

Mammalian intestinal allometry, phylogeny, trophic level and climate

María J. Duque-Correa, Daryl Codron, Carlo Meloro, Amanda McGrosky, Christian Schiffmann, Mark S. Edwards and Marcus Clauss

Article citation details

Proc. R. Soc. B **288**: 20202888.

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Review timeline

Original submission: 19 November 2020

Revised submission: 9 January 2021

Final acceptance: 19 January 2021

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

Review History

RSPB-2020-2888.R0 (Original submission)

Review form: Reviewer 1 (Heather Smith)

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?

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

Thank you for inviting me to review this wonderful manuscript. It is a much-needed empirical evaluation of some widely-held assumptions regarding mammalian GIT morphology. The manuscript helps to tease apart some of the numerous influences on various quantitative GIT variables. It is an excellent paper which will make a significant contribution to the field.

I have no major substantive changes. The methods and interpretations are sound, and the paper is clear and well written. Instead, below I provide my impressions and thoughts.

I was not surprised that the c(a)ecum failed to follow the positive allometric patterns of the other intestinal regions. The cecum is an unusual component of the GIT in that its digestive role is only part of its overall function in the body, with immune support and possible bacterial reservoirs also contributing. I wonder if the authors may wish to discuss these additional functions further in their explanations of why the scaling of the cecum differed from other intestinal sections. I'm also curious as to whether there is a difference between laurasiatherians and euarchontoglires in this variable. There is a general assumption that the former have smaller ceca for their body sizes, but I'm not certain whether this has been empirically tested using such a larger dataset.

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This reviewer has declined anonymity: It is Heather Smith.

Reference cited: Hunt A, Al-Nakkash L, Lee AH, Smith HF. 2019. Phylogeny and herbivory are related to avian cecal size. *Scientific Reports* 9:4243.

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?

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

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Is it clear?

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Do you have any ethical concerns with this paper?

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Comments to the Author

General:

This is an important and useful paper, and generally well-written.

Making the data available is especially important.

The R code used for analyses should also be made available, not just referencing packages (cf. line 422).

This study is an example of "ecomorphology" and also "evolutionary physiology," but those terms are not used. I would suggest citing some review papers on those fields and making the connection. As currently written, it just goes straight into GIT without an appeal to biologists who see themselves as more general.

Specific:

84 Data is plural so "Data were only used if ..." Check for other cases in the manuscript, e.g., line 90.

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Garland, Jr., T., A. F. Bennett, and E. L. Rezende. 2005. Phylogenetic approaches in comparative physiology. *Journal of Experimental Biology* 208:3015–3035.

Rezende, E. L., and J. A. F. Diniz-Filho. 2012. Phylogenetic analyses: comparing species to infer adaptations and physiological mechanisms. *Comprehensive Physiology* 2:639–674.

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Table S1 and others: I know what AICc and delta AICc are in general, but I don't understand what is in the columns with those labels here. Please explain with footnotes to the tables (and also in the text).

Decision letter (RSPB-2020-2888.R0)

05-Jan-2021

Dear Dr Clauss:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers

are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please 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.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the 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.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (<https://royalsociety.org/journals/ethics-policies/>). You should pay particular attention to the following:

Research ethics:

If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:

If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:

It is a condition of publication that you make available the data and research materials supporting the results in the article. Please see our Data Sharing Policies (<https://royalsociety.org/journals/authors/author-guidelines/#data>). Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (<https://royalsociety.org/journals/ethics-policies/data-sharing-mining/>). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

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.

For more information please see our open data policy <http://royalsocietypublishing.org/data-sharing>.

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. Please try to submit all supplementary material as a single file.

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].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,

Dr Daniel Costa

mailto:proceedingsb@royalsociety.org

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

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Table S1 and others: I know what AICc and delta AICc are in general, but I don't understand what is in the columns with those labels here. Please explain with footnotes to the tables (and also in the text).

Author's Response to Decision Letter for (RSPB-2020-2888.R0)

See Appendix A.

Decision letter (RSPB-2020-2888.R1)

19-Jan-2021

Dear Dr Clauss

I am pleased to inform you that your manuscript entitled "Mammalian intestinal allometry, phylogeny, trophic level and climate" 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

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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.

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,
Dr Daniel Costa
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
(There are no comments.)

