A place for everything and everything in its place: spatial organization of individuals on nests of the primitively eusocial wasp *Ropalidia marginata*

Nitika Sharma and Raghavendra Gadagkar

Review timeline

Original submission:	30 January 2019
1st revised submission:	24 May 2019
2nd revised submission:	3 August 2019
3rd revised submission:	22 August 2019
Final acceptance:	22 August 2019

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

Review History

RSPB-2019-0257.R0 (Original submission)

Review form: Reviewer 1 (James D. Crall)

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?
Acceptable

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?
    Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
See attached file (See Appendix A)

Review form: Reviewer 2

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?
Acceptable

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

Is the length of the paper justified?
No

Should the paper be seen by a specialist statistical reviewer?
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Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
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> **Is it accessible?**
> N/A
>
> **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 paper describes the spatial organization of wasps on their nest. The authors find that most wasps show site fidelity even though brood is randomly distribute throughout the nest – thus the location of the brood does not seem to determine site fidelity. In addition the found a positive relationship between ovarian development and spatial core size. Last, workers tended to avoid queens and spatial overlap in cores was small.

The authors clearly put in a lot of time and effort into collecting the detailed spatial and behavioral data and analyzing it. The data is rich and deep. However, I found the paper to be written as a list of many small findings, without clear connections between them, rather than a cohesive scientific story with hypotheses. Currently it reads like a collection of finding with no connecting theme. It would be helpful to emphasize what brings all these findings together. I would have also liked to see the results placed in a broader framework. What can other scientists who do not study wasps (or social insects) learn from this work? What are some broad principles that this work uncovered? One thing to consider is to include fewer findings that are tightly linked to one another.

The organization of the paper could be improved substantially. The introduction needs to start with a much broader picture and end with the questions and hypotheses that are being tested. It would help to explain how each measure reported on addresses the questions that drove this work. There is a list of 5 questions in the methods somewhere but the mapping between the measures and questions is not clear. Similarly, it would be helpful to guide the reader in the result section and help them understand what questions each result addresses. It would also be helpful to add some figures in the results, where appropriate – for example when reporting on the correlations. Finally, almost every paragraph of the discussion begins with a few sentences that belong in the introduction. Had those sentences been brought in the introduction, the goals of the study would have been clearer.

While this seems like a long list, I think that with a major re-organization, and reading up on more broad literature, the results of the study are robust and the amount of data is impressive. Below I provide detailed comments to assist in revising this work.
Minor comments:
L4: add a sentence that connects the first and second sentences to explain why are social insects an interesting system for examining these questions.
L7-9: too specific for an abstract
L11-13: Start with the positive results and only then go into the negative results.
L15-16: this tradeoff could be introduced earlier.
L45-50: It would be helpful to know the study questions before going into all these details to help the reader understand why you are providing them with all this information.

L50-51: how might these questions be relevant to other systems?

L66: on a grid or exact x, y coordinates?

L70: in it's own core area? Wouldn't this be 50% by definition? This calculation needs to be clarified.

L72: how where these random paths generated?

L75: this paragraph needs to be unpacked. Sentences are too long and there are too many topics in this paragraph. Furthermore, it would help to clarify what biological question each item in the list at the end of the paragraph set out to test. I would suggest introducing these general biological questions clearly in the introduction.

L76-77: what is the binomial response variable? How do you define spatial fidelity? Why is this binomial rather than degree of fidelity?

L78: how do you define and quantify a 'behavioral profile?

L82: how is 'collective colony distribution' defined and quantified

L87: consider flipping the order of this sentence and all others like it to begin with why this was done (statement that starts with 'to…')

L88: why five and how was their positions determined?

L98: what research question is the information in this paragraph addressing?

L109: how is 'behavioral profile' defined?

L112: R is the software that needs to be cited – see their help for how to cite it properly. RStudio is simply the developing environment. Also, what packages were used? Was the statistical analysis also conducted in R or in another software? If in R, what packages?

L118-120: this information already appeared in the methods

L121-122: This information belongs in the methods, not results.

L135-139: would be helpful to report the statistics that support all these statements here. Also seems like results that could be presented in an illuminating figure.

L212-219: these findings seem very interesting – it would have been nice to have some idea on what might drive this relationship building up to this.

L238-242: Belong in the introduction

L250-252: Belong in the introduction

L259: other tasks? Not clear

L268: this paragraph belongs with the previous one

L271-272: introduce this hypothesis in the introduction!

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L281: introduce this hypothesis in the introduction!

L283-285: Belong in the introduction

L294-295: Belong in the introduction

L302-305: are there implications of this work beyond wasps?

Decision letter (RSPB-2019-0257.R0)

20-Mar-2019

Dear Ms Sharma:

I am writing to inform you that your manuscript RSPB-2019-0257 entitled "A place for everything and everything in its place: spatial organization of individuals on nests of the primitively eusocial wasp Ropalidia marginata" has, in its current form, been rejected for publication in Proceedings B. This action has been taken on the advice of the Associate Editor and two referees, who have recommended that substantial revisions are necessary. With this in mind, we are willing to

consider a resubmission, provided that the comments of the Associate Editor and referees are fully addressed.

It is important to note that this is not a provisional acceptance. The resubmission will be treated as a new manuscript. If possible, we will invite the same referees to review the resubmitted manuscript, however, new reviewers will be sought if the original referees are unable to provide reports.

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.

Sincerely,
Victoria Braithwaite

========================
Professor V A Braithwaite
Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
The two experts that evaluated this manuscript both find the data of interest, but they raise a number of important issues with the presentation of the study and the scientific storyline, which requires a major restructuring and rewriting of parts of the paper. They give excellent advice on how the presentation could be improved, which I would like to ask the authors to fully take into account in a thorough revision of this manuscript. Furthermore, referee 1 makes an important point that the relationship between spatial fidelity and core area needs to be clarified. Given the severity of the comments I cannot recommend publication of this paper in its present form, but I suggest the authors resubmit a thoroughly revised version of this manuscript, which will be sent for full review again, if possible to the same referees as before.

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Reviewers' Comments to Author:

Referee: 1
See attached file

==

Referee: 2

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Author's Response to Decision Letter for (RSPB-2019-0257.R0)

See Appendix B.

RSPB-2019-1212.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?
Acceptable

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

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

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

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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
Overall, I believe the manuscript is substantially improved.

However, I do have some remaining concerns that I think should still be addressed. I think many of the overall issues highlighted by Reviewer 2 on organization and structure remain, and the paper could be improved by expanding and clarifying the discussion of motivating hypotheses in the introduction, and discussion.

