
Round #2

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by Fabien Condamine, 28 Nov 2022 11:11
Manuscript: **https://www.biorxiv.org/content/10.1101/2022.05.09.490912v2** version 2

Decision for your submission at PCi Evol. Biol. #548

Dear Benjamin and Benoît,

Thank you for submitting your revised work (manuscript #548) to PCi Evol. Biol.

I have sent back for re-review to the previous 5 expert reviewers. We have now received the comments from 4 of them, which you will find associated to this decision.

All the reviewers expressed again positive comments about the manuscript, on which I agree, and 3 referees added a few more comments that should not be the most difficult to address.

However, I also agree with the remaining comments raised during this new round of review, and I would like to see a revised version of the manuscript. I think it's important to clarify several aspects of the study as suggested by the reviewers.

After this revision, I am opitmistic that it will lead to a recommendation since I think I will not send it back for re-review (the referees have already done a great job, and I thank them for it). I hope these reviews will help you to improve your study.

I look forward to see a revised version of your manuscript. If you have any questions, please do not hesitate to reach me.

All the best,
Fabien Condamine, for PCi Evol. Biol.

Dear Fabien,

Thank you for taking on this new review round. We have now addressed the new comments raised by the reviewers point by point. In particular, we have added clarity on predictions (following remarks of reviewer 1), and on the limits/discussion of the models (OU, MC, following comments of reviewers 1/4). In addition, we have revised the methods section to make it clearer and moved some parts to the supplementary materials to have a lighter version, as suggested by reviewer 4. Yet, we did not venture into reshaping the narrative around the striatum only, as this reviewer also suggested, as we felt that this would not be wise now that everyone has (more or less) agreed on the form of the manuscript. Finally, we have added sections to fit the requirements of PCI (Funding, code availability etc.) as requested in PCI guidelines.

With our very best,

Benjamin and Benoît.

Reviews

Reviewed by anonymous reviewer, 26 Nov 2022 00:23

I have read with great interest the revised version of the manuscript Primate sympatry shapes the evolution of their brain architecture. I thank the authors for their positive response to previous comments and commend them for the hard work addressing them. I think the work is clearer, however I still have a few questions that I believe need to be addressed before the work is suitable for recommendation.

Thank you for this next round of review and the constructive comments. We have addressed them in the following lines, point by point.

Firstly, to me it is not clear why competition is expected to lead to directional changes, i.e. either enlarged or decreased brain structure or brain size. As I understand it competition may lead to character displacement, to avoid competing for specific resources with members of a given species. However, not all competing individuals are predicted to modify specific characters and even less so in the same direction and degree. Indeed, individuals of the more successful competitor would face no selection to change. Thus, I wonder if the prediction resulting from high sympatry might not be increased variance in brain structures or brain sizes across a set of sympatric species, rather than enlarged or reduced brain structure or brain sizes. In support of this idea, if I am not mistaken, this is what the authors actually found for body size, a trait that is probably more directly linked to resource use in primates (or at least the Discussion seems to suggest this in lines 497-500).

We do agree that competition might not necessarily be associated with a directional selection. In fact, this is purposely why we also included a "Matching Competition" model, which assesses whether the trait under study (here the size of some brain regions) would diverge between taxa because of disruptive selection (because of competition). Thus, to highlight further this possibility as soon as the introduction, we lengthened the idea of niche partitioning, highlighting the possibility of complete divergence (see lines 84-94).

The point above leads me to my second point of concern. The authors have chosen to use both body size and whole brain size to control for allometric effects in their analyses of brain structure sizes. However, I was left wondering whether this is justified given they found that competition actually impacts body size evolution, as would be predicted, but actually rather differently than they predict for brain structure sizes. I acknowledge that the fact that results are the same when using either variable as a control for allometric effects, which I honestly found a bit puzzling given the effect of competition on body size evolution.

We must admit that we shared the puzzle with the reviewer at first, and were also surprised that the results remained similar. However, as we mentioned, the study of the relative size of the brain when weighting by body mass gives access to energy reallocation within the whole body and the brain, while it gives only access to within-brain when weighting by the whole brain size. The similarity of the results may thus highlight that sympatry mostly affected within-brain energy allocation, and not the total energy allocation toward the whole brain itself (coherently with the insensitivity of the EQ to sympatry). We thus rephrased lines 404-407 which was initially "Therefore, our results suggest that species sympatry simultaneously impacted between-tissues and within-brain reallocations for the hippocampus and the striatum."

