Re: Infectious disease transmission and behavioral allometry in wild mammals
Han, Barbara; Park, Andrew; Jolles, Anna; Altizer, Sonia

Dear Dr. Boots,

Thank you for editing our manuscript and for providing us with the opportunity to submit a revised version. We have addressed all of the comments and suggestions by the associate editor and reviewers (detailed below in blue italicized font). We have also made more explicit our original plans to post all data and code publicly in compliance with JAE data sharing policies and at the specific request of the reviewer. We feel that these constructive comments have improved the manuscript and we hope you will now find our paper suitable for publication in the Journal of Animal Ecology.

Thank you very much for your efforts in the communication of our work.

All the best,

Barbara Han

ASSOCIATE EDITOR COMMENTS TO THE AUTHORS

The revised manuscript has now been seen by one previous reviewer and myself, and we are largely in agreement that the authors have done a good job of revising their manuscript in response to the previous comments - in particular in the justification of using the defensibility index. The reviewer does though raise some additional points that should be addressed, including some further consideration about possible alternative/additional scaling relationships relating to the macroparasite analysis. I have to say I agree with these points, not least because the results of the empirical tests of these predictions were mixed, to say the least. Certainly for macroparasite species richness the predictions are largely upheld, but it seems the empirical data of prevalence largely conflict with the predictions, and I think this is rather glossed over, particularly in the Abstract and first paragraph of the Discussion. For example, contrary to what is stated around line 290, I don't think these specific results provide compelling support the suggestion that home rage size is inversely linked with infection risk. So, I would urge that some of these more general statements are appropriately caveated or toned down.

> ***We have included additional text in the Abstract (lines 36-38) and the first page of the Discussion (line 389-391) to caveat model predictions with contrasting results from the prevalence analysis. We also refer to page 3 of the Discussion (line 434 to the end of the paragraph) for additional text explaining what could be causing helminth prevalence to increase with body size in carnivores.***
>
> ***Did the editor mean line 390, not 290? In general, given how intuitive it seems, we were also surprised at the lack of empirical evidence for a positive relationship between home range size and infection risk in mammals, and have done our best to draw attention the empirical support for this finding throughout the paper. In lines 96-101 of the Introduction we lay out existing empirical evidence for a relationship between home range size and infection risk in mammals. Here we cited 3 studies and a review paper discussing this relationship across multiple mammal clades. We discuss these studies in greater detail in lines 131-147 of the Data sub-section of the Methods, and reiterate these points again in the Discussion (lines 393-399) to remind the reader of this counterintuitive yet empirically well-supported background.***

However, I also wonder whether there is some extra insight these comparisons can provide - the empirical data suggests that parasite species richness decreases with body size (matching the predictions), so increases with intensity of home range use. Converesely, the patterns of parasite prevalence don't match the model predictions, so presumably decrease with intensity of home range use. Does this tell us something about how host behaviour/home range use affects risk of exposure v. diversity of exposure? As with the reviewer, I think it is important to comment a bit more about these macroparasite results, particularly given the mis-matches between macroparasite data and predictions.

> ***For all taxa, the results from prevalence data were corroborated by parasite richness data and model predictions except for macroparasite prevalence in the carnivores. It could be that carnivore macroparasite prevalence patterns are revealing something interesting about their behavior and home range usage, though we hesitate to make any specific statements without additional corroborative results. We have included discussion on the macroparasite results for carnivores in particular, in response to suggestions from Reviewer 1 (see lines 434-446).***

REFEREES' COMMENTS TO AUTHORS
Reviewer: 1

CONFIDENTIAL COMMENTS TO AUTHORS

The authors edits have largely addressed my concerns in providing greater clarity in their methods. In particular, I think the authors now done a very good job in explaining why the intensity of habitat use is a better proxy of the probability of acquiring parasite's free livings stages than the absolute distance traveled in a day - I am very satisfied with their answer.

