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My niche: individual spatial niche specialization affects within- and between-species interactions

Annika Schirmer, Julia Hoffmann, Jana A. Eccard and Melanie Dammhahn

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3rd revised submission:	12 December 2019
Final acceptance:	12 December 2019

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

Review History

RSPB-2019-0620.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Marginal

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

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

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
No

Is it clear?
Yes

Is it adequate?
No

Do you have any ethical concerns with this paper?
No

Comments to the Author
In this paper, the authors measure multiple populations of two species of voles to test whether individual differences in boldness behaviour influence their space use in the wild. I think the study is quite interesting and having so much behavioural data on wild animals is quite rare. Additionally, understanding how individual differences in behaviour influence inter-specific interactions is an area of major interest at the moment so it is very timely. At the moment, however, I think the manuscript needs quite a bit of work in terms of streamlining and clarifying the introduction and perhaps more importantly, better clarity in the methods and statistics. I think there are quite some interesting things here, but I just really can't parse out exactly what they were testing with their different statistical models. However, if this can be done, then I think this could be a strong paper.

Major comments:

1 - The intro feels a little scattered at the moment. The first paragraph is about behaviour in general, and it seems like mainly at the within-species level, but then the final line of the paragraph says something about behaviour mediating among-species interactions. The second paragraph then is about spatial behaviour in particular and sort of mostly still focusing at the within-species level (I think?) but then again, the last line of the paragraph is about among-species interactions. Then finally in the third paragraph the authors start talking about behaviour mediating among-species interactions (which I agree, is one of the most understudied aspects of individual behavioural variation). It was also a little unclear how the authors were considering individual "space use" – do they consider this a behavioural trait? Or something different from behavioural differences? Are they saying that some (other) aspect of behaviour predicts individual space use, or that individual space use *is* the behavioural measure? So altogether, by the time I got to the end of the introduction it was unclear to me exactly what the authors were going to measure as behaviour, and then exactly how they were going to measure within- and among- species interactions. An ideal introduction would have given me enough clues that I could predict your study design before you actually describe it in the methods.

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Results: Unfortunately it is just really difficult for me to follow exactly what statistical models were performed and exactly what hypotheses or predictions each model was testing. Right now, the results just feel very much like a laundry list of testing whether each (and every) predictor has some effect on each (and every) measure of space.

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The authors used a combination of mark-recapture and VHF tracking data to quantify intra- and interspecific spatial overlap among individuals of two rodent species. A subset of the animals also had their personality (boldness) assayed at least twice. Each type of data has limitations, but together they present a reasonably clear story about how boldness is related to within and between species patterns of spatial overlap. Although there is considerable interest in how consistent individual differences in personality (or the related concept of behavioral syndromes) might affect space use (movements, habitat preferences, spatial overlap) and ultimately species interactions, to date, relatively few studies have actually quantified how personality relates to space use and/or spatial overlap. Thus on this basis, this study is in the right ballpark to be publishable in a top journal like Proc B. My criticism, however, is that the authors have, in my view, extrapolated and focused on implications regarding niche specialization and species interactions that go well beyond what their data actually show. I would strongly recommend a substantial scaling back of the Discussion and conclusions (including the title) to focus on their actual results with some, but much less speculation on what these results might show about niches or species interactions. I will first discuss the study itself and then elaborate a bit more on my criticism about interpretations.

The authors use three methods to infer relationships between personality and spatial overlap. Each has substantial weaknesses, but putting them all together tells a reasonably consistent story. Although I believe the basic result that boldness relates to spatial overlap, I think the authors should provide a bit more discussion of the limitations of their data.

The first method involves analyses of nearest neighbor distances (NND) using a mean of only 4 captures per individual for only 126 of, I think, about 250 of the animals of these 2 species in these trapping sites. A simple point is that it would be valuable to tell readers how many animals of the two focal species were trapped on site at least once and for each site, what proportion were recaptured often enough to calculate a center of activity for those individuals. Having only roughly ½ of the animals included in the analysis clearly reduces the accuracy of all NND estimates – for many, perhaps most animals, their nearest neighbor might not be part of the data set. In addition, having a mean of only 4 captures per individual is obviously rather shaky for establishing a central location that might be a shifting location over the season. For animals that were captured more often, the authors could subsample to gauge the effect of having a smaller number of captures on their assessment of a central location. Captures were done from August to November. Clearly, if some NNDs were calculated based on animal captures for different individuals that were a few months apart, this poses potential problems. The upshot is that this

metric has weaknesses: although it has larger sample sizes, it is still missing many animals, and each animal's data are rather shaky. The authors might discuss these limitations somewhere in their paper.

A second method involves VHF tracking that produce 96 locations per day with an accuracy of 9.4 +/- 7.3m. Given that NND were often < 10 m, is this accuracy good enough? Perhaps I didn't look carefully enough, but how large were typical home ranges (95% or 50% KDE)? Knowing that would help readers get a better sense of our comfort level with an accuracy +/- 10 meters. Even with this source of random error (that isn't too bad relative to other tracking studies), I would characterize this as a high resolution quantifying of home ranges. The obvious weakness, however, is that this was only done for 36 animals (out of perhaps 150 at these 3 focal study sites – again, it would be nice to know the total number of animals of these two species at these sites). And, this was only done for 4 days for any given individual. It was not clear if this was the same 4 days for all animals, or different days for different animals. In any case, this is clearly a limited data set for assessing spatial overlaps with the purpose of understanding niches and competition. The authors calculated dyadic spatial overlaps for pairs of these 36 animals, but these might be of limited value if most of these dyads did not involve the animals' nearest neighbors, or even animals that were anywhere near a given focal.

A third method involved combining the two types of data by looking at the number of animal home range centers (based on the limited number of recaptures of each of a large number of animals) that were found within the 95% or 50% KDE of the intensively tracked animals (but these were only for a few animals and only for 4 days). Although this method suffered from some of the problems of the 1st two methods, it struck me as relatively good data, though limited by having only 4 days of intensive tracking, and by presumably counting animals that were captured throughout the 3 month season in the calculation of animals that were found in the focal animals' home ranges. That is, I am guessing that many of the animals that were calculated to be in the focal animal's home range were not actually captured during the 4 day period of intensive tracking of the focal animal. Still, this method works well enough as long as the home range locations and sizes of the focals are very stable over the entire season. Are they?

Overall, I am not deeply worried about these limitations because I do not see any reason why they would bias the results towards seeing a relationship between boldness and spatial patterns. Still, I suggest that the authors should discuss the limitations of their methods.

My larger criticism is the extrapolation of spatial overlap to niche specialization and the strength of competition. I am not deeply in the field of niche specialization, but to me, evidence on this would involve information on niches, habitat use or perhaps diets. Specialization seems like it would imply that individuals use habitats in a highly nonrandom way and that there are substantial individual differences in their pattern of nonrandom habitat use. The patterns of spatial overlap reported here do not obviously say much if anything about that. The authors apparently had a recent paper addressing this (ref 37), but the current manuscript does not, in my view, add to it. The further jump to patterns of intra- versus interspecific competition is also tenuous. I am reminded of the classic 1960s/1970s debates on the meaning of niche overlap relative to competition. Some believers in niche theory suggested that high overlap results in strong competition, but others noted that the opposite could also be true – that high competition results in low overlap (competitors avoid or displace each other), so high overlap would reflect low competition. Still others noted that overlap might be unrelated to competition. To me, the resolution of this 'debate' was the recognition of the need for some experiments to directly test the strength of competition. I recognize that the authors are not claiming that they have the final answers about personalities and niche specialization and competition, but many of their conclusions, and much of their discussion goes pretty close to assuming that they have strong

inferences about how spatial overlap relates to competition. Again, I strongly suggest that they substantially scale back the ambitiousness of their discussion and conclusions about competition.

Some minor points:
Regarding a statistical detail: for looking at dyadic spatial overlaps for the 36 tracked animals, they had 418 dyads. I am not sure that this is the correct way to think about it – but I suppose each of the 36 animals could be paired with each of the 35 others = 1260 pairings, but accounting for not double-counting the same pair, leaves us with 630 pairings. Can the authors clarify what criteria were used to identify the 418 that were used in analyses?

A key paper reviewing ideas and data on personalities and space use is Toscano et al. 2016, I think.

The authors present analyses for intraspecific overlaps, interspecific overlaps, and both combined. They might consider not showing the results for overlap with all individuals combined in the main text (i.e., move it to an Appendix). This is not a strong suggestion.

Beyond inferring that patterns of spatial overlap yield insights for niche specialization and competition, the authors also suggest more than once that the fact that bolder animals have larger home ranges suggests that they have access to more resources. They note that this assumes homogeneous habitat quality for the bold versus shy individuals. Is this a good assumption? Others have noted the expectation that animals with higher resource densities in their home range will reduce their home range size since they do not need as a large a home range to meet their energy demands. In parallel with the issue about the relationship between spatial overlap and competition, a key is the direction of cause-effect: does home range size determine resource availability or vice versa? Does spatial overlap determine competition or vice versa?