There also remain some issues on the definition of metrics for spatial fidelity, I believe. In particular, in regards to the test statistic, the authors' response has sufficiently addressed my previous concerns about why the core area is, on average, greater than 50% (although I think it's worth making it more explicit in the manuscript that the "core area" statistic differs from 50%, see note below).

However, the response has not sufficiently addressed my other concern about the test statistic. In particular, variation in the test statistic is almost entirely explained by variation in core area size, rather than occupancy rate of the core area (see my previous comments). In addition, I find the occupancy rate to the be slightly confusing to interpret (i.e., what does it mean that some individuals have an occupancy rate of 1 of their core area, given that core area is intended to estimate 50% occupancy?). My suspicion, in light of the additional and informative information the authors have provided in terms of the biased KDE estimator they use (href), is that variation in occupancy rate is primarily driven by variance in the bias of this estimator across different datasets, and I find the interpretation of this metric fairly unintuitive.

Given this, would it not be more straightforward and facilitate ease of interpretation to simply report the core area size, and then perform statistical test directly on core area, rather than the test statistic? This would still allow for an explicit statistical test of whether individual wasps display

"spatial fidelity" (i.e., have a core area smaller than expected by chance). If not, I think the authors should provide a clearer explanation of why the test statistic is preferable over simply performing statistical tests on core area, and how to interpret the occupancy rate component of the test statistic.

Specific comments:
L8: Should modify here to clarify that the core area does not actually contain, on average, 50% of observations

L53-55: I think the background for these multiple potential hypothesis should be introduced and motivated more fully, given the centrality for the manuscript.

L77-79: Given the points raised above, I don't think this description accurately conveys what the metric tests. As quantified, a wasp would be scored as displaying significant "spatial fidelity" just by having a small core area, and not exclusively by "using its core area more intensively than expected by chance alone," given that most of the variation in the test statistic comes from variation in core area size, not from occupancy rate.

L185: What is the relationship between activity and core area size?

L336-337: Not totally clear to me why the specific result on organizational immunity and no other positive, significant results found are emphasized here.

Figs 2-4: For all figures, I would suggest clarifying what is being plotted (presumably these are effect plots?), and in particular including specifically indicating with the dotted lines and shaded regions (95% CI?) indicate.

Review form: Reviewer 2

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?
Acceptable

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?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
While I'm happy with the answers provided in the response letter to my previous comments, many of the answers were not incorporated into the text. The reason I raised those questions was because the text was not clear about these points and should be revised so that other readers won't have the same questions come up. However, much of the reasoning provided in the response letter is not presented in the paper for other readers to see.

The introduction still does not do a good enough job at introducing the questions the paper set out to study. While I appreciate that the hypotheses were moved to the introduction, the reader is not provided with the justification for why these questions are addressed. What are the broader knowledge gaps the paper is set out to address? Background for each of the 5 hypotheses you set out to test is still missing - why you asked them and what is already known and not known for each particular questions should be presented in the introduction. For example, the way the introduction is currently written, there is no way for a reader to know what you mean by 'organizational immunity'. What is organizational immunity? What spatial patterns would be expected if there was organizational immunity? What is already known about the link between space use and organizational immunity? Similar questions need to be addressed for each of the 5 hypotheses in the introduction, otherwise, it is not clear why you chose to study these hypotheses.

The sub headings in the results section all imply causation when only correlations can be inferred.

Line by line comments:
Line 4: the transition to the second sentence of the abstract is not clear. Why is this 'Although'? seems like the same line of reasoning as the first sentence.
Line 11: list these hypotheses
Line 30: The topic sentence here is not a stand alone. I would suggest not opening it with a contrasting phrase, rather write it as a statement that does not depend on the previous paragraph. E.g. start on 'non-random' and replace 'similar' with something along the lines of 'important'.
Line 39: what are the fitness consequences of this organization? you state in the topic sentence that there are fitness consequences but those are not referred back to in this paragraph.
Line 40: what does non-random distribution of tasks have to do with being highly eusocial? The logic of this sentence is not clear.
Line 42: not clear how wasps provide these opportunities, or why these opportunities would be important to address.

Line 55: the link between space use and the earlier parts of this paragraph is not clear. You start by telling us about the wasps and then go on to telling us about your hypotheses, but why study these hypotheses in this system, is not clear. What are the gaps your study addresses? In addition, each of these hypotheses requires a much more detailed introduction. So for example, instead of talking about a specific study system (elk and wolves) in the first paragraph, introducing the mechanisms that underlie spatial fidelity in more general terms would be more appropriate for this study.

While it is great to have the hypotheses listed here in the introduction the goal of the introduction is to provide background and justification for why you asked the questions and not just list them.

Line 126: not clear from the structure of the sentences if the pooling is of all 155 wasps or of 3 days for each wasp.

Line 131: why is this 'as expected'?

Line 151: grammar of the sentence needs fixing

Figures 1 and 2: I appreciate the addition of these figures to the main text and would suggest having the same y axis on all subplots in each of these figures. It would also be helpful to plot the actual data and not just the model fits (on figure 3 as well). In addition, the text size on the labels could be larger.

Line 161: the phrasing of this suggests causation, but you are only showing correlation. Please edit this, for example to something along the lines of: 'relationship between dominance interactions and spatial distance'.

Line 166: what do you mean by 'trophic interactions'? trophallactic?

Lines 171-172: again stated as a causative statement when what you show is correlative.

Line 185: not clear what you mean by 'inherent'. Do you mean individual variation?

Line 196: 'in order to' suggests causation again when only correlation can be inferred.

Line 223: again, causation vs correlation, could it be that the workers are avoiding the queen rather than the queen avoiding the workers?

Line 232: how could you distinguish who avoided whom?

239-247: this information belongs in the introduction.

255-257: this information belongs in the introduction to justify one of your hypotheses.

Paragraph on 274: the logic of the paragraph seems to move from one topic to another. In addition, it is not clear why you use 'also' in the topic sentence.

Line 297: you did not look at pheromones so this is an odd way to start a discussion on this topic.

Lines 323-327: considering disease transmission was not examined explicitly, this part of the discussion doesn't seem to directly follow from this study.

Conclusions should be more forward looking and broaden the discussion beyond the study system.

Decision letter (RSPB-2019-1212.R0)

15-Jul-2019

Dear Ms Sharma:

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 continue to raise concerns with your manuscript. We have decided that you may have one further opportunity to revise your manuscript to address the issues that have been raised.