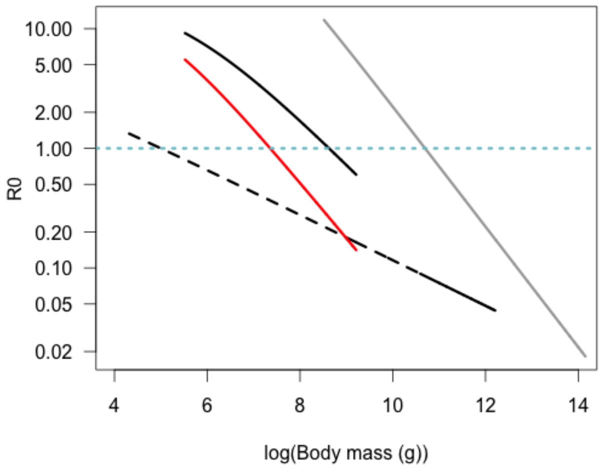
I still think that the draconian separation of the processes driving transmission for micro- and macro-parasites - namely social group size for directly transmitted pathogens and intensity of habitat use only for environmentally transmission macroparasites - may be a bit too extreme: while I agree that the intensity of habitat use decreases with body size, I still believe that that the increase in the social group size might play a role also for the transmission of macroparasites through free living stages. I am probably a bit naïve but, as I mentioned in my first report, I still believe that a large herd of 500-1000 African buffalo may provide fantastic opportunities also for macroparaste to boost their transmission. So, in my vision, I see two allometric processes driving transmission in opposite directions: the decrease in the intensity of habitat use with host body size decreases the probability of transmission, but the increase in social group size with body size might actually increase the probability of transmission.

> ***We completely agree. We have inserted additional text in the Discussion (beginning in line 466) to draw attention to the fact that these transmission processes are not separate in nature, and indeed, macro and microparasite transmission are more than likely simultaneously occurring in any host group.***

Anyway, I also see that the absolute value of the exponent of the allometric relationship between body size and intensity of habitat use is larger than then that of the allometric relationship between body size and social group size. Therefore, even if both processes were occurring at the same time as I am inclined to believe, I think that the outcome would still be a negative exponent, that is, that probability of transmission should decrease with host body size for macroparasite. Therefore, although the actual value of the exponent would be different, the main conclusions of this paper would still old true. Anyway, as the relationship between Ro and log body mass might not be linear (at least it seems so in Figure 3 in the case of primates for macroparasites), I am wondering whether a reduction in the magnitude of the allometric coefficient and a change in the intercept might have an impact on the actual outcome of the analysis for macroparasite as depicted in the right panel of Figure 3. It seems to me that it might be worth exploring this aspect but I hope the authors will excuse me if my comments arise from my oversight or inability to understand some fundamental element in the derivation of their model. If this is the case and I am completely wrong, I apologize for the inconvenience, just let me know.

> ***We agree that the absolute values of scaling exponents differ between the driver explored for microparasite transmission (social group size) and that for macroparasite transmission (intensity of home range use). However, direct comparison of exponents is not especially***

informative as they are embedded in very different expressions for R_0 (Fig. 2). In particular, for R_0 for macroparasite transmission, the transmission rate (beta) appears in the numerator and denominator and increasing the value of scaling parameters (illustrated here with a 20% increase in primate allometric parameters – red line) actually reduces the R_0 for a given body mass. The reviewer is correct when they allude to the fact that the degree of nonlinearity in the relationship shown in Fig. 3B is affected by the value of these allometric parameters since the red line is more linear than its corresponding line (solid black).



For the sake of thoroughness, I have few more minor comments that the authors might want to take into consideration.

There is only a partial correspondence between the allometric exponents reported in Table inserted in the lower left corner of Figure 2 and those reported in the panel of Figure 1: while for the combination of primates and microparasite the regression coefficients are the same, they are slightly different for ungulates. In addition, the match is perfect also for the combination of primates/carnivor and macroparasites, but the intercept is 2.89 for ungulates in Figure 2 while 4.89 in Figure 1: maybe I am missing something, but I suggest the authors to double check it.

Thank you for catching these important typos. The 3 values in the small table inserted in Fig. 2 have been updated to match the coefficients reported in Fig. 1.

PSR, firstly used in Table 1 is never explicitly defined , neither in the main body of the paper, nor in the Table legend. While it becomes clear by reading Appendix S1, the authors might want to explicitly define it in the legend of Table 1.

We have clarified that PSR stands for "parasite species richness" in the legend of Table 1.

There is a "c" in the corner of the lower left panel of Figure 1: this should be either removed or all the panels should be numbered.

We have added back the a, b, and d labels to the panels.