I apologize that I did not have the time to give line by line suggestions on grammar and style as some reviewers do. Overall, the paper is reasonably well written, though again, the Discussion is too long and speculative.

Decision letter (RSPB-2019-0620.R0)

25-Apr-2019

Dear Ms Schirmer,

I am writing to inform you that your manuscript RSPB-2019-0620 entitled "My niche: within-species individual spatial niche specialisation affects within and between species interactions" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice ofthe Associate Editor and the referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional

circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Yours sincerely,
Loeske Kruuk
Editor

Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
Dear authors,

Two reviewers and myself have read the paper. We all think it is a timely paper and has the potential to be a good contribution to ProcB, but not in its current form. At the moment it is unclear what was tested exactly and why (reviewer 1) and the conclusions extend beyond the results (reviewer 2). These are very crucial points that are raised and should be dealt with, after which it remains to be seen whether the MS continues to be seen as a potentially good contribution to our journal. Given that both above points can possible be remedied by rewriting, I recommend to reject the paper with the possibility to resubmit. Both reviewers provided detailed constructive reviews that include a list of additional specific points that help to improve the MS.

best wishes,
Martijn van de Pol

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
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however, I think the manuscript needs quite a bit of work in terms of streamlining and clarifying the introduction and perhaps more importantly, better clarity in the methods and statistics. I think there are quite some interesting things here, but I just really can't parse out exactly what they were testing with their different statistical models. However, if this can be done, then I think this could be a strong paper.

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The authors present analyses for intraspecific overlaps, interspecific overlaps, and both

combined. They might consider not showing the results for overlap with all individuals combined in the main text (i.e., move it to an Appendix). This is not a strong suggestion.

Beyond inferring that patterns of spatial overlap yield insights for niche specialization and competition, the authors also suggest more than once that the fact that bolder animals have larger home ranges suggests that they have access to more resources. They note that this assumes homogeneous habitat quality for the bold versus shy individuals. Is this a good assumption? Others have noted the expectation that animals with higher resource densities in their home range will reduce their home range size since they do not need as a large a home range to meet their energy demands. In parallel with the issue about the relationship between spatial overlap and competition, a key is the direction of cause-effect: does home range size determine resource availability or vice versa? Does spatial overlap determine competition or vice versa?

I apologize that I did not have the time to give line by line suggestions on grammar and style as some reviewers do. Overall, the paper is reasonably well written, though again, the Discussion is too long and speculative.

Author's Response to Decision Letter for (RSPB-2019-0620.R0)

See Appendix A.

RSPB-2019-2211.R0

Review form: Reviewer 1

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
Yes

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

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
No

Do you have any ethical concerns with this paper?
No

Comments to the Author
The authors have done a great job of revising their introduction. By and large it is much clearer so well done!

I do however, still have some concerns. First about the presentation of their predictions and then again about their methods.

First, I think their predictions could really benefit from some more clarity. The authors state on Line 137 that "the main focus of our study was whether behavioural-dependent individual spatial niche occupation in both species affects their spatial interactions with con- and hetereospecifics". But then the prediction that they stated on Line 143 is still unclear "We predicted that irrespective of species, larger home ranges and core areas of bolder individuals overlap more with those of heterospecific individuals." So does this mean that the authors believe that boldness influences home range which then influences overlap? Or does it mean that among bold animals, those with larger home ranges will have greater overlap? Or does it mean that among those with larger home ranges those that are bolder will have greater overlap? This perhaps seems like a nit-picky point, but I think clarifying exactly the direction of the predictions is critical. The best hypotheses describe some mechanism to explain why something is the way it is, and then the predictions are what logically follow if that hypothesis were true. So it needs to be clearly explained whether the authors think that boldness drives the overlap, or the larger home range, or what.

In the statistical methods:

Line 255: please state explicitly here exactly which behavioural variables this was done for. I think it is the behavioural measures that were collected from the open field and not the CMR right?

Line 266: Here the authors state that "since [the] behavioural tests were done before VHF tracking commence, we could not use a multivariate mixed model approach". This is just categorically not true. The paper that authors cite even include a tutorial with R code in the supplementary material to show exactly who to do this. Dingemanse & Docthtermann's 2013 paper in J. Animal Ecology also has supplementary material showing how to do this (Supplementary Text s17: "Do it yourself: Bivariate models where two phenotypic attributes were both assayed repeatedly but never at the same time). So you can very much use a multivariate approach on behaviors/traits that were collected at different times – the key is that you will be limited to

partitioning the variance only at the among-individual level, but not the within-individual level. But, the among-individual level is what the authors truly care about, so I don't see this as a problem. The paper that the authors cite also explicitly says that using BLUPs as response/predictor variables for further statistical tests is not a good idea (which is exactly what the authors are doing). All of the authors' interpretations hinge on how they are measuring "individual boldness" so this is really a critical point and using bivariate mixed models (which does seem possible here) is really the gold standard for the field and would really make this is rock solid paper in terms of how to measure individual behavioral differences in the field.

Line 283: by individual boldness here the authors mean the BLUPs right? This should be stated explicitly

Line 299: I think the "not" in this sentence is out of place? "The larger sample size allowed us to NOT include individual boldness, species, and sex as fixed factors as well as a three-way interaction between these main factors." I also assume based on this wording that the authors also included all 2-way interactions?

Line 345: change "less" to "fewer"

Review form: Reviewer 3

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
No

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
This is a revised version of a manuscript "My niche: individual spatial niche specialisation affects within and between species interactions". It presents results of research on the effects of boldness on intra- and inter-specific home range overlap. It turns out that relatively to shy individuals, home ranges of bold individuals have little overlap with conspecifics, but high overlap with heterospecifics. This is an interesting example of the ecological significance of individual differences in behavior: through their effects on space use, they might affect intra- and interspecific competition. The Authors interpret their findings in the context of species coexistence.

The manuscript has already received two very thorough reviews and has been substantially changed in response. I know that it can be frustrating to have another person request another, completely different set of changes, so I kept my comments to the minimum.

MAJOR COMMENT
The discussion of individual variation as a mechanism of species coexistence (lines 22-24, 34-36, 395-397, 447-487) strikes me as simplified and based on intuitive arguments presented in opinion papers rather than on results of quantitative analyses (e.g. Hart et al. 2016, Maynard et al. 2019) or empirical data (e.g. Hausch et al. 2018). The Authors assert that increased individual variation leads facilitates coexistence because it limits similarity among competitors. However, the opposite might be true. As an example, Hart et al. (2016) used a mathematical model to demonstrate that intraspecific variation makes coexistence more difficult in three different ways. Among them, intraspecific niche variation increases rather than reduces similarity among competitors.

So, I think that the specific link between individual variation in space use and species coexistence proposed in the manuscript is speculative, and suggest toning it down (e.g. presenting it as only one of possible outcomes) or presenting more concrete arguments.

References:
Hart, S. P., Schreiber, S. J., & Levine, J. M. (2016). How variation between individuals affects species coexistence. Ecology Letters, 19(8), 825-838.

Hausch, S., Vamosi, S. M., & Fox, J. W. (2018). Effects of intraspecific phenotypic variation on species coexistence. Ecology, 99(6), 1453–1462. doi:10.1002/ecy.2346

Maynard, D. S., Serván, C. A., Capitán, J. A., & Allesina, S. (2019). Phenotypic variability promotes diversity and stability in competitive communities. Ecology Letters.

DETAILED COMMENTS
Line 65: only a few studies?
Line 256 & 260: this information is found in tables A2 and A3, not A6 and A7. By the way, please double-check the values in A2. There are rows where results are highly significant even though

SE are very large (e.g. latency to investigate in A. agrarius) and rows where SE=0, but CI are quite wide (e.g. center crossings in A. agrarius).
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Line 419: this info is in Fig. A3, not Fig. A2.
Line 431: should be "boldness scales positively with the number of heterospecific neighbors"?
Line 496: I get that there is a link between boldness and dominance in intraspecific interactions, but why would two bold individuals of different species be competitively balanced?

