



David Jansen <david.awam.jansen@gmail.com>

Functional Ecology FE-2018-00828

Functional Ecology <onbehalf@manuscriptcentral.com>

Mon, Oct 1, 2018 at 11:30 AM

Reply-To: admin@functionalecology.org

To: heybobby99@gmail.com

Cc: heybobby99@gmail.com, david.awam.jansen@gmail.com, mercy.akinyi@duke.edu, laurence.gesquiere@duke.edu, alberts@duke.edu, Elizabeth.A.Archie.2@nd.edu

01-Oct-2018

Dear Dr Bobby Habig,

FE-2018-00828

Multi-scale predictors of parasite risk in wild male savanna baboons (*Papio cynocephalus*)

Habig, Bobby; Jansen, David; Akinyi, Mercy; Gesquiere, Laurence; Alberts, Susan; Archie, Elizabeth

Your manuscript has now been assessed by two reviewers and one of our associate editors. While all involved found that the subject and the study model were quite relevant, the reviewers raised important issues regarding the adequacy of the measurements and the analytical methods to shed light on the processes determining parasite load in baboons, as suggested by the authors.

I thus regret that I must decline your paper from Functional Ecology. I refer you to the editor's and reviewers' comments for an explanation of the concerns that led to this decision. Please note that Functional Ecology presently receives many more manuscripts for review than we are able to publish and there must be compelling reasons to accept a paper; these include the novelty, importance and general interest of the paper. This means that some manuscripts that are otherwise sound are nonetheless rejected.

Thank you for allowing us to consider your manuscript. I hope you find the editor's and reviewers' comments helpful as you prepare your paper for submission to another journal.

Yours sincerely,

Dr Enrico Rezende
Senior Editor

ASSOCIATE EDITOR COMMENTS FOR THE AUTHORS**Comments to the Author:**

This manuscript examines predictors of parasite load in male savanna baboons using long-term data from an established study population with known behavioral, social, and environmental traits. This unique dataset allows the authors to examine a suite of predictors of parasite risk in males, from those acting at individual scales, group scales, or at the scale of the population.

One reviewer and I found the questions asked to be potentially important and interesting. However, both reviewers raised a number of concerns about the study, from methodology to scope and interpretation. Reviewer 1 raised critical issues with model construction and the potential for over-parameterization, as well as the broader context in which the study was placed. Reviewer 2 raised substantial concerns about the methods used to quantify parasite load, which form the basis of the study. While I do not agree that egg counts have no utility, the authors should at least address the ability of egg counts (in some cases, at only single time points) to provide a meaningful proxy of parasite load. Further, the authors frequently assume that higher egg counts represent "costs of reproduction" to males, but those costs will only be present if these particular parasite species have meaningful fitness consequences in males of this species. Has that been demonstrated? Finally, there are several places throughout the manuscript where causal links are implied by the detected correlations. The authors should be a bit more circumspect when discussing the correlations, which may sometimes derive from a third factor entirely. Although many of the methodological concerns are likely addressable, the manuscript did not effectively communicate the overall significance of the combination of results for the broader field of ecology, and this limited overall enthusiasm for the manuscript.

REVIEWERS' COMMENTS TO THE AUTHORS

Reviewer: 1

Comments to the Corresponding author

This paper will be of great interest to readers because it combines social behavioral, demographic, endocrine, and ecological factors to determine their effects on parasite infection risk in male yellow baboons. Whereas many other papers simply look at single factors, this paper examines multiple variables in combination and investigates the determinants of parasitism from multiple levels – individual hosts, groups and populations. Thus, this paper would add to the recently growing body of literature on parasitism in primates and mammals.

One concern I have with the paper as it is written now is that it seems that it was not necessarily written with a broader audience in mind when it could have been. The larger topic should be of interest to many – those who study behavioral ecology and beyond. More references of specific species and what has been found with regard to some of the factors discussed in this study, would help to place understanding in a broader context. Although the authors explain each factor in the introduction and then discuss or explain each finding in the discussion, more literature could have been included to place the results in a broader context to enable us to understand how these data compare both to other published studies as well as to understand the broader impacts of such a study, which is based on solid long-term data.

Additionally, sometimes a rather simplistic view of causal pathways is provided without too much discussion or mention of caveats. Although the authors explain each of their significant findings, what would be interesting is to also see a deeper discussion of what those findings mean. For instance, the finding that males that move around more have fewer parasites compared to males that reside longer in a group is an interesting one. What are the implications of this for long-term group residents? From the perspective of reducing infection risk, is it then better for individuals to move around more?