Table 1 is reported twice in the PDF package I downloaded from the Journal's web site. There are two results in the table that are reported in light grey, I do not understand whether it is a typo or whether this brings any information. I assume that the two slashes "//" means that there were not enough data (or no data) to test the regression/correlation.

> ***We mistakenly uploaded Table 1 twice: in the main text and as a separate PDF. We have deleted Table 1 from the text, updated the formatting, and replaced // with "NA". We also found an error in the table, and have replaced "Spearman's rank correlation" in row 3a with "Multivariate regression". We clarified in the legend that, for question 3a, we performed multivariate regressions on all clades expect the primates, which violated normality assumptions. For primates we therefore performed nonparametric statistics (Spearman's rank correlation), and found there was no correlation between residual PSR and body mass.***

Quite interestingly, the relationship between body size and Ro is also allometric in the case of pathogen, with the slope for the ungulates allegedly steeper than in the case of primates (I believe 0.19 vs. 0.13 respectively). Anyway, the authors do not comment nor report this result anywhere in the ms nor in the supplementary information, while it might worth commenting it and discussing what the implications are (if any).

> ***We weren't able to find these particular slope values for primates or ungulates. If we've understood correctly, we can compare the R_0 values between primates and ungulates, which differ in slope values due to allometric scaling. Thus, for primates and ungulates of similar body size, primates will exhibit a greater microparasite R_0 compared to ungulates due to the allometric scaling of their social group sizes (now included in the Discussion, lines 429-431). For the macroparasite scaling (defensibility index), there are many fewer primate and ungulate species which share similar body sizes, but for the narrow region where the largest primates overlap with the smallest ungulates, ungulates reflect greater macroparasite R_0 values due to the allometric scaling of defensibility index. Hopefully this is what the reviewer is referring to?***

It would be useful if the authors declare which type of statistical software was used for their analyses. Figures look like they were made in R CRAN, but I might be wrong.

> ***The reviewer is correct, everything was done using R. We now reference this explicitly at the end of the Methods section.***

Last but not least, it would be really great if the authors will make available the whole database used in the present analysis as online supplementary information (along with the code to analyze it, if in R). This would allow the reader to double check the statistical analyses and, the scientific community to leverage on the excellent work presented in this ms. I understand that the authors might want to keep the database private if they plan to publish further papers out of the same dataset, which would be totally legitimate given the enormous effort required to assemble it. Anyway, I think that the scientific community would immensely benefit from data sharing and public access to scientific data, especially because it might be so difficult to gather them. Therefore, I respectfully ask the authors to assess the possibility of publishing their dataset but I will understand if they refuse to do so.

> ***The majority of these data are already available online (PanTHERIA, and the Global Mammal Parasite Database), but because the data for this study are combined in a unique way we will also post the newly constructed synthetic datasets together with all of the R code to Dryad as well as to Han's website at the Cary Institute. We hope this will encourage others to make use of these data and perhaps build on this work.***

In conclusion, I am satisfied with their revision and, thus, I strongly recommend the ms for publication after having fixed these minor issues.

> ***We are very grateful for the thoughtful and extraordinarily collegial reviews, which served to greatly improve this paper. Thank you.***

Responses to reviewer comments (round 1)

Dear Dr. Boots,

We have revised our manuscript, "*Infectious disease transmission and behavioral allometry in wild mammals*" in response to comments given by two reviewers and the Associate Editor. I have pasted reviewer comments below (in italics) and placed our responses beneath each point.

Associate Editor Comments for Authors:

This manuscript has been seen by 2 reviewers, who both saw good merit in the paper. However, both reviewers also raised a number of points that would need to be addressed, particularly concerning the need to justify and clarify some of the analyses and metrics used, and some of the model assumptions.

In particular, I echo Reviewer 1's query about the D-index (the ratio of range length to home range size), and the assumption that contact rate will increase with this relative metric rather than, for example, absolute day range length.

