

## The development of affiliative and coercive reproductive tactics in male chimpanzees

Rachna B. Reddy, Kevin E. Langergraber, Aaron A. Sandel, Linda Vigilant and John C. Mitani

### Article citation details

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### Review timeline

Original submission: 16 June 2020  
1st revised submission: 29 October 2020  
2nd revised submission: 2 December 2020  
Final acceptance: 3 December 2020

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

## Review History

### RSPB-2020-1428.R0 (Original submission)

#### Review form: Reviewer 1

##### Recommendation

Major revision is needed (please make suggestions in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Excellent

**General interest: Is the paper of sufficient general interest?**

Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**

Excellent

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

#### **Comments to the Author**

Review of RSPB-2020-1428, Reddy et al., "The development of affiliative and coercive reproductive tactics in male chimpanzees"

This is a very well written paper that describes a thorough study of the mating behavior of adolescent wild chimpanzees. The authors frame the study in a way that illustrates its potential appeal to a broad audience. I have very few specific comments (which is very rare), so I must commend the authors on all aspects of the presentation of this study.

However, there is one issue that I feel must be addressed before this study is published, and it is potentially a serious problem. Among chimpanzee researchers, it is well known that the 'unusually large' Ngogo chimpanzee community recently underwent a fission into two separate communities. For years before this occurred, the community had two distinct subgroups, or 'neighbourhoods'. As a result, members of one neighbourhood (particularly females) rarely saw members of the other. It is my understanding that the present study took place during the period right before the fission, and I wonder how much of the finding that rates of grooming and aggression predict paternity can be attributed to the fact that some male-female dyads rarely (if ever) saw each other, and therefore had few opportunities to groom, be aggressive, or mate. The effects of age and rank will not be affected by the subgrouping, however.

If I am correct (apologies if I'm not), then the authors must control for neighbourhood membership in the analyses.

#### **Specific comments**

Line 232 – Please address why you didn't not exclude maternal sisters. In Walker et al. 2017 (which you cite), of 65 offspring, only 1 was conceived by a maternal brother, and the authors conclude that this is because of inbreeding avoidance.

Line 248 – Muller et al. and Feldblum et al. both found that the timing of aggression within a female's cycle (e.g. cycling, not receptive; cycling, receptive) was important. They both concluded that aggression was a long-term strategy to coerce females to mate, rather than forced copulation. You included 'time spent in oestrous' as an explanatory variable, but it would be interesting to see a more nuanced treatment of the timing of male aggression toward females.

Line 356 – “two behavioral strategies”. I would like to see more discussion of alternative strategies that males might employ. There is a growing literature on the importance of male-male bonds in chimpanzees, and many have suggested that coalitions among males may enhance mating opportunities for lower-ranking males. For example, a recent paper from Gombe (Bray et al. 2016, in Proceedings B) showed that males that had a close relationship with the alpha male had higher mating success than expected for their rank. Might this also be happening at Ngogo? Not just friends of the alpha male, but maybe those who are friends with high ranking males? And what about coalitionary mate guarding, which has been described in this population? Things to mention in the discussion, if not in the analyses themselves.

## Review form: Reviewer 2

### Recommendation

Major revision is needed (please make suggestions in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Excellent

**General interest: Is the paper of sufficient general interest?**

Good

**Quality of the paper: Is the overall quality of the paper suitable?**

Marginal

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

Yes

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

Yes

**Is it clear?**

No

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

### Comments to the Author

This paper attempts to distinguish the effects of both aggression and affiliative behavior on the mating and reproductive success of adolescent male chimpanzees. This is a worthy goal, and the

Ngogo community contains a sufficiently large sample of adolescents to gain insight into their reproductive strategies. I don't think the paper can be published in its current form, due to problems with the behavioral methods, but these are fixable.

The authors use a relatively straightforward measure of aggression, but their measure of affiliation is a composite index that combines proximity and grooming. This method was borrowed from the baboon literature, but is questionable in the current context, where the authors are attempting to differentiate the effects of aggressive and affiliative behaviors. The problem is that chimpanzee males often maintain proximity to females in contexts such as mate guarding that are clearly agonistic. And males must necessarily be in proximity to females to be aggressive toward them. So proximity is not an unambiguous measure of a positive, affiliative relationship in the way that grooming is. Combining proximity and grooming into a single index makes it impossible to evaluate whether the effect on mating success is driven by both measures, by the measure that is clearly affiliative (grooming), or the measure that is ambiguous. It isn't clear why an index is necessary when there are only two variables, and the modeling approach adopted by the authors could easily consider them separately. I think this has to be done to convincingly show that affiliative behavior is having the effect that is claimed. (Separating these measures would also facilitate the interpretation of the model estimates, as it isn't really clear what a 1 unit increase in the CAI means.)

