



Peer Community In Ecology

Reproductive flexibility shapes primate survival in a changing climate driven by environmental unpredictability

Cédric Sueur  based on peer reviews by 2 anonymous reviewers

Jules Dezeure, Julie Dagorrette, Lugdiwine Burtschell, Shahrina Chowdhury, Dieter Lukas, Larissa Swedell, Elise Huchard (2024) Flexible reproductive seasonality in Africa-dwelling papionins is associated with low environmental productivity and high climatic unpredictability. *bioRxiv*, ver. 2, peer-reviewed and recommended by Peer Community in Ecology. <https://doi.org/10.1101/2024.05.01.591991>

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As seasonal cycles become increasingly disrupted, our understanding of the ecology and evolution of reproductive seasonality in tropical vertebrates remains limited (Bronson 2009). To predict how changes in seasonality might impact these animals, it is crucial to identify which elements of their varied reproductive patterns are connected to the equally varied patterns of rainfall seasonality (within-year fluctuations) or the significant climatic unpredictability (year-to-year variations) characteristic of the intertropical region.

Dezeure et al. (2024) provide a comprehensive examination of reproductive seasonality in papionin monkeys across diverse African environments. By investigating the ecological and evolutionary determinants of reproductive timing, the authors offer novel insights into how climatic factors, particularly environmental unpredictability, shape reproductive strategies in these primates. This study stands out not only for its methodological rigour but also for its contribution to our understanding of how primates adapt their reproductive behaviours to varying environmental pressures. The findings have broad implications, particularly in the context of ongoing climate change, which is expected to increase environmental unpredictability globally. The innovative approach of this paper lies in its multifaceted examination of reproductive seasonality, which integrates data from 21 wild populations of 11 papionin species. The study employs a robust statistical framework, incorporating Bayesian phylogenetic generalised linear mixed models to control for phylogenetic relatedness among species. This methodological choice is crucial because it allows the authors to disentangle the effects of environmental variables from evolutionary history, providing a more accurate picture of how current ecological factors influence reproductive strategies.

The study's focus on environmental unpredictability as a determinant of reproductive seasonality is particularly noteworthy. While previous research has established the importance of environmental seasonality (Janson and Verdolin 2005), this paper breaks new ground by showing that the magnitude of year-to-year variation in rainfall – rather than just the seasonal distribution of rainfall – plays a critical role in determining the intensity of reproductive seasonality. This finding is supported by the significant negative correlation between reproductive seasonality and environmental unpredictability, which the authors demonstrate across multiple populations and species. The results of this study are important for several reasons. First, they challenge the traditional view that reproductive seasonality is primarily driven by within-year environmental fluctuations. By showing that inter-annual variability in rainfall is a stronger predictor of reproductive timing than intra-annual variability, the authors suggest that primates, like papionins, have evolved flexible reproductive strategies to cope with the unpredictable availability of resources. This flexibility is likely an adaptive response to the highly variable environments that many African primates inhabit, where food availability can vary dramatically not just within a year but from year to year. Second, the study highlights the role of reproductive flexibility in the evolutionary success of papionins. The authors provide compelling evidence that species within the *Papio* genus, for example, exhibit significant variability in reproductive timing both within and between populations. This variability suggests that these species possess a remarkable ability to adjust their reproductive strategies in response to local environmental conditions, which may have contributed to their widespread distribution across diverse habitats in Africa. This finding aligns with the work of Brockman and Schaik (2005), who argued that reproductive flexibility is a key factor in the success of primates in unpredictable environments.

The study also contributes to our understanding of the evolutionary transition from seasonal to non-seasonal breeding in primates. The authors propose that the loss of strict reproductive seasonality in some papionin species may represent an adaptive shift toward greater reproductive flexibility. This shift could be driven by the need to maximise reproductive success in environments where the timing of resource peaks is difficult to predict. The authors' findings support this hypothesis, as they show that populations living in more unpredictable environments tend to have lower reproductive seasonality. The broader implications of this study (Dezeure et al. 2024) extend beyond the specific case of papionin monkeys. The findings have relevance for the study of reproductive strategies in other long-lived, tropical mammals that face similar environmental challenges. As climate change is expected to increase the frequency and intensity of environmental unpredictability, understanding how species have historically adapted to such conditions can provide valuable insights into their potential resilience or vulnerability to future changes.

Many primate species are already facing significant threats from habitat loss, hunting, and climate change. By identifying the environmental factors that influence reproductive success, Dezeure et al. (2024) study can help inform conservation strategies aimed at protecting the most vulnerable populations. For example, conservation efforts could focus on maintaining or restoring habitat features that promote reproductive flexibility, such as access to a variety of food resources that peak at different times of the year (Chapman et al.).