> AUTHOR RESPONSE: This is an excellent point that we have now clarified in the paper. We used defensibility index instead of absolute day range length because the distance traversed within 24 hrs subsumes important differences in behaviors affecting transmission if home range size is not accounted for. For two species with identical day range lengths, one with a very small home range will mean it is frequently resampling a smaller area, whereas another species with a large home range will likely be encountering 'new' habitat across a large area.
>
> Although one might expect that animals with larger day range length or home range size alone might encounter a greater diversity of parasite species, in fact, past empirical studies in mammals showing that home range size scales negatively with infection risk for many primates, ungulates, and carnivores (citations listed in lines 97-98). Here, we also reference a more recent study (Bordes et al. 2009) which found no support for a positive relationship between home range size and parasite species richness, instead reporting the opposite trend of large home ranges linked with reduced parasite richness and lower risk of helminth infection in primates, ungulates, carnivores, and rodents.
>
> Importantly, for any given parasite species, we might expect that the probability of infection (and continual re-infection) will increase as a host uses a given habitat more

intensely, as hosts will be shedding infectious stages into the environment that are frequently re-acquired. In support of this prediction, Ezenwa et al. (2004b) found that ungulates that showed greater territoriality (regularly patrolling a finite habitat) had more intense infections by parasitic helminths and protozoa. Therefore, we feel that the use of the D-index is the best predictor of this type of habitat re-sampling that can lead to a build up of infectious stages and greater encounters by hosts.

We have tried to better set up our approach beginning in line 90 to the end of the Introduction. We also made sure that our justification for using the D-index instead of day range length was more clearly stated in the Methods in lines 128-143.

The authors find negative relationships between body size and this metric, which could arise either from a negative relationship between body size and range length, or from a positive relationship between body size and home range size. Could the authors explore which it is (presumably they have the data to do so)? It may be that these different relationships have different implications for pathogen contact rate and, as suggested by Reviewer 1, may reconcile the difference between predicted and observed macro-parasite scaling with body size.

AUTHOR RESPONSE: For the mammal groups represented in our study we found positive relationships between both (i) home range size and body size, and (ii) day range length and body size (although the home range size vs. body size relationship was not significant in primates). Thus, the negative scaling of defensibility index described in Figure 1b is driven by allometry in the ratio of the numerator (day range length) and the denominator (home range size), with home range size increasing more rapidly with body size than day range length. As expected, home range size and day range length also scale positively with each other for all clades (except the primates in which there was no allometric scaling of day range length). We describe DRL and home range size analyses in lines 321-328 and 384-388, and have generated an additional figure (Figure S1) and summarized results of regression analyses in an additional appendix (Appendix S2).

I am also wary that really this is only half of the story - the paper considers how host body size affects contact rate (via changes in group size, etc.), but largely ignores how it affects other key parameters. There is some attempt to explore the effect of body size on host mortality for the macro-parasite model, and mention that body size may affect pathogenesis (and also presumably recovery rate, worm mortality, worm fecundity etc...), but those acknowledgments don't get away from the fact that the analyses as they stand are incomplete. As such it is not clear quite what this analysis establishes. While it is presumably not possible to quantify these additional relationships, I would appreciate more acknowledgment of these limitations, and ideally some consideration, either verbally or theoretically, of how these additional relationships could modify the predictions.

AUTHOR RESPONSE: This is a valid point that we have now tried to better address in the revised paper. As the editor notes, it is difficult to quantify all possible scaling relationships that affect host-parasite transmission dynamics, and our present analysis

> advances prior work (that incorporated scaling in demographic rates) by also considering behavioral relationships that underlie transmission. Parasite development and within-host dynamics is challenging to address directly. In our analysis, we did not have access to the kinds of data (linking host body size to infectious period, recovery, parasite longevity, infectious stage production) needed to explore these parasite-oriented relationships. However, we agree that it is important to draw better attention to the potential importance of these factors and limitations of the current work (see lines 244-249).
>
> As suggested, we now discuss how host allometry might affect the within-host infection dynamics (lines 158-165, 246-249). We also illustrate a specific combination of contact rate and disease-induced mortality rate to show how the addition of parasite scaling relationships could modify our predictions of R_0, whilst pointing out both data limitations and the potential for parasite species-specific responses (beginning in line 445).