Decision letter (RSPB-2019-2211.R0)

16-Oct-2019

Dear Ms Schirmer,

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

We are all agreed that this is a very interesting topic and that the manuscript is potentially suitable for Proc B. Some of the reviewers' comments on the revision relate to presentation and clarity, and these should be straightforward to address. A more substantial issue that the revision has highlighted is some of the statistical methods: the Associate Editor and referee set this out clearly below, but the association between boldness and spatial data needs to assessed from the individual-level covariance in a multivariate model. Use of BLUPs can be anti-conservative (I know this from my own work), whereas a multivariate approach allows appropriate estimates of the statistical uncertainty, and it is now widely accepted that this is the appropriate method. I appreciate that the issue should have been picked up with the first version of the manuscript, but the extension of your MCMCglmm analysis to a bivariate model should be straightforward (see the referee's comments). It would be useful to include common names in the abstract (rather than just 'rodents'). The Associate Editor has various useful suggestions of further possibilities to consider, which would be interesting (see below); I leave these your discretion, but you do need to include the bivariate model rather than the BLUPs as a minimum.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

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

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

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

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

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

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

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

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

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the

accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

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

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

Best wishes,
Professor Loeske Kruuk
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
Dear authors,

Thank you for your revision, it has greatly improved the manuscript. Both reviewers and myself have read the revision and have only few remaining points, but these are still important points. One group of points (see both reviewers) is related to the writing of the MS, specifically, the discussion of individual variation as a mechanism of species coexistence and clarity of the predictions.
A second point is more analytical, and could potentially require re-analysis. Reviewer 2 points out this MS uses a stepwise analytical approach, and is quite critical of the use of BLUPs (the use of such shrinkage estimators has been criticized for good reasons, and usage of BLUPS also interfere with uncertainty propagation). I agree with this and even would like to point out that the whole analysis is a three step approach, ant he propogation of uncertainty is not only an issue with using BLUPs for further analyses, but also for the PCAs. First PCAs are used for variable reduction to identify a single 'boldness' variable, then BLUPS of the PCA scores are used to extract individual level boldness scores, and these are then correlated to spatial characteristics. As reviewer 2 points out, ideally one analyses everything in one single model. Reviewer 2 suggests that this can be done for the personality and space use variables using a bivariate mixed model. The authors currently state this is impossible given that VHF data was collected at different times, but the reviewer disagrees. Why would this not be possible in a bivariate model with boldness and e.g. NND? We need to get to the bottom of this. More generally, I was wondering whether a multivariate structural equation model may be able to include all spatial variables and personality variables (you could even use latent variables for boldness and exploration and model its relation to the behavioural measurements and thereby include the 'PCA-like' variable reduction model within this SEM; though I acknowledge that this is not a simple thing to do)? The reason to challenge you to explore this synthetic approach is not in the least because sample sizes are not always the largest in your dataset and therefore uncertainty propagation could be rather important.

AE's Minor comments:
-L105 insides or insights?

- L. 305 Models were simplified via stepwise backward selection by removing interactions when they did not increase model fit based on the Akaike Information Criterion (AIC), with dAIC > 2 between nested models [43]. I do not understand why model selection philosphies are mixed here, and why with dAIC > 2 between nested models was used. For model comparison the model with the lowest AIC is best.
- In results, sample sizes are generally mentioned in the main text, while they are already mentioned in figure legends (redundancy)

Reviewer(s)' Comments to Author:

Referee: 3

Comments to the Author(s).
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DETAILED COMMENTS

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Line 496: I get that there is a link between boldness and dominance in intraspecific interactions, but why would two bold individuals of different species be competitively balanced?

Referee: 1

Comments to the Author(s).
The authors have done a great job of revising their introduction. By and large it is much clearer so well done!

I do however, still have some concerns. First about the presentation of their predictions and then again about their methods.

First, I think their predictions could really benefit from some more clarity. The authors state on Line 137 that "the main focus of our study was whether behavioural-dependent individual spatial niche occupation in both species affects their spatial interactions with con- and hetereospecifics". But then the prediction that they stated on Line 143 is still unclear "We predicted that irrespective of species, larger home ranges and core areas of bolder individuals overlap more with those of heterospecific individuals." So does this mean that the authors believe that boldness influences home range which then influences overlap? Or does it mean that among bold animals, those with larger home ranges will have greater overlap? Or does it mean that among those with larger home ranges those that are bolder will have greater overlap? This perhaps seems like a nit-picky point, but I think clarifying exactly the direction of the predictions is critical. The best hypotheses describe some mechanism to explain why something is the way it is, and then the predictions are what logically follow if that hypothesis were true. So it needs to be clearly explained whether the authors think that boldness drives the overlap, or the larger home range, or what.

In the statistical methods:

Line 255: please state explicitly here exactly which behavioural variables this was done for. I think it is the behavioural measures that were collected from the open field and not the CMR right?

Line 266: Here the authors state that "since [the] behavioural tests were done before VHF tracking commence, we could not use a multivariate mixed model approach". This is just categorically not true. The paper that authors cite even include a tutorial with R code in the supplementary material to show exactly who to do this. Dingemanse & Docthtermann's 2013 paper in J. Animal Ecology also has supplementary material showing how to do this (Supplementary Text s17: "Do it yourself: Bivariate models where two phenotypic attributes were both assayed repeatedly but

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Line 345: change "less" to "fewer"

Author's Response to Decision Letter for (RSPB-2019-2211.R0)

See Appendix B.

RSPB-2019-2211.R1 (Revision)

Review form: Reviewer 1

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
I really applaud the authors for their revisions. Their new analyses are by far the most appropriate for the data they have, and I think will help make this paper stand out as a really excellent and rigorous example of the study of behavioral variation in the field!

Decision letter (RSPB-2019-2211.R1)

09-Dec-2019

Dear Ms Schirmer

I am pleased to inform you that your manuscript RSPB-2019-2211.R1 entitled "My niche: individual spatial niche specialisation affects within and between species interactions" has been accepted for publication in Proceedings B.

Thank you for the work you have put into the revisions of this paper: I'm really pleased that you were able to implement the multivariate models as suggested, and your changes have resulted in an excellent manuscript. The Associate Editor and referee have now recommended publication, but the AE has also suggested some minor revisions to your manuscript. Therefore, I invite you to respond to the AE's comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into https://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally

submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation
It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
• DNA sequences: Genbank accessions F234391-F234402
• Phylogenetic data: TreeBASE accession number S9123
• Final DNA sequence assembly uploaded as online supplemental material
• Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311
NB. From April 1 2013, peer reviewed articles based on research funded wholly or partly by RCUK must include, if applicable, a statement on how the underlying research materials – such as data, samples or models – can be accessed. This statement should be included in the data accessibility section.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link. Please see https://royalsociety.org/journals/ethics-policies/data-sharing-mining/ for more details.

6) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit https://royalsociety.org/journals/authors/author-guidelines/.

Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,

Professor Loeske Kruuk
Editor, Proceedings B
mailto:proceedingsb@royalsociety.org

Associate Editor:
Board Member: 1
Comments to Author:
Dear authors,
This revision is read by the most critical reviewer and myself. We agree that the authors have taken on board the key points (incl. using multivariate mixed model)s , and both the reviewer and I think the comments have been adressed.
I only have a list of minor remarks remaining that should be easy to deal with (see below).

minor points:
-L27 NE-Germany,_. Please spell out NE in the abstract,
-L153 “by” should this word be deleted?
-L317 For completeness, we ran all models also with exploration as a fixed factor instead of boldness as a response variable in bivariate models “. Exploration as fixed factor or as a response variable? I did not understand this sentence.
-For reproducibility It would be good to provide the code of the statistical mixed models as supplementary material . Also I could not find where the data will be stored.
-L332 I was a bit unclear why both SE and CI are presented, especially SE is not the most informative as the +SE and -SE are asymmetric for repeatability (as it is zero-positive).
-In figure 1 panels have no label (a), (b) etc. this would allow for more specific referencing in the results.
-L348. There is no Fig. 5 in the MS.
-L355, which fixed factors?
-Looking at Figure 1 some of the correlations are rather weak. Would it not be more informative to convert the covarianes to correlations in table 1 as these are more easily to interpret? Now we can mainly see from table 1 if covariance estimates are different from zero, but have little clue on whether these are strong or weak associations.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
I really applaud the authors for their revisions. Their new analyses are by far the most appropriate for the data they have, and I think will help make this paper stand out as a really excellent and rigorous example of the study of behavioral variation in the field!

Author's Response to Decision Letter for (RSPB-2019-2211.R1)

See Appendix C.

Decision letter (RSPB-2019-2211.R2)

12-Dec-2019

Dear Ms Schirmer

I am pleased to inform you that your manuscript entitled "My niche: individual spatial niche specialisation affects within and between species interactions" has been accepted for publication in Proceedings B.

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Sincerely,
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

Response to referees

My niche: individual spatial niche specialisation affects within and between species interactions (Manuscript ID RSPB-2019-0620)

Annika Schirmer, Julia Hoffmann, Jana A. Eccard & Melanie Dammhahn
Animal Ecology, Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany

We thank the editors and referee for their thorough comments and helpful suggestions to improve our manuscript. For each of their comments, we provide detailed responses, which are in bold after "**Authors**". Original comments of the referees are kept in italics.

