THE ROYAL SOCIETY PUBLISHING

PROCEEDINGS B

Substrate use drives the macroevolution of mammalian tail morphological diversity

Sarah T. Mincer and Gabrielle A. Russo

Article citation details Proc. R. Soc. B 287: 20192885. http://dx.doi.org/10.1098/rspb.2019.2885

Review timeline

Original submission: 1st revised submission: 2nd revised submission: 16 January 2020 Final acceptance:

1 October 2019 10 December 2019 17 January 2020

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

Review History

RSPB-2019-2301.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? Good

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

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

Is the length of the paper justified? Yes

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

Reports © 2020 The Reviewers; Decision Letters © 2020 The Reviewers and Editors; Responses © 2020 The Reviewers, Editors and Authors. Published by the Royal Society under the terms of the Creative Commons Attribution License http://creativecommons.org/licenses/by/4.0/, which permits unrestricted use, provided the original author and source are credited

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? No

Do you have any ethical concerns with this paper? No

Comments to the Author

The tail length variation in mammals have been noticed and well studied before, and previous studies showed various ecological and behavioral factors influencing the significant length evolution in different mammalian clades. However, there hasn't been an understanding on the tail length diversity at a large phylogenetic scale. For this reason, this manuscript 'Substrate use drivers the macroevolution of mammalian tail morphological diversity' by Mincer and Russo presented an updated investigation on how the tail diversity evolved among and within different mammalian clades and could provide a holistic view on this aspect. This is an interesting paper which used phylogenetic comparative methods to address mechanisms underlying the evolution of tails in mammals. However, I have some major and minor concerns which I hope they address before this manuscript can be accepted for publication by Proceedings B:

My major concerns comes from that the authors employed RTL (relative tail length) only in the examination of the effect of climate on TL while other analyses used TL (tail length) in stead. Although the author mentioned in line 72-73 of page 2 that RTL is an appropriate measure for quantifying tail length, they also thought that RTL was unable to provide an explicit look at how TL scales to BL or BM. I do not think they have provide rationale for their treatment. Now that the RTL is an appropriate measure for quantifying tail length, it should be included in the analysis and see whether they are better or worse than TL in analyses. At least they should provide references which made such conclusion.

Other minor concerns:

1) Page 1, line 5-6, considering the important function and adaptive significance of mammalian tails, I do not think they are really phylogenetically informative.

2)Page 2, line 49 and line 57 both mentioned they used species with genomic data. I do not see the genomic data have been employed in the subsequent analyses. Could the authors please provide further information on how they use the genomic data for their analyses?

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? 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. 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? Yes Is it adequate? Yes

Do you have any ethical concerns with this paper? No

Comments to the Author

Review of RSPB-2019-2301

Thank you for the opportunity to review the manuscript, "Substrate use drives the macroevolution of mammalian tail morphological diversity" by Mincer and Russo. In this manuscript, the authors' goals for this study were to 1) test the hypothesis that ecological and behavioral variables influence tail morphology within and across mammalian orders, 2) explore patters of interaction between morphological, behavioral, and ecological variables, and 3) document tail length diversity in specific mammalian lineages. The authors were successful in reaching each of these goals using a large sample of 1200+ mammalian species sampled in proportion to their occurrence in nature across a diverse range of mammalian families and orders, and by utilizing sophisticated phylogenetic comparative methods. In sum, the authors have presented a well-reasoned, adequately tested, and succinctly written summary of their findings: that morphological diversity in mammalian tail length is driven by substrate use.

My only concern about this manuscript relates to the scaling analysis. The authors use phylogenetic generalized least squares to evaluate allometric scaling of tail length to body length and body mass. But all of these variables have error terms associated with them, and unless r-values are above 0.9 (and they are not reported here in the S1 table), it might be appropriate to re-evaluate the allometric scaling with reduced major axis (model II) regression instead of pGLS. An

RMA approach will not control for phylogenetic contrasts, but it will provide a suitable second test of the allometric analysis that I think is warranted here to verify results.

Decision letter (RSPB-2019-2301.R0)

11-Nov-2019

Dear Miss Mincer:

I am writing to inform you that your manuscript RSPB-2019-2301 entitled "Substrate use drives the macroevolution of mammalian tail morphological diversity" 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 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.