REFEREES' COMMENTS TO AUTHORS

Reviewer: 1

This is a very neat paper, very well written with a clear presentation of goals, methods and results. Firstly, the authors empirically derived scaling coefficients for estimates of social group size and ranging intensity for three groups of mammals (primates, carnivores and ungulates) through an existing global trait database. Secondly, they applied these relationships to scale the transmission parameter relative to host body size. Thirdly, they explored the consequences of this behavioral allometry for invasibility of host populations by microparasites transmitted directly through close contact, and by macroparasites transmitted environmentally. Finally they provided an empirical test of model predictions for micro- and macro-parasites and controlled for possible sampling biases. They found that, according to model prediction, prevalence and pathogen richness should increase with body size (as mediated by social group size) for microparasites, while they should decrease with body size (as mediated by intensity of home range use). Model predictions were supported by empirical evidence as for the microparasite model, but not for the macroparasite one. The authors provide a honest and comprehensive explanation of why this should be the case.

I think that the papers is very nice, it provides a significant advancement in science and deserves publication on JAE once a small number of potential issues are clearly addressed by the authors.

The less defensible hypothesis seems to me that on the relationship between the contact rate "f" and, ironically, the defensibility coefficient. I want to bring upfront that I might be completely wrong but I am not convinced that transmission is expected to increase proportionally to a relative measure of home range use. If free living stages are randomly distributed in the territory and an individual randomly moves within its home range, it seems to me that, as much as in any prey-predator model, the per-capita probability of encounter *depends, in addition to the density of free living stage, upon the space covered/distance traversed by the host per unit time, namely, an absolute measure of the intensity of home range use.*

As such, I would have used directly the metric of animal movement per day range length, i.e. the distance traversed by an animal with a 24 hour period, and not its ratio over the home range size.

> AUTHOR RESPONSE: As noted in the response to the editor's comments, day range length provides a measure of the distance covered in 24 hours but it does not account for the home range size across which an animal is traversing - so it cannot give a measure of the intensity of home range usage. D-index takes both home range size and distance traversed into account in a simple ratio, and thereby providing the best available measure of the intensity of home range use. To explain this further, the distance traversed within 24 hrs can subsume very different behaviors across species if home range size is not accounted for. For example, for two animals with identical day range lengths, one with a very small home range will mean it could be resampling a small area many times over, while another species with a large home range may always be encountering 'new' habitat across a large area. When trying to assess the intensity of range usage, home range size must be accounted for. D-index does this, while day range length does not. We have now better justified our use of this ratio as an index of the intensity of habitat use and its expected relationship to parasite exposure in the text in both the final paragraph of the Introduction, and in the Methods lines 128-143.

Assuming that day range length scale allometrically with host body size, this alone might transform the relationship between R_0 and host body size for macroparasite from a decreasing to an increasing one, in accordance with empirical observations. I might be completely wrong, but I do not see why an aggregation of thousands of wildebeest in the Serengeti should not be a feast also for macroparasites in terms of opportunities of infection.

> AUTHOR RESPONSE: We agree that this pattern – a negative relationship between infection risk and home range use – is non-intuitive, but it is previously-documented in the literature for helminthic parasites of multiple mammal species (review and meta-analysis in Bordes et al. 2005). As noted in the response to the editor's comments, we have now also better explored the relationships between body size and each component of the the D-index ratio, and address this more fully in the Introduction (beginning line 90), Methods (beginning line 128), Results (beginning line 321), and the Discussion (beginning line 384).

I am also partially puzzled by the micro-parasite model: while I understand the idea of looking at acute diseases with dynamics much faster than host demography, the model reported in Fig. 2 somehow does not account for the impact that the pathogen might have on host demography itself, so it seems to me that it account for only part of the overall story. By using the Kermack and McKendrick (1927) model reported in Fig. 2a, isn't the underlying assumption that disease induced mortality is negligible – which would be in contradiction *with the majority of acute diseases - or is disease induced mortality implicitly included in the "gamma" parameter? And even if so, wouldn't this capture only the first wave of the epidemic and fail to properly describe the long term endemic solutions with all the implications on the discussion about disease prevalence and richness?*

> AUTHOR RESPONSE: The reviewer is correct in pointing out that we do not explicitly include disease-induced mortality in the model or in the expression for R_0 presented in Fig. 2a. However, as the reviewer notes, including disease-induced mortality would have the effect of increasing the overall loss rate from the infectious class, and in this particular simple model, its inclusion can be approximated by considering larger values of the parameter γ. We now mention this limitation in the main text (lines 207-209), but note that for a fixed overall loss rate, the relationship between R_0 and body mass is preserved (i.e. driven by the numerator of R_0, not the denominator, which contains the loss terms). Importantly, we acknowledge that accounting for scaling relationships on within-host dynamics (and resulting effects on host recovery, mortality and parasite shedding) would be a useful goal, but one that is beyond the scope of data available for this study. As noted in the response to the last comment from the editor, we discuss this earlier in the paper (lines 158-165, 246-249) and more fully in the Discussion, beginning in line 445.