Referee 1:

Major comments:

*1 - The intro feels a little scattered at the moment. The first paragraph is about behaviour in general, and it seems like mainly at the within-species level, but then the final line of the paragraph says something about behaviour mediating among-species interactions. The second paragraph then is about spatial behaviour in particular and sort of mostly still focusing at the within-species level (I think?) but then again, the last line of the paragraph is about among-species interactions. Then finally in the third paragraph the authors start talking about behaviour mediating among-species interactions (which I agree, is one of the most understudied aspects of individual behavioural variation). It was also a little unclear how the authors were considering individual "space use" – do they consider this a behavioural trait? Or something different from behavioural differences? Are they saying that some (other) aspect of behaviour predicts individual space use, or that individual space use *is* the behavioural measure? So altogether, by the time I got to the end of the introduction it was unclear to me exactly what the authors were going to measure as behaviour, and then exactly how they were going to measure within- and among- species interactions. An ideal introduction would have given me enough clues that I could predict your study design before you actually describe it in the methods.*

Authors: The idea of individual niche differentiation links within- and between species levels. First, if individuals occupy only part of a species ecological niche, competitive interactions within species are affected and behaviour should mediate these interactions. Second, within species variation in ecological niche components should affect interactions between species (e.g., between competitors, between predators and prey). In this introduction we therefore always attempted to cover and link these two fundamental aspects. For example, the first paragraph is not "about behaviour" and "at the within-species level" because already in the second sentence (lines: 47-50), we make very explicit that …"variation in how individuals of a population interact with abiotic and biotic components of the environment will affect fundamental ecological interactions, such as within- and between species competition and predator-prey relationships [2–7]". We thank the reviewer very much for pointing out what he/she reads in our introduction and we made great effort to rephrase and clarify aspects that were misleading.

We interpret individual differences in space use as a fitness-relevant aspect of individual niche specialisation (see also Spiegel et al. 2015) because it subsumes how a particular individuals of a population interacts with abiotic and biotic components of the environment. In our view, space use is not a behavioural trait but the outcome of a series of behavioural decisions (where to forage, how to avoid predation). How these behavioural decisions are made is partly determined by inter-individual differences in exploration and boldness, which are the behavioural traits. We added a paragraph specifically on that in the introduction (lines 104 – 114).

I think what the authors did was 1) estimated "boldness" in individuals of two species of co-occurring voles.

Authors: That is what we did, we clarified in the introduction which behavioural traits we assumed to have a large impact on space use, movement and spatial interactions (boldness and exploration) and therefore focused on in this study. Through a previous study we know that for our study species boldness is a strong predictor for space use and movement, which is why put the main focus on the effects of this trait (lines 104-114, 133-136, 268-270).

I would recommend the authors streamline their introduction to really have each paragraph focus on one particular idea and remove redundancies. To me, the strongest introduction would first focus on how behaviour can mediate within-species interactions and individual niche size. Then they could focus on how behaviour and individual niches may influence among-species interactions. Then they can introduce their particular study system and explain how they will measure individual behaviour (boldness) and individual space niches (telemetry and mark-recap). Maybe this is what the authors tried to do, in which case there are probably just some small tweaking of wording that needs to be done (e.g. remove mention of among-species interactions from the paragraphs focusing on within-species interactions).

Authors: See also comments above. Actually the order of paragraphs suggested by the reviewer is the one we had/have in mind. We tried to strengthen the presentation of our thoughts by rephrasing some sentences, deleting some misleading phrases, and adding some details.

Measuring boldness was a major component of this paper, but I felt like boldness was hardly introduced at all in the introduction. In fact, the first mention of "boldness" does not come until Line 141 when the authors are outlining their specific questions. So to me, it felt like this measurement of boldness "came out of nowhere". The entire introduction is about individual space use, but the authors really use boldness as the main predictor in their models so boldness needs to be a major part of the introduction (this might also help address my comment below re: line 70).

Authors: See also comment above. We stressed the focus on boldness as the main behavioural trait at several places in the manuscript (lines 104-114, 133-136, 268-270).

2 - Statistical analyses: In general, I think it is so helpful when authors explicitly state WHY they are performing each test. That is, what exactly is this model helping them test? So on Line 246 the authors state "we used LMM/GLMMs to test our predictions" but please state exactly what

those predictions are again! A good way to do this is to say something like "In order to test our prediction that individual boldness will predict individual space use, we used a linear mixed model with mean trapping point as the response variable and individual boldness as the fixed effect of interest. We additionally include thse other fixed effects etc etc etc" Something like that would majorly help the reader follow exactly what you are doing and WHY.

As it is now, it was really hard for me to parse exactly what all these different models were telling me and how I should interpret the results of them.

Authors: We thank the reviewer for pointing out that our statistical models were not described in sufficient detail. We revised the whole section (methods section 2.6.2, lines 272 - 316) about the statistical models emphasizing which model addresses which predictions and described and justified model structures in more detail.

Minor comments:

Line 70: this statement of "here we did this in this study" seemed to come very early in the introduction. Especially considering the authors then use another 4 paragraphs to set up their study subsequently. Additionally, the phrasing of this particular line seemed circular at first " ….aimed to test whether individual differences in space use facilitate the occupation of individual spatial niches…" So, to me, this read as the authors are using measures of individual space use to see whether that is a good measure of individual space use?? I would honestly remove this line from here – this line is then also essentially repeated at Line 124 where I think it is much more appropriate.

Authors: We deleted the respective sentence and introduce the aim of the study only later on in the introduction (lines 122- 126.

Line 88 & 110: I would be a little careful making such explicit reference to "competition over resources" and "diet" as diet was not explicitly measured in this study at all. All the authors know is that the voles are occupying the same territories and therefore presumably competition over resources/diet should be important, but this is probably just one aspect of competition – they could also be partitioning their territories because of competition over shelter, or predation risk, or mate availability or any number of unmeasured things. If the authors want to focus on diet, then they would have needed to have some measure of gut contents or something similar.

Authors: Indeed, we did intend to refer to competition over all types of resources, including food, shelter, predator-free area etc. We thank the reviewer for pointing out that our phrasing of this point was not clear enough. We did not intend to make explicit references to diet. To our understanding of the term resources summarises more than just those that can be consumed by an animal. The term resource competition therefore was meant to incorporate competition for food, shelter, predator-free area etc. By explicitly mentioning various examples of resources (lines 80-81, 107), we hope to have clarified this issue. Given the studies at hand, available examples from empirical research solely focus on diet, however.

Line 106: "Changes in the degree of individual niche variation across ecological gradients might lead to changes in interspecific competitive interactions" This line really made me think that the authors were going to measure changes in the degree of individual niche variation over time or over some ecological gradient. But they actually didn't do that. So they may just want to rephrase so that the readers aren't expecting one thing, and then get another.

Authors: We thank the reviewer for pointing out, that this sentence was misleading. We rephrased the sentences to direct the focus more on the aspects relevant to our study (lines 98-102).

Line 231: The authors state here that they estimate repeatability for each behavioural variable and then used these behavioural variables into a PCA – but I thought that there were only two behavioural variables that they measured (as stated on Line 183 – "latency head" and "latency body" were measured and (Line 188) "variables from the open-field tests…are omitted here"). So it seems a bit silly to do a PCA on just two behavioural variables? Or if more behavioural variables were included then these need to be explicitly stated here.

Authors: For brevity reasons, we left out many details on the behavioural tests. In fact, we quantified seven behavioural variables in each test. Subsequently, we did a PCA with all behavioural variables to obtain two meaningful components. Variables separated in a way that variables from the open field part of the test (latency-center, number of center crossings, number of sections and activity) loaded on the first component and variables observed in the dark-light part of the test (latency-head, latency-body) loaded on the other component. Based on the variables that represent the components the first one was interpreted as a measure for exploration and the second component as one for boldness. Since exploration had no effect on the response variables in our study or on those measured in a previous study (Schirmer et al. 2019). We refrained from showing results on the effect of exploration. We rephrased the sections to clarify it (lines 184-201). Results of repeatability estimates of single variables and of the PCA are in the electronic supplements.

Line 211: Wow, 10m error rate is really quite high given that these animals are so tiny (that has to be several hundred body lengths right?). It just feels like there is a lot of error that is being propagated in the system (high error rate in the tracking data, and then using BLUPs of this data to predict other things….)

Authors: We are aware that the error of our tracking system is rather high compared to the dimensions of our study subjects. However, we are confident that the observation of space use, movement and static interaction patterns with this method is still valid. The estimation error is the same for all individuals in the study. Effects of consistent individual differences on space use and interaction patterns that were found despite the rather high noise in the data suggest that the found effects are rather large and robust. Furthermore, our method is the only way to estimated space use and spatial interactions in our study species, since direct observation of the animals is not possible due to their lifestyle. Tracking systems with a higher spatial resolution are not applicable for our study species yet. We added some comments on that to the manuscript (lines 222-227).
BLUPs were not calculated based on the tracking data, BLUPs were extracted from the data set of the individual difference test. This data set has much less noise than the data set of space use and movement.

Line 219: The authors state here that they "calculated total, intra- and inter-specific home range overlaps" When I read this initially, I thought this meant that there were 3 measures for the entire study. But then based on the results, rather it looks like the authors actually estimates lots of different home range overlap variables (e.g. between dyadic pairs Line 325). This needs to be explicitly spelled out here.

Authors: We thank the reviewer for pointing out the lack of clarity. We did calculate three different overlap metrics but these metrics were calculated for each dyad of simultaneously tracked individuals. The dyads result from the method of home range overlap calculation. For each individual the overlap to each simultaneously tracked individual per site is calculated in a dyad, therefore for each individual there are several dyads calculated for the home range overlaps. Those dyads were treated as repeated measures of an individual in the statistical analyses. We clarified that aspect by stating:

"For each individual, these spatial overlap metrics were obtained by calculating its home range overlap with every other simultaneously tracked individual at the study site. Repeated sampling of individuals was corrected for in statistical models." (lines 243-246).