References:

Brockman D, Schaik C (2005) Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates

Bronson FH (2009) Climate change and seasonal reproduction in mammals. *Philos Trans R Soc B Biol Sci* 364:3331–3340. <https://doi.org/10.1098/rstb.2009.0140>

Chapman CA, Gogarten JF, Golooba M, et al Fifty+ years of primate research illustrates complex drivers of abundance and increasing primate numbers. *Am J Primatol* n/a:e23577. <https://doi.org/10.1002/ajp.23577>

Jules Dezeure, Julie Dagorrette, Lugdiwine Burtschell, Shahrina Chowdhury, Dieter Lukas, Larissa Swedell, Elise Huchard (2024) Flexible reproductive seasonality in Africa-dwelling papionins is associated

with low environmental productivity and high climatic unpredictability. bioRxiv, ver.2 peer-reviewed and recommended by PCI Ecology <https://doi.org/10.1101/2024.05.01.591991>

Janson C, Verdolin J (2005) Seasonality of primate births in relation to climate. In: Schaik CP van, Brockman DK (eds) Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp 307–350

Reviews

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.1101/2024.05.01.591991>

Version of the preprint: 1

Authors' reply, 27 August 2024

Please find our answer to the reviewers in the PDF attached, and the paper with track change (highlighted in yellow).

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Decision by **Cédric Sueur** , posted 20 June 2024, validated 21 June 2024

Revision needed

The manuscript presents an innovative study on climate factors and reproductive seasonality in Papionins, with well-structured content and clear objectives. Reviewer 1 finds the methods section needing improvement, particularly the statistical analysis justification, and suggests minor editorial changes. Reviewer 2 notes the title's misleading implication of causality and critiques the definition of seasonality and data heterogeneity handling. Both reviewers appreciate the study's potential but emphasize the need for clearer methodological explanations and critical discussion of data quality and terminological definitions. Addressing these issues could enhance the study's contribution to understanding primate reproductive seasonality.

Reviewed by anonymous reviewer 2, 14 June 2024

Title and abstract

Does the title clearly reflect the content of the article? yes

Does the abstract present the main findings of the study? Yes

Introduction

Are the research questions/hypotheses/predictions clearly presented? Yes

Does the introduction build on relevant research in the field? Yes

Materials and methods

Are the methods and analyses sufficiently detailed to allow replication by other researchers? Yes

Are the methods and statistical analyses appropriate and well described? No (see below)

Results

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? I don't know

Are the results described and interpreted correctly? Yes

Discussion

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? Yes

Are the conclusions adequately supported by the results (without overstating the implications of the findings)? Yes

The article presents a study analyzing the effect of climate factors seasonality on the reproductive seasonality of Papionins in Africa. The objective is to test the hypothesis that unpredictability of climate seasonality decreases reproduction seasonality which allows greater flexibility to match vegetation productivity peak with conception, lactation or weaning. The work is based on data extracted from literature and from databases (remote sensing, climate). The text is very well structured and referenced. The results are clearly exposed and in-depth discussed. I am not a specialist of this subject and not able to fully judge relevance of the discussion, but I feel the work innovative and find the approach very solid. The discussion also comprises a part making a parallel between Papionins and early humans, both having left the forests for the savannahs and sharing flexible or low reproductive seasonality. For me, only the Methods section needs improvements:

L187 to 193 The explanations must be improved. I understand the principle that the monthly vectors are summed to compute the mean rbirth and that it diminishes when the births occur all along the year. But I would think that monthly lengths would be computed using something like the monthly proportion of annual births.

L313 The choice of a Poisson distribution must be justified. Otherwise, I do not understand why a Poisson distribution is used since rbirth is continuous and the Poisson distribution is discrete. I suggest the use of the beta distribution with logit link which is flexible and appropriate for random variables with continuous bounded distributions. It is not necessary to transform variables with values comprised between 0 and 1 (if there are 0, Smithson & Verkuilen 2006, Psychological Methods 11, 54-71 suggest $y=(y*(N-1)+0.5)/N$ with N the sample size). Perhaps the use of the beta regression would improve the results

Minor remarks

L35 change 'the environmental measures' to 'environmental variations'

L140 suppress the new paragraph

L212 change 'In addition' to 'Yet'

L349 All along the Results and the Discussion sections, I would prefer the use of the scientific names rather than the common names since those ones are not given in the Tables and in the Figures

Table 1: give the signification of Krain

Figure 4 Perhaps the use of abbreviations for the sites would improve clarity

Reviewed by anonymous reviewer 1, 19 June 2024

Title and abstract

Does the title clearly reflect the content of the article? Yes, No (**The title suggests an analysis of causal relationships, but it is more of a correlative analysis**), I don't know

Does the abstract present the main findings of the study? Yes, No (please explain), I don't know

Introduction

Are the research questions/hypotheses/predictions clearly presented? Yes, No (please explain), I don't know

Does the introduction build on relevant research in the field? Yes, No (please explain), I don't know