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 a short 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,
Victoria Braithwaite

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Professor V A Braithwaite
mailto: proceedingsb@royalsociety.org

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Associate Editor Board Member, Comments to Author:

This paper has been reviewed by the two experts who already commented on the original version of this resubmission. While referee 2 (previously referee1) sees improvement, both referees feel that quite a number of their comments was not incorporated (at least not in the text; some questions were answered in the letter but these questioned aimed at pointing out gaps in the text). Both feel that the introduction still lacks essential elements, including a clear identification of the gap in our knowledge (note that the lack of research in a particular organism as mentioned in line 42 is not the type of gap I am talking about but rather a conceptual gap) as well as an explanation and justification of the tested hypotheses, which should also be expanded in the discussion. After my own reading, I found that the little information about the hypotheses that was present in the original introduction has even been deleted. Just listing them, together with a reference, as it is now is clearly not sufficient. Referee 1 gives an example for one of the hypotheses illustrating what kind of information would be needed for all 5 hypotheses. Furthermore there are still questions about the metrics used to analyse space use. Moreover, there are many detailed comments of both referees to be taken into account. Although both referees were not fully satisfied with the revision, their general tenor was to give the authors a second chance to solve the highlighted issues. It is the policy of PRSB to allow only up to two major

changes to a manuscript, so I would like to urge the authors to closely adhere to the advice and comments by both referees when revising this manuscript and to fully satisfy all concerns. If the authors feel that this is not possible given the length restrictions of the journal then they may consider submitting to a journal that does not have such restrictions.

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Reviewers' Comments to Author:

Referee: 2

While I'm happy with the answers provided in the response letter to my previous comments, many of the answers were not incorporated into the text. The reason I raised those questions was because the text was not clear about these points and should be revised so that other readers won't have the same questions come up. However, much of the reasoning provided in the response letter is not presented in the paper for other readers to see.

The introduction still does not do a good enough job at introducing the questions the paper set out to study. While I appreciate that the hypotheses were moved to the introduction, the reader is not provided with the justification for why these questions are addressed. What are the broader knowledge gaps the paper is set out to address? Background for each of the 5 hypotheses you set out to test is still missing - why you asked them and what is already known and not known for each particular questions should be presented in the introduction. For example, the way the introduction is currently written, there is no way for a reader to know what you mean by 'organizational immunity'. What is organizational immunity? What spatial patterns would be expected if there was organizational immunity? What is already known about the link between space use and organizational immunity? Similar questions need to be addressed for each of the 5 hypotheses in the introduction, otherwise, it is not clear why you chose to study these hypotheses.

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Line 55: the link between space use and the earlier parts of this paragraph is not clear. You start by telling us about the wasps and then go on to telling us about your hypotheses, but why study these hypotheses in this system, is not clear. What are the gaps your study addresses? In addition, each of these hypotheses requires a much more detailed introduction. So for example, instead of talking about a specific study system (elk and wolves) in the first paragraph, introducing the mechanisms that underlie spatial fidelity in more general terms would be more appropriate for this study.

While it is great to have the hypotheses listed here in the introduction the goal of the introduction is to provide background and justification for why you asked the questions and not just list them.
Line 126: not clear from the structure of the sentences if the pooling is of all 155 wasps or of 3 days for each wasp.
Line 131: why is this 'as expected'?
Line 151: grammar of the sentence needs fixing
Figures 1 and 2: I appreciate the addition of these figures to the main text and would suggest having the same y axis on all subplots in each of these figures. It would also be helpful to plot the actual data and not just the model fits (on figure 3 as well). In addition, the text size on the labels could be larger.
Line 161: the phrasing of this suggests causation, but you are only showing correlation. Please edit this, for example to something along the lines of: 'relationship between dominance interactions and spatial distance'.
Line 166: what do you mean by 'trophic interactions'? trophallactic?
Lines 171-172: again stated as a causative statement when what you show is correlative.
Line 185: not clear what you mean by 'inherent'. Do you mean individual variation?
Line 196: 'in order to' suggests causation again when only correlation can be inferred.
Line 223: again, causation vs correlation, could it be that the workers are avoiding the queen rather than the queen avoiding the workers?
Line 232: how could you distinguish who avoided whom?
239-247: this information belongs in the introduction.
255-257: this information belongs in the introduction to justify one of your hypotheses.
Paragraph on 274: the logic of the paragraph seems to move from one topic to another. In addition, it is not clear why you use 'also' in the topic sentence.
Line 297: you did not look at pheromones so this is an odd way to start a discussion on this topic.
Lines 323-327: considering disease transmission was not examined explicitly, this part of the discussion doesn't seem to directly follow from this study.
Conclusions should be more forward looking and broaden the discussion beyond the study system.

===
Referee: 1

Overall, I believe the manuscript is substantially improved.

However, I do have some remaining concerns that I think should still be addressed. I think many of the overall issues highlighted by Reviewer 2 on organization and structure remain, and the paper could be improved by expanding and clarifying the discussion of motivating hypotheses in the introduction, and discussion.

There also remain some issues on the definition of metrics for spatial fidelity, I believe. In particular, in regards to the test statistic, the authors' response has sufficiently addressed my previous concerns about why the core area is, on average, greater than 50% (although I think it's worth making it more explicit in the manuscript that the "core area" statistic differs from 50%, see note below).

However, the response has not sufficiently addressed my other concern about the test statistic. In particular, variation in the test statistic is almost entirely explained by variation in core area size, rather than occupancy rate of the core area (see my previous comments). In addition, I find the occupancy rate to the be slightly confusing to interpret (i.e., what does it mean that some individuals have an occupancy rate of 1 of their core area, given that core area is intended to estimate 50% occupancy?). My suspicion, in light of the additional and informative information

the authors have provided in terms of the biased KDE estimator they use (href), is that variation in occupancy rate is primarily driven by variance in the bias of this estimator across different datasets, and I find the interpretation of this metric fairly unintuitive.

Given this, would it not be more straightforward and facilitate ease of interpretation to simply report the core area size, and then perform statistical test directly on core area, rather than the test statistic? This would still allow for an explicit statistical test of whether individual wasps display "spatial fidelity" (i.e., have a core area smaller than expected by chance). If not, I think the authors should provide a clearer explanation of why the test statistic is preferable over simply performing statistical tests on core area, and how to interpret the occupancy rate component of the test statistic.

Specific comments:
L8: Should modify here to clarify that the core area does not actually contain, on average, 50% of observations

L53-55: I think the background for these multiple potential hypothesis should be introduced and motivated more fully, given the centrality for the manuscript.

L77-79: Given the points raised above, I don't think this description accurately conveys what the metric tests. As quantified, a wasp would be scored as displaying significant "spatial fidelity" just by having a small core area, and not exclusively by "using its core area more intensively than expected by chance alone," given that most of the variation in the test statistic comes from variation in core area size, not from occupancy rate.

L185: What is the relationship between activity and core area size?

