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.

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/)

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

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.

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?

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.

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.

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

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.

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".

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?

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.

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%?

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.

Results

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

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

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.

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.

Discussion:

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

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?

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).

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!

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

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.

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.

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.

Supplement:

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

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?

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).