I also found somewhat surprising that the authors propose that competition could lead to reduced brain structure or brain sizes due to depleted resources and the energy constraints of maintaining a large brain. There is indeed plenty of evidence supporting the claim of high costs of brain growth, development and maintenance. However, competition would result in depleted resources for individuals that are less successful in competing but not necessarily for all competitors.

Given previous comments, and comments from other reviewers, now we introduce three predictions: possible increase, decrease or divergence (i.e. character displacement; which we initially tested with the MC model) of brain sizes with sympatry. Thus, this includes the possible scenario here mentioned by the reviewer (now lines 91-94).

This would also depend on the degree to which resources can be defended and thus how competition plays out. In fact, whether resources are defendable or not would actually have a very strong effect on the predicted outcome of sympatry and thus resource competition. There is no mention regarding whether resources can be defended or not. I.e. can members of one group effectively monopolize one or a group of fruiting trees impeding individuals of other species to access the resource? Or rather, is competition more scramble where arriving first gives precedence and thus greater access to resources and groups leave to search for other food sources when too many groups arrive, such as in a producer scrounger game?

We agree that the fact that resources may or may not be monopolisable may contribute to blurring the evolutionary scenario we have proposed. We provide indeed only a simplified version, and acknowledge (lines 512-518) that several other processes may disrupt the proposed picture. We are not aware of any available data on interspecies resource defence in primates, for which scramble competition may be the dominant form. However, as resource defence may also affect species cognition (as we point out, citing Ashton et al., 2020), we open up this possibility, mentioning the case of the hummingbird for which interspecies territoriality and resource defence have been demonstrated (line 539).

In the Discussion the authors state that their results clearly emphasize the compromise due to high energetic demands of the brain as the largest structures, the cerebellum and neocortex, as well as whole brain size, are best fitted by an OU model. They propose that this may suggest a stabilization towards an optimal size resulting from an equilibrium between costs and benefits. It is not clear to me why they expect the optimum to be the same for all species. Certainly, the benefits of a given relative brain size will differ among species given differing selection factors. Costs could also potentially differ if species are not all equally successful in acquiring resources. Finally, great care must be taken when interpreting the results of these models, one thing is the pattern that is observed but another is the process that may be responsible for said pattern (see e.g. Revell et al 2008). Furthermore, there are studies suggesting care must be taken when interpreting the results of OU models (see e.g. Cooper et al. 2015).

We agree with the reviewer that there is some confusion around the OU model, and we may have failed to highlight them. Furthermore, as the environment in which the frugivore species studied live may vary, the selection on relative brain size may also vary, and a multi-peak OU model would indeed be more appropriate. However, in this framework, such models are not yet implemented. Here, the OU could potentially represent the average of these multi-peak OUs. We have thus modified lines 338-340 to add some precision. In parallel, as the aim of this model, and other models not dependent on sympatry in fact, was to test whether or not sympatry helped describing the evolutionary history of brain size (by comparing their fit), the fact that the OU itself is the best model is therefore anecdotal. Rather, it is important that the sympatry-dependent models are not. To avoid further confusion and not emphasise those results “individually”, we have therefore deleted this paragraph and modified paragraphs lines 393-397 to highlight the confront with the sympatry effect.

Reviewed by Paula Gonzalez, 12 Nov 2022 13:39

Comments to the Author

The authors addressed all of my comments. I think the rationale of the paper is much clearer. The strengths and limitations of the data and methods used are now discussed which can contribute to further studies on the evolution of primate cognition. Here below are minor comments.

We thank the reviewer for this note.

Introduction.

I suggest to mention the energy reallocation alternatives (relative to body mass or within the brain) in the introduction.

Agreed, we have now added the sentence lines 61-63.

P 5 L94:101. I suggest to clarify whether the expectations refer to absolute or relative size (or both) of the hippocampus. The same comment applies to Predictions 2 and 3.

Done, we now added « relative ».

Results.
P 29 Table 1. According to the caption the table shows the results of the phylogenetic regressions for size of some brain areas, but the variables were transformed to the size relative to body mass. If this is the case, please clarify that the results correspond to relative size of some brain areas.