L336-337: Not totally clear to me why the specific result on organizational immunity and no other positive, significant results found are emphasized here.

Figs 2-4: For all figures, I would suggest clarifying what is being plotted (presumably these are effect plots?), and in particular including specifically indicating with the dotted lines and shaded regions (95% CI?) indicate.

Author's Response to Decision Letter for (RSPB-2019-1212.R0)

See Appendix C.

Decision letter (RSPB-2019-1212.R1)

19-Aug-2019

Dear Ms Sharma

I am pleased to inform you that your manuscript RSPB-2019-1212.R1 entitled "A place for everything and everything in its place: spatial organization of individuals on nests of the

primitively eusocial wasp Ropalidia marginata" has been accepted for publication in Proceedings B.

The Associate Editor has recommended publication, but also suggests some minor revisions to your manuscript. Therefore, I invite you to respond to their 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 editor and upload a file "Response to Editor". 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,
Victoria Braithwaite

Professor V A Braithwaite
Editor, Proceedings B
mailto:proceedingsb@royalsociety.org

Associate Editor, Comments to Author:

I am by and large satisfied with the revision. The introduction reads well now, also the abstract is much clearer, and the points by the referees have been well incorporated. So I am happy to recommend acceptance pending the minor revisions outlined below.

1) Abstract: reads well now but ends sort of without end, with the results. What is the general conclusion of this study?

2) Line 82: unenveloped? This does not seem to be an English word. Is this a terminus technicus? It needs some explanation

3) Re the new text: "This is to be expected because wasps that show spatial fidelity spend more time in their core areas than expected by chance alone, while wasps that do not show spatial

fidelity spend no more time in their core areas than expected by chance alone, thus it follows that the core areas of wasps showing spatial fidelity should be smaller than those of wasps who do not show spatial fidelity."

This is a lengthy explanation for something not really important (i.e., to explain the "as expected" from the previous version. I understand what you mean, because I worked with kernels previously myself, but for someone who has not, it may sound tautological. I suggest to delete these lines completely.

4) line 362: It is not possible to start this sentence with "Nor". See my suggestion in text file

5) line 353: "in den-sharing possums (***give latin name in brackets***)

6) For a better read, I made a number of very small edits in the text (I used the track-changes word document, which I attach here), taking care not to change the content. In case I may still have changed the content feel free to ignore that edit.

Author's Response to Decision Letter for (RSPB-2019-1212.R1)

See Appendix D.

Decision letter (RSPB-2019-1212.R2)

22-Aug-2019

Dear Ms Sharma

I am pleased to inform you that your manuscript entitled "A place for everything and everything in its place: spatial organization of individuals on nests of the primitively eusocial wasp Ropalidia marginata" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

Your article has been estimated as being 9 pages long. Our Production Office will be able to confirm the exact length at proof stage.

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Paper charges
An e-mail request for payment of any related charges will be sent out shortly. The preferred payment method is by credit card; however, other payment options are available.

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.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

General comments:
       Overall, I think the manuscript is interesting and timely: there is growing interest in spatial dynamics within social insect nests, although study so far has been relatively restricted to ants and bees. Exploring these dynamics, and the ties between spatial dynamics and reproductive physiology and task performance in a primitively eusocial insect nest provides an interesting and informative perspective on these questions.
       I do, however, think there are several aspects of the manuscript that should be addressed to improve the manuscript. First, I'm a bit confused by several aspects of the definition and interpretation of spatial fidelity here. I've included some more specific notes below, but in general it's hard for me to interpret currently to what extent spatial fidelity here is independent of core area. If it's primarily driven by calculations of core area, that should be clarified throughout to make for easier interpretation of results.
       Second, I'm a bit surprised that so few results are presented as figures in the main text. Several of the supplementary figures are important for supporting the key findings of the paper. I would suggest that some of the supplementary figures (especially Figures S2-5) be moved to the main text, at the discretion of the authors in deciding which are most important to support key findings.
       I have included more detailed description of these and other comments throughout the manuscript below.

Specific comments
L4-5: I think it would be useful to motivate the importance of space-use here a bit beyond the fact that it is now being investigated. I.e., why is spatial fidelity and space-use potentially important?
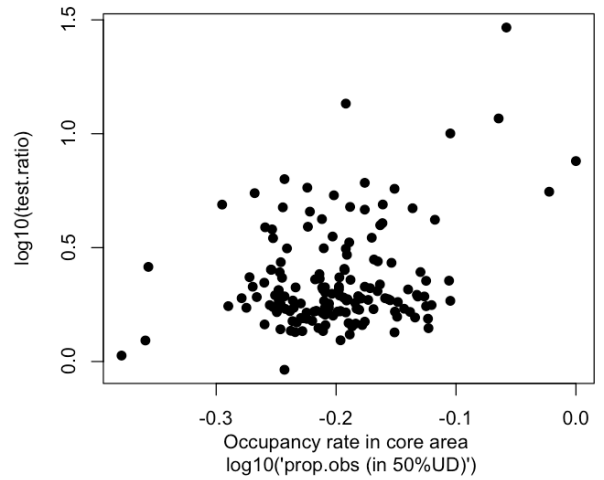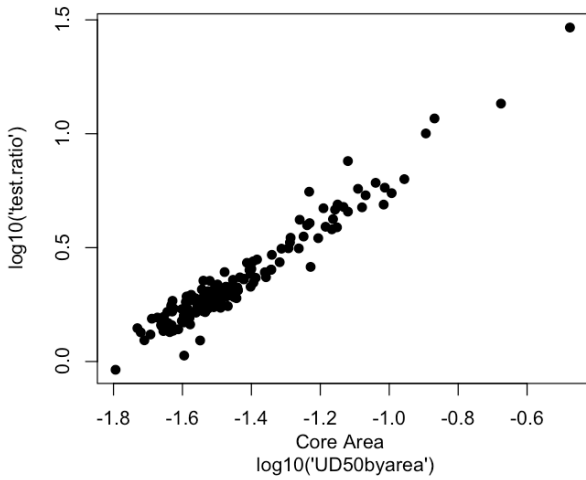
L7-8: "locating a wasp" makes it sound as though it could be the core are for all wasps, regardless of identity. Edit to clarify that this is individual-specific?