There was no description of the importance of diet or habitat quality anywhere, with the exception of touching upon nutrition in passing, even though it is known that these can be important determinants of parasitism. Age is a factor that is considered in this paper. However, diet affects the physical quality of males (e.g., older males may forage on poorer quality nutrition) and will thus be a contributing factor to increased parasitism. Also, environmental factors considered in the paper – temperature and rainfall – have direct impact on food availability, and thus on the physical condition as well as immune responses in animals. However, there was no discussion of this in the paper.

One of the strengths of this study comes from the fact that the data were provided from males residing in 11 groups. However, differences in group characteristics were not really taken into consideration in the analyses apart from group size and sex ratio. How much overlap was there in range use among the groups? It's possible that the greater the overlap the higher the parasitism. Overall the habitat occupied by these groups may be uniform, but there may be differences in micro-habitat and micro-climate in the home ranges occupied by the different groups, as well as differences in food abundance and quality, which can affect parasitism. What about access to human-derived foods which some groups may consume at higher rates than others? If there are differences among the groups in exposure to parasites from human-derived foods, it needs to be addressed. One way is by controlling for group identity. Even if a quantitative analysis of these factors is not possible, it would be informative to see a description and possible effects of any differences discussed in the paper.

Abstract

Line: 28: Change 'life histories' to 'demography' because it refers to male dispersal/immigration.

Introduction

I understand the limitations due to space, but the introduction should start broader and include the importance of studying parasitism (in terms of effects on individual fitness and effects on populations) and bring in other animals.

In the introduction, it would be good to see a brief discussion of how infection by these parasites happens in primates and what some of the negative consequences of infection are. I know the authors have included these details in a table in supplementary materials, but it is always good to read a brief summary in the main body of the paper to understand the significance of studying something like this.

Even though the authors explain each factor and their potential relationship with parasite infection risk throughout the introduction, it may be nice to see in the last paragraph of the introduction a quick list or summary of the factors that the

authors specifically test and what their specific predictions would be based on yellow baboon biology and the specific social and environmental conditions in Amboseli.

Lines 44-45: Perhaps better to specify 'immunological costs' because all three references have to do with disease and immunology. Although there could be other costs that could be included here to make the first sentence of the paper broader.

Lines 54-55: Is there really only one study? The authors write "handful of studies" but provide only one example reference.

Lines 65-67: I think more references can be provided for this.

Figure 1: I like this figure for visualizing the various levels of factors. I have a couple of questions about it. (1) What is meant by "more dense environmental exposure" under large group size? Is the density of parasites greater? Is that due to the larger number of host individuals in larger groups harboring larger numbers of parasites and thus larger groups represent larger habitats of parasites? (2) Under host-levels processes in high rank, a missing component is the relationship between rank and GC hormones and parasites. High rank may be associated with higher GCs which in turn may be associated with higher parasite load.

Lines 92-100: Rank instability is mentioned here but no explanation is given of what effects might be expected on parasitism due to instability. There may be differences in the effects of social instability on parasitism by male rank, with higher ranking males experiencing different parasitism than lower ranking males. And these can be tied to hormone pathways with both cortisol and testosterone showing different expression in higher ranking versus lower ranking males in response to instability.

Lines 95-96: But see Rifkin et al. 2012 (*The American Naturalist* 180: 70-82). Group size may not be such a strong predictor of parasitism (especially in mammals).

Line 104: Change 'moisture' to 'precipitation' if authors mean rainfall.

Lines 107-109: Extremely hot temperatures may not necessarily be linked to lower parasite loads, unless we are talking about unnaturally elevated temperatures. Higher temperatures are in fact often linked with higher parasite incidence at various stages of their life cycle. See, for instance, Poulin 2006 (*Parasitology* 132: 143-151).

Lines 116-117: Add 'simultaneously' to the end of the sentence.

Line 136: Taxon name. Why not include the common name yellow baboons? I know they are often referred to as savanna baboons in the literature, but it would be good to have the more specific common name included here as well since savanna can refer to more than one taxon. It may also be helpful for online searches.

Line 141: Yellow baboons are polygynandrous. Not all baboons are.

Lines 141-143: Males don't exhibit sexual dimorphism, the species does.