Materials and methods

Are the methods and analyses sufficiently detailed to allow replication by other researchers? Yes, No (please explain), I don't know

Are the methods and statistical analyses appropriate and well described? Yes, No (**see review as text**), I don't know

Results

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? Yes, No (please explain), I don't know

Are the results described and interpreted correctly? Yes, No (**see review as text**), I don't know

Discussion

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? Yes, No (**see review as text**), I don't know

Are the conclusions adequately supported by the results (without overstating the implications of the findings)? Yes, No (please explain), I don't know

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

By Dezeure and colleagues

The main research question of the study is interesting. The authors tried not only to categorize African papionin species into seasonal and non-seasonal breeders and determine the degree of reproductive seasonality within and among species but also tried to correlate (temporally) certain reproductive events with climatic and NDVI information. The paper is nicely written and the narrative is easy to follow.

The quality of such analyses, however, depends largely on the availability, quality and quantity of data on reproductive events. Quantity and quality can vary largely, e.g., from one species corresponding data of only one population (groups) from 20 years is available, from another species data from 5 populations (groups) for only one or two years, from a third species just data from captivity. Therefore, the question arises how to weigh these differences, or should one ignore them at all? Given this problem, the authors might discuss how such data heterogeneity might affect their results.

I also think that another general question is when to speak of seasonality. How is seasonality defined? This is a difficult question and the authors used here a circadian statistic parameter (r_{birth}) to differentiate seasonal from non-seasonal breeders. However, they did not use r_{birth} directly, but the associated p-value. P 14 L 334-336 "Populations were categorized as seasonal breeders when P-values associated with the Rayleigh test were <0.05 , meaning that the null hypothesis of a uniform birth distribution could be rejected". It might be statistically correct, but since the P-value not only depends on the effect size (here r_{birth}) but also the sample size, using only the P-values to categorize seasonality is in my view inappropriate. For instance, the distribution of 32 births in Gashaka-Gumti reveals a r_{birth} of 0.2167 and a P-value of 0.2237 and is thus per the definition of the authors non-seasonal. However, the distribution of 118 births in Gilgil reveals an even smaller r_{birth} of 0.1873 but a P-value of 0.0159 and makes the population a seasonal breeder. In addition, when comparing the distributions of births over the 12 months of the year for Gilgil and Gashaka, as depicted in Fig 2, it remains rather questionable to categorize the Gilgil population as seasonal and the Gashaka population as non-seasonal. The question remains, how large should the r_{birth} (effect size) be to qualify for seasonality? Another question arises when the authors speak about evolution, in particular the evolution of a flexible reproductive phenology.

P4 L90-91 "flexible reproduction may be more advantageous than strictly seasonal reproduction"

What do you mean by flexibility? On an individual basis or population basis. It might be difficult for a female to decide whether to mate or not if she then has no clue what the conditions will be in 6 months.

P18 L422-424 "Such flexibility would imply that each population, or even each individual may be able to adjust phenology to current environmental conditions."

Should this mean, that an individual female may decide that this year I will start later with reproduction because it seems that the year will be difficult? Usually, such "flexibility" is found at the population level. Some individuals will reproduce at that time of the year and others at another time. If there is selection pressure on the timing, those individuals who reproduce at the optimal time would have a fitness benefit. We can find flexibility within and among individuals, and within and among populations. It would be very helpful here, to get some more information on how the authors think such a process would work.

Aim II of the study is to tackle the question: What are the main environmental factors responsible for variation in the intensity of reproductive seasonality?

This suggests that the authors try to look for causal relationships between environmental factors and reproductive seasonality. I think this is not possible at this stage. It is more of a correlative relationship that the authors describe.

In my view, the paper has good potential. If the authors will be able to be a bit more critical with their study (data quality, definition of terms, definition of seasonality etc) the study might become a valuable contribution to our knowledge of the seasonality of primate reproduction and will further reveal that most of the African papionins are relatively independent of seasons when reproducing.

Minor comments

P6 L138 primate taxon instead of primates

P7 L169 Where do the data for *Rungwecebus* come from? I doubt there are data available, not even from captivity.

P8 L181 A definition or description of what the authors mean by "birth peak" and "intensity of birth seasonality" would be helpful.

P14 L345 "females tended to conceive during, soon before, or soon after the annual food peak" NDVI is a relatively good measure of plant productivity, however, whether this always coincides with the annual food peak is at least debatable. In temperate zones, NDVIs might be highest at the beginning of summer, but many trees carry fruit later in the year. The more or less strong relationship between NDVI and food peaks (phenology data) needs at least to be addressed.

P15 L358-359 "... closely related species have more similar patterns of reproductive seasonality. However, such a value is also compatible with some phylogenetic flexibility." What do you mean here? If phylogeny has a strong impact, can we then speak of the adaptation of species to certain ecological conditions?