journal of Primatology*, *39*(1), 105–126. doi:
826 10.1007/s10764-018-0018-x
- 827 Jolly, C. J. (2001). A proper study for mankind: Analogies from the Papionin monkeys and their
828 implications for human evolution. *Yearbook of Physical Anthropology*, *44*, 177–204. doi:
829 10.1002/ajpa.10021
- 830 Jordan, V. E., Walker, J. A., Beckstrom, T. O., Steely, C. J., McDaniel, C. L., St Romain, C. P., ...
831 Worley, K. C. (2018). A computational reconstruction of *Papio* phylogeny using Alu insertion
832 polymorphisms. *Mobile DNA*, *9*(1). doi: 10.1186/s13100-018-0118-3
- 833 King, G. E. (2022). Baboon perspectives on the ecology and behavior of early human ancestors.
834 *Proceedings of the National Academy of Sciences of the United States of America*, *119*(45). doi:
835 10.1073/pnas.2116182119
- 836 Kingdon, J., Happold, D., Butynski, T. M., Hoffmann, M., Happold, M., & Kalina, J. (2012).
837 *Mammals of Africa*.
- 838 Lee, P. C. (1996). The meanings of weaning: growth, lactation, and life history. *Evolutionary*
839 *Anthropology*, *5*(3), 87–98. doi: [https://doi.org/10.1002/\(SICI\)1520-6505\(1996\)5:3<87::AID-](https://doi.org/10.1002/(SICI)1520-6505(1996)5:3<87::AID-EVAN4>3.0.CO;2-T)
840 [EVAN4>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1520-6505(1996)5:3<87::AID-EVAN4>3.0.CO;2-T)
- 841 Loe, L. E., Bonenfant, C., Mysterud, A., Gaillard, J. M., Langvatn, R., Klein, F., ... Stenseth, N. C.
842 (2005). Climate predictability and breeding phenology in red deer: Timing and synchrony of
843 rutting and calving in Norway and France. *Journal of Animal Ecology*, *74*(4), 579–588. doi:
844 10.1111/j.1365-2656.2005.00987.x
- 845 Lukas, D., & Clutton-Brock, T. (2017). Climate and the distribution of cooperative breeding in
846 mammals. *Royal Society Open Science*, *4*(1). doi: 10.1098/rsos.160897
- 847 Lycett, J. E., Weingrill, T., & Henzi, S. P. (1999). Birth patterns in the Drakensberg Mountain

- 848 baboons (*Papio cynocephalus ursinus*). *South African Journal of Science*, 95(8), 354–356.
- 849 McNutt, J. W., Groom, R., & Woodroffe, R. (2019). Ambient temperature provides an adaptive
850 explanation for seasonal reproduction in a tropical mammal. *Journal of Zoology*, 309(3), 153–
851 160. doi: 10.1111/jzo.12712
- 852 Pereira, R. J. P., Dos Santos Zanetti, E., & Furlan Polegato, B. (2010). Female reproduction. In J. M.
853 Barbanti Duarte & S. Gonzalez (Eds.), *Neotropical Cervidology* (1st ed., Vol. 1).
854 FUNEP/IUCN. Retrieved from <https://www.researchgate.net/publication/273143129>
- 855 Petersdorf, M., Weyher, A. H., Kamilar, J. M., Dubuc, C., & Higham, J. P. (2019). Sexual selection in
856 the Kinda baboon. *Journal of Human Evolution*, 135(102635). doi: 10.1016/j.jhevol.2019.06.006
- 857 Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using
858 the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in*
859 *Ecology and Evolution*. doi: 10.1016/j.tree.2005.05.011
- 860 R Core Team. (2019). *R: A language and environment for statistical computing*. Retrieved from
861 <https://www.r-project.org/>
- 862 Reitsema, L. J. (2012). Introducing Fecal Stable Isotope Analysis in Primate Weaning Studies.
863 *American Journal of Primatology*, 74(10), 926–939. doi: 10.1002/ajp.22045
- 864 Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things).
865 *Methods in Ecology and Evolution*, 3, 217–223. doi: 10.1111/j.2041-210X.2011.00169.x
- 866 Revell, L. J. (2024). phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and
867 other things). *PeerJ*, 12. doi: 10.7717/peerj.16505
- 868 Rhine, R. J., Norton, G. W., Wynn, G. M., & Wynn, R. D. (1989). Plant feeding of yellow baboons
869 (*Papio cynocephalus*) in Mikumi national park, Tanzania, and the relationship between seasonal
870 feeding and immature survival. *International Journal of Primatology*, 10(4), 319–342. doi:
871 10.1007/BF02737420
- 872 Rogers, J., Muthuswamy, R., Harris, R. A., Mailund, T., Leppälä, K., Athanasiadis, G., ... Worley, K.

