

Montpellier, April 21st 2022

Dear Dr Paquet,

We are grateful to you and the two reviewers for providing comments for our manuscript “Sexual coercion in a natural mandrill population”. We have modified our manuscript to adopt most of the suggestions and our responses are detailed in the text below (in red, following each comment). In the few cases where we did not follow a suggestion, we provide a detailed justification.

Please let us know if you require any further information and thank you again for your consideration.

Kind regards,
Nikolaos Smit



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?).

We have now corrected the legend. Indeed, in the columns starting with “harsh”, only severe aggression is taken into account.

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?

We have now changed the model, and this error should not appear anymore.

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

We have now corrected the typos.

2) Script 2ndPredictionStats.R

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

We have added the “.csv” in the name.

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)

We have now corrected all of these typos and have also carefully read the manuscript and scripts throughout to correct others.

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

We reran the models for predictions 1 and 3 including the time of observation as a fixed effect instead and we have adjusted the tables accordingly. The results remained similar, suggesting that our models are robust to different approaches used to control for variation in observation time.

MAIN TEXT:

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

We have included this information (L187).

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

A justification for the use of these fixed factors was added “We further controlled for the following fixed effects: female dominance rank (high-, medium- or low-ranking) to test if higher-ranking males are preferentially targeted by males, parity (nulliparous or parous) to test if parous females are preferentially targeted by males, SR to test if the number of males in relation to females in the group influences the probability of occurrence of male aggression...” (L191-195).

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 occurring during the observations (if it did happen more than once at times), then you could use that information as well.

Please see our answer to a similar comment above, regarding the inclusion of a fixed effect instead of an offset term. Changing the offset term into a fixed effect did not affect our results, suggesting that our model is robust to different approaches used to control for variation in observation time.

There were too few cases where more than one event of aggression was observed (from 734 cases where there was at least one aggression event observed, only 118 included at least two aggression events) to consider a Poisson distribution.

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.

We have rephrased to be clear that we refer to the probability that a female was observed with an injury for the first time that day "...the probability that a female got injured (observed injured for first time) on a given day..." (L204).

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

We have changed the sentence as suggested "We then tested whether males who were more aggressive also had a higher mating probability with their victim..." (L210-211).

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 aggression 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.

We agree that aggression and familiarity are likely to be associated, however, we do not expect aggression to be a simple, direct outcome of proximity. Particularly, we do not adopt the mechanistic view that variation in interaction rates and by extension in aggression rates is caused by variation in spatial proximity (i.e. where two individuals happening to be close together by chance would interact), given that a massive body of work in socio-ecology has contributed to show that animal groups are highly socially structured, meaning that the social surroundings of an individual are unlikely to be random, but instead reflect the existence of highly differentiated relationships between group members. In other words, spatial proximity is more likely to result from differential interaction rates than the reverse. In addition, we are working on a follow-up study that directly addresses this point by focusing on the links between the characteristics of dyadic intersexual relationships and male coercion. This study indeed indicates that females seem to be assaulted more by the males that share a social bond with them, which mirrors previous findings from baboons, chimpanzees, and humans. These elements have been added to the discussion (L364-374).

Line 187: briefly say why using OSR instead of SR in this analysis.

We have added this information "...OSR (since we focused only on swollen females for that prediction) ..." (L221).

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 statistician and there are for sure better qualified people to help!).

Please see our response to a similar comment above.

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?

Swollen periods are short in mandrills. Therefore, on the 801 identified heterosexual dyads, 138 of them were not observed during the swollen period of the female. In order to filter out low-sampled dyads, we calculated the median observation time of the 801 dyads and it was a bit higher than 30 minutes (1927 seconds). We tried different thresholds close to the median (25, 30 or 35 minutes) and our results remained similar. We considered that choosing a higher threshold, that would reduce the number of potential dyads under the half of the identified ones, would not allow us to fit our designed model including six fixed and three random effects. Finally, when we run our model without using any threshold for the time of observation, the results are similar.

We have changed the sentence as follows: “We restricted our analyses to those heterosexual dyads that were observed for at least 30 minutes of focal time during the female swollen period to avoid biases due to under-sampling that would prevent us from estimating reliably mating probability.” (L227-229).

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 exercise any choice? I would replace "solely" by "potentially" but if I am misunderstanding you can just clarify.

We have rephrased the sentence as suggested “...to test whether males with aggressive phenotypes have higher mating success than less aggressive males, potentially because aggression may act as a sexually selected trait and may be chosen by females.” (L260-262).

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")).

We have followed this comment: the whole section was placed in the main text and the use of the optimizer was justified “Whenever necessary we increased the number of iterations and/or we changed the optimizer of the model to achieve model convergence of the model and improve its fit.” (L270-271).