Relatedly, the discussion of the aggression finding is relatively straightforward, as it appears that males use aggression strategically as sexual coercion. The discussion of the affiliation finding is frustrating, however, because it focuses on "dyadic relationships" rather than individual strategies. From the data in the paper we cannot tell whether these relationships are (1) driven mostly by males maintaining proximity with and grooming females (in which case males might be pursuing an affiliative strategy), (2) driven mostly by females maintaining proximity with and grooming males (a very different mechanism), or (3) relatively equal contributions from both sexes. Is it not possible to calculate Hinde's Indices to show who is responsible for dyadic affiliation? Presumably the authors have data on who was grooming and who was being groomed in each dyad, which might shed light on male and female strategies.

Finally, in the analyses and the discussion the Ngogo chimpanzees are treated as a single community. However, recent presentations from Ngogo researchers described a clear fission into two separate communities that had at least started during this study period. I think the authors must address this issue in some way. Given that the social indices incorporate average measures across all dyads, it seems misleading to treat zeros from males and females who are potentially members of separate communities as equivalent to zeros from males and females who are in the same community. Zeros from members of different communities drive down the average measures across the community, potentially exaggerating the strength of dyadic bonds. There may be a good reason to treat all individuals in the study as members of the same community, but the rationale for this should be explained, along with any potential pitfalls.

Specific comments:

Line 87: It is misleading to say that marine iguanas "masturbate before mating to achieve speedy ejaculation." Rather, young males in this species keep matings brief by using ejaculate kept in readiness in their cloacal pouches. Wikelski et al. describe this as "functionally equivalent to masturbation," but the mechanism is distinct and internal (i.e. the iguanas are not stimulating their own genitals).

Lines 100-101: Here and in the abstract the authors focus on chimpanzee males' use of force to coerce unwilling females to mate or go on consortship. Much of the literature cited by the authors, however, suggests that this is not the primary mechanism of sexual coercion. Instead, most aggression is used to keep females from mating promiscuously. This has the effect of increasing a male's relative mating success, but by constraining female sexuality, not by overcoming a female's reluctance to mate. This dynamic may differ between adult and adolescent

males, but the two possibilities should be acknowledged.

Lines 161-173: How long were “focal observation sessions”? It is clear that these were not all-day focals, so can you provide a little more detail about how their length was determined and how they ended?

Line 186: Does “spatial proximity” mean within 5 meters? It sounds like it from the previous section, but this should be explicitly defined.

Line 307: Would read better as “were older than 20 years and rarely fathered offspring...”

Figure on Page 36: Why is the x-axis labeled at irregular intervals? And what is the line floating above age 22? The axis labels and other text are very small compared to the rest of the figure. On a journal page this will be unnecessarily difficult to read. Why not increase the font size?

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## Decision letter (RSPB-2020-1428.R0)

11-Aug-2020

Dear Dr Reddy:

I am writing to inform you that your manuscript RSPB-2020-1428 entitled "The development of affiliative and coercive reproductive tactics in male chimpanzees" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A ‘response to referees’ document including details of how you have responded to the comments, and the adjustments you have made.

- 2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
- 3) Line numbers in your main document.
- 4) Data - please see our policies on data sharing to ensure that you are complying (<https://royalsociety.org/journals/authors/author-guidelines/#data>).

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Sincerely,  
 Dr Robert Barton  
 mailto: [proceedingsb@royalsociety.org](mailto:proceedingsb@royalsociety.org)

Associate Editor

Comments to Author:

This well-written and interesting manuscript reports correlations between mating success of adolescent male chimpanzees and several traits, including male age and aggressive and affiliative behaviors. Both of the reviewers and I found the manuscript to be valuable and of broad appeal to the readership of Proceedings B. However, there are a few potentially serious problems with the analyses, which I summarize as follows. First, both reviewers note that this community of chimpanzees underwent a fissioning event after this study was conducted; the social division of the group into two "neighborhoods" before the split could have affected the affiliative social networks described here, and should be controlled for in analyses. Second, the measure of affiliation used here combines both grooming and proximity, which (as explained by reviewer 2) potentially confounds affiliation and aggression in ways that seem unnecessary, since they could be analyzed separately. Finally, I found the modeling approach to be somewhat arbitrary, and would recommend full model subsetting. Since these concerns have the potential to alter the conclusions of the paper, I would encourage the authors to revise the manuscript according to the reviewers' recommendations and resubmit it.