About the test on host of well-studied parasites (end of page 12), I do not fully understand the goal of the test, i.e. whether it is to check for biases (and if so, as I think, the authors could explicitly say so when they present the test and/or when they discuss its results) or to corroborate the analysis by using a subset of very well studied species of host and/or parasites. Again, as much as in the previous two cases, I might be completely wrong and miss-understand the main point: if so, I shall be very grateful to the authors if they can help me (and possibly the general reader) to properly understand the implications of each of the two previous assumptions and the goal of the test on host of well-studied parasites.

> AUTHOR RESPONSE: Yes, the reviewer is correct. We examined a subset of well-studied parasite species in an effort to address sampling bias in hosts (not parasites). In particular, we aimed to control for the possibility that larger hosts are better studied, and therefore, their parasite species might also be better studied, thus leading to higher estimates of parasite species richness for larger host species. In particular, specialist parasites of smaller-bodied hosts might not be well represented in the literature, whereas by focusing on common parasites for which diagnostics is We attempted to clarify this further by adding text to the Methods (lines 30-313).

I have also some reservation on the benefits of splitting the data for different mammal groups. While in general there is no doubt that accounting for the individuality of the different mammal groups, in practice by doing so it seems to me that the authors partially reduce the power of their analysis. While all significant, the allometric relationship for social group size for primates explain only 17% of the variance, and that for population density even less, only 7%, so this makes me wonder how much information these allometric relationship actually provide.

> AUTHOR RESPONSE: We considered combining the clades initially, and agree that combining as suggested here would increase statistical power and R^2 in some cases. After some consideration, we felt that a more detailed view for the R0 analyses would be informative, to account for the likelihood of behavioral variation among clades. As noted by Reviewer 1, allometric scaling patterns for social group size and population density in primates were much less apparent compared to the ungulates and the carnivores respectively, but by having access to these clade-specific patterns, readers can get a sense for how invasibility predictions for primates compare to the other clades, which have stronger and more significant allometry. To give a sense for regression results when clades are considered together, we have now added a description of the global trends in the legend of Figure 1.

As similar relationships (at least for population density and life expectancy) have been already published in the literature for different taxa, it would suggest the authors to comment how their findings provide confirmation of previous analysis or whether their depart from existing literature. This is true also for the allometric relationship for population density for carnivore with a remarkably high allometric coefficient (-0.82), in agreement with other studies showing that carnivores have a steeper relationship with body size with respect to herbivores for example, but it could be nice to comment how much and, specifically, how different with respect to the present study.

I wonder about this because I do not fully understand to what extent the results of this study depend upon the specific subset of species for which it was possible to derive the required data or, if this is not the case, whether we can consider the relationships reported in Fig. 1 as the new golden standard - as I hope! - to be used in future studies of allometric scaling with host body size (at least until a newly refined relationship will be published) – per se a sufficiently strong reason to grant publication to the present study. It might also be the case that it is not really important what is the actual allometric coefficient as long as the relationships are decreasing or increasing and if, so, the authors might explicitly mention it.

> AUTHOR RESPONSE: The scaling coefficients we identify are similar to those from previously published work, although there is a range of published values for any given coefficient. As noted by the reviewer, we found carnivore population density to scale allometrically by -0.82, which falls within the range of coefficients published by Peters 1986 (approximately -1.16 using unpublished data on carnivores, and -0.91 when all mammals are considered together) and those reported in primary literature (e.g., -0.75 reported by Carbone and Gittleman (2002). In the revised manuscript, we note the similarity of our scaling coefficients to previous work (e.g., lines 330-332 of the Results).
>
> To further address this comment, in discussing potential future work (in the Discussion section) we note that when synthesizing multiple allometric relationships contributing to parasite transmission, in some cases qualitative effects are likely sufficient and in other cases quantitative comparisons become important (lines 369-376).