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

We have rephrased the sentence as suggested “By contrast, swollen females were not significantly more targeted by other groupmates...” (L285-286).

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

We have rephrased the sentence “We found support for sexual intimidation in mandrills: the rate of male aggression received by a female during the time window preceding her swollen period (...) was significantly and positively correlated to the probability of copulation of the dyad during that swollen period...” (L298-302).

Line 248: predict instead of predicted.

We have corrected this typo.

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.

We have rephrased the sentence as suggested "This indicates that immediate aggression (i.e. during the swollen period) did not clearly influence female mating pattern..." (311-312).

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".

We have now rephrased "Lastly, we did not find evidence for a female preference for aggressive male phenotypes..." (L332).

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

We have rephrased accordingly "Third, our analysis suggests that increased and repeated male aggression before the receptive period increases male mating success with the targeted female at times where she is most likely fertile." (L347-349).

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

We have rephrased as follows "...we did not find evidence supporting a female preference for particularly aggressive males." (L359-360).

Line 298: rephrase the causal statement.

We have rephrased the sentence: "...our results suggest that repeated aggression over extended periods increases mating probability to aggressors once females become fertile..." (L377-378).

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.

We rephrased as suggested "We found that male mandrills use severe aggression towards swollen females more often on average than chacma baboons (...). Yet, swollen female mandrills are injured ca. three times less on average than chacma baboons..." (L382-383 and L386-887)

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.

We have moved all the methods in the main text, except the tests for harassment, punishment and the "aggressive male phenotype" hypothesis.

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.

For the 25 individuals the exact date of birth was known and not estimated, we have now corrected the relevant lines "The exact date of birth was known for 25 individuals." (L151-152).

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.

Given the large variation of cycles' length across females, it was impossible to provide accurate figures.

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 aggression rate towards all groupmates. Could you show this estimate and confidence intervals before and after inclusion here?

We have added the requested information: "...but the rate of aggression towards the dyad female was marginally significant (Estimate=1.529, CI95%=[-0.039;3.097], Chisq=3.654, p-value=0.056) in comparison to the model without the overall aggression rate where the dyadic aggression rate was clearly significant (Table 3)." (L62-65 in the supplementary material).

Reviewed by anonymous reviewer, 23 Mar 2022 15:22

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.

Although this comment raises an interesting and relevant question to our study, a complete answer would go beyond the scope of this manuscript (studying the efficiency of sexual coercion as a male reproductive strategy). Indeed, there are studies from both captive and wild mandrills showing that alpha males sire a majority of offspring in their social group (L91-92).

We have now added one more analysis showing that alpha males are more aggressive than non-alpha males toward females during the mating season. Given the aforementioned skew in favor of alpha males, sexual coercion appears to be an effective mating strategy. We have also added a new paragraph in the discussion relevant to this question (L404-415).

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.

Although we felt a bit reluctant to dismiss or overlook previous findings on female mate choice in mandrills when drafting this manuscript, we generally agree with this comment regarding the weight of evidence for female mate choice in mandrills. We have therefore re-framed our study without highlighting female mate choice, as well as we added in the discussion a paragraph highlighting the points made by the referee (L425-436).

Reviewed by Micaela Szykman Gunther, 21 Mar 2022 16:45

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.

We agree that 5-min focal sampling may appear brief, however, this is clearly the best compromise that we found given 1. mandrill's close habitat (i.e. longer focals would automatically result in higher chances to lose the focal individual during a given observation period) and 2. the large number of individuals in our study group (~200-250).

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.

Please see our response to a similar comment above.

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 alpha male sires, indeed, a majority of offspring each year, both in captivity and in our study group, as emphasized in our introduction ("Male reproductive skew is high, since the alpha male monopolizes 60-70% of reproductions (Charpentier et al. 2020; Charpentier et al. 2005)" (L91-92)). In light of this comment, we have now added one model (L244-257) testing if alpha males are more aggressive than non-alpha males toward females during the mating season. Our results suggest that an alpha male is more aggressive towards adult females than a non-alpha male (L326-328). We have also added some relevant lines in the discussion (L404-415).

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

Below this point, we paste the comments of the second reviewer from the pdf file of the manuscript

Need scientific names accompanying?

We have added the scientific names "...intimidation was recently reported in chimpanzees (*Pan troglodytes*) and chacma baboons (*Papio ursinus*)..." (L25-26).

Males are still considered subadult at 9 years? Why include subadult males? Do they try to mate too? How did you age immigrant males?