Results: Unfortunately it is just really difficult for me to follow exactly what statistical models were performed and exactly what hypotheses or predictions each model was testing. Right now, the results just feel very much like a laundry list of testing whether each (and every) predictor has some effect on each (and every) measure of space.

Authors: We extended the information on which models were calculated and why and hope that it clarifies the presented results. Furthermore, based on the comments from a second reviewer, we shortened the whole result section which hopefully makes it easier to understand.

Referee 2:

The authors used a combination of mark-recapture and VHF tracking data to quantify intra- and interspecific spatial overlap among individuals of two rodent species. A subset of the animals also had their personality (boldness) assayed at least twice. Each type of data has limitations, but together they present a reasonably clear story about how boldness is related to within and between species patterns of spatial overlap. Although there is considerable interest in how consistent individual differences in personality (or the related concept of behavioral syndromes) might affect space use (movements, habitat preferences, spatial overlap) and ultimately species interactions, to date, relatively few studies have actually quantified how personality relates to space use and/or spatial overlap. Thus on this basis, this study is in the right ballpark to be publishable in a top journal like Proc B.

Authors: We thank the reviewer for his/her encouraging comments on the significance of our study.

My criticism, however, is that the authors have, in my view, extrapolated and focused on implications regarding niche specialization and species interactions that go well beyond what their data actually show. I would strongly recommend a substantial scaling back of the

Discussion and conclusions (including the title) to focus on their actual results with some, but much less speculation on what these results might show about niches or species interactions. I will first discuss the study itself and then elaborate a bit more on my criticism about interpretations.

Authors: We think that the implications of within-species niche specialisation on between-species interactions are a fascinating and so far less explored area of research. We agree that some aspects of our discussion were rather speculative but they were intended to stimulate more testing and thinking about the feedbacks between within-species variation and between-species interactions. As suggested by the reviewer, we tuned back and removed speculative aspects from the discussion (see also below).

The authors use three methods to infer relationships between personality and spatial overlap. Each has substantial weaknesses, but putting them all together tells a reasonably consistent story. Although I believe the basic result that boldness relates to spatial overlap, I think the authors should provide a bit more discussion of the limitations of their data.

Authors: We are aware that each of our methodological approaches has limitations and weaknesses, which is an immanent problem true for most field-based studies, particularly those that have to rely on indirect methods because the behaviour of their study subjects is not readily observable. Indirect methodology prevails in a vast number of field studies addressing individual niche specialisation (e.g., via stable isotopes) or spatial patterns (e.g., via GPS), or behavioural variation (e.g., via standardized tests of wild animals in laboratory environments or via ACC). We used a field-based approach because of its ecological validity and made an attempt to combined many methods to help us overcome shortcomings of each single one. As suggested by the reviewer (see also below), we address methodological limitations in more detail in the methods section and the discussion (###) and provide additional "sensitivity" analyses of estimating spatial patterns based on CMR data in the supplementary material. Moreover, we explain in detail below why we think that some of the "limitations" pointed out by the reviewer (e.g., about the temporal patterns or an apparently incomplete subsample, which in fact is a selection of adults only) are actually based on misunderstandings. We hope we have clarified the text in this version of the manuscript to prevent such misunderstandings.

The first method involves analyses of nearest neighbor distances (NND) using a mean of only 4 captures per individual for only 126 of, I think, about 250 of the animals of these 2 species in these trapping sites. A simple point is that it would be valuable to tell readers how many animals of the two focal species were trapped on site at least once and for each site, what proportion were recaptured often enough to calculate a center of activity for those individuals.

Authors: In total we captured 270 individuals, of which 227 were recaptured often enough to calculate a mean trapping point (captured at least twice). Detailed information for each trapping grid is now provided in ESM (Tab. A1).

Having only roughly ½ of the animals included in the analysis clearly reduces the accuracy of all NND estimates – for many, perhaps most animals, their nearest neighbor might not be part of the data set.

Authors: In the analysis determining the nearest neighbour of an individual 227 out of 270 captured individuals from all study sites were included. The subsequent statistical analysis testing the predictions that boldness influences the nearest neighbour distance was than done on a subset of this data. The subset contained only those individuals of known behavioural type whose nearest neighbour was also of known behavioural type (n = 126), i.e. only residential, adult individuals. The probability, that the nearest neighbour of an individual was not the actual residential nearest neighbour (i.e. the main competitor) is therefore rather slim in our data set. We clarified that in the method section by stating:

"Based on CMR data, we calculated for each individual tested for behavioural differences a proxy for its centre of spatial activity as the arithmetic mean trapping point (mean ± SD: 4.3 ± 3.9 captures/individual; n = 227; for sensitivity analysis see Fig. A5). As a measure of the strength of interaction between spatially interacting individuals, we calculated the distance between each individual and its nearest neighbour (con- and heterospecific). Spatial analyses were conducted in the program QGIS (version 2.18.14). Since we are interested in general longer term interaction patters, we restricted subsequent statistical analyses of these spatial interactions to adult individuals of known behavioural type because we assume that only these residential individuals (n = 126) have temporary stable home ranges within our study sites. Hence, we excluded juveniles and transient individuals (captured only once). " (lines 230-230)

In addition, having a mean of only 4 captures per individual is obviously rather shaky for establishing a central location that might be a shifting location over the season. For animals that were captured more often, the authors could subsample to gauge the effect of having a smaller number of captures on their assessment of a central location.

Authors: We thank the reviewer for the suggestion. We added a new analysis to the supplement material (Fig. A2) that compared the calculated mean trapping point of each individual based on different numbers of recaptures for the subset of animals that were recaptured at least 8 times. This analysis supports that the calculated mean trapping points based on 4 captures are sufficiently accurate. We agree with the reviewer, that the centre of activity of an animal can shift with season, however in our study these seasonal differences are rather unlikely. On each study site capturing, personality testing and VHF tracking of individuals stretched only over a time period of approximately two weeks and study sites were visited consecutively. Therefore, all space use data of each individual animal that was part of the study represents more or less a snapshot of its space use and spatial interactions which excludes seasonal dependent shifts and changes. We clarified the process of trapping, individual difference testing and tracking in the method section (line 163-166).

Captures were done from August to November. Clearly, if some NNDs were calculated based on animal captures for different individuals that were a few months apart, this poses potential problems. The upshot is that this metric has weaknesses: although it has larger sample sizes, it is still missing many animals, and each animal's data are rather shaky. The authors might discuss these limitations somewhere in their paper.

Authors: This remark is due to a misunderstanding. Although captures were done from August to November, we did all data collection of a particular site within ca. 2 weeks. Since we put all effort in one site at a time, we created a data set that represents a quasi complete picture of the spatial interactions and behavioural variation at a time for each site but we

had to visit the different study sites sequentially over a couple of months. All spatial interactions that were calculated between individuals (NND, home range overlap) refer to individuals that were on the same study site at the same time. As mentioned above, study sites were visited consecutively, which resulted in the whole study stretching from August to November. On each study site however, the trapping, testing and tracking of individuals was done within approximately 2 weeks and done simultaneously for all individuals on the respective site. We added more information in the method section to clarify these aspects (lines 163-166; 206-208; 211-212).

A second method involves VHF tracking that produce 96 locations per day with an accuracy of 9.4 +/- 7.3m. Given that NND were often < 10 m, is this accuracy good enough? Perhaps I didn't look carefully enough, but how large were typical home ranges (95% or 50% KDE)? Knowing that would help readers get a better sense of our comfort level with an accuracy +/- 10 meters. Even with this source of random error (that isn't too bad relative to other tracking studies), I would characterize this as a high resolution quantifying of home ranges.

Authors: We are aware that the error rate of our tracking system is rather high and resulting in high resolution quantifying of home ranges. However, we are confident that the observation of space use, movement and static interaction patterns with this method is still valid. Despite the rather high noise in the tracking data we found effects of consistent individual differences on space use and interactions pattern which suggests that the found effects are robust. Due to their lifestyle, direct observations of animals is not possible in our study species and tracking systems with higher spatial resolutions are not applicable yet. Therefore the VHF tracking method represents the only way to estimate space use, movement and spatial interactions. The limits set by the tracking method therefore have to be accepted but we believe they are outweighed by the scientific value gained from it. We added the mean home range (bank voles: 2125.47 ± 1811.6 m^2, striped field mice: 2737.10 ± 2045.62 m^2) and core area sizes (bank voles: 530.48 ± 472.13 m^2, striped field mice: 599.62 ± 445.84 m^2) for both species in the results section of the manuscript (lines 335-338).

The obvious weakness, however, is that this was only done for 36 animals (out of perhaps 150 at these 3 focal study sites – again, it would be nice to know the total number of animals of these two species at these sites). And, this was only done for 4 days for any given individual. It was not clear if this was the same 4 days for all animals, or different days for different animals. In any case, this is clearly a limited data set for assessing spatial overlaps with the purpose of understanding niches and competition. The authors calculated dyadic spatial overlaps for pairs of these 36 animals, but these might be of limited value if most of these dyads did not involve the animals' nearest neighbors, or even animals that were anywhere near a given focal.