We have now adjusted the legend stating, “Species sympatry correlates negatively with the **relative** size of some brain areas”.

Reviewed by anonymous reviewer, 07 Nov 2022 15:22

This is the revised version of the previous manuscript. The first version was already very good, but I had a few concerns mainly regarding simpatry and niche partitioning. I think in this new version these concerns were satisfactorily tackled when possible or at least acknowledged when the problem was not immediately solvabl . I really like the final result and I think this will be a valuable contribution to the literature. While some doubts might remain regarding how convincing the results are, I think it is now up to the readers to make that call. The authors did a good work presenting the limitations and a balanced and honest interepretation. Also, I also was satisfied reading the author's response to the other reviewer's concerns, which I shared. So I have no further comments and I would definitively reccomend the publication of such a valuable contribution to macroevolutionary studies on primate brain evolution.

Thanks for inviting me to review this interesting manuscript.

We are sincerely grateful for the time taken to help us improve the quality of this work!

Reviewed by Orlin Todorov, 28 Nov 2022 05:24

Hello,

here is my second round of review of the manuscript "Primate sympatry shapes the evolution of their brain architecture" submitted to PCI Evol Bio. Detailed comments can be found in the attached pdf file.

Cheers,
Dr Orlin S. Todorov

We thank the reviewer for the time taken, their constructive comments, and particularly the multiple references provided to elaborate their criticism, which gave us material to work on.

To whom it may concern,

Here are my general and specific comments on the manuscript entitled “Primate sympatry shapes the evolution of their brain architecture”. Apologies for the slight delay, but the manuscript is very involved and it took more time than expected to look into.

Introduction:

The introduction is well written, follows a clear line and provides comprehensive reasoning behind most hypotheses tested. I have a major point related to the definition of cognition (the absence thereof) and have included some specific line by line comments:

General: I would have loved to see a working definition of cognition the authors are using. There is a great amount of controversy surrounding the use of this term (especially within biologists) so I believe providing a working definition will make the authors' thesis clearer.

We built our rationale with the conception of cognition as defined by Shettleworth (2010) as “the set of mechanisms that enable individuals to perceive, learn and memorise information, and make decisions”. We have now added it lines 35-36.

Line 50 - *"Although the relevance of this assumption is heavily limited within species, in part because of plasticity (Gonda, Herczeg, and Merilä 2013), this holds true when comparing different species (e.g. in primates, Reader and Laland, 2002)."* I would add 'within taxonomically similar groups' as it is also problematic to infer 'cognitive ability' from relative brain size alone among larger taxonomic groups (see https://pubmed.ncbi.nlm.nih.gov/21252471/)

We modified accordingly.

Line 64 - *"granivores, insectivores, etc."* - maybe list all the categories?

We have now done it (“[…] (frugivores, folivores, nectarivores, granivores, insectivores, omnivores)”).

Line 93 - *"hence high cognition"* - in the absence of a working definition of 'cognition' I don't

understand the usage of 'higher' or 'lower' in this context.

We have now given a definition (see comment above).

Line 96 - *"In this case, the size of the hippocampus (reflecting long-term memory abilities) should be larger the higher the sympatry intensity"* - this is not necessarily true as increased long-term memory demands might 'push' some of the hippocampal processing to the neocortex, leading to more 'corticalised' species with actually smaller hippocampi (relative to the other sub-components or rest of the brain) - see https://www.sciencedirect.com/science/article/pii/S0896627304005793. I see that you mention such a possibility in line 101 and 110 but maybe add a line for this other possible pathway to hippocampal size decrease?

From our understanding, it seems that the relationship between the hippocampus and the neocortex (more exactly the prefrontal cortex) is more complicated than a unilateral flow from the hippocampus

to the prefrontal cortex. Both might act in connivance (Kitamura et al., 2017) As such, both the hippocampus and the prefrontal cortex should be under the same selective regime and follow the same changes in size. Yet, we added this idea to prediction 2 lines 101-103. Furthermore, we also added it to the discussion lines 421-422.

Line 104 - Another use of 'high' and 'low' cognition.

Methods:
Line 133 - I would have appreciated a table (or similar) listing all packages used for analyses with the corresponding version. This could substantially improve reproducibility.

We now provided it in Supplementary Material and have stated it in the main text line 126.

