Peer Community In
Ecology

Rare behaviours can have strong effects: evidence for sexual coercion in mandrills

Matthieu Paquet based on reviews by Micaela Szykman Gunther and 1 anonymous reviewer

A recommendation of:

Sexual coercion in a natural mandrill population

Nikolaos Smit, Alice Baniel, Berta Roura-Torres, Paul Amblard-Rambert, Marie J. E. Charpentier, Elise Huchard *(2022), bioRxiv, 2022.02.07.479393, ver. 5 peer-reviewed and recommended by Peer Community in Ecology*
https://doi.org/10.1101/2022.02.07.479393

Data used for results
https://doi.org/10.5281/zenodo.6607803
Scripts used to obtain or analyze results
https://doi.org/10.5281/zenodo.6607803

Submitted: 11 February 2022, Recommended: 30 May 2022

Published: 31 May 2022

Cite this recommendation as:
Matthieu Paquet (2022) Rare behaviours can have strong effects: evidence for sexual coercion in mandrills. *Peer Community in Ecology, 100099.* ***https://doi.org/10.24072/pci.ecology.100099***

Recommendation

Sexual coercion can be defined as the use by a male of force, or threat of force, which increases the chances that a female will mate with him at a time when she is likely to be fertile, and/or decrease the chances that she will mate with other males, at some cost to the female (Smuts & Smuts 1993). It has been evidenced in a wide range of species and may play an important role in the evolution of sexual conflict and social systems. However, identifying sexual coercion in natural systems can be particularly challenging. Notably, while male behaviour may have immediate consequences on mating success ("harassment"), the mating benefits may be delayed in time ("intimidation"), and in such cases, evidencing coercion requires detailed temporal data at the individual level. Moreover, in some species male aggressive behaviours may subtle or rare and hence hardly observed, yet still have important effects on female mating probability and fitness. Therefore, investigating the occurrence and consequences of sexual coercion in such species is particularly relevant but studying it in a statistically robust way is likely to require a considerable amount of time spent observing individuals.

In this paper, Smit et al. (2022) test three clear predictions of the sexual coercion hypothesis in a natural population of Mandrills, where severe male aggression towards females is rare: (1) male aggression is more likely on sexually receptive females than on females in other reproductive states, (2) receptive females are more likely to be injured and (3) male aggression directed towards females is positively related to subsequent probability of copulation between those dyads. They also tested an alternative hypothesis, the "aggressive male phenotype" under which the correlation between male aggression towards females and subsequent mating could be statistically explained by male overall aggressivity. In agreement with the three predictions of the sexual coercion hypothesis, (1) male aggression was on average 5 times more likely, and (2) injuries twice as likely, to be observed on sexually receptive females than on females in other reproductive states and (3) copulation between males and sexually receptive females was twice more likely to be observed when aggression by this male was observed on the female before sexual receptivity. There was no support for the aggressive male hypothesis.

The reviewers and I were highly positive about this study, notably regarding the way it is written and how the predictions are carefully and clearly stated, tested, interpreted, and discussed.

This study is a good illustration of a case where some behaviours may not be common or obvious yet have strong effects and likely important consequences and thus be clearly worth studying. More generally, it shows once more the importance of detailed long-term studies at the individual level for our understanding of the ecology and evolution of wild populations.

It is also a good illustration of the challenges faced, when comparing the likelihood of contrasting hypotheses means we need to alter sample sizes and/or the likelihood to observe at all some behaviours. For example, observing copulation within minutes after aggression (and therefore, showing statistical support for "harassment") is inevitably less likely than observing copulations on the longer-term (and therefore showing statistical support for "intimidation", when of course effort is put into recording such behavioural data on the long-term). Such challenges might partly explain some apparently intriguing results. For example, why are swollen females more aggressed by males if only aggression before the swollen period seems associated with more chances of mating? Here, the authors systematically provide effect sizes (and confidence intervals) and often describe the effects in an intuitive biological way (e.g., "Swollen females were, on average, about five times more likely to become injured"). This clearly helps the reader to not merely compare statistical significances but also the biological strengths of the estimated effects and the uncertainty around them. They also clearly acknowledge limits due to sample size when testing the harassment hypothesis, yet they provide precious information on the probability of observing mating (a rare behaviour) directly after aggression (already a rare behaviour!), that is, 3 times out of 38 aggressions observed between a male and a swollen female. Once again, this highlights how important it is to be able to pursue the enormous effort put so far into closely and continuously monitoring this wild population.

Finally, this study raises exciting new questions, notably regarding to what extent females exhibit "counter-strategies" in response to sexual coercion, notably whether there is still scope for female mate choice under such conditions, and what are the fitness consequences of these dynamic conflicting sexual interactions. No doubt these questions will sooner than later be addressed by the authors, and I am looking forward to reading their upcoming work.