Minor comments:

67: please clarify; reproducing with "nulliparous" females seems contradictory

85-92: many examples of male alternative mating tactics occur in taxa where size predicts mating success and smaller males may follow an entirely different developmental trajectory (i.e. sneaking or female mimicry). Here it may be more relevant to focus on examples in which younger males adopt alternative mating tactics that are not fixed for the rest of their lifetimes, like the bushbuck example and others from mammals.

121: does this use of nulliparous mean that the offspring of these matings (i.e. sired by adolescent males with previously non-reproductive females) do not survive? How can a female be nulliparous if she reproduces?

134: more information on this population, including when the study was conducted relative to when fission occurred, would be useful here

191-195: see comment by reviewer 2. It seems relatively simple to separate measures of grooming and proximity.

248-282: the sets of variables included in candidate models seems arbitrary. Why not use full model subsetting to evaluate parameters? Some of the predictors also seem potentially correlated.

372: this paragraph seems to contradict itself by stating that aggression is not effective for young males who are "not yet physically mature and are unlikely to dominate females," then stating that aggression increases mating success for young males who direct aggression towards females that they can dominate. Clarify.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

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However, there is one issue that I feel must be addressed before this study is published, and it is potentially a serious problem. Among chimpanzee researchers, it is well known that the 'unusually large' Ngogo chimpanzee community recently underwent a fission into two separate communities. For years before this occurred, the community had two distinct subgroups, or 'neighbourhoods'. As a result, members of one neighbourhood (particularly females) rarely saw members of the other. It is my understanding that the present study took place during the period right before the fission, and I wonder how much of the finding that rates of grooming and aggression predict paternity can be attributed to the fact that some male-female dyads rarely (if ever) saw each other, and therefore had few opportunities to groom, be aggressive, or mate. The effects of age and rank will not be affected by the subgrouping, however.

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Referee: 2

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## Author's Response to Decision Letter for (RSPB-2020-1428.R0)

See Appendix A.

## RSPB-2020-2679.R0

### Review form: Reviewer 1

#### **Recommendation**

Accept as is

#### **Scientific importance: Is the manuscript an original and important contribution to its field?**

Excellent

#### **General interest: Is the paper of sufficient general interest?**

Excellent

#### **Quality of the paper: Is the overall quality of the paper suitable?**

Excellent

#### **Is the length of the paper justified?**

Yes

#### **Should the paper be seen by a specialist statistical reviewer?**

No

#### **Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

**Comments to the Author**

Thank you for your careful consideration of our comments. I am entirely satisfied with the revision. Well done!

## Review form: Reviewer 2

**Recommendation**

Accept with minor revision (please list in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Good

**General interest: Is the paper of sufficient general interest?**

Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**

Good

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

**Comments to the Author**

The authors have done a thorough job in addressing reviewer comments, and this revision is an improvement on the initial submission. The methods are clearer, as we have more detail about the community split, and the analyses are more convincing, as grooming is now a separate predictor, rather than part of a composite index. I do wonder why proximity data were removed entirely, when they could have been included in the models as an independent predictor. It is informative if males are in similar proximity with some females, yet show higher levels of grooming or aggression with a subset of these.

I have a few minor suggestions that I think would improve the paper further:

Line 141: The authors note that adolescent males “cannot compete effectively with larger, stronger adult males or serve as effective coalitionary partners.” There is no citation here, but Enigk et al. (2020) (*Anim. Behav.*) recently showed this for coalitions.

Line 195: “During focal following sessions, we recorded all chimpanzees who were observed together with the focal male during the hour-long focal following episodes. These individuals were defined to be in association, or in the same subgroup with focal subjects.” Can you be more specific about how subgroups were defined? Who was considered to be “in association”?

Line 220: 9 out of 4744 is 0.19%, not 0.001%.

Line 418: “Anecdotally, when female chimpanzees received aggression from an adult male who did not have a strong affiliative bond with them, they often just screamed and ran away. Females receiving similar aggression from a male with whom she shared a strong affiliative relationship, however, react in an entirely different way. When attacked, these females remain in place, lunge toward their male partners while clutching their arms, rocking back and forth, and screaming repeatedly until making choking sounds.” The discussion suggests that affiliative bonds are responsible for this anecdotal observation, but aren’t these males also the ones who were generally directing more aggression toward the females? It seems just as likely that a female is less disturbed by receiving aggression from a male who is rarely aggressive toward her because she expects that he will not be as violent or as persistent in his aggression.