Materials and Methods

Generally, means should be reported with standard errors (or deviations) and ranges, along with sample sizes. Please include in your methods in the section on statistical analysis that male identity was controlled for in the models by including it as a random factor.

It appears that group identity was not controlled for. That should also be included as a random factor in the models. This study is about group-level processes (among other factors). It is not just total group size that's important. Characteristics of each group such as ranging, the types of foods eaten (higher versus lower quality diet), etc. will impact parasite infection of members of each of those groups. Thus, I would think group identity would be an essential factor to control for!

Lines 182-185: What makes them especially common? It appears that these four parasites are more common than any other parasite, with each having >50% prevalence in the males. Please specify beyond simply stating that they were especially common.

Line 184: Does strongyles include multiple species? How many types of Strongylids were seen in the samples?

Line 196: The mean age was 12.87 years. Does this include all 97 males? Need to give N's for all means. It would be better to see a breakdown of age by the two samples – mean age of males of known age and mean age of males with

estimated age.

Line 200: No description of methods used to obtain ranks, or the statistics. How linear were the ranks?

Lines 209-211: How many groups did a male reside in during a year on average?

Lines 211-213: What is the average consecutive male residency?

Lines 215-219: No numbers given for RIA results for hormones. It is customary to report the inter-assay and intra-assay coefficients of variation for RIAs. Were the same fecal samples used for hormone analyses as for parasite analysis? Or were hormone data averaged over weeks or month to relate to parasite load?

Lines 222-224: What was the variation in group size, i.e., what were the smallest and largest group sizes? It would be nice to see a range for such things.

Lines 224-227: So only changes in male rank were considered to be a source of social instability? What about male immigration which directly impacts male-male competition and leads to social upheaval?

Lines 227-228: Sex ratio was used as a group-level predictor of parasitism. However, the operational sex ratio may be more interesting to look at when determining the effects of competition. The number of receptive females is usually much less than the total number of adult females in a baboon group, which affects male-male competition.

Line 237-239: Does the range of maximum temperatures (28.95-35.83 Celsius) refer to daily or monthly temperature?

Lines 242-243: The first measure is *T. trichiura* intensity. Please mention that you are measuring 'intensity' here. All measures (terms) of parasitism, such as intensity and prevalence, should be defined at the outset. Secondly, this measure needs to be defined better. Is egg count the number of eggs per some specific weight of feces?

Lines 244-245: Are all Strongylids considered to be one taxon and therefore count as one when calculating parasite richness?

Lines 260-261: What were the correlation coefficients and p values?

Table S2: this table is very useful as a reference for understanding the many variables used in the models. Would it be possible to include this in the main body of the paper rather than as supplementary material?

Results

Lines 294-295: From Table 1 it appears that strongyles are the second most common parasites, whereas the authors have written that it is the least common of the four types.

Table 2 should also report confidence intervals.

Line 332-337: Is it possible to get an idea of how many groups males typically lived in previously? It seems from Figure 3D that having lived in only one group before is much worse than having lived in two or more groups before (although the error bars are quite large for group sizes 2 and >3). This is something that would be interesting to see a further discussion of.

Discussion

The discussion can be expanded to include more comparative literature as well as to explain findings based on what has been found in other studies. For example, Arlet et al. 2015 found that parasite incidence was greater in immigrant males in mangabeys, and Setchell et al. 2010 found that male mandrills with higher GC levels had higher diversity of parasites. It could also be helpful to draw in more non-primate literature here to understand broader implications, especially as the research on parasitism in mammals has been growing within the past decade or so.

Some of the larger questions that the authors refer to in the introduction that would have been interesting to see addressed are not properly addressed based on their findings. The fact that male dominance rank has no effect on parasite risk in yellow baboons is significant and different from what other studies have found in other primates. What does this result mean? Do we need to be more careful when interpreting the results of other studies that have found such an effect because it could be an artifact of not having controlled for a variable such as age which (rather than rank) may be the real influencing factor? Or are there differences in social or ecological factors that could explain such a difference?

Lines 393-397: But see Arlet et al. 2015. How does this present study compare with that? Arlet et al. 2015 examined many of the same factors in mangabeys. What can be learned from that?

Line 403-405: The relationship between long-term residence in a group (i.e., not dispersing frequently) and higher parasitism does not necessarily mean multiple dispersals are good for males as may be implied from such a result. Group identity was not controlled for in the analyses. Is it possible that residence in specific groups leads to males have higher parasites because those groups specifically harbor more parasites?