Appendix A

RSPB-2020-2888
Reply to Reviewers

Dear Dr. Costa,

Thank you for giving us the opportunity to revise our manuscript and respond to the Reviewers' comments.

Please find below the revised manuscript (including main text, figures, supplementary materials) with all revised text in **grey shading**. Our response to specific reviewer comments are given in the table on the next pages, linking with the line numbers of that document. Identical versions (of main text, figures, supplementary materials – all separately) were uploaded in the system.

Both reviewers asked for additional calculations, which were done and added to the Supplementary Material. The original data was, this time, not added as appendices to the re-submission, but was uploaded to Dryad as suggested as:

Duque-Correa MJ, Codron D, Meloro C, McGrosky A, Schiffmann C, Edwards MS, Clauss M (2021) Mammalian intestinal allometry, phylogeny, trophic level and climate. Dryad Dataset <https://doi.org/10.5061/dryad.z8w9ghxb8>

The sharing link at this stage is

https://datadryad.org/stash/share/mOF3gf-L3yGyoT47bZTxFA2WsYuDO__kRzY4xeEK8AA

We thank you for your time and hope the manuscript now meets the requirements of the Proceedings of the Royal Society B: Biological Sciences.

Sincerely,

María Duque-Correa & Marcus Clauss

See detailed responses to reviewers down below

PS: Co-author Christian Schiffmann had already been named on the title page in the author line of the originally submitted manuscript, but M. Clauss had apparently forgotten to enter him as author in the system.

Reviewer 1:

Thank you for inviting me to review this wonderful manuscript. It is a much-needed empirical evaluation of some widely-held assumptions regarding mammalian GIT morphology. The manuscript helps to tease apart some of the numerous influences on various quantitative GIT variables. It is an excellent paper which will make a significant contribution to the field.

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I was pleased to see that the authors included volancy as a variable. There is an apparently intriguing compromise between the additional energy requirements of flying and the need for reduced overall body weight.

Reviewer's comment (lines refer to the original submission)	Our response	Changes made in the text (lines refer to the revised version)
<p>I was not surprised that the c(a)ecum failed to follow the positive allometric patterns of the other intestinal regions. The cecum is an unusual component of the GIT in that its digestive role is only part of its overall function in the body, with immune support and possible bacterial reservoirs also contributing. I wonder if the authors may wish to discuss these additional functions further in their explanations of why the scaling of the cecum differed from other intestinal sections.</p> <p>I'm also curious as to whether there is a difference between laurasiatherians and euarchontoglires in this variable. There is a general assumption that the former have smaller caeca for their body sizes, but I'm not certain whether this has been empirically tested using such a larger dataset.</p>	<p>1. We added the analyses to the legend of Fig. S6 (and an additional panel to Fig. S6), where we give the scaling relationships for coprophagic and non-coprophageous mammals now but also the requested ones for Laurasiatheria and Euarchontoglires, in connection to the Smith et al. 2017 findings. One can see that in GLS, the predicted scaling difference exists, whereas this is no longer the case in PGLS. We added the Laurasiatheria-Euarchontoglires comparison to the same figure. Note that in the more limited taxonomic datasets, geometric scaling is typically included in the scaling confidence interval.</p> <p>2. Beyond the explanation we give with respect to coprophagy, which we find convincing, we would like not to discuss these other functions, because we cannot link them reasonably to differences between the groups in our own thinking. Given that we make the data available for others, other researchers are welcome to use this to explore other functional roles of the caecum.</p>	<p>Addition made to the legend of Fig. S6: Using GLS, the scaling between the two functional mammal groups had different confidence intervals for both the factor and the exponent, and geometric scaling was included in the confidence interval for non-coprophageous species (non-coprophageous: caecum length = 6.4 [5.6 to 7.3] $BM^{0.29 [0.25 \text{ to } 0.33]}$; coprophageous: caecum length = 10.0 [9.1 to 10.9] $BM^{0.20 [0.17 \text{ to } 0.23]}$); using PGLS, geometric scaling was included in the confidence interval for both groups, there were no differences in the scaling exponent, and the numerical difference in the factor was not maintained by the confidence intervals (non-coprophageous: caecum length = 4.5 [1.3 to 15.5] $BM^{0.29 [0.24 \text{ to } 0.33]}$; coprophageous: caecum length = 7.8 [2.5 to 24.1] $BM^{0.29 [0.25 \text{ to } 0.33]}$); (B) across Laurasiatheria and Euarchontoglires (because more evolutionary changes in the caecal appendix occurred in the latter compared to the former [19]). Euarchontoglires have longer caeca, and a shallower scaling, but confidence intervals overlap in PGLS (GLS: Lauras. caecum length = 4.1 [3.0 to 5.7] $BM^{0.40 [0.32 \text{ to } 0.49]}$, Euarch. caecum length = 10.7 [9.7 to 11.9] $BM^{0.20 [0.16 \text{ to } 0.25]}$; PGLS: Lauras. caecum length = 5.6 [2.8 to 11.1] $BM^{0.30 [0.24 \text{ to } 0.36]}$, Euarch. caecum length = 11.6 [7.7 to 17.6] $BM^{0.29 [0.24 \text{ to } 0.35]}$).</p>
<p>Hunt and colleagues (2019) investigated a similar relationship in birds and found no correlation between volancy and cecal size. Although flying capabilities vary much more among avian taxa than mammals, the results may still be relevant.</p>	<p>We apologize for not being aware of this study. We cited it now, in proper context.</p>	<p>addition made l. 386: In birds, this does not necessarily apply to the caecum [70].</p>