The figures are much clearer, but in Figure 1 can you use different symbols for first time and multiparous mothers so that if the figure is printed without color the points can be distinguished?

**Decision letter (RSPB-2020-2679.R0)**

25-Nov-2020

Dear Dr Reddy

I am pleased to inform you that your manuscript RSPB-2020-2679 entitled "The development of affiliative and coercive reproductive tactics in male chimpanzees" has been accepted for publication in *Proceedings B*.

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into <https://mc.manuscriptcentral.com/prsb> and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

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- 2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.
- 3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

- 4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

- 5) Data accessibility section and data citation

It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository (<https://royalsociety.org/journals/authors/author-guidelines/#data>).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:

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- Final DNA sequence assembly uploaded as online supplemental material
- Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311

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If you wish to submit your data to Dryad (<http://datadryad.org/>) and have not already done so you can submit your data via this link

[http://datadryad.org/submit?journalID=RSPB&manu=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document not available)) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link. Please see <https://royalsociety.org/journals/ethics-policies/data-sharing-mining/> for more details.

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Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,

Dr Robert Barton

mailto:proceedingsb@royalsociety.org

Associate Editor

Board Member

Comments to Author:

The authors have nicely revised their paper to address all of the concerns raised in the previous reviews. I appreciate the clarifications that have been made throughout, and agree with the authors that their modeling approach is sound. One reviewer recommends some final (minor) changes; if the authors are able to address these, we will be happy to accept the paper for publication.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).

Thank you for your careful consideration of our comments. I am entirely satisfied with the revision. Well done!

Referee: 2

Comments to the Author(s).

The authors have done a thorough job in addressing reviewer comments, and this revision is an improvement on the initial submission. The methods are clearer, as we have more detail about the community split, and the analyses are more convincing, as grooming is now a separate predictor, rather than part of a composite index. I do wonder why proximity data were removed entirely, when they could have been included in the models as an independent predictor. It is informative if males are in similar proximity with some females, yet show higher levels of grooming or aggression with a subset of these.

I have a few minor suggestions that I think would improve the paper further:

Line 141: The authors note that adolescent males “cannot compete effectively with larger, stronger adult males or serve as effective coalitionary partners.” There is no citation here, but Enigk et al. (2020) (*Anim. Behav.*) recently showed this for coalitions.

Line 195: “During focal following sessions, we recorded all chimpanzees who were observed together with the focal male during the hour-long focal following episodes. These individuals were defined to be in association, or in the same subgroup with focal subjects.” Can you be more specific about how subgroups were defined? Who was considered to be “in association”?

Line 220: 9 out of 4744 is 0.19%, not 0.001%.

Line 418: “Anecdotally, when female chimpanzees received aggression from an adult male who did not have a strong affiliative bond with them, they often just screamed and ran away. Females receiving similar aggression from a male with whom she shared a strong affiliative relationship, however, react in an entirely different way. When attacked, these females remain in place, lunge toward their male partners while clutching their arms, rocking back and forth, and screaming repeatedly until making choking sounds.” The discussion suggests that affiliative bonds are responsible for this anecdotal observation, but aren’t these males also the ones who were generally directing more aggression toward the females? It seems just as likely that a female is less disturbed by receiving aggression from a male who is rarely aggressive toward her because she expects that he will not be as violent or as persistent in his aggression.

The figures are much clearer, but in Figure 1 can you use different symbols for first time and multiparous mothers so that if the figure is printed without color the points can be distinguished?

## Author's Response to Decision Letter for (RSPB-2020-2679.R0)

See Appendix B.

## Decision letter (RSPB-2020-2679.R1)

03-Dec-2020

Dear Dr Reddy

I am pleased to inform you that your manuscript entitled "The development of affiliative and coercive reproductive tactics in male chimpanzees" has been accepted for publication in *Proceedings B*.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact [procb\\_proofs@royalsociety.org](mailto:procb_proofs@royalsociety.org)

Your article has been estimated as being 10 pages long. Our Production Office will be able to confirm the exact length at proof stage.