References

Smit N, Baniel A, Roura-Torres B, Amblard-Rambert P, Charpentier MJE, Huchard E (2022) Sexual coercion in a natural mandrill population. bioRxiv, 2022.02.07.479393, ver. 5 peer-reviewed and recommended by Peer Community in Ecology. https://doi.org/10.1101/2022.02.07.479393

Smuts BB, Smuts R w. (1993) Male Aggression and Sexual Coercion of Females in Nonhuman Primates and Other Mammals: Evidence and Theoretical Implications. In: Advances in the Study of Behavior (eds Slater PJB, Rosenblatt JS, Snowdon CT, Milinski M), pp. 1–63. Academic Press. https://doi.org/10.1016/S0065-3454(08)60404-0

Reviews

Toggle reviews

Evaluation round #3

DOI or URL of the preprint: ***https://doi.org/10.1101/2022.02.07.479393***

Version of the preprint: 3

Author's Reply, 26 May 2022

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Dear Dr Paquet,

Please find below the revised manuscript and the our answers after your last comment. The updated version has already passed screening in bioRxiv and 'will be online shortly'.

Thank you,
Nikolaos Smit

Decision by Matthieu Paquet, 26 May 2022

Dear authors,

Many thanks for your submission.

I am deeply sorry for not noticing this earlier but I would just have one final suggestion for improvement:

In Figure 1c the occurence of copulations is shown on the x axis and the aggression rate on the y axis. Similarly in the text lines 303-305, you present the mean aggression rate of dyads that copulated vs dyads that did not. Yet, was was tested (and is indeed correct) is whether aggression rate statistically explained the probability to copulate later on, not the other way round. Therefore I feel that a figure showing copulation rate on the y axis as a functon of agression rate on the x axis would better illustrate the analysis (even if it may not look as "nice" as copulation is a binary variable. Similarly, it would be more relevant and adequate given the test performed to provide in the text was the expected copulation probability was for dyads with no aggression vs dyads with an aggression rate of e.g 1 per hour (or another more biologically relevant rate).

Do you think it could be possible (and relevant) to make such a change? Meanwhile I am already writing the recommendation, so hopefully the recommendation will not be delayed at all.

Apologies again and best wishes,

Matthieu

Evaluation round #2

DOI or URL of the preprint: ***https://doi.org/10.1101/2022.02.07.479393***

Version of the preprint: 2

Author's Reply, 23 May 2022

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Dear

Decision by Matthieu Paquet, 23 May 2022

Dear Authors,

Your preprint entitled “Sexual coercion in a natural mandrill population” has been reviewed again by one of the previous reviewers who only provided a few minor comments to address on a PDF document.

In addition I also have the two following comments:

Line 87: perhaps use a more "geographical" terminology as the term "Old World" reflects a colonial perspective.

Line 228: please state in the text (as you did in your response to one of my previous comments) that results remained similar when using slightly different thresholds and whithout using any threshold.

Once these comments are addressed, I will be very happy to recommend your preprint.

I wish you a very nice day,

Matthieu

Reviewed by Micaela Szykman Gunther, 21 May 2022

I appreciate the additions to this revised manuscript. I think the authors have addressed the comments by the reviewers and editor.

I have a few minor questions/comments/edits that I will included in an attached document.

Download the review

Evaluation round #1

DOI or URL of the preprint: ***https://www.biorxiv.org/content/10.1101/2022.02.07.479393v1***

Version of the preprint: 1

Author's Reply, 31 Mar 2022

Download author's replyDownload tracked changes file
Dear Dr Paquet,

I personally apologize for not submitting a tracked changes document. I realized upon the re-submission process that this was requested. In addition, I am using as my main editing software LaTeX while the exchanges with the coauthors took place via docx, therefore, it is complicated to obtain such a result. In most of the responses in the attached reply, however, you can find both the changed text quoted and the corresponding lines within the main document. Please accept my sincere apologies and thank you again for your time.

Given that I could upload only one revised document, I merged the main and supplementary pdf into one file that you can find attatched below.

Kind regards,
Nikolaos Smit

Decision by Matthieu Paquet, 31 Mar 2022

Dear Authors,

Your preprint entitled “Sexual coercion in a natural mandrill population”has now been reviewed and the reviewers’ comments are appended below. As you will see, both reviewers are highly positive about the study, and I share their views, notably regarding the way it is written and how the predictions are carefully stated and tested. Yet they have several comments that need to be addressed carefully before your preprint can be recommended. Please note that the second reviewer also commented on the PDF and you should be able to download this review.