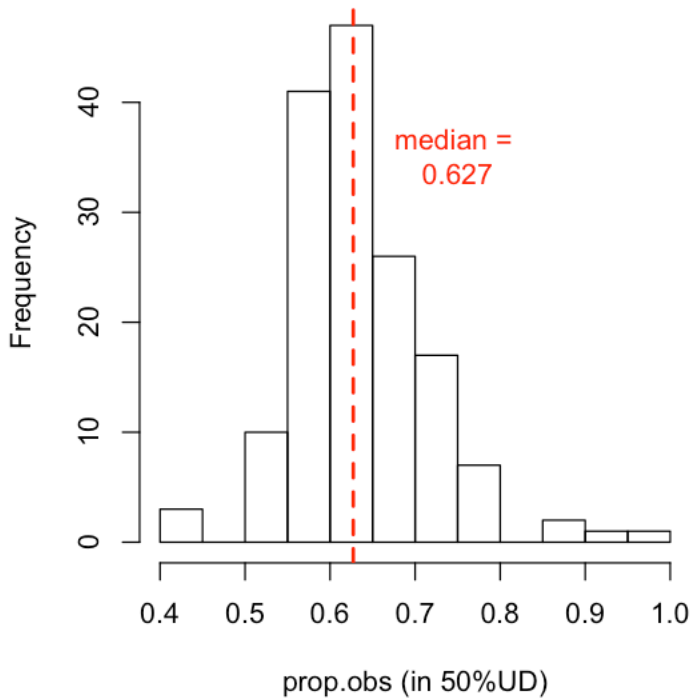L26: "majorly" - perhaps "primarily" instead?

L66: Is this 25,492 total locations, or locations per wasp? Wording makes it sound like the latter, but based on Fig 1 it doesn't appear that there are 25k locations for each wasp...

L70: "... the proportion of observed locations of the wasp that fell in the core area polygon..." – Perhaps I'm misinterpreting this metric, but I understand the 'core area' as a polygon that contains 50% of the total locations for a focal wasp. If that's correct, shouldn't this number always be 0.5? So this metric is essentially equivalent to the inverse of the core area (= 0.5*1/(size of the core area))? In this case, is it correct to interpret the spatial fidelity tests as essentially whether the core areas are smaller than expected by a random walk distribution?

Looking at the raw data, it appears that the 'test.ratio' statistic is indeed very strongly correlated with the estimated core area (left panel), but only weakly correlated with the occupancy rate in the estimate core area (right panel):

Or is the difference that the core area is based on occupancy probabilities derived from the density estimate (KDE), rather than raw data? Again looking at the raw data, the mean occupancy rate of the core area is on average substantially higher than what I would assume is the null expectation of 50%):

How should we interpret deviation from this expectation? Does this suggest some kind of bias in the KDE estimation? And if so, to what extent are these results sensitive to smoothing parameters?

L71-73: Are the simulated data here generated from a random walk model? If so, how is this parameterized? Or, is this just compared to a random, uniform distribution of points within the nest area? Also, are the core areas recalculated for these simulated test ratios (based on the simulated locations), or is the core area from the empirical data retained, and only the # of observations located within the core area varies in the simulated data?

L75: "fitted" should be "fit"

L121-122: Is this the same statistic described in lines 71-73? If so, is it correct that this test statistic could be interpreted either as a shift in rates of location in the core area (compared to the null expectation of 50% based on the definiition of core area) OR the estimated size of the core area (i.e., wasps with a small core area would score higher on the statistic described in lines 71-73 than a random-walk)?

L123: For wasps that didn't show spatial fidelity, how much of these might be explained by lack of statistical power to identify significant differences from the random distributions? Is there a relationship between the number of locations sampled per individual, and the probability of finding spatial fidelity? An alternative - and I think perfectly acceptable - approach would just be to test for spatial fidelity at the whole population, rather than the individual (for example using an anova type approach, among other possibilities), and to interpret either core area or the 'test ratio' as a continuous metric of spatial fidelity, rather than spatial fidelity being described as a binary state that wasps either have or don't have.

L129-131: Again, should be clarified that this is expected from the test statistic (as described in L 71-73), if I'm interpreting correctly

L135-141: These patterns again seem generally consistent with the spatial fidelity metric and nest area being (negatively) correlated.

L215: "was" should be "were"

L238-243: I think this section should be edited to clarify the limitations of previous approaches, given that estimates of area are also central to spatial fidelity as defined here (see discussion above).

L255-257: Refs [6] and [7] in bumblebees (generally considered primitively eusocial) are an exception to this.

L259: Although there is a significant relationship between spatial fidelity and foraging, suggesting at least some ties between task performance and spatial fidelity.

Appendix B

<div align="center">

Authors' responses to editor's and reviewers' comments

(responses in **bold**)

</div>

Associate Editor :

Comments to Author:

The two experts that evaluated this manuscript both find the data of interest, but they raise a number of important issues with the presentation of the study and the scientific storyline, which requires a major restructuring and rewriting of parts of the paper. They give excellent advice on how the presentation could be improved, which I would like to ask the authors to fully take into account in a thorough revision of this manuscript. Furthermore, referee 1 makes an important point that the relationship between spatial fidelity and core area needs to be clarified. Given the severity of the comments I cannot recommend publication of this paper in its present form, but I suggest the authors resubmit a thoroughly revised version of this manuscript, which will be sent for full review again, if possible to the same referees as before.

Thank you very much for the suggestions. We have restructured the scientific storyline now and also differentiated core areas and spatial fidelity more clearly. We do not assume that all individuals use their core areas more than expected by chance alone. We therefore used a statistical test to assess the proportion of wasps that in fact used their core areas more than expected by chance. We use the phrase 'spatial fidelity' to define use of core areas more than expected by chance alone. This has been further clarified in the manuscript (see lines 7-9 and 73-85). More generally, we have also made an effort to improve the clarity of our writing.

Referee 1:

General comments:

Overall, I think the manuscript is interesting and timely: there is growing interest in spatial dynamics within social insect nests, although study so far has been relatively restricted to ants and bees. Exploring these dynamics, and the ties between spatial dynamics and

reproductive physiology and task performance in a primitively eusocial insect nest provides an interesting and informative perspective on these questions.

I do, however, think there are several aspects of the manuscript that should be addressed to improve the manuscript.

First, I'm a bit confused by several aspects of the definition and interpretation of spatial fidelity here. I've included some more specific notes below, but in general it's hard for me to interpret currently to what extent spatial fidelity here is independent of core area. If it's primarily driven by calculations of core area, that should be clarified throughout to make for easier interpretation of results.

We do not assume that all individuals in fact use their core areas more than expected by chance alone. We therefore used a statistical test to assess the proportion of wasps that in fact used their core areas more than expected by chance. We use the phrase 'spatial fidelity' to define use of core areas more than expected by chance alone. This has been further clarified in the manuscript (see lines 7-9 and 73-85).