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Proceedings B

mailto:proceedingsb@royalsociety.org

# Appendix A

## *Responses to Reviewer & Editor Comments*

Associate Editor

Comments to Author:

This well-written and interesting manuscript reports correlations between mating success of adolescent male chimpanzees and several traits, including male age and aggressive and affiliative behaviors. Both of the reviewers and I found the manuscript to be valuable and of broad appeal to the readership of Proceedings B. However, there are a few potentially serious problems with the analyses, which I summarize as follows. First, both reviewers note that this community of chimpanzees underwent a fissioning event after this study was conducted; the social division of the group into two "neighborhoods" before the split could have affected the affiliative social networks described here, and should be controlled for in analyses. Second, the measure of affiliation used here combines both grooming and proximity, which (as explained by reviewer 2) potentially confounds affiliation and aggression in ways that seem unnecessary, since they could be analyzed separately. Finally, I found the modeling approach to be somewhat arbitrary, and would recommend full model subsetting. Since these concerns have the potential to alter the conclusions of the paper, I would encourage the authors to revise the manuscript according to the reviewers' recommendations and resubmit it.

***As noted in the cover letter, we have addressed all three of these concerns.***

***First, we indicate that the Ngogo chimpanzee community fissioned after the end of this study in 2018. Chimpanzees in the two new groups therefore continued to interact with each other during the observations made here. To account for the possible effect of the fissioning process, we control for association in all of the candidate models we consider (Lines 179-187; 280-282).***

***Second, we revised our mating success analysis and use grooming time to assay affiliative bonds following Reviewer 2's suggestion. Results derived from the new analyses do not differ from those reported before (Lines 284-290; 371-393).***

***Third, we explain how we constructed our candidate models in the model comparison analysis. We have revised our methods section and provided a detailed description and justification for the inclusion each candidate model in the Supplementary Online Materials (Lines 268-301, SOM Candidate Model Description). Instead of adopting an all-model subset approach, we constructed a constrained number of models based on an a priori understanding of male chimpanzee behavior and the factors that are likely to affect their mating success. Using this knowledge, we constructed our candidate models by carefully considering these factors and how they could potentially interact.***

Minor comments:

67: please clarify; reproducing with "nulliparous" females seems contradictory

***In the revision, we note that adolescent males mate with nulliparous females and reproduce with first-time mothers (Lines 73-74).***

85-92: many examples of male alternative mating tactics occur in taxa where size predicts mating success and smaller males may follow an entirely different developmental trajectory (i.e. sneaking or female mimicry). Here it may be more relevant to focus on examples in which younger males adopt alternative mating tactics that are not fixed for the rest of their lifetimes, like the bushbuck example and others from mammals.

***We have deleted these examples from species where males using different strategies may have permanent fixed phenotypes. We provide an additional mammalian example instead of Sika deer who may sneak copulations while young and/or subordinate (Lines 95-97).***

121: does this use of nulliparous mean that the offspring of these matings (i.e. sired by adolescent males with previously non-reproductive females) do not survive? How can a female be nulliparous if she reproduces?

***As we have noted above, in the revised manuscript we refer to females who were nulliparous while males mated with them. These females became first-time mothers after giving birth. We have corrected this phrasing throughout the manuscript (Lines 73-74, 136, 137, 157-158, 250, 322, 324, 334, 400, 407)***

134: more information on this population, including when the study was conducted relative to when fission occurred, would be useful here

***We have provided additional details on the timing of the community fission and how subgrouping that preceded it may have affected mating. We also include how we controlled for the potential effect of the fissioning process by including association time in all of the appropriate models (Lines 179-187; 280-282).***

191-195: see comment by reviewer 2. It seems relatively simple to separate measures of grooming and proximity.

***In the revised manuscript we use grooming time instead of the affiliation index to assay affiliative bonds between males and females (Lines 284-290; 371-393).***

248-282: the sets of variables included in candidate models seems arbitrary. Why not use full model subsetting to evaluate parameters? Some of the predictors also seem potentially correlated.

***As noted in our cover letter and above, the construction of the candidate models was in fact not arbitrary. Instead these models were carefully crafted by combining factors that we have hypothesized will influence male mating success.***

***In the revision, we have provided a detailed explanation for how each model was constructed. We have also verified that the predictors were not correlated (Lines 268-301, 314-315, SOM Candidate Model Description).***

372: this paragraph seems to contradict itself by stating that aggression is not effective for young males who are "not yet physically mature and are unlikely to dominate females," then stating that aggression increases mating success for young males who direct aggression towards females that they can dominate. Clarify.