In addition I also have the following comments:

CODE REVIEW:

1) In the script 1rstPredictionStats.R

aggrBinAM: Did the female received aggression from adult males towards the female this day
harshBinAM: Did the female received aggression from adult males towards the female this day
aggrBinYMF: Did the female received aggression from groupates other than adult males towards the female this day
harshBinYMF: Did the female received aggression from from groupates other than adult males towards the female this day

The descriptions of these variables are identical but their values are not identical. Please clarify their differences (agression vs "severe" agression?).

Line 76: I get an error message "Error in etapred + sim.reff : non-conformable arrays". Can you ensure this function can be run and the fit of the model assessed?

Lines 143 and 144 the name of the model output is incorrect.

2) Script 2ndPredictionStats.R

Line 16: .csv is missing (STATinjCyF <- read.csv(2ndPredictionTable.csv))

Line 29: # month: Month of observations (not orservations)

Line 31 and 32: sex ratio instead of ration

3) Script 3rdPredictionStats.R

Line 18 correct the name "3rdPrediction" instead of "3ndPrediction"

Line 24 arrival? (correct other typos also if possible)

Line 60: having a fixed effect seems safer than an offset in a binomial likelihood with logit link (see comment below).

MAIN TEXT:

Line 157: spell out GLMM the first time you use it.

Line 160-161: briefly justify why you need to control for these variables.

Line 162: It seems indeed relevant to try to "offset" the probability to observe the event by the length of the observation period. However, I am not certain this would be the right way to proceed with a Bernouilli (binomial) distribution and logit link. Unfortunately, I am not aware of ways to easily "offset" in such cases. Given the very low (about 2%?) probability of observing at least one event within an observation period, I guess the probability to observe 2 of these events is very close to zero (did it ever occur in the present dataset?)? In such case you could instead use a Poisson distribution and then having log(time) as offset would be fine (and no need to scale it I think). If you do have the information of the number of events occuring during the observations (if it did happen more than once at times), then you could use that information as well.

Line 171: is it the probability that she got injured that day or that she was seen with an injury that day? My question is, can we be sure the injury happened on that day? If so, it can be left but if not it may be best to rephrase for clarity.

Line 176: perhaps change mating success for mating probability (if this is what is meant) for clarity?

Line 176-177: for prediction 3, can it be controlled for the familiarity between the 2 individuals? (i.e. their probability/number of interactions). My question is: could the positive relationship between rate of agression and mating probability be solely due to the fact that these two individuals interact more (any "neutral" interaction rate would also be associated with mating probability)? If it could be a possibility, please state it in the discussion. If not, please clarify why not in the method section.Line 187: briefly say why using OSR instead of SR in this analysis.

Lines 191-193: again the offset may be problematic here, although in this case I understand why it may be more interesting to look at effects on the probability to mate than at the number of matings. Perhaps it is best to just use time as a fixed explanatory variable here? That sounds fine by me but otherwise one could build a more customized statistical model (I could think about it if you decide to go down this road, but I am not a statistican and there are for sure better qualified people to help!).

Line 193: this needs some clarification and if possible references. What would be the biases due to too short observations and why is 30 minutes a reasonable threshold to prevent such bias?

Line 211: I understand why you would expect such result if female choose to mate with aggressive males, but it could be that aggressive male mate more, irrespective of whether females can exerce any choice? I would replace "solely" by "potentially" but if I am misunderstanding you can just clarify.

Line 217: State here (instead of in the appendix) that "whenever a singular fit was observed, we reran the relevant model with the bglmer function of the blme package [7]". I'd actually recommend having the whole "Statistical Analysis" section of the appendix in the main text. Also briefly justify the use of the "optimizer" (control==glmerControl(optimizer="bobyqa")).

Line 226: were not "significantly/clearly" more targeted, or similar rewording (one should not accept the null hypothesis).

Line 239: avoid causal language (positively influence). It is very nicely avoided elsewhere in the result section.

Line 248: predict instead of predicted.

Line 250: if by "strongly" you refer to the statistical significance I would avoid it (as it should rather refer to effect size) and use "significantly", "clearly" or similar wording instead.

Line 255: it may be personal but perhaps avoid using the word "failed" here. Not finding statistically "significant" effects should not be perceived as a "failure".

Line 278: it is not shown that male agression "improves" male mating success. Either change "we showed" for e.g. "our analysis suggests" or change "improves" for a non-causal statement.

Line 289 and 297: again, perhaps don't use the word "failed".

Line 298: rephrase the causal statement.

Line 303 and 307: "on average" more often, or similar wording, as the difference between the two is not tested and the standard deviations provided suggest overlap of the estimates.