Lines 415-418: No references provided.

Lines 438-439: Do younger males forage more on the arthropod vectors of *A. caucasica*?

Lines 433-434: How socially connected are older males compared to younger males? There is also a difference in the types of relationships that older versus younger males have. Younger males may interact more with young adult/subadult females, whereas older males may interact more with infants and juveniles or service relationships with specific older females. All of this would impact how and which parasites are transmitted to different types of males in the group.

Lines 447-448: Is there a rank effect when age is not controlled?

Lines 451-453: How many other groups, on average, do these males reside in?

Lines 455-458: See also Nunn and Dokey 2006 (Biology Letters 2: 351-354).

Lines 459-465: While it is true that social isolation of dispersing males will limit social contact and thus may reduce parasitism, it is also possible that this same social isolation (along with other problems and dangers of dispersal) may be physiologically stressful for males which in turn may lead to higher parasitism (via immunosuppression). If males are moving around between groups, it suggests that they are having a challenging time entering a group or being accepted in a group. So, both as a result of not being socially accepted while in a previous group and during dispersal time when the male is alone, these males may actually be spending a large proportion of time alone and not interacting with others which may be stressful.

Lines 461-463: Males are both socially and sexually isolated when newly immigrated into a group if they have not been socially accepted (which is often the case, and which often leads to these males dispersing repeatedly and more frequently than others). Thus, their risk of parasite infection should be lower.

Lines 463-465: This is an odd hypothesis. Males in good condition would be more likely to be accepted into the group as they would be attractive to at least some of the females in the group and they would also be good competitors in aggressive interactions against other males, making it more likely for these new males to become more long-term members of these new groups.

Lines 481-485: This entire section on the effects of low precipitation on increased parasitism is very interesting. However, the brief explanation feels rather unsatisfactory. Please elaborate, if possible, on the causal pathways and the significance of such a finding on other primates/mammals that also live in dry environments or experience seasonal extremes of rainfall. As climate change becomes an increasingly important issue, more focus seems to be placed on understanding the impacts of rising temperatures and wetness on the spread of parasites. The results from this study would add to that understanding on a factor that is considered less often – that the lack of rainfall can also increase parasitism.

Line 487: In terms of parasite richness, how do the Amboseli baboons compare with other primates? Coinfection by multiple parasites seems to be relatively common. Is parasite richness higher in these yellow baboons compared to other primates?

Lines 493-496: The authors write that their finding that parasite species do not compete and negatively covary is surprising. However, it is quite common to find multiple parasites in single hosts. High parasite richness is common in gregarious species with large degrees of social contact. Parasite richness is determined by several characteristics of the hosts (body size, group size, home range size, diet, etc).

Reviewer: 2

Comments to the Corresponding author

My primary concerns regard the parasitological methods, and thus prevent me from recommending publication. First, some animals were apparently sampled once. This is problematic because of the eggs and cysts are shed intermittently, and a proper diagnose can only be made when multiple samples are obtained, preferably on non-consecutive days, from

the same animal. Second, the authors use *Trichuris* egg counts, drawing many conclusions using them (e.g., even as a signal for cost in male mating effort). Egg counts are not proper markers of host condition or disease state, which is why professional parasitologists do not report them. Simply put, there are no good experiments that can demonstrate the utility of egg counts, and we have known this for a long time. This brings me to the third point: it is unclear if any of the authors did the laboratory work, as these are not indicated in the author contribution section. Did any of them do the actual parasitological analyses?

Other items:

1. How was *Trematoda* spp. diagnosed?
2. How was *Strongyloides fuelleborni* diagnosed without fecal culture?
3. How was *Strongyles* diagnosed?
4. *Strongyloides fuelleborni* is misspelled in Table 1.
5. Why are the data for females being published separately? Of course I understand the behavioral, reproductive, and endocrinological differences, but analyzing the abiotic effects would benefit from a combined analysis, not two separate publications.

=====

Editorial Office email: admin@functionalecology.org

Functional Ecology is a journal of the British Ecological Society.

The British Ecological Society is a limited company, registered in England No. 1522897 and a Registered Charity No. 281213. VAT registration No. 199992863. Information and advice given to members or others by or on behalf of the Society is given on the basis that no liability attaches to the Society, its Council Members, Officers or representatives in respect thereof.