Reviewer 2:

This is an important and useful paper, and generally well-written.

Reviewer's comment (lines refer to the original submission)	Our response	Changes made in the text (lines refer to the revised version)
Making the data available is especially important.	<p>Exactly, this is why we submitted the original data file along with the submission. For the revision, we have uploaded the data, the data references and the phylogenetic tree, as a Dryad Dataset using the link provided by Proc R Soc B, and cite it correspondingly.</p> <p>The sharing link at this stage (not yet accepted) is https://datadryad.org/stash/share/mOF3gf-L3yGyoT47bZTxFA2WsYuDO_kRzY4xeEK8AA</p>	<p>addition made: setup of Dryad Dataset Duque-Correa MJ, Codron D, Meloro C, McGrosky A, Schiffmann C, Edwards MS, Clauss M (2021) Mammalian intestinal allometry, phylogeny, trophic level and climate. Dryad Dataset https://doi.org/10.5061/dryad.z8w9ghxb8:</p> <p>and addition in manuscript: l. 437: are publicly available [77].</p>
The R code used for analyses should also be made available, not just referencing packages (cf. line 422).	We can (and did) do this, although this basically means repeating code from the instructions to use the cited packages. However, due to some details, this may actually add value.	R code added at the end of the Supplementary Material.
This study is an example of "ecomorphology" and also "evolutionary physiology," but those terms are not used. I would suggest citing some review papers on those fields and making the connection. As currently written, it just goes straight into GIT without an appeal to biologists who see themselves as more general.	Good point. We added the word "ecomorphological" to the abstract, "ecomorphology" to the key words, started the Background section with a corresponding sentence and citation, and also made additions in the discussions.	<p>addition in the manuscript: l.439: and is given in the Supplementary Material.</p> <p>change made in abstract l. 25: ecomorphological</p> <p>change made to keywords l. 44: ecomorphology</p> <p>addition made in Background l. 46: Ecomorphological diversity is considered the main driver of species diversity, and diet is considered as one of the most important components of an animal's niche [1].</p> <p>addition made l. 412: At the same time, they indicate that these associations – or convergences – cannot be considered ubiquitous or 'fixed laws'. Rather, data scatter suggests that different morphophysiological solutions exist for the same ecological challenge – a typical finding of ecomorphological studies.</p>
84 Data is plural so "Data were only used if ..." Check for other cases in the manuscript, e.g., line 90.	Yes, we apologize for the mistake. This was corrected throughout.	changes made throughout the text at multiple locations (l. 88, 92, 94, 95, 100, 103, 131, 204: data were
123 I suggest that the authors also do analyses for some of the major branches of the tree, e.g., Rodentia, Carnivora. Additional interesting relationships may be found. If they don't fit in the paper, they could be supplemental materials.	Yes, this is a good point. We did that already, but we failed to mention this at this location in the methods. The result of these analyses had already been included in the "Trophic level" section and on table S4 and figure S2.	addition made in method section l. 131: and (iv) various individual taxonomic groups