Subadult males are those males that have fully reached their adult size but have not yet conspicuous red faces (Setchell & Dixson 2002). We have included these males because, first, some of them newly immigrate around this age in mandrills (males may immigrate earlier but due to their size, they are not

yet competitive) and second, they enter into the competitive, mating and reproductive arenas around this age (*Setchell et al 2005*). We have now added this information (L131-133).

We attribute male age according to body size, condition and patterns of tooth eruption and wear. For your information, males aged 9-10 yrs are very easily spotted because of clear morphological characteristics (e.g. full adult size but no conspicuous colors on their face).

You describe agonistic interactions but not sexual interactions. What sexual behaviors were recorded?

We have added this information (only mounts were considered) “The observers systematically recorded copulations of males with females (n=275).” (L134-135).

Will females fight violently, producing visible wounds, even occasionally? Either way, it would be worth mentioning.

We have added this information “We never observed violent female-female aggression resulting in an injury.” (L183-184). However, as mentioned in the manuscript: “Female relatives form tight social relationships (..), including aggressive coalitions against males that can, exceptionally, lead to male’s death...” (L97-99).

Only adult males? Not subadults? >9 years old? More details on age determination and inclusion of males needed above, as I highlighted already.

We have now rephrased to clarify that, indeed, in all our analyses, we have included subadult and adult males. See also our answer above to the previous relevant comment.

How was female dominance rank established? This should also be included in female section in Methods.

We have now included in the main text details from the supplementary material concerning the establishment of dominance ranks (L141-147).

You haven't stated above if your observations consistently observed most copulations. If you were potentially missing many copulations, that would affect your analysis here.

Because of the close environment where mandrills live, we probably miss copulation events, possibly affecting our results. However, we have controlled for the total focal observation time of the heterosexual dyads in our analyses.

We have now added this information “The observers systematically recorded copulations of males with females (n=275).” (L134-135).

How male dominance was established should also be included in the above section on males that I suggested including.

We have now included in the main text details from the supplementary material concerning the establishment of dominance ranks (L141-147)

Are resident and immigrant adult males treated the same by other males? By females? How is position in the male dominance hierarchy established (same as my previous question)?

Regarding the dominance rank, see the answers above.

In an earlier version of our model for the 3rd prediction (testing if male aggression increases mating success), we included male residency (resident vs immigrant) as a fixed factor. However, we removed that factor for the following reasons. First, it did not add any explanatory power to the model. Most importantly, our definition of residency considers which males are present in the group at the end of the previous birth season, versus which males arrive in the group during the current mating season. This definition, which is useful to capture which males are integrated in the current social dynamics and which males are not, nevertheless fails to capture male familiarity to the female members of the group. Indeed, mandrill males commonly enter and leave several times during their life (Brockmeyer et al 2015), meaning that some males that are considered as immigrants by our definition can be very familiar to groupmates. Measuring male familiarity is difficult because we can easily miss short stays by males who stay on the periphery of the group. Generally, we feel like the resident vs immigrant status is a complex issue in mandrill males, and beyond the scope of this manuscript. We are currently running follow-up studies where we plan to tackle this question more thoroughly than by just adding a fixed effect in one of the models presented here. We hope this choice is understandable.

Please state earlier in the methods the approximate date range of the mating season. Is this only once per year?

Indeed, the mating season occurs only once a year but lasts for several months. We clarified earlier in the methods “...mating season (Brockmeyer et al 2015); which generally lasts every year from April to September Dezeure et al 2022)...” (L90). The mating season is a gradual event starting with a few females cycling up to a certain number of cycling females that varies across years depending on e.g. environmental factors. Attributing specific dates to each mating season appears thus hazardous and is beyond the scope of this study.

I see a lot of reference to the supplementary materials. As I read them now, I think much of the background information there should be here in the main manuscript. Why refer to a supplemental text? I had to dig to find it. Perhaps just for the analyses that did not go as planned, as for the male aggression hypothesis.

We have moved all the requested information in the main text.

But females seem to be mating mostly with alpha males? Male rank influences likelihood of mating. Did alpha males also show more aggression towards females (prior to swelling)?

Our results indeed show that alpha males copulate significantly more with adult females in comparison to non-alpha males. Alpha male also sire the majority of offspring in the group each year, both in captivity and in our study population, as emphasized in our introduction (“Male reproductive skew is high, since the alpha male monopolizes 60-70% of reproductions (Charpentier et al. 2020; Charpentier et al. 2005)” (L91-92)). We have now added to our revised manuscript a model (L244-257) showing that alpha males are more aggressive than non-alpha males toward females during the mating season (L326-328) and we have also added some relevant lines in the discussion (L404-415).