- 873 C. (2019). The comparative genomics and complex population history of *Papio* baboons. *Science*
874 *Advances*, 5, 1–14. Retrieved from <http://advances.sciencemag.org/>
- 875 Rosetta, L., Lee, P. C., & Garcia, C. (2011). Energetics during reproduction: A doubly labeled water
876 study of lactating baboons. *American Journal of Physical Anthropology*, 144(4), 661–668. doi:
877 10.1002/ajpa.21475
- 878 Rutberg, A. T. (1987). Adaptive Hypotheses of Birth Synchrony in Ruminants: An Interspecific Test.
879 *The American Naturalist*, 130(5), 692–710. doi: 10.1086/284739
- 880 Setchell, J. M., Lee, P. C., Wickings, E. J., & Dixson, A. F. (2002). Reproductive Parameters and
881 Maternal Investment in Mandrills (*Mandrillus sphinx*). *International Journal of Primatology*,
882 23(1), 51–68. doi: 10.1023/A:1013245707228
- 883 Spady, T. J., Lindburg, D. G., & Durrant, B. S. (2007). Evolution of reproductive seasonality in bears.
884 *Mammal Review*, 37(1), 21–53. doi: 10.1111/j.1365-2907.2007.00096.x
- 885 Spinage, C. A. (1973). The role of photoperiodism in the seasonal breeding of tropical African
886 ungulates. *Mammal Review*, 3(3), 71–85. doi: 10.1111/j.1365-2907.1973.tb00174.x
- 887 Struhsaker, T. T. (1997). Ecology of an African rain forest: logging in Kibale and the conflict between
888 conservation and exploitation. *Journal of Tropical Ecology*, 14(4), 561–561. doi:
889 10.1017/S0266467498240399
- 890 Swedell, L. (2011). African papionins: diversity of social organization and ecological flexibility. In C.
891 J. Campbell, A. Fuentes, K. C. MacKinnon, S. Bearder, & R. Stumpf (Eds.), *Primates in*
892 *perspective* (Vol. 2, pp. 241–277). Oxford: Oxford University Press. Retrieved from
893 <https://www.researchgate.net/publication/285789215>
- 894 Thel, L., Chamaillé-Jammes, S., & Bonenfant, C. (2022). How to describe and measure phenology?
895 An investigation on the diversity of metrics using phenology of births in large herbivores. *Oikos*,
896 2022(4). doi: 10.1111/oik.08917
- 897 Thompson, M. E., & McCabe, G. M. (2013). Reproductive seasonality in wild Sanje mangabeys

- 898 (Cercocebus sanjei), Tanzania: Relationship between the capital breeding strategy and infant
899 survival. *Behaviour*, 150(12), 1399–1429. doi: 10.1163/1568539X-00003102
- 900 Tinsley Johnson, E., Snyder-Mackler, N., Lu, A., Bergman, T. J., & Beehner, J. C. (2018). Social and
901 ecological drivers of reproductive seasonality in geladas. *Behavioral Ecology*, 29(3), 574–588.
902 doi: 10.1093/beheco/ary008
- 903 Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., & Lytle, D. A. (2017). Seasonality and
904 predictability shape temporal species diversity. *Ecology*, 98(5), 1201–1216.
- 905 Trébouet, F., Malaivijitnond, S., & Reichard, U. H. (2021). Reproductive seasonality in wild northern
906 pig-tailed macaques (*Macaca leonina*). *Primates*. doi: 10.1007/s10329-021-00901-1
- 907 van Noordwijk, M. A. (2012). From maternal investment to lifetime maternal care. In *The evolution of*
908 *primate societies* (pp. 321–342). Chicago, London: The University of Chicago Press.
- 909 Van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests:
910 Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and*
911 *Systematics*, 24(1), 353–377. doi: 10.1146/annurev.es.24.110193.002033
- 912 van Schaik, C. P., & van Noordwijk, M. A. (1985). Interannual variability in fruit abundance and the
913 reproductive seasonality in Sumatran Long-tailed macaques (*Macaca fascicularis*). *J. Zool.,*
914 *Lond. (A)*, 206(4), 533–549. doi: 10.1111/j.1469-7998.1985.tb03557.x
- 915 Wells, J. C. K., & Stock, J. T. (2007). The biology of the colonizing ape. *Yearbook of Physical*
916 *Anthropology*, 50(1), 191–222. doi: 10.1002/ajpa.20735
- 917 Wiederholt, R., & Post, E. (2011). Birth seasonality and offspring production in threatened neotropical
918 primates related to climate. *Global Change Biology*, 17(10), 3035–3045. doi: 10.1111/j.1365-
919 2486.2011.02427.x
- 920 Wright, P. C. (1999). Lemur Traits and Madagascar Ecology: Coping With an Island Environment.
921 *Yearbook of Physical Anthropology*, 42, 31–72. doi: 10.1002/(sici)1096-
922 8644(1999)110:29+<31::aid-ajpa3>3.0.co;2-0

923 Zerbe, P., Clauss, M., Codron, D., Bingaman Lackey, L., Rensch, E., Streich, J. W., ... Müller, D. W.
924 H. (2012). Reproductive seasonality in captive wild ruminants: Implications for biogeographical
925 adaptation, photoperiodic control, and life history. *Biological Reviews*, 87(4), 965–990. doi:
926 10.1111/j.1469-185X.2012.00238.x

927