Authors: The restriction of the sample size is due to the tracking method. Only individuals of a certain body mass can carry the tracking collars and with an increasing number of tracked individuals the resolution of the tracking data gets lower. The system therefore requires a balance between quantity of tracking locations and quantity of individuals that can be tracked at the same time.

Individuals that were tracked on one study site were always tracked simultaneously for the same four days. We emphasized that in the method section (lines 211 -212). Therefore, individuals that did overlap are expected to interact spatially. We agree with the reviewer, that the limited sample size of tracked individuals does not verify that overlapping individuals are actually the ones interacting the most. However, to address that limitation in our data we included the analysis of number of neighbours in the home ranges of tracked individuals. This combination of tracked and captured individuals allowed to consider not only other tracked individuals but nearly all adult residential individuals as potential interaction partners. Since results of home range overlaps and number of neighbours within home ranges show the same effect for boldness, especially on the intraspecific scale, we are rather confident that although we have high resolution estimates of home ranges, their overlaps are of value and the found effects for the influence of boldness on home range overlaps are valid.

A third method involved combining the two types of data by looking at the number of animal home range centers (based on the limited number of recaptures of each of a large number of animals) that were found within the 95% or 50% KDE of the intensively tracked animals (but these were only for a few animals and only for 4 days). Although this method suffered from some of the problems of the 1st two methods, it struck me as relatively good data, though limited by having only 4 days of intensive tracking, and by presumably counting animals that were captured throughout the 3 month season in the calculation of animals that were found in the focal animals' home ranges. That is, I am guessing that many of the animals that were calculated to be in the focal animal's home range were not actually captured during the 4 day period of intensive tracking of the focal animal. Still, this method works well enough as long as the home range locations and sizes of the focals are very stable over the entire season. Are they?

Authors: As mentioned in the comments above, all trapping, testing and tracking of individuals at a respective site happened within two weeks. Seasonal changes in home ranges and population structures are therefore negligible. Over the 4 days of tracking, home ranges were stable and did not change in size.

The mean trapping points of individuals within the home range of a tracked individual belong to animals which were captured immediately before tracking of the focal individuals started. On each site the experimental procedures were always done on successive days (13 ± 3). The probability of those individuals actually interacting if they spatially intersect is therefore rather high. We added more explanation in the methods regarding the time frame of the experiment (lines 163-166).

Overall, I am not deeply worried about these limitations because I do not see any reason why they would bias the results towards seeing a relationship between boldness and spatial patterns. Still, I suggest that the authors should discuss the limitations of their methods.

Authors: As detailed above, we agree with the reviewer because we think that the results obtained should be rather conservative, given the fact that there are some limitations of the methodology (e.g., in the precision of the tracking data).

My larger criticism is the extrapolation of spatial overlap to niche specialization and the strength of competition. I am not deeply in the field of niche specialization, but to me,

evidence on this would involve information on niches, habitat use or perhaps diets. Specialization seems like it would imply that individuals use habitats in a highly nonrandom way and that there are substantial individual differences in their pattern of nonrandom habitat use. The patterns of spatial overlap reported here do not obviously say much if anything about that. The authors apparently had a recent paper addressing this (ref 37), but the current manuscript does not, in my view, add to it.

Authors: In the current manuscript we present data on differences in habitat characteristics of different behavioural types in the study species. We analysed whether the level of ground cover and the maximum vegetation height differed in home ranges of the individuals based on their boldness score. We found that ground cover within the home ranges positively depends on boldness while maximum vegetation height showed a negative relationship. The pattern was the same for both study species and is a major part for concluding individual spatial niche occupation. The results are present in the supplement material (Fig. A3). Since the intraspecific patterns that result from personality-dependent movement and space use, i.e. individual spatial niche specialisation, are not the main focus of this paper and are largely discussed in the cited paper, we refrain from showing results on the microhabitats in the main paper and rather have it in the supplements.

The further jump to patterns of intra- versus interspecific competition is also tenuous. I am reminded of the classic 1960s/1970s debates on the meaning of niche overlap relative to competition. Some believers in niche theory suggested that high overlap results in strong competition, but others noted that the opposite could also be true – that high competition results in low overlap (competitors avoid or displace each other), so high overlap would reflect low competition. Still others noted that overlap might be unrelated to competition. To me, the resolution of this 'debate' was the recognition of the need for some experiments to directly test the strength of competition.

Authors: We agree with the reviewer, that we did not measure actual competition between our study species. However, other studies suggest that our study species do compete strongly over resources (Gliwicz J. 1981; Kozakiewicz A. 1987; Jancewicz E, Gliwicz J. 2017) and that indirect interactions thereby play the most important part (Kozakiewicz A, Boniecki P. 1994). One way to assess indirect interactions is to measure static proxies for them, like the overlap of home ranges. Only individuals that spatially intersect can interact especially indirectly via for example scent marks and exploitation competition, which should be the case between individuals of our study species. We added a section to the discussion clarifying our take on spatial interactions and competition (400-414; 427-435). We agree that an experimental approach is necessary to determine the level of competition between both study species and how consistent individual differences are connected to it. Such an approach is what we are currently working on and so far results support the assumption that the level of home range overlap represent the competition level of individuals from our study species.

I recognize that the authors are not claiming that they have the final answers about personalities and niche specialization and competition, but many of their conclusions, and much of their discussion goes pretty close to assuming that they have strong inferences about how spatial overlap relates to competition. Again, I strongly suggest that they substantially scale back the ambitiousness of their discussion and conclusions about competition.

Authors: Testing directly the strength of competition was not possible in our case since it would have required a completely different study design which would not have been feasible. However, we take the concerns of the reviewer seriously and revised the discussion accordingly.

Some minor points:

Regarding a statistical detail: for looking at dyadic spatial overlaps for the 36 tracked animals, they had 418 dyads. I am not sure that this is the correct way to think about it – but I suppose each of the 36 animals could be paired with each of the 35 others = 1260 pairings, but accounting for not double-counting the same pair, leaves us with 630 pairings. Can the authors clarify what criteria were used to identify the 418 that were used in analyses?

Authors: We thank the reviewer for pointing out, that this was not presented clear enough. Spatial overlaps were only calculated between individuals that were on the same study site, i.e. those which shared the same habitat and which potentially could interact. On three of our five study sites individuals were tracked via VHF telemetry, therefore the sample size of 36 individuals refers to individuals from three subpopulations. Only individuals from the same subpopulation can potentially interact, restricting the number of considerable dyads to 418.

A key paper reviewing ideas and data on personalities and space use is Toscano et al. 2016, I think.

Authors: We thank the reviewer for suggesting this publication. We added it to the references, however in our opinion it is more a key paper for personalities and individual dietary specialisation rather than for personalities and space use. We therefore added it to the references in that context (line 476).

The authors present analyses for intraspecific overlaps, interspecific overlaps, and both combined. They might consider not showing the results for overlap with all individuals combined in the main text (i.e., move it to an Appendix).

Authors: We thank the reviewer for this suggestion and complied with it.

Beyond inferring that patterns of spatial overlap yield insights for niche specialization and competition, the authors also suggest more than once that the fact that bolder animals have larger home ranges suggests that they have access to more resources. They note that this assumes homogeneous habitat quality for the bold versus shy individuals. Is this a good assumption? Others have noted the expectation that animals with higher resource densities in their home range will reduce their home range size since they do not need as a large a home range to meet their energy demands. In parallel with the issue about the relationship between spatial overlap and competition, a key is the direction of cause-effect: does home range size determine resource availability or vice versa? Does spatial overlap determine competition or vice versa?

Authors: We do not have data on the distribution of resources (food, shelter) on the study sites. We base the assumption of higher access to resources by bolder individuals on the assumption of higher competitive ability of bolder individuals. This is supported by other studies as well as unpublished data from us (Microtus arvalis, J.A. Eccard, unpublished data), but also by the higher spatial exclusivity of bolder individuals on the intraspecific scale as well as the increased interactions on the interspecific scale. For both a higher competitive ability is advantageous for bolder individuals and a higher competitive ability is in turn connected to higher resource access. Furthermore, resources do not only refer to food, they also include shelter and predator free area or cover from predators respectively. Since we measured the level of vegetation cover in the home ranges of study individuals our results might refer more to resources in the context of predation risk rather than food. We clarified our definition of resources and revised parts of the discussion:
"Based on the positive relationship between boldness and competitive ability [25], it would be plausible that bolder individuals occupy microhabitats of better quality and/or have higher access to resources (e.g., food, shelter, predator-free area). With the data at hand, we found differences in vegetation cover between home ranges of bold and shy behavioural types (Fig. A2), suggesting that individuals face differences in predation risk." (lines 415-419).

I apologize that I did not have the time to give line by line suggestions on grammar and style as some reviewers do. Overall, the paper is reasonably well written, though again, the Discussion is too long and speculative.

Authors: We thank the reviewer taking the time to read and comment on our manuscript. We revised the discussion thoroughly and shortened it.