APPENDIX: I agree with the reviewer and that most if not all of the appendix can be in the main text. It is relatively short and there is no page limit for the preprint.

Line 26: how do you estimate error (if it is from ref. 1 cite it at the first sentence already) and what is "a few" days? Be specific.

Lines 33-36: again avoid using "a few" days and "several" says and rather provide a mean and/or a range of number of days for each statement.

Lines 103-104: in addition, what seems particularly interesting to show here (rather than p values) is how the effect of the rate of aggression towards the dyad female get affected by including the agression rate towards all groupmates. Could you show this estimate and confidence intervals before and after inclusion here?

I look forward to reading the revised version of this preprint.

Best wishes,

Matthieu

Reviewed by anonymous reviewer, 23 Mar 2022

In this manuscript, the authors test three predictions of the sexual coercion hypothesis in a natural population of Mandrills. They found support for the occurrence of sexual coercion in this population as (1) males were more likely to target sexually receptive females with aggression (both severe and not), (2) sexually receptive females were more likely to be injured and, (3) male aggression directed towards females before their swollen periods predicted the probability of copulation between those dyads. The authors also tested the alternative prediction that females are choosing to mate with the most aggressive males but found no support for this. Nor did the authors find support for the idea that males punish females for copulating with other males.

I thoroughly enjoyed reading this paper. It was well-written, and the data was well-analyzed and appropriate to address the question of sexual coercion. I think this is an important contribution to the literature on sexual coercion and additional strong evidence of this behavior in a cercopithecoid showing extensive sexual dimorphism and overall low rates of severe aggression by males to females.

One small point is that I was wondering if the authors have any data on paternity or conception rates. This data would solidify the argument that sexual coercion is an effective mating strategy for males that results in increased reproductive success. I don't think this data is necessary but perhaps a single line including reference to other studies that might have shown that alpha males sire the majority of offspring if that information is available.

A larger point is about how the paper is framed suggesting that mandrills are a species where sexual coercion and female choice are co-occurring. I find this problematic because I believe the data showing female choice in mandrills is weak. The cited study was done on a semi-free ranging population with only five males where they showed that females were more likely to approach males with more colorful faces. However, given the small sample size and the fact that the most colorful males were the highest ranking and therefore, likely, the most aggressive, I don't think the authors could rule out the role of sexual coercion. Even for the male that lost rank and didn't lose color, females were not more likely to mate with that male after he fell in status. The authors of this manuscript also cite personal observations that females will sometimes interrupt copulations as evidence of female choice. However, I think it's possible that this behavior is also the result of male coercion if, for example, a female interrupts a copulation with a male if another male who has a history of aggression.

This brings up a larger issue with the nature of these kinds of studies in general. Many studies of female choice in primates use the metric of approaches towards males as evidence of choice. However, if males have been aggressive towards females, especially in the way that is shown in this paper where males are directing aggression in periods preceding the sexual swelling period, then females may approach males not because of a preference but rather out of fear. The authors of this paper discuss that some species, like chimpanzees, show evidence of both female choice and sexual coercion, but this is actually a methodological difference between these studies. Some studies show evidence of females approaching particular males as evidence of female choice and other studies show that females copulate more often with males that are most aggressive towards them. Without data on aggression, the data on female approaches alone is insufficient to demonstrate female choice in any study. And in fact, it's hard to imagine given the size difference between males and females, that females would be able to exert choice at all. Given what I consider very weak evidence of female choice in this species, I would not frame this paper in this light.

Reviewed by Micaela Szykman Gunther, 21 Mar 2022

The authors presented an interesting study on sexual intimidation in a primate society. They carefully addressed several predictions of two contrasting hypotheses and presented data from several years of data collection to support the sexual intimidation hypothesis.

The Introduction set up the research question nicely and built on past research in related systems.

Regarding the Methods: It's clear that the data collection protocols were not explicitly set up to answer this question, and the 5-minute focal animal surveys were a bit brief to consider both aggression and mating success. Yet, they seemed to obtain adequate data to test their predictions, despite some low sample sizes.

I didn't feel that sufficient details were provided in the Methods to allow replication. Interestingly, many questions I had could be answered in the Supplementary Material. I would prefer that those details be put into the manuscript itself, as it doesn't seem that readers need to go to the supplementary material to find details that are required to understand the methods of the paper. Authors may review my notes in the attached pdf regarding which I details I thought should be included.

Regarding the results: there were some details on male rank (alpha vs not) and aggression/mating, but I was wondering about the proportion of aggression/matings with the alpha male. The alpha male seemed to dominate matings, as well as mate-guarding of females, and I wonder if that potentially confounded analyses of male rank. More clarity on this point would be useful.

The Discussion rounded out the paper well and supported the results.

Download the review