Line 155-156 - ECV is converted to brain mass by the multiplication of volume by the specific gravity of brain mass (1.036 g/mL). Not by additionally multiplying it by 10**-3. See https://www.journals.uchicago.edu/doi/10.1086/685655 for example. By multiplying each raw unit of brain volume by 1.036 you are converting from units of volume (mm3) to units of mass (gr). So, multiplying by 10**-3 is not necessary. I agree that it does not affect the significance and only the magnitude of the estimate, so as long as you are not interpreting estimates, it should be OK. Nonetheless, in my opinion, this should be corrected.

Our data were in mm^3. Thus, as mentioned by the reviewer, the 1.036 value is when the units are in mL. Since 1 mm^3 = 0.001 mL, we had to multiply by 0.001 to have mL and then proceeded to the conversion with the gravity of brain mass. Thus, our conversion should be in line with what is intended.

Line 185 - I guess you need to capitalise Google Earth Professional?

Done, thank you.

Line 263 - I have a conceptual problem with this line of *reasoning "The MC model considers the repulsion of traits of sympatric lineages..."* - applying such Matching Competition model would imply that what is actually selected for/against in evolution would be 'brain size' (or sub-region), while in reality brain size is not being directly selected for/against - it is specific behaviours or 'cognitive ability' that are under direct selection (i.e. can be incorporated as traits in such models) and not the suspected by-product of this selection, in this case - quantity of brain tissue. This is a conceptual issue and I don't expect any actionable change in the manuscript, but for the sake of conceptual clarity, I believe this general approach is misleading.

We agree with the reviewer that the changes we are looking at in terms of brain size variations is the sum of many traits that depend on many genes under potentially various and independent selective pressures. Thus, by modelling such a complex trait we are clearly looking only at the resulting variations, and it would be indeed incorrect to interpret such variations as the outcome of a directional and homogenous selective pressure. We have clarified this in the Discussion section (in the first paragraph about the limits, see lines 509-511).

Line 283 - *"Prior to fitting, trait parameters were log-transformed to reach more symmetrical distributions."* - usually, log transformation of allometric data is being done, so exponential variables can be plotted and analysed on log-log scales, using linear techniques, not for 'more symmetrical distributions".

Indeed, this is a confusion of our own. We have now replaced it by “to account for allometry”, this sentence, as here the log transformation is intended for allometric control.

Line 297 - *'represents the average'* - did you take the mean or did you use another pooling technique? What do we know about the error distribution among and within these levels of uncertainty, and if 'means' were used, was it justified?

We computed the mean weight for all this model, for which we could compute a confidence interval, following a traditional statistical rationale. Because this is misleading (and we explained it in the legend of Figure 4) we rephrased it lines 246-252.

Line 322 - *"(square-rooted to reach symmetrical distribution)"* - I don't understand why you need the distribution of species numbers to be 'symmetrical'? You would expect issues with linear regressions from non-normality of the residuals, but I don't think you need to square-root 'number of species' to achieve some sort of 'symmetry' in the distribution.

Here, however, we disagree with the reviewer. Symmetrical distributions are often of interest to limit leverage effect, which is visible with the non-normality of residuals and, often but not necessarily, induced by skewed data too if a Gaussian model is fitted. As we observed deviations in the distribution of residuals compared to expected with a Gaussian model, we performed such transformations to remove this bias. We thus maintained our explanation and added "to reach symmetrical distribution **to limit leverage effects**").

Line 324 - *'For a given species A, sympatry with another species B was considered when at least 10% of the range of species A, overlaps with the range of species B'* - why the 10% threshold? Is it used in the literature? Why not 5%, 15% or 20%?

The choice of 10% was meant to match the (arbitrary) lowest threshold used to assign biogeographic areas to a given species. Based on preliminary investigations, this 10% allowed us to not consider species as interacting only because of a gross estimation of their distribution range provided by IUCN. We did not investigate sensitivity to such a parameter to limit computational demand. Nevertheless, we had already analysed sentivity to the threshold overlap with biogeographic areas, which revealed no influence (see Supplementary Material).

Line 363 and General - at this point I am genuinely challenged by the multitude and diversity of modelling and analytical techniques used in this paper - various regression approaches (pgls, phylolm, MCMCglmm), evolutionary model fitting (several different approaches and several R packages, including model and rates of evolution), ancestral state reconstructions (diet and ranges with several different assumptions), estimation of diversification rates (ClaDS). I am not convinced that such overly complicated approach does the study and its accessibility to a specialised audience a favour. I would have recommended a much narrower scope, limited to no more than a few statistical techniques, so as to be able to easily make a point using the available data, without the myriad of transformations, different approaches and data manipulation techniques.