Second, I'm a bit surprised that so few results are presented as figures in the main text. Several of the supplementary figures are important for supporting the key findings of the paper. I would suggest that some of the supplementary figures (especially Figures S2-5) be moved to the main text, at the discretion of the authors in deciding which are most important to support key findings.

We had previously avoided figures in the main text to stay within the stipulated six-page limit imposed by the journal but in response to the reviewer, we have now added some figures that support major results (Figs. 2-4) in the main text.

I have included more detailed description of these and other comments throughout the manuscript below.

Specific comments

L4-5: I think it would be useful to motivate the importance of space-use here a bit beyond the

fact that it is now being investigated. I.e., why is spatial fidelity and space-use potentially important?

As suggested, we have now described the importance of studying space use in social insects (see lines 4-5 and 30-43).

L7-8: "locating a wasp" makes it sound as though it could be the core area for all wasps, regardless of identity. Edit to clarify that this is individual-specific?

We have now rephrased this sentence for improved clarity (see lines 7-9).
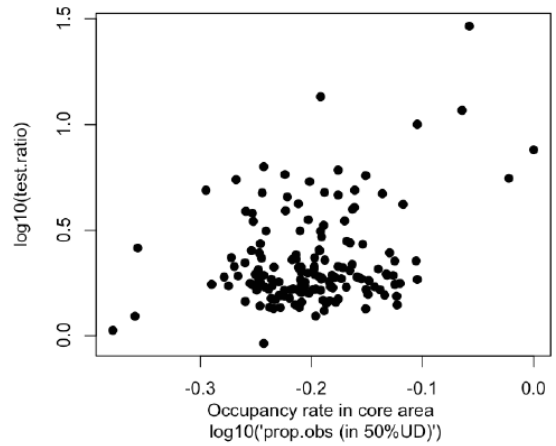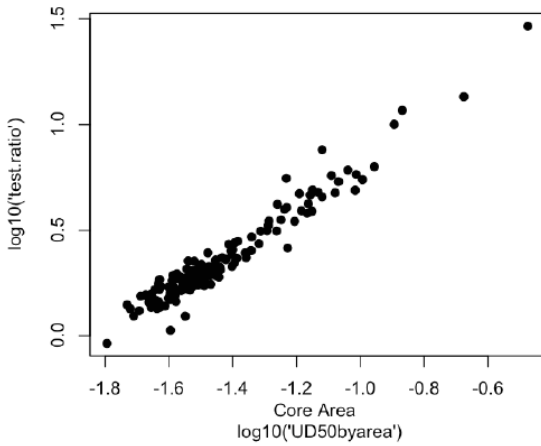
L26: "majorly" - perhaps "primarily" instead?

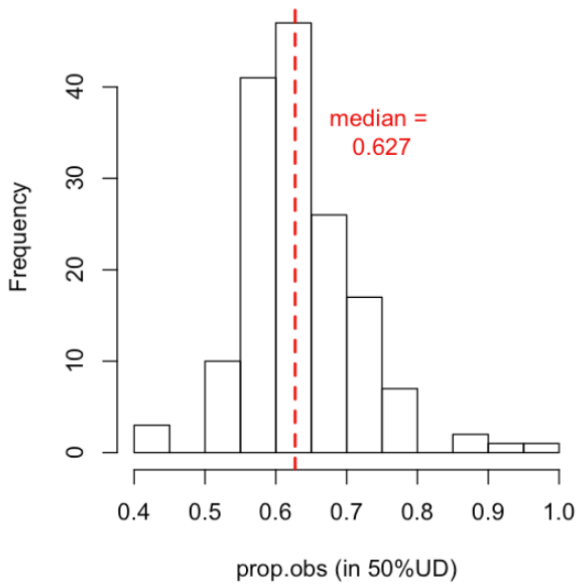**Rephrased as suggested (lines 39 and 56).**

L66: Is this 25,492 total locations, or locations per wasp? Wording makes it sound like the latter, but based on Fig 1 it doesn't appear that there are 25k locations for each wasp...

The total number of locations for all wasps put together was 25,492. This has now been clarified in the manuscript (lines 74-77).

L70: "... the proportion of observed locations of the wasp that fell in the core area polygon..." – Perhaps I'm misinterpreting this metric, but I understand the 'core area' as a polygon that contains 50% of the total locations for a focal wasp. If that's correct, shouldn't this number always be 0.5? So this metric is essentially equivalent to the inverse of the core area (= 0.5*1/(size of the core area))? In this case, is it correct to interpret the spatial fidelity tests as essentially whether the core areas are smaller than expected by a random walk distribution? Looking at the raw data, it appears that the 'test.ratio' statistic is indeed very strongly correlated with the estimated core area (left panel), but only weakly correlated with the occupancy rate in the estimate core area (right panel):

Or is the difference that the core area is based on occupancy probabilities derived from the density estimate (KDE), rather than raw data? Again looking at the raw data, the mean occupancy rate of the core area is on average substantially higher than what I would assume is the null expectation of 50%):

How should we interpret deviation from this expectation? Does this suggest some kind of bias in the KDE estimation? And if so, to what extent are these results sensitive to smoothing parameters?

The smoothing parameter used for the KDE in our study is href which is calculated as href $= ([s_x^2 + s_y^2]/2)^{1/2} \times n^{-1/6}$ (where s_x^2, s_y^2 are estimates of the variances of the x, y locational

data). This smoothing method is known to overestimate the area but is better than traditional methods because it objectively calculates the href for each individual based on the individual variation in spatial data. The Least Squares Cross Validation method (or LSCV) although overcomes the overestimation issue but is known to often fail to converge (pathological LSCV) because of several overlapping locations in the data and thus cannot be relied on. In our case as well, the LSCV failed to converge. The developer of adehabitatHR (the package used to delineate core areas) points out that- According to Seaman and Powell (1998) "This is a difficult problem that has not been worked out by statistical theoreticians, so no definitive response is available at this time" (see lines 34-45 in electronic supplementary material).

Href is thus the most objective approach to calculating smoothing parameter for our data. Calculating 'test ratio' particularly frees us from the overestimation limitation of href because we calculate intensity of use (as proportion of locations per unit core area) to deduce whether an animal shows spatial fidelity. Thus, we do not automatically assume that all wasps use their core areas more intensely than expected by chance alone. We explicitly check for this, using the test ratios and indeed, we find that only 62% of the wasps can really be said to show spatial fidelity. Thus, by explicitly checking for spatial fidelity, we believe that our method of measuring use intensity is a more conservative, robust and reliable method than merely delineating core areas.

L71-73: Are the simulated data here generated from a random walk model? If so, how is this parameterized? Or, is this just compared to a random, uniform distribution of points within the nest area? Also, are the core areas recalculated for these simulated test ratios (based on the simulated locations), or is the core area from the empirical data retained, and only the # of observations located within the core area varies in the simulated data?