To upload a resubmitted manuscript, log into http://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 Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely, Professor Hans Heesterbeek mailto: proceedingsb@royalsociety.org

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

The tail length variation in mammals have been noticed and well studied before, and previous studies showed various ecological and behavioral factors influencing the significant length evolution in different mammalian clades. However, there hasn't been an understanding on the

tail length diversity at a large phylogenetic scale. For this reason, this manuscript 'Substrate use drivers the macroevolution of mammalian tail morphological diversity' by Mincer and Russo presented an updated investigation on how the tail diversity evolved among and within different mammalian clades and could provide a holistic view on this aspect. This is an interesting paper which used phylogenetic comparative methods to address mechanisms underlying the evolution of tails in mammals. However, I have some major and minor concerns which I hope they address before this manuscript can be accepted for publication by Proceedings B:

My major concerns comes from that the authors employed RTL (relative tail length) only in the examination of the effect of climate on TL while other analyses used TL (tail length) in stead. Although the author mentioned in line 72-73 of page 2 that RTL is an appropriate measure for quantifying tail length, they also thought that RTL was unable to provide an explicit look at how TL scales to BL or BM. I do not think they have provide rationale for their treatment. Now that the RTL is an appropriate measure for quantifying tail length, it should be included in the analysis and see whether they are better or worse than TL in analyses. At least they should provide references which made such conclusion.

Other minor concerns:

1) Page 1, line 5-6, considering the important function and adaptive significance of mammalian tails, I do not think they are really phylogenetically informative.

2)Page 2, line 49 and line 57 both mentioned they used species with genomic data. I do not see the genomic data have been employed in the subsequent analyses. Could the authors please provide further information on how they use the genomic data for their analyses?

Referee: 2

Comments to the Author(s) Review of RSPB-2019-2301

Thank you for the opportunity to review the manuscript, "Substrate use drives the macroevolution of mammalian tail morphological diversity" by Mincer and Russo. In this manuscript, the authors' goals for this study were to 1) test the hypothesis that ecological and behavioral variables influence tail morphology within and across mammalian orders, 2) explore patters of interaction between morphological, behavioral, and ecological variables, and 3) document tail length diversity in specific mammalian lineages. The authors were successful in reaching each of these goals using a large sample of 1200+ mammalian species sampled in proportion to their occurrence in nature across a diverse range of mammalian families and orders, and by utilizing sophisticated phylogenetic comparative methods. In sum, the authors have presented a well-reasoned, adequately tested, and succinctly written summary of their findings: that morphological diversity in mammalian tail length is driven by substrate use.

My only concern about this manuscript relates to the scaling analysis. The authors use phylogenetic generalized least squares to evaluate allometric scaling of tail length to body length and body mass. But all of these variables have error terms associated with them, and unless rvalues are above 0.9 (and they are not reported here in the S1 table), it might be appropriate to reevaluate the allometric scaling with reduced major axis (model II) regression instead of pGLS. An RMA approach will not control for phylogenetic contrasts, but it will provide a suitable second test of the allometric analysis that I think is warranted here to verify results.

Author's Response to Decision Letter for (RSPB-2019-2301.R0)

RSPB-2019-2885.R0

Review form: Reviewer 1

Recommendation

Accept as is

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

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

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

I am satisfied with the revisions by the authors and would like to recommend for publication of this revised submission by Proceedings B.

Review form: Reviewer 2

Recommendation Accept as is Scientific importance: Is the manuscript an original and important contribution to its field? Good

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

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.

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 responded satisfactorily to my critique. I am satisfied with the additions of adjusted r2 values in the tables.

Decision letter (RSPB-2019-2885.R0)

10-Jan-2020

Dear Miss Mincer

I am pleased to inform you that your Review manuscript RSPB-2019-2885 entitled "Substrate use drives the macroevolution of mammalian tail morphological diversity" has been accepted for publication in Proceedings B.

The referees do not recommend any further changes. Therefore, please proof-read your manuscript carefully and upload your final files for publication. 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 me know immediately.

To upload your manuscript, log into http://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, upload a new version through your Author Centre.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

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. Please note that PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file from the main text and the file name should contain the author's name and journal name, e.g authorname_procb_ESM_figures.pdf

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. Please see: https://royalsociety.org/journals/authors/author-guidelines/

4) Data-Sharing and data citation

It is a condition of publication that data supporting your paper are made available. Data should be made available either in the electronic supplementary material or through an appropriate repository. Details of how to access data should be included in your paper. Please see https://royalsociety.org/journals/ethics-policies/data-sharing-mining/ for more details.

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=RSPB-2019-2885 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.

5) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit https://royalsociety.org/journals/authors/author-guidelines/.

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

Sincerely, Professor Hans Heesterbeek mailto:proceedingsb@royalsociety.org Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s). The authors have responded satisfactorily to my critique. I am satisfied with the additions of adjusted r2 values in the tables.