We agree that the article is now a heavy load. This is a combination of internal discussions and then the reviewing process. We have revised the main text accordingly and have only kept what was necessary to reproduce the analyses, and provided in supplementary further assessment of stability/uncertainty, and replication with different metrics.

Results

Line 372 - I believe you mean 'dataset' and not 'database'.

Indeed, thank you.

Line 373 - Maybe rephrase to 'when considering the analyses on brain area sizes relative to body size'.

Done, thank you.

Line 401 - *"The fact that these biggest areas are best described by the Ornstein-Uhlenbeck process suggests a stabilisation towards an optimal size"* - see my comment on Line 263 in the Methods section, but this is the same remark - trying to fit an OU model on brain size/or partitions relating to aspects of cognition, would assume one is expecting an 'adaptive evolution' of the trait (brain/partition size). To my knowledge no size of brain area (brain size as a whole) is under direct selection in relation to cognition - behaviour is - so it cannot be adaptive, and I don't think it is correct to assume OU process. Brain size variation might be suspected to follow an OU-process like evolution in respect to other selective pressures, that would in turn directly select for brain size (small or large) i.e. body size, cranial capacity/shape, even arguably certain sensory systems.

The lack of direct selection on brain size, but more specifically on other traits cascading on brain size, was discussed in a previous critique of the MC model. We have also reworded these current lines following the comment of reviewer 1 and removed the first few sentences of the discussion, commenting specifically on the OU results, as they could be misinterpreted when they are only peripheral to the main results (lines 392-397).

General - My concern from line 363 in the methods section is again revealed in the whole results section - reporting of results is done comprehensively, clearly and in reasonable amount of detail, but the amount and variety of analytical and modelling techniques makes reading through and following the results very cumbersome. Having to repeat a lot of the specific transformations and exclusion/inclusion criteria and thresholds from the methods section makes the section confusing, and waters down the important findings of the study.

Again, a sobering recommendation would be to limit the scope of the paper to the few important findings, obtained through the most appropriate, most rigorous few techniques.

We have now removed as much as possible of the sensitivity analyses into the supplements.

Discussion:

Line453 - *"between the energy it incurs"* - Maybe 'between the energy costs it incurs"?

Yes indeed, this was a typo. Thank you for catching it!

Line 454 - *"the evolution of the biggest brain areas, the cerebellum and the neocortex"* – the cerebellum is not a brain area, call it a structure, maybe?

We changed “areas” for “regions” in the whole document.

Line 489 - *"We show that a higher intensity of sympatry is actually associated with smaller sizes of the hippocampus"* - interestingly, using body mass to control for allometry, you get a significant effect of % overlapping range on hippocampus (**p=0.058**, again, as remarked by other reviewers, this is arguably significant, especially given the small sample size of his test - N=50), while it is NOT significant when you control with brain size (p=0.09). You state in the manuscript that **the results obtained are similar**, while they are **clearly not** (**they might be considered similar, as technically, both corrections yield an absence of effect**). Additionally, one reason for decrease of hippocampal size (evolutionary speaking) without any necessary 'decrease in cognitive ability' might be increase in corticalisation. I.e. processing that is usually done in the hippocampus gets shifted onto the cortex (cerebral or cerebellar).

We had corrected the phrasing previously, to tone down the idea of significance, as indeed pointed out by one reviewer. However, in a null hypothesis framework as carried out here, both p-values obtained could be considered as trends (on the contrary, because of the small sample size, for which extremely low pvalues would be unreachable).

With regards to corticalisation, we refer the reviewer to a previous answer. It is now mentioned both in the introduction and discussion.

Line 517 - As I am reading the manuscript now, the link with striatum is the only one that stands, and I would advise focusing the whole narrative on this finding. It is quite intriguing as it is!

As we stated in the response to the Editor, we fear that such changes in the narrative would be inadequate at this stage of revision. In addition, despite pvalues indicating only trends, the pattern evidenced for the hippocampus is consistent within analyses (when thresholds varied) as well as between analyses (e.g. linear models or models of trait evolution). Thus, we kept our narrative on the discussion focusing on both, the hippocampus and striatum.