<p>131 and on I don't understand the logic for the sequential analyses. It's OK to just do plain allometry, with only body mass as an independent variable. But, after that, they should do a full model with all of the other predictors.</p>	<p>The point is, as explained in the method section, availability. If we had all data for all species, of course we would do a full model with all variables. But data availability basically varies with each variable, so that the "full model" approach would either necessitate "estimating" a large number of missing data (an approach we do not want to pursue) or reducing the dataset to the smallest common species denominator, which would mean excluding a lot of published data. Our "piecemeal" approach is how we think this should be done, even though it – clearly – makes the narrative more difficult, as one has to consider, all the time, which dataset we are talking about. However, that kind of complexity is, in our view, the best approach to comparative analyses. By giving the original data, we facilitate other approaches.</p>	<p>no change</p>
<p>144 This methods paragraph should cite some publications that review phylogenetic statistical methods, such as these: Garland, Jr., T., A. F. Bennett, and E. L. Rezende. 2005. Phylogenetic approaches in comparative physiology. <i>Journal of Experimental Biology</i> 208:3015–3035. Rezende, E. L., and J. A. F. Diniz-Filho. 2012. Phylogenetic analyses: comparing species to infer adaptations and physiological mechanisms. <i>Comprehensive Physiology</i> 2:639–674. They could also refer more to the Appendix in Lavin et al. 2008, which explains things nicely. The readers need that, not just citations of computer programs.</p>	<p>Good point. We added a sentence and the two new references mentioned by the reviewer, and another one on the topic by some of our group.</p>	<p>Addition made l. 148: Comparative analyses need to consider the phylogenetic structure of the datasets that are analyzed [41-43].</p>
<p>159 Add the K statistic of this paper and compare with values in their appendix: Blomberg, S. P., T. Garland, Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. <i>Evolution</i> 57:717–745.</p>	<p>We added Blomberg's K to the method, result and discussion section for the full datasets for each intestinal section.</p>	<p>Additions made in methods l. 151: In all PGLS models, as phylogenetic signal, lambda (λ) was estimated by maximum likelihood. Additionally, we used the R package 'phytools' [46] to estimate the phylogenetic signals Blomberg's K [47] and Pagel's λ [48] for the complete datasets and the dataset of those species for which small intestine, caecum, and colon/rectum data were available. Additions made in results l.167: Both Pagel's λ (at values of 0.97 to 0.99) and Blomberg's K (0.58 to 0.76) indicated a distinct phylogenetic pattern in the data; the two methods differed only for the caecum length, for which K, but not λ, indicated lower values than for the other intestinal sections (Table S1). addition made l. 294: Both phylogenetic signals, K and λ, indicated that closely related species share a common intestinal morphology. In the Supplementary Material, Table S1 was added with the different phylogenetic signals.</p>

160 Change While to Although	We do not think that “although” is a good link between the two facts here. In order to comply nevertheless, we also deleted the “while” and just made two simple sentences.	Change made l. 172: There was no evident spacing in intestinal length between marsupials and placentals (Fig. S2A). Afrotheria and Xenarthra had comparatively short intestines (Fig. S2B), and phylogenetic clustering was evident both within the Laurasiatheria and the Euarchontoglires (Fig. S2C-E).
246 Change the section to be named "Limitations of the Present Study"	Ok.	Change made l. 259: Limitations of the present study
368 Possible example of "multiple solutions" -- may want to search and cite some papers, again, to help generalize the present findings to ecomorphology/evolutionary physiology.	Good point. We made an addition.	Addition made l. 412: Our investigation demonstrates associations between intestinal anatomy and dietary niches that have been claimed in the biological literature for long. At the same time, they indicate that these associations – or convergences – cannot be considered ubiquitous or ‘fixed laws’; rather, data scatter suggests that different morphophysiological solutions exist for the same ecological challenge– a typical finding of ecomorphological studies.
Table S1 and others: I know what AICc and delta AICc are in general, but I don't understand what is in the columns with those labels here. Please explain with footnotes to the tables (and also in the text).	Thank you for pointing this out. Each table now has its own footnote, explaining the AICc and its delta in that specific table.	Footnotes added to all table in the supplement, e.g. AIC _c : small sample corrected Akaike’s information criterion (for analyses using the same species, indicated by the same n, a lower AIC _c indicates a better model fit); ΔAIC _c : indicates the difference in AIC _c to the model with the lowest AIC _c (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC _c cannot be compared between GLS and PGLS models.