Referee: 1

Comments to the Author(s). I am satisfied with the revisions by the authors and would like to recommend for publication of this revised submission by Proceedings B.

Sincerely, Proceedings B mailto: proceedingsb@royalsociety.org

Decision letter (RSPB-2019-2885.R1)

17-Jan-2020

Dear Miss Mincer

I am pleased to inform you that your manuscript entitled "Substrate use drives the macroevolution of mammalian tail morphological diversity" 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

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

Open Access

You are invited to opt for Open Access, making your freely available to all as soon as it is ready for publication under a CCBY licence. Our article processing charge for Open Access is £1700. Corresponding authors from member institutions

(http://royalsocietypublishing.org/site/librarians/allmembers.xhtml) receive a 25% discount to these charges. For more information please visit http://royalsocietypublishing.org/open-access.

Paper charges

An e-mail request for payment of any related charges will be sent out shortly. The preferred payment method is by credit card; however, other payment options are available.

Electronic supplementary material:

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.

You are allowed to post any version of your manuscript on a personal website, repository or preprint server. However, the work remains under media embargo and you should not discuss it with the press until the date of publication. Please visit https://royalsociety.org/journals/ethics-policies/media-embargo for more information.

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

Sarah T. Mincer Response to referees 12/09/19 RSPB-2019-2301 Substrate use drives the macroevolution of mammalian tail morphological diversity

Referee 1

Comment 1: *My major concerns comes from that the authors employed RTL (relative tail length) only in the examination of the effect of climate on TL while other analyses used TL (tail length) in stead. Although the author mentioned in line 72-73 of page 2 that RTL is an appropriate measure for quantifying tail length, they also thought that RTL was unable to provide an explicit look at how TL scales to BL or BM. I do not think they have provide rationale for their treatment. Now that the RTL is an appropriate measure for quantifying and see whether they are better or worse than TL in analyses. At least they should provide references which made such conclusion.*

Response: We agree that we needed to provide additional rational as to why we used body size measures in our analyses. We added lines 73-78 to provide additional rationale for the use of tail length rather than RTL our analyses. The use of a ratio is not always accepted as the best measure because of scaling differences [1]. While we have information for how tail length may scale with body size for particular groups [2-4], there is no information for this relationship at a larger phylogenetic scale. We therefore wanted to examine patterns of covariance between tail length and body size measures based on different ecological and behavioral variables that may influence tail length [5]. Using a ratio such as RTL to control for body size does not allow us to test for variation in the allometric scaling of tail length to body size, and a pANCOVA is a stronger test of this variation [1]. And, results of our study indicate that tail length does not scale isometrically, and instead exhibits a negative allometry across phylogeny (Results and discussion: lines 157-161). We suggest that that the relationship between tail length and body size measures (e.g., body length and body mass) requires an independent perspective of each variable.

Comment 2: *Page 1, line 5-6, considering the important function and adaptive significance of mammalian tails, I do not think they are really phylogenetically informative.*

Response: We disagree that tail length (which includes presence versus absence) is not phylogenetically informative. Tail loss is a commonly cited derived trait that characterizes all hominoids, including humans, living apes, and our fossil ancestors [6-11]. Thus, previous work uses tail absence versus presence to classify living and fossil taxa and can provide information about the phylogenetic position of taxa - potentially as members of the ape and human clade (i.e., it is phylogenetically informative). To further support this assertion, we added citations on page 1, line 6 that utilize tail loss as a trait to characterize particular hominoid taxa. This study also provides support for the idea that tail length is functionally significant, and in this sense we agree with the review. The use of tail loss to characterize and classify taxa also supports its status as a

derived trait that is phylogenetically informative, thus we assert that tail length (including presence versus absence) is "both functionally and phylogenetically informative" (page 1, line 6).

Comment 3: Page 2, line 49 and line 57 both mentioned they used species with genomic data. I do not see the genomic data have been employed in the subsequent analyses. Could the authors please provide further information on how they use the genomic data for their analyses?

Response: Thank you for pointing this out. The phylogeny used for all phylogenetic comparative methods was taken from Smaers, Turner [12], which utilized genomic data, morphology, and/or existing taxonomy to adjust previously constructed trees [13] and create a single resolved tree. For more detail regarding this procedure see Faurby and Svenning [13]. We have revised lines 50 and 56-57 of our manuscript to remove mention of genomic data for clarification, as genomic data was not *directly* used in our analyses of tail length.