***We have clarified that the comparison we make is between young, adolescent males and young adult males (Lines 416-420)***

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

Review of RSPB-2020-1428, Reddy et al., "The development of affiliative and coercive reproductive tactics in male chimpanzees"

This is a very well written paper that describes a thorough study of the mating behavior of adolescent wild chimpanzees. The authors frame the study in a way that illustrates its potential appeal to a broad audience. I have very few specific comments (which is very rare), so I must commend the authors on all aspects of the presentation of this study.

However, there is one issue that I feel must be addressed before this study is published, and it is potentially a serious problem. Among chimpanzee researchers, it is well known that the 'unusually large' Ngogo chimpanzee community recently underwent a fission into two separate communities. For years before this occurred, the community had two distinct subgroups, or 'neighbourhoods'. As a result, members of one neighbourhood (particularly females) rarely saw members of the other. It is my understanding that the present study took place during the period right before the fission, and I wonder how much of the finding that rates of grooming and aggression predict paternity can be attributed to the fact that some male-female dyads rarely (if ever) saw each other, and therefore had few opportunities to groom, be aggressive, or mate. The effects of age and rank will not be affected by the subgrouping, however.

If I am correct (apologies if I'm not), then the authors must control for neighbourhood membership in the analyses.

***We have addressed this issue above in our cover letter and in a comment to the Associate Editor above.***

Specific comments

Line 232 – Please address why you didn't not exclude maternal sisters. In Walker et al. 2017 (which you cite), of 65 offspring, only 1 was conceived by a maternal brother, and

the authors conclude that this is because of inbreeding avoidance.

***Thank you for catching this. We in fact excluded maternal sisters, but failed to note this in the original submission. We now note this in the revision (Line 204).***

Line 248 – Muller et al. and Feldblum et al. both found that the timing of aggression within a female's cycle (e.g. cycling, not receptive; cycling, receptive) was important. They both concluded that aggression was a long-term strategy to coerce females to mate, rather than forced copulation. You included 'time spent in oestrous' as an explanatory variable, but it would be interesting to see a more nuanced treatment of the timing of male aggression toward females.

***In previous research that serves as a basis for this paper, we showed that males direct aggression to females when females were cycling and when they were pregnant and lactating (Reddy & Mitani 2020). We now note this in our revised Introduction (Lines 143-148). The relatively short duration of our study, however, limits us from conducting an analysis using females in different reproductive states as done, for example, by Feldblum and colleagues (2014). We now address this limitation and highlight it as an avenue for further study in the revised Discussion (Lines 473-481).***

Line 356 – “two behavioral strategies”. I would like to see more discussion of alternative strategies that males might employ. There is a growing literature on the importance of male-male bonds in chimpanzees, and many have suggested that coalitions among males may enhance mating opportunities for lower-ranking males. For example, a recent paper from Gombe (Bray et al. 2016, in Proceedings B) showed that males that had a close relationship with the alpha male had higher mating success than expected for their rank. Might this also be happening at Ngogo? Not just friends of the alpha male, but maybe those who are friends with high ranking males? And what about coalitionary mate guarding, which has been described in this population? Things to mention in the discussion, if not in the analyses themselves.

***We now note that our findings suggest that “at least two” mating tactics appear to be successful for adolescent male chimpanzees (Lines 397-398). In addition, we indicate the importance of male coalitions in reducing male-male competition in the Introduction (Lines 108-111), citing both Watts 1998 and Bray and colleagues 2016. We point out, though, that adolescent and young adult males are likely to be precluded from forming coalitions often, as they retain “outsider” status (Kawanaka 1993) (Line 122).***

Referee: 2

Comments to the Author(s)

This paper attempts to distinguish the effects of both aggression and affiliative behavior on the mating and reproductive success of adolescent male chimpanzees. This is a

worthy goal, and the Ngogo community contains a sufficiently large sample of adolescents to gain insight into their reproductive strategies. I don't think the paper can be published in its current form, due to problems with the behavioral methods, but these are fixable.

The authors use a relatively straightforward measure of aggression, but their measure of affiliation is a composite index that combines proximity and grooming. This method was borrowed from the baboon literature, but is questionable in the current context, where the authors are attempting to differentiate the effects of aggressive and affiliative behaviors. The problem is that chimpanzee males often maintain proximity to females in contexts such as mate guarding that are clearly agonistic. And males must necessarily be in proximity to females to be aggressive toward them. So proximity is not an unambiguous measure of a positive, affiliative relationship in the way that grooming is. Combining proximity and grooming into a single index makes it impossible to evaluate whether the effect on mating success is driven by both measures, by the measure that is clearly affiliative (grooming), or the measure that is ambiguous. It isn't clear why an index is necessary when there are only two variables, and the modeling approach adopted by the authors could easily consider them separately. I think this has to be done to convincingly show that affiliative behavior is having the effect that is claimed. (Separating these measures would also facilitate the interpretation of the model estimates, as it isn't really clear what a 1 unit increase in the CAI means.)