We did not use a random walk model. Instead, each simulation for each wasp, involved sampling n locations with replacement (n being the number of frames in which a wasp was sighted on the nest) randomly, from all pooled locations of all wasps. Both core areas and

proportion of locations therein, were recalculated for each simulation. So the total number of frames (out of 300 scanned frames) for which a wasp was located on the nest was kept consistent between observed and simulated data.

So each (of 1000) simulation assumes that the animal could have been located n times (observed sightings of a wasp) in any of the locations ever occupied by any of the wasps on a nest and could vary from a sparse distribution, through intermediate to clumped (preferential space use). Because the core areas are recalculated in each simulation for each wasp, the proportion of locations inside this core area also vary. Only the total number of sightings is retained and the test ratio is recalculated thereafter for each simulation. Once we had the simulated test ratios for each of 155 wasps, we classified each wasp as showing spatial fidelity if its observed test ratio was greater than 95% of the simulated test ratios for that wasp (lines 78-85).

L75: "fitted" should be "fit"

Corrected (line 89)

L121-122: Is this the same statistic described in lines 71-73? If so, is it correct that this test statistic could be interpreted either as a shift in rates of location in the core area (compared to the null expectation of 50% based on the definition of core area) OR the estimated size of the core area (i.e., wasps with a small core area would score higher on the statistic described in lines 71-73 than a random-walk)?

As explained above, we interpret the test statistic as follows: a wasp is considered to show spatial fidelity if its observed test ratio is greater than 95% of the simulated test ratios for that wasp. This is because we wanted to classify wasps into binary categories of showing fidelity or not, rather than have spatial fidelity as a continuous variable. Thus, our test ratio can be interpreted as the intensity of use such that wasps showing spatial fidelity have a greater proportion of locations inside a smaller core area.

L123: For wasps that didn't show spatial fidelity, how much of these might be explained by lack of statistical power to identify significant differences from the random distributions?

We are not sure of the answer to this question. However, we treat the result that 62% of the wasps show spatial fidelity as a conservative estimate; maybe, more wasps show spatial fidelity, but at least 62% do.

Is there a relationship between the number of locations sampled per individual, and the probability of finding spatial fidelity?

There is no relation between the locations sampled per individual and its probability to show spatial fidelity. We used generalized linear mixed effects model with nest as random effect to test if the tendency of a wasp to show spatial fidelity depended on the number of times it was sighted on the nest but we did not find evidence for the same.

glmer(Spatial fidelity (0 or 1) ~ sampled locations of a wasp + (1|nest),family=binomial)

	Estimate	Std. error	z value	Pr(>|z|)
Intercept	0.24	0.41	0.58	0.56
Total sampled locations	0.003	0.002	1.14	0.25

An alternative - and I think perfectly acceptable - approach would just be to test for spatial fidelity at the whole population, rather than the individual (for example using an anova type approach, among other possibilities), and to interpret either core area or the 'test ratio' as a continuous metric of spatial fidelity, rather than spatial fidelity being described as a binary state that wasps either have or don't have.

Maybe, but our goal was to distinguish between wasps that showed and did not show spatial fidelity. Therefore, we adopted the more stringent binary approach after statistical testing to establish that although core areas may be generated for all animals in response to even random aggregation of locations, these animals need not show spatial fidelity. The lack of such rigorous hypothesis testing has been criticized in greater detail in some studies (Richardson *et al.*, 2017). Additionally, we do not lose biological significance of this information by having a binary cut off. We emphasize in our study that the same population might benefit or not from showing spatial fidelity based on their biological roles in the society. For instance, feeders may not prefer to preferentially use a part of the nest if their task involves patrolling the entire nest (see lines 266-272).

L129-131: Again, should be clarified that this is expected from the test statistic (as described in L 71-73), if I'm interpreting correctly

Yes, this is expected (although not guaranteed) and we have said so in the manuscript (lines 75-85).

L135-141: These patterns again seem generally consistent with the spatial fidelity metric and nest area being (negatively) correlated.

The two are indeed negatively correlated.

$$\text{Test ratio} = \frac{\text{proportion of all observed locations of the wasp that fall in the core area polygon}}{\text{proportion of total nest area that is occupied by the delineated core area polygon}}$$

L215: "was" should be "were"

Corrected (line 189)

L238-243: I think this section should be edited to clarify the limitations of previous approaches, given that estimates of area are also central to spatial fidelity as defined here (see discussion above).

This section has now been edited to explain that rigorous hypothesis testing is important to differentiate preferential use from random use (lines 241-254).

L255-257: Refs [6] and [7] in bumblebees (generally considered primitively eusocial) are an exception to this.

Yes, we agree. This has been clarified (line 57).

L259: Although there is a significant relationship between spatial fidelity and foraging, suggesting at least some ties between task performance and spatial fidelity.

We agree and have said so in revised manuscript (lines 259-263).

Referee 2:

This paper describes the spatial organization of wasps on their nest. The authors find that most wasps show site fidelity even though brood is randomly distribute throughout the nest – thus the location of the brood does not seem to determine site fidelity. In addition they found a positive relationship between ovarian development and spatial core size. Last, workers tended to avoid queens and spatial overlap in cores was small.

The authors clearly put in a lot of time and effort into collecting the detailed spatial and behavioral data and analyzing it. The data is rich and deep. However, I found the paper to be written as a list of many small findings, without clear connections between them, rather than a cohesive scientific story with hypotheses. Currently it reads like a collection of finding with no connecting theme. It would be helpful to emphasize what brings all these findings together. I would have also liked to see the results placed in a broader framework. What can other scientists who do not study wasps (or social insects) learn from this work? What are some broad principles that this work uncovered? One thing to consider is to include fewer findings that are tightly linked to one another.

The organization of the paper could be improved substantially. The introduction needs to start with a much broader picture and end with the questions and hypotheses that are being tested. It

would help to explain how each measure reported on addresses the questions that drove this work. There is a list of 5 questions in the methods somewhere but the mapping between the measures and questions is not clear. Similarly, it would be helpful to guide the reader in the result section and help them understand what questions each result addresses. It would also be helpful to add some figures in the results, where appropriate – for example when reporting on the correlations. Finally, almost every paragraph of the discussion begins with a few sentences that belong in the introduction. Had those sentences been brought in the introduction, the goals of the study would have been clearer.