Appendix B

Response to referees

My niche: individual spatial niche specialisation affects within and between species interactions (Manuscript ID RSPB-2019-2211)

Annika Schirmer, Julia Hoffmann, Jana A. Eccard & Melanie Dammhahn
Animal Ecology, Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany

We thank the editor and referees for their thorough comments and helpful suggestions to improve our manuscript. For each of their comments, we provide detailed responses, which are in bold and italic after "**Authors**". Original comments of the referees are kept in regular font.

Associate Editor

Comments to Author:

Dear authors,

Thank you for your revision, it has greatly improved the manuscript. Both reviewers and myself have read the revision and have only few remaining points, but these are still important points. One group of points (see both reviewers) is related to the writing of the MS, specifically, the discussion of individual variation as a mechanism of species coexistence and clarity of the predictions.

Authors: We thank both reviewers and the associate editor for taking the time to read and comment on our manuscript. We thoroughly revised the manuscript according to the suggestions and reworked the whole statistical analysis as well as the complete result section. The discussion was revised as well.

A second point is more analytical, and could potentially require re-analysis. Reviewer 2 points out this MS uses a stepwise analytical approach, and is quite critical of the use of BLUPs (the use of such shrinkage estimators has been criticized for good reasons, and usage of BLUPS also interfere with uncertainty propagation). I agree with this and even would like to point out that the whole analysis is a three step approach, ant he propogation of uncertainty is not only an issue with using BLUPs for further analyses, but also for the PCAs. First PCAs are used for variable reduction to identify a single 'boldness' variable, then BLUPS of the PCA scores are used to extract individual level boldness scores, and these are then correlated to spatial characteristics. As reviewer 2 points out, ideally one analyses everything in one single model. Reviewer 2 suggests that this can be done for the personality and space use variables using a bivariate mixed model. The authors currently state this is impossible given that VHF data was collected at different times, but the reviewer disagrees. Why would this not be possible in a bivariate model with boldness and e.g. NND? We need to get to the bottom of this. More generally, I was wondering whether a multivariate structural equation model may be able to include all spatial variables and personality variables (you could even use latent variables for boldness and exploration and model its relation to the behavioural measurements and thereby include the 'PCA-like' variable reduction model within this SEM; though I acknowledge that this is not a simple thing to

do)? The reason to challenge you to explore this synthetic approach is not in the least because sample sizes are not always the largest in your dataset and therefore uncertainty propagation could be rather important.

Authors: We thank the editor and reviewer 2 for the detailed comments and the helpful suggestions for improving our statistical analyses. We have thoroughly revised the statistical analyses of the data and adopted the bivariate model approach suggested by reviewer 2. The focus of the statistics is now on the covariance between boldness and space use parameters and does no longer assume that one predicts the other (section 2.6.2). We decided to use the PCA scores of the second component as a quantitative measure of boldness in the Bayesian models rather than the single measured variables from the individual difference test, since the test itself measures six variables and picking one of them as a measure of boldness would neglect the underlying grouping structure of the data. In fact, the boldness score is composed of two correlated behavioural variables only. We checked whether the single variables that comprise the boldness score (latency to stick the head out of the pipe and the latency to leave the pipe with the whole body) co-vary similarly to the combined boldness score with the spatial parameters and obtained qualitatively similar results. We prefer to present the results for the combined boldness score from the PCA in the main test, but have included the results for the single variables in the supplements (Tab. A7).

AE's Minor comments:

-L105 insides or insights?

Authors: We corrected the wording and changed it into insights.

- L. 305 Models were simplified via stepwise backward selection by removing interactions when they did not increase model fit based on the Akaike Information Criterion (AIC), with dAIC > 2 between nested models [43]. I do not understand why model selection philosphies are mixed here, and why with dAIC > 2 between nested models was used. For model comparison the model with the lowest AIC is best.

Authors: **We reanalysed all models incorporating a Bayesian framework, as a result the whole statistic section *(section 2.6.2)* was revised and the section mentioned above is no longer part of the manuscript.**

- In results, sample sizes are generally mentioned in the main text, while they are already mentioned in figure legends (redundancy)

Authors: We thank the reviewer for pointing that out. We refrained from mentioning the sample sizes in the figure legends and only state them in the main text.

Reviewer(s)' Comments to Author:

Referee: 3

Comments to the Author(s).

This is a revised version of a manuscript “My niche: individual spatial niche specialisation affects within and between species interactions”. It presents results of research on the effects of boldness on intra- and inter-specific home range overlap. It turns out that relatively to shy individuals, home ranges of bold individuals have little overlap with conspecifics, but high overlap with heterospecifics. This is an interesting example of the ecological significance of individual differences in behavior: through their effects on space use, they might affect intra- and interspecific competition. The Authors interpret their findings in the context of species coexistence.

Authors: We thank the reviewer for recognizing the merits of our findings.

The manuscript has already received two very thorough reviews and has been substantially changed in response. I know that it can be frustrating to have another person request another, completely different set of changes, so I kept my comments to the minimum.

MAJOR COMMENT

The discussion of individual variation as a mechanism of species coexistence (lines 22-24, 34-36, 395-397, 447-487) strikes me as simplified and based on intuitive arguments presented in opinion papers rather than on results of quantitative analyses (e.g. Hart et al. 2016, Maynard et al. 2019) or empirical data (e.g. Hausch et al. 2018). The Authors assert that increased individual variation leads facilitates coexistence because it limits similarity among competitors. However, the opposite might be true. As an example, Hart et al. (2016) used a mathematical model to demonstrate that intraspecific variation makes coexistence more difficult in three different ways. Among them, intraspecific niche variation increases rather than reduces similarity among competitors.

So, I think that the specific link between individual variation in space use and species coexistence proposed in the manuscript is speculative, and suggest toning it down (e.g. presenting it as only one of possible outcomes) or presenting more concrete arguments.

References:

Hart, S. P., Schreiber, S. J., & Levine, J. M. (2016). How variation between individuals affects species coexistence. Ecology Letters, 19(8), 825-838.

Hausch, S., Vamosi, S. M., & Fox, J. W. (2018). Effects of intraspecific phenotypic variation on species coexistence. Ecology, 99(6), 1453–1462. doi:10.1002/ecy.2346

Maynard, D. S., Serván, C. A., Capitán, J. A., & Allesina, S. (2019). Phenotypic variability promotes diversity and stability in competitive communities. Ecology Letters.

Authors: We thank him/her for suggesting this literature, some of which had only been published after this manuscript entered the reviewing process. We agree with the reviewer that the jury is still out on whether or not intra-specific trait variation promotes or hinders species coexistence. This is mainly due to a paucity of mechanistic modelling. We revised the section of the discussion on species coexistence and nuanced our argumentation. Moreover, we briefly review the outcome of the available analytical models (lines 452 – 474).

DETAILED COMMENTS

Line 65: only a few studies?

Authors: We revised the sentence to: "Although we know much about how individual behavioural differences affect within-species interaction (e.g., summarized in [17]), fewer studies explored whether and how they modify interactions between species."

Line 256 & 260: this information is found in tables A2 and A3, not A6 and A7. By the way, please double-check the values in A2. There are rows where results are highly significant even though SE are very large (e.g. latency to investigate in A. agrarius) and rows where SE=0, but CI are quite wide (e.g. center crossings in A. agrarius).

Authors: We corrected the table references in the text and checked table A2. We thank the reviewer for pointing out the inconsistencies and corrected the errors.

Line 261: BLUPs are known to be anti-conservative and this should be acknowledged (Hadfield et al. 2009, Houslay et al. 2017 – the later one is already cited in the manuscript).

Authors: We reanalysed our data, ending up with bivariate models assessing the covariance between boldness and spatial parameters, therefore BLUPs are no longer used in this manuscript (section 2.6.2).

Line 278 – ...but there is no info on the distribution families and link functions in Table A5?

Authors: Due to the re-analysis of the data, table 5 was revised, now representing the model structures of the bivariate models.

Line 299: should be "allowed us to include"?

Authors: We revised the sentence accordingly.

Line 417-418: this statement is very cryptic: can you briefly explain what were the differences in vegetation cover and how they can affect predation risk?

Authors: We added some more explanation on the potential connection between vegetation cover and predation risk by adding the following:

"With the data at hand, we found a positive covariance between boldness and percentage of ground cover in home ranges but a negative covariance with maximum vegetation height in home ranges (Fig. A2). These differences in microhabitat occupation of bold and shy individuals could be connected to different predation risks, since the accessibility of predators might differ between microhabitats. Microhabitats with higher levels of maximum vegetation height might be more accessible for ground predators, while those with high ground cover but less maximum vegetation height might be more accessible for avian predators.." (lines 406 – 413).

Line 419: this info is in Fig. A3, not Fig. A2.

Authors: We corrected the figure reference.

Line 431: should be "boldness scales positively with the number of heterospecific neighbors"?

Authors: We thank the reviewer for pointing out this crucial mistake. We corrected the wording to: "In contrast to the within-species pattern, we found that boldness varied positively with interspecific

overlap of home ranges and number of heterospecific neighbours in an individual's home range." (lines 423 – 425)

Line 496: I get that there is a link between boldness and dominance in intraspecific interactions, but why would two bold individuals of different species be competitively balanced?