***As noted above, we have substituted grooming time to assess affiliative bonds as suggested by this reviewer.***

Relatedly, the discussion of the aggression finding is relatively straightforward, as it appears that males use aggression strategically as sexual coercion. The discussion of the affiliation finding is frustrating, however, because it focuses on "dyadic relationships" rather than individual strategies. From the data in the paper we cannot tell whether these relationships are (1) driven mostly by males maintaining proximity with and grooming females (in which case males might be pursuing an affiliative strategy), (2) driven mostly by females maintaining proximity with and grooming males (a very different mechanism), or (3) relatively equal contributions from both sexes. Is it not possible to calculate Hinde's Indices to show who is responsible for dyadic affiliation? Presumably the authors have data on who was grooming and who was being groomed in each dyad, which might shed light on male and female strategies.

***Our consideration of this affiliative behavior as indicative of a bond was based on prior analyses of behavior between these same pairs (Reddy & Mitani 2020). In this paper, we showed that bond strength is associated with increased equability in grooming between males and females. Thus, both individuals appear to invest in these relationships. We now allude to this and other observations that we used to assess whether affiliative behavior between males and females reflect dyadic bonds in the revised Introduction. (Lines 143-148).***

Finally, in the analyses and the discussion the Ngogo chimpanzees are treated as a

single community. However, recent presentations from Ngogo researchers described a clear fission into two separate communities that had at least started during this study period. I think the authors must address this issue in some way. Given that the social indices incorporate average measures across all dyads, it seems misleading to treat zeros from males and females who are potentially members of separate communities as equivalent to zeros from males and females who are in the same community. Zeros from members of different communities drive down the average measures across the community, potentially exaggerating the strength of dyadic bonds. There may be a good reason to treat all individuals in the study as members of the same community, but the rationale for this should be explained, along with any potential pitfalls.

***We have addressed this issue above.***

Specific comments:

Line 87: It is misleading to say that marine iguanas “masturbate before mating to achieve speedy ejaculation.” Rather, young males in this species keep matings brief by using ejaculate kept in readiness in their cloacal pouches. Wikelski et al. describe this as “functionally equivalent to masturbation,” but the mechanism is distinct and internal (i.e. the iguanas are not stimulating their own genitals).

***We have deleted this sentence (Line 95-97).***

Lines 100-101: Here and in the abstract the authors focus on chimpanzee males’ use of force to coerce unwilling females to mate or go on consortship. Much of the literature cited by the authors, however, suggests that this is not the primary mechanism of sexual coercion. Instead, most aggression is used to keep females from mating promiscuously. This has the effect of increasing a male’s relative mating success, but by constraining female sexuality, not by overcoming a female’s reluctance to mate. This dynamic may differ between adult and adolescent males, but the two possibilities should be acknowledged.

***We indicate that males sexually coerce females to mate with them and NOT with others (Lines 112-113). We also emphasize in the discussion, as we did in our original submission, that a major limitation of our study is our inability to address this aspect of sexual coercion, and that future studies will need to examine its effect on paternity success (Original MS, Lines 446-464; Revision, Lines 457-473).***

Lines 161-173: How long were “focal observation sessions”? It is clear that these were not all-day focals, so can you provide a little more detail about how their length was determined and how they ended?

***We added additional information to clarify the length of focal observation sessions. (Lines 198-201).***

Line 186: Does “spatial proximity” mean within 5 meters? It sounds like it from the previous section, but this should be explicitly defined.

***We have deleted this section as we now use grooming as a measure of affiliative bonds.***

Line 307: Would read better as “were older than 20 years and rarely fathered offspring...”

***We have made this correction. (Lines 330-332)***

Figure on Page 36: Why is the x-axis labeled at irregular intervals? And what is the line floating above age 22? The axis labels and other text are very small compared to the rest of the figure. On a journal page this will be unnecessarily difficult to read. Why not increase the font size?