We have changed the narrative of the paper to include references from across the animal kingdom both in the introduction as well as while discussing our results [ref 1-8, 26, 27, 30-35]. We have clearly divided the paper in first establishing preferential space use by rigorous hypothesis testing and thereafter testing 5 hypotheses that were previously put forth to explain non-random space use in social insects (lines 46-57). The results section now has each result listed under a question it answers, particularly in context of a hypothesis being tested. The implications of our results beyond social insects have also been discussed (lines 321-330).

While this seems like a long list, I think that with a major re-organization, and reading up on more broad literature, the results of the study are robust and the amount of data is impressive. Below I provide detailed comments to assist in revising this work.

Minor comments:
L4: add a sentence that connects the first and second sentences to explain why are social insects an interesting system for examining these questions.

Changed as suggested (line 4-5)

L7-9: too specific for an abstract

We have edited the abstract to reflect comments from both reviewers.

L11-13: Start with the positive results and only then go into the negative results.

Abstract has been re-written as suggested (lines 11-14).

L15-16: this tradeoff could be introduced earlier.

Abstract has been re-written as suggested.

L45-50: It would be helpful to know the study questions before going into all these details to help the reader understand why you are providing them with all this information.

Manuscript has been edited as suggested (lines 46-57)

L50-51: how might these questions be relevant to other systems?

Our finding that the potential queens do not necessarily avoid the queens may be because the queen rubs her pheromone on the nest surface. The opposite result might be obtained where queens release pheromones directly into the air, making them the only source of queen pheromones. Thus, non-random space use is expected to vary depending on the detailed behavior and physiology of different species and hence, we have not speculated too much about other systems.

L66: on a grid or exact x, y coordinates?

Exact x-y coordinates to the resolution of a pixel. 1cm=125 pixels

L70: in it's own core area? Wouldn't this be 50% by definition? This calculation needs to be clarified.

Yes, in a wasp's own core area. Yes, it is expected that the proportion of locations inside the core area may be around 50% but this is not guaranteed. The smoothing parameter used for the KDE in our study is href which is calculated as href = $([s_x^2 + s_y^2]/2)^{1/2} \times n^{-1/6}$ (where s_x^2, s_y^2 are estimates of the variances of the x,y locational data). This smoothing method is known to overestimate the area but is better than traditional methods because it objectively calculates the href for each individual based on the individual variation in spatial data. The Least Squares Cross Validation method (or LSCV) although overcomes the overestimation issue but is known to often fail to converge (pathological LSCV) because of several overlapping locations in the data and thus cannot be relied on. In our case as well, the LSCV failed to converge. The developer of adehabitatHR (the package used to delineate core areas) points out that- According to Seaman and Powell (1998) "This is a difficult problem that has not been worked out by statistical theoreticians, so no definitive response is available at this time" (see lines 34-45 in electronic supplementary material).

Href is thus the most objective approach to calculating smoothing parameter for our data. Calculating 'test ratio' particularly frees us from the overestimation limitation of href because we calculate intensity of use (as proportion of locations per unit core area) to deduce whether an animal shows spatial fidelity. In order to first establish if individuals of this species indeed show spatial fidelity within their nest, our method of measuring use intensity is a more conservative, robust and reliable method.

L72: how where these random paths generated? Also, are the core areas recalculated for these simulated test ratios (based on the simulated locations), or is the core area from the empirical data retained, and only the # of observations located within the core area varies in the simulated data?

Each simulation for each wasp, involved sampling n locations with replacement (n being the number of frames in which a wasp was sighted on the nest) randomly, from all pooled locations of all wasps. Both core areas and proportion of locations therein, were recalculated for each simulation. So the total number of frames (of 300 scanned frames) for

which a wasp was sighted on the nest was kept consistent between observed and simulated data.

So each (of 1000) simulation assumes that the animal could have been located n times (observed sightings of a wasp) in any of the locations ever occupied by any of the wasps on a nest and could vary from a sparse distribution, through intermediate to clumped (preferential use). Because the core areas are recalculated in each simulation for each wasp, the proportion of locations inside this core area also vary. Only the total number of sightings is retained and the test ratio is recalculated thereafter for each simulation. Once we had the simulated test ratios for each of 155 wasps, we classified each wasp as showing spatial fidelity if its observed test ratio was greater than 95% of the simulated test ratios for that wasp (see lines 78-85).

L75: this paragraph needs to be unpacked. Sentences are too long and there are too many topics in this paragraph. Furthermore, it would help to clarify what biological question each item in the list at the end of the paragraph set out to test. I would suggest introducing these general biological questions clearly in the introduction.

We have made these changes according to your suggestions (see lines 88-110).

L76-77: what is the binomial response variable? How do you define spatial fidelity? Why is this binomial rather than degree of fidelity?

The binomial response variable is whether a wasp shows spatial fidelity or not. We did not use a degree of fidelity because our goal was to distinguish between wasps that showed and did not show spatial fidelity. Therefore, we adopted the more stringent binary approach after statistical testing to establish that although core areas may be generated for all animals in response to even random aggregation of locations, these animals need not show spatial fidelity. The lack of such rigorous hypothesis testing has been criticized in greater detail in some studies (Richardson *et al.*, 2017). Additionally, we do not lose biological significance of this information by having a binary cut off. We emphasize in our study that

the same population might benefit or not from showing spatial fidelity based on their biological roles in the society. For instance, feeders may not prefer to preferentially use a part of the nest if their task involves patrolling the entire nest (lines 265-272).

L78: how do you define and quantify a 'behavioral profile?

Behavioural profile of a wasp is defined as the extent of its performance of various tasks. It is measured as the frequency per hour of feeding larvae, frequency per hour of dominance behaviour shown, frequency per hour of nest maintenance, frequency per hour of aggression received, proportion of time spent foraging (away from nest).

Behavioural data to assess the time budget of wasps was recorded in the form of scans – where the behaviour that a wasp performed at the first glance was recorded every 6 minutes by playing the entire 30 hours of video for each of six nests. Rare behaviours like aggression displayed or dominance behaviour (DB), aggression received or subordinate behaviour (S-), feeding larvae (FL), maintenance of the nest (MA) etc., were recorded in the form of all occurrence sessions (AOS) lasting 5 minutes at a time, where every performance of each of these behaviours by any individual was recorded during the replay. The sequence of scans and AOS sessions was randomly intermingled. At the end of 3 days, 150 scans and 150 AOS respectively, were obtained for each nest. The proportions of time spent by each wasp on each behaviour were calculated from the scans and the frequencies per hour with which each wasp performed each rare behaviour, were calculated from the AOS sessions (also in electronic supplementary material lines 21-30).

L82: how is 'collective colony distribution' defined and quantified

The centroid of all locations (x and y coordinates) occupied by all wasps pooled across three days of observation is called the colony centre (added now as Fig. S3 in supplementary material).