I have to say that it is somehow disappointing that the present study cannot include ungulates in the analysis of macroparasite diseases because of the lack of data to compute the D-index, as I assume (maybe erroneously) that herbivores, especially grazers, are more likely than carnivore to pick up free living infective stages (in the case, for instance, of intestinal nematodes) given their feeding mode. If it is assumed that the distance traversed by the host per unit time increases allometrically with host body size, wouldn't this allow to include also ungulate in the analysis?

> AUTHOR RESPONSE: We agree with the reviewer that ungulates are indeed affected by a high diversity of macroparasites, although carnivores and primates also have many, many macroparasites too. Initially were not able to compute the D-index owing to the limited data available on ungulate day range lengths in the published literature. However, we found one study collating data on day range lengths for a number of ungulate species (Carbone et al. 2005), so we have updated our manuscript to include D-Index analyses on this group. In addition to updated figures (Fig 1, Fig 3, Table 1, and Appendix 1), see lines 144-146 in Methods, lines 321-328, 338-344, 374-376 in Results, and lines 386-391 and 414-416 in the Discussion.

As a minor point, I observe the strange way of reporting Ro in Fig. 2, namely: in Fig. 2a at the end of the equation, in Fig. 2b in the middle, with "H" and "d" in the left-hand-side not expressed as a function of host body size, as they are in the equation reported at page 10. I also note that a similar equation for Ro for the microprasite model is not reported in the main body of the paper, presumably at page 8 where I would have expected to see it for symmetry with the macroparasite model.

> AUTHOR RESPONSE: Figure 2 equations only illustrate how transmission was scaled allometrically to reflect host behaviors. The full model is described within the main text (pages 10-11). We did this purely to reduce the business of Figure 2. We added the allometric scaling for parameters in the microparasite model in line 195, which increases the symmetry of model presentations, as suggested. We have also updated the legend for Figure 2 to make more explicit that the figure illustrates how scaling coefficients are incorporated into the transmission term, beta (lines 634-635).

I agree with the authors' comments that there might be (and actually are) other scaling laws to account for and include in the model, so their paper does not necessarily say the very last word on the subject. Yet, I believe that advancements in science are accomplished also through incremental steps and, thus, the fact that not all the theoretically possible allometric relationships have been explicitly included in the model should not prevent publication of a work that otherwise presents great elements of novelty. – Giulio De Leo

Reviewer: 2

This manuscript uses relationships between body size and 1) social group size, and 2) intensity of home-range use, to model changes in the contact process and hence transmission *parameters, and consequently effects on R0, for microparasite and macroparasite infections. Observing a negative relationship between body size and the intensity of home-range use, and population density; and a positive relationship between body size and social group size, and longevity, the authors go on to predict positive relationships between body size and R0 for microparasites, and negative relationships between body size and R0 for macroparasites.*

The manuscript is very well prepared, clear, appropriately concise, and well-written. The figures are well chosen and prepared. Considerable care has been taken to control for biases where possible.

I'm not an expert on the comparative method, but I'm a little surprised that it is generally regarded as not necessary to be concerned about phylogenetic correlation when analyzing data of these sort. The authors state that since their goal is not to 'confirm that relatedness is an underlying driver of allometric scaling' .. it is appropriate to retain the phylogenetic signal. They seem to have precedent on their side (and in fairness don't make statistical inferences about the allometric relationships).

> AUTHOR RESPONSE: The reviewer is correct in noting that we were purely interested in identifying the allometric relationships from the raw data, rather than drawing inferences from data with the phylogenetic signal removed. It is true that more closely related species are more likely to share physical and behavioral characteristics such as body size and group size (as would be estimated by phylogenetic signal). However, analyses to estimate scaling coefficients with the phylogenetic signal removed would offer a different slope than those based on the observed measures alone.

I wonder whether the authors have thought about extending their analysis to consider the effect of body size on critical community size? There are simplistic analytic expressions for CCS in the literature that could be used with equivalent legitimacy as the authors expressions for R0.

> AUTHOR RESPONSE: This is an interesting idea. In general, critical community sizes have been studied and estimated in seasonally-forced systems and shown to depend strongly on details of infectious periods, including distribution (as discussed in Keeling & Rohani, 2008 "Modeling infectious diseases"). The scaling of infectious period distributions with body size is insufficiently studied to allow us to make progress at this time, but we agree that it's an interesting idea for future work.

Minor points: double period on line 256.

> The extra period has been removed.