Referee 2

Comment 1: *My* only concern about this manuscript relates to the scaling analysis. The authors use phylogenetic generalized least squares to evaluate allometric scaling of tail length to body length and body mass. But all of these variables have error terms associated with them, and unless r-values are above 0.9 (and they are not reported here in the S1 table), it might be appropriate to re-evaluate the allometric scaling with reduced major axis (model II) regression instead of pGLS. An RMA approach will not control for phylogenetic contrasts, but it will provide a suitable second test of the allometric analysis that I think is warranted here to verify results.

Response: You have raised an important point here regarding error. We have revised tables S1 and S2 in the supplementary information to include adjusted r^2 values for each variable as requested. However, we believe that pGLS is the most appropriate method to evaluate allometric scaling. Although previous studies have utilized a reduced major axis (RMA) approach in cases where there is error in both variables, RMA is not an accurate estimator of allometric regression slopes because it can be biased when there is error caused by biological variation (i.e., error caused by unknown, biological sources) in the model [14]. Other work has indicated that a phylogenetic generalized least squares (pGLS) approach used here is a stronger and more accurate way to test for allometric shifts in tail length while taking phylogeny into account [15, 16].

References

[1] Packard, G.C. & Boardman, T.J. 1987 The misuse of ratios to scale physiological data that vary allometrically with body size. *New directions in ecological physiology* 61.

[2] Demes, B., Jungers, W.L., Fleagle, J.G., Wunderlich, R.E., Richmond, B.G. & Lemelin, P. 1996 Body size and leaping kinematics in Malagasy vertical clingers and leapers. *Journal of Human Evolution* 31, 367-388.

[3] Preuschoft, H., Witte, H., Christian, A., & Fischer, M. 1996 Size influences on primate locomotion and body shape, with special emphasis on the locomotion of 'small mammals'. *Folia Primatologica* 66, 93-112.

[4] Hayssen, V. 2008 Patterns of body and tail length and body mass in Sciuridae. *Journal of Mammalogy* 89, 852-873.

[5] P'elabon, C., Firmat, C., Bolstad, G.H., Voje, K.L., Houle, D., Cassara, J., Le Rouzic, A. & Hansen, T.F. 2014 Evolution of morphological allometry. *Annals of the New York Academy of Science* 1320, 58–75.

[6] Williams, S.A., Middleton, E.R., Villamil, C.I. & Shattuck, M.R. 2016 Vertebral numbers and human evolution. *American journal of physical anthropology* 159, 19-36.

[7] Williams, S.A. & Russo, G.A. 2015 Evolution of the hominoid vertebral column: the long and the short of it. *Evolutionary Anthropology: Issues, News, and Reviews* 24, 15-32.

[8] Russo, G.A. 2015 Postsacral vertebral morphology in relation to tail length among primates and other mammals. *The Anatomical Record* 298, 354-375. (doi:10.1002/ar.23004).

[9] Russo, G.A. 2016 Comparative sacral morphology and the reconstructed tail lengths of five extinct primates: *Proconsul heseloni, Epipliopithecus vindobonensis, Archaeolemur edwardsi, Megaladapis grandidieri,* and *Palaeopropithecus kelyus. Journal of Human Evolution* 90, 135-162. (doi:10.1016/j.jhevol.2015.10.007).

[10] Ward, C.V., Walker, A. & Teaford, M. 1991 *Proconsul* did not have a tail. *Journal of Human Evolution* 21, 215-220.

[11] Nakatsukasa, M. 2003 Definitive evidence for tail loss in *Nacholapithecus*, an East African Miocene hominoid. *Journal of human evolution* 45, 179-186.

[12] Smaers, J.B., Turner, A.H., Gómez-Robles, A. & Sherwood, C.C. 2018 A cerebellar substrate for cognition evolved multiple times independently in mammals. *eLife* 7, e35696.
[13] Faurby, S. & Svenning, J.-C. 2015 A species-level phylogeny of all extant and late Quaternary extinct mammals using a novel heuristic-hierarchical Bayesian approach. *Molecular phylogenetics and evolution* 84, 14-26.

[14] Hansen, T.F. & Bartoszek, K. 2012 Interpreting the evolutionary regression: the interplay between observational and biological errors in phylogenetic comparative studies. *Systematic Biology* 61, 413-425.

[15] Hansen, T.F. 1997 Stabilizing selection and the comparative analysis of adaptation. *Evolution* 51, 1341-1351.

[16] Smaers, J.B. & Rohlf, F.J. 2016 Testing species' deviation from allometric predictions using the phylogenetic regression. *Evolution* 70, 1145-1149.