***We have revised this figure so that axes are labeled at regular intervals. We had initially added tick marks between ages 10 and 20 to highlight the distinction between adolescent and young adult male (16-20y) siring patterns, but realize this was confusing. See Revised Figure 1.***

Figure on Page 39: This figure is confusing because it isn't immediately clear what the floating labels “strong affiliative bond” and “no affiliative bond” refer to. And it isn't immediately clear whether the blue and yellow dots for adolescent male and young adult male are just there for the color, and refer to both sets of lines, or just indicate the dotted lines (since the legend uses dots). (Why are some lines dotted and some solid?) If the figure is printed in black and white, it is difficult to tell what the legend refers to. All of this can be interpreted with some effort and concentration by the reader, but why not make it easy? Adolescents could be dashed lines and adults solid lines for both types of bonds, which would clarify the legend, if it also used dashed and solid lines. The two sets of lines should be clearly labeled by bond type (by drawing an arrow from the label to the lines, or some other device).

***We have revised this figure so that there are four panels instead of two and that it does not rely on colors to differentiate both affiliative bond strength and male age in a single graph. See Revised Figure 4.***

## **Appendix B**

### *Responses to Reviewer Comments*

***Thank you for your careful and thoughtful feedback on our paper. We have addressed the comments of Reviewer 2 in our revision. We indicate how we have changed the manuscript below. We indicate changes in the marked version of the manuscript itself by highlighting them in yellow.***

Associate Editor

Board Member

Comments to Author:

The authors have nicely revised their paper to address all of the concerns raised in the previous reviews. I appreciate the clarifications that have been made throughout, and agree with the authors that their modeling approach is sound. One reviewer recommends some final (minor) changes; if the authors are able to address these, we will be happy to accept the paper for publication.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).

Thank you for your careful consideration of our comments. I am entirely satisfied with the revision. Well done!

Referee: 2

Comments to the Author(s).

The authors have done a thorough job in addressing reviewer comments, and this revision is an improvement on the initial submission. The methods are clearer, as we have more detail about the community split, and the analyses are more convincing, as grooming is now a separate predictor, rather than part of a composite index. I do wonder why proximity data were removed entirely, when they could have been included in the models as an independent predictor. It is informative if males are in similar proximity with some females, yet show higher levels of grooming or aggression with a subset of these.

***As described in our previous revision and here, our goal was to investigate whether affiliative bonds between males and females impact mating success. Grooming frequency reflects these bonds. In contrast proximity alone, as Reviewer 2 pointed out in our initial submission, may reflect mate-guarding behavior by males in addition to affiliation. To remove ambiguity, we have chosen to delete proximity from our analyses, as its inclusion would complicate interpretation of the results (Reddy & Mitani 2020; Revision 2, Lines 285-290).***

I have a few minor suggestions that I think would improve the paper further:

Line 141: The authors note that adolescent males “cannot compete effectively with larger, stronger adult males or serve as effective coalitionary partners.” There is no citation here, but Enigk et al. (2020) (Anim. Behav.) recently showed this for coalitions.

***We have added this citation (Revision 2, Lines 121, 577-581).***

Line 195: “During focal following sessions, we recorded all chimpanzees who were observed together with the focal male during the hour-long focal following episodes. These individuals were defined to be in association, or in the same subgroup with focal subjects.” Can you be more specific about how subgroups were defined? Who was considered to be “in association”?

***We have specified that individuals within “visual range” were considered to be in association (Revision 2, Lines 209-210).***

Line 220: 9 out of 4744 is 0.19%, not 0.001%.

***Thank you for catching this. We have made this correction (Revision 2, Line 237).***

Line 418: “Anecdotally, when female chimpanzees received aggression from an adult male who did not have a strong affiliative bond with them, they often just screamed and ran away. Females receiving similar aggression from a male with whom she shared a strong affiliative relationship, however, react in an entirely different way. When attacked, these females remain in place, lunge toward their male partners while clutching their arms, rocking back and forth, and screaming repeatedly until making choking sounds.” The discussion suggests that affiliative bonds are responsible for this anecdotal observation, but aren't these males also the ones who were generally directing more aggression toward the females? It seems just as likely that a female is less disturbed by receiving aggression from a male who is rarely aggressive toward her because she expects that he will not be as violent or as persistent in his aggression.

***We have clarified that our framing of these anecdotes reflects one of many possible interpretations (Revision 2, Lines 439-440). We appreciate Reviewer 2's insight which will inform our future research on the dynamics of specific aggressive events.***

The figures are much clearer, but in Figure 1 can you use different symbols for first time and multiparous mothers so that if the figure is printed without color the points can be distinguished?

***We have revised this figure so that first-time mothers are designated by squares and multiparous mothers by circles (Revision 2, Figure 1, Line 489).***