Authors: The competitive balance between bold individuals of different species is based on the shown connection between boldness and competitive ability, irrespective of the species. Webster et al. (2009) showed that bolder individuals were competitively stronger in interspecific competition scenarios compared to shy individuals. Behavioural variation along the bold-shy axes could therefore be connected to variation in competitive ability of individuals. If two species vary similarly on the behavioural axis, the same might be true for variation in competitive ability. This would mean that individuals of similar behavioural type have similar competitive ability, i.e. are competitively balanced. In terms of species coexistence mechanisms this suggests that consistent inter-individual differences in behaviour could act as an equalising mechanism of species coexistence, balancing competitive differences on the individual level. We revised sections of the discussion to clarify that (lines 452 – 483).

Referee: 1

Comments to the Author(s).

The authors have done a great job of revising their introduction. By and large it is much clearer so well done!

Authors: We thank the reviewer for recognizing the improvements.

I do however, still have some concerns. First about the presentation of their predictions and then again about their methods.

First, I think their predictions could really benefit from some more clarity. The authors state on Line 137 that "the main focus of our study was whether behavioural-dependent individual spatial niche occupation in both species affects their spatial interactions with con- and hetereospecifics". But then the prediction that they stated on Line 143 is still unclear "We predicted that irrespective of species, larger home ranges and core areas of bolder individuals overlap more with those of heterospecific individuals." So does this mean that the authors believe that boldness influences home range which then influences overlap? Or does it mean that among bold animals, those with larger home ranges will have greater overlap? Or does it mean that among those with larger home ranges those that are bolder will have greater overlap? This perhaps seems like a nit-picky point, but I think clarifying exactly the direction of the predictions is critical. The best hypotheses describe some mechanism to explain why something is the way it is, and then the predictions are what logically follow if that hypothesis were true. So it needs to be clearly explained whether the authors think that boldness drives the overlap, or the larger home range, or what.

Authors: We thank the reviewer for pointing out that our predictions were not precise enough. We revised this section of the introduction and made the predictions more precise and comprehensible.

"We hypothesized that individual differences in behaviour are functionally integrated with intra- and interspecific spatial interactions of co-occurring bank voles and striped field mice. We predicted that irrespective of species, boldness positively co-varies with the overlap of home ranges and core areas

of heterospecific individuals due to the positive relationship between boldness and home range size. For the overlap of home ranges and core areas of conspecific individuals, we predicted a negative covariance with boldness, due to the higher spatial exclusivity on the intraspecific scale ([36]; Fig. A1). Based on the assumption of a link between boldness and competitive ability [25], we predicted that bolder individuals of both species spatially interact more with heterospecific individuals and less with conspecific individuals. Specifically, we expected a positive covariance between boldness and the number of neighbours (intra- and interspecific) within their home ranges and core areas, as well as by a positive covariance between boldness and the distances between the home range centre of a focus individual and those of neighbouring individuals (con- or heterospecific). We did not expect exploration to co-vary with spatial interactions within and between species based on a previous study [36]." (lines 142 – 156)

In the statistical methods:

Line 255: please state explicitly here exactly which behavioural variables this was done for. I think it is the behavioural measures that were collected from the open field and not the CMR right?
Authors: We clarified the sentence. "We estimated repeatability for each behavioural variable observed during the individual difference test (section 2.3) using the R package rptR…" (lines 258 – 259).

Line 266: Here the authors state that "since [the] behavioural tests were done before VHF tracking commence, we could not use a multivariate mixed model approach". This is just categorically not true. The paper that authors cite even include a tutorial with R code in the supplementary material to show exactly who to do this. Dingemanse & Docthtermann's 2013 paper in J. Animal Ecology also has supplementary material showing how to do this (Supplementary Text s17: "Do it yourself: Bivariate models where two phenotypic attributes were both assayed repeatedly but never at the same time). So you can very much use a multivariate approach on behaviors/traits that were collected at different times – the key is that you will be limited to partitioning the variance only at the among-individual level, but not the within-individual level. But, the among-individual level is what the authors truly care about, so I don't see this as a problem. The paper that the authors cite also explicitly says that using BLUPs as response/predictor variables for further statistical tests is not a good idea (which is exactly what the authors are doing). All of the authors' interpretations hinge on how they are measuring "individual boldness" so this is really a critical point and using bivariate mixed models (which does seem possible here) is really the gold standard for the field and would really make this is rock solid paper in terms of how to measure individual behavioral differences in the field.

Authors: We thank the reviewer for the helpful suggestions. According to the recommendations, we revised all statistical analyses adapting a bivariate approach. We now focus on the covariance between boldness and spatial interaction parameters, rather than the effect of boldness as a predictor on spatial parameters (section 2.6.2). Qualitatively, all results presented before, using BLUPS, are similar to the estimated covariances.

Line 283: by individual boldness here the authors mean the BLUPs right? This should be stated explicitly

Authors: We revised the whole statistical analysis and no longer use BLUPs (section 2.6.2).

Line 299: I think the "not" in this sentence is out of place? "The larger sample size allowed us to NOT include individual boldness, species, and sex as fixed factors as well as a three-way interaction between

these main factors." I also assume based on this wording that the authors also included all 2-way interactions?

Authors: We corrected the sentence.

Line 345: change "less" to "fewer"

Authors: We changed the wording in the sentence.

Appendix C

Response to referees

My niche: individual spatial niche specialisation affects within and between species interactions (ID RSPB-2019-2211.R1)

Annika Schirmer, Julia Hoffmann, Jana A. Eccard & Melanie Dammhahn
Animal Ecology, Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany

We thank the editor and referee for their comments and helpful suggestions during the revision process. For each of the remaining comments, we provide detailed responses, which are in bold and italic after "**Authors**". Original comments of the referees are kept in regular font.

Associate Editor:

Board Member: 1
Comments to Author:

Dear authors,

This revision is read by the most critical reviewer and myself. We agree that the authors have taken on board the key points (incl. using multivariate mixed models), and both the reviewer and I think the comments have been addressed.

Authors: We thank the Associated Editor for the assessment and the helpful suggestions during the revisions. We are pleased that the major comments were addressed satisfactorily by us.

I only have a list of minor remarks remaining that should be easy to deal with (see below).

minor points:

-L27 NE-Germany,_. Please spell out NE in the abstract,

Authors: We spelled out NE.

-L153 "by" should this word be deleted?

Authors: Yes it should be and we deleted it.

-L317 For completeness, we ran all models also with exploration as a fixed factor instead of boldness as a response variable in bivariate models ". Exploration as fixed factor or as a response variable? I did not understand this sentence.

Authors: We forgot to delete "as a fixed factor". We thank the reviewer for pointing out the mistake and lack of clarity. We ran models with exploration as a response variable. Similarly to the bivariate models with boldness and spatial parameters as response variables, we calculated bivariate models with exploration and spatial parameters as response variables.

-For reproducibility It would be good to provide the code of the statistical mixed models as supplementary material. Also I could not find where the data will be stored.

Authors: We provide the R code for one model as an example in the supplementary material (A13). The data is stored in the open research data portal of the Leibniz Center for Agricultural Landscape Research (ZALF), which is the common data base for the research initiative BioMove of which this study is part of. The data can be accessed via the following links: https://www.doi.org/10.4228/ZALF.DK.129; https://www.doi.org/10.4228/ZALF.DK.131. This is also stated in the data statement of the manuscript.

-L332 I was a bit unclear why both SE and CI are presented, especially SE is not the most informative as the +SE and -SE are asymmetric for repeatability (as it is zero-positive).

Authors: We followed the suggestion of the reviewer and refrained from presenting SEs for the repeatability results. We revised the results section accordingly, as well as the table (Tab. A2) in the supplement presenting the repeatability results of the single variables measured in the individual difference test.

-In figure 1 panels have no label (a), (b) etc. this would allow for more specific referencing in the results.

Authors: We thank the reviewer the suggestions. We added labels (a-f) to each panel of the figure and adjusted the referencing in the manuscript accordingly. Instead of referring to just the figure, we now refer to the specific panel in the figure.

-L348. There is no Fig. 5 in the MS.

Authors: We thank the reviewer for pointing out the error in referencing. The reference is supposed to be for Fig. A5 in the supplement material. We corrected that.

-L355, which fixed factors?

Authors: We specified the fixed factors.

-Looking at Figure 1 some of the correlations are rather weak. Would it not be more informative to convert the covarianes to correlations in table 1 as these are more easily to interpret? Now we can mainly see from table 1 if covariance estimates are different from zero, but have little clue on whether these are strong or weak associations.

Authors: We added the correlation coefficients in table 1 to give a representation of the strength of association between variables.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

I really applaud the authors for their revisions. Their new analyses are by far the most appropriate for the data they have, and I think will help make this paper stand out as a really excellent and rigorous example of the study of behavioral variation in the field!

Authors: We thank the reviewer for the assessment and all the helpful suggestions that help improve the manuscript.