Line 546 - Very good section (Limitations) underlining the major limitations in such inquiries!

Thank you.

Comments on my previous comments (using the old line numbers from the previous round)

Ln138 (from my previous comments): In the context of your study - I don't think that expecting brain sub-component to 'compete' for energy with 'the rest of the body' is a realistic expectation (see https://www.science.org/doi/10.1126/science.7777856). They are not independent organs or systems after all. According to both the expensive tissue and expensive brain hypotheses, when such 'competition' exists it is on the level of organ-organ (physiological system vs physiological system) level - i.e. brain vs gut, immune system vs fat storage propensity etc. The brain as a whole is under the same/similar developmental constraints and different sub-components are differentially integrated/modular (https://pubmed.ncbi.nlm.nih.gov/31213287/) in relation to the whole CNS and as a results - to each other. Thus, I don't think that it is realistic to expect that each brain subcomponent, evolutionary speaking, competes for the 'overall somatic energy budget' independent of the rest of the brain (or other parts thereof). Nonetheless, it is commendable that you have included analyses using the relative sub component size to the whole brain size.

If the distribution of energy can vary between groups of organs, it can also vary within one organ group. A difference in distribution within an organ group could therefore be viewed as a variation in distribution on a more specific scale (here only a part of the organ group vs another part of the same or different organ group), since these scales are cross-sectional. Our argument is that division by body mass provides insight into changes within both (and indistinguishable from) the whole body and the brain, whereas division by whole brain size provides a more rapid insight into the distribution of energy within the brain. Note that a non-uniform response of all brain areas when dividing by body mass would already indicate changes in energy distribution within the brain, whereas a uniform response would only indicate changes in energy distribution between the brain and other organs. By providing both reports in the new version of the manuscript, we believe we provide all the information necessary to discuss the expensive tissue/brain and mosaic hypotheses. Therefore, we have not made any changes.

566-571 (from my previous comments): I find this discussion point very important and well addressed, but I wonder, if you have these data (on dental wear, which can be used to infer ancestral diet states of certain fossil species), why did you not integrate it in your ancestral state estimation? Instead of eyeballing the data and 'verifying' the validity of the inference, such inclusion would 'calibrate' your estimations and you wouldn't need to assess its suitability manually.

The honest answer is that we had not thought about it prior to submission. Doing it after review would have implied re-running all models, a computationally extremely demanding task. Thus, we first assessed *a posteriori* if our inference was right. Since we observed no major deviation, we considered our approach sufficiently good to avoid rerunning the models

Ln234 and Additional methods comment (from my previous review) regarding using imputation: *"We are aware of these techniques, unfortunately, most of the missing data concern the output variable (brain size), thus using such methods won't be applicable in this context."*

Using multiple imputation is always recommended and applicable, and it is a popular misconception that it should not be used when imputing dependent (or independent) variables. (see https://pubmed.ncbi.nlm.nih.gov/30657714/). I would highly recommend using multiple imputation, if not in this study, then in your further inquiries.

We thank the reviewer for redirecting us towards the adequate literature! We are still a bit confused with potential circularity issues but it is something that we will definitely test (e.g. by simulating missing values) in the future as a way to increase the dataset size.

Supplement:

Figure 7 a and b in the supplement seems to be missing?

Indeed, our apology, Figure 7 actually disappeared from the file. We have now reinserted it. Note that we reorganized supplementary files for clarity, hence figure numbering changed.

Section ACCOUNTING FOR ALLOMETRY IN MODELS OF BRAIN SIZE EVOLUTION - *'Considering the ratio of body mass to body mass gives information'* - I think you mean brain mass the first time?

Indeed, we have corrected it. Thank you!

Same section - I appreciate the authors going the extra mile and illustrating their point with simulated data, even though I believe it is unnecessary. My recommendation would be to include something along the lines of this sentence from their *supplement "This is also in line with the phylogenetic models of trait evolution considering sympatry, which in the current state-of-the-art are not designed to account for additional variables of our choice, and for which we thus had to use relative brain size."* in the main text. Then just add a sentence that the method is still reliable for the sake of their question (i.e. when estimating effects of 'third' variables irrespective of the specific allometry between body and brain size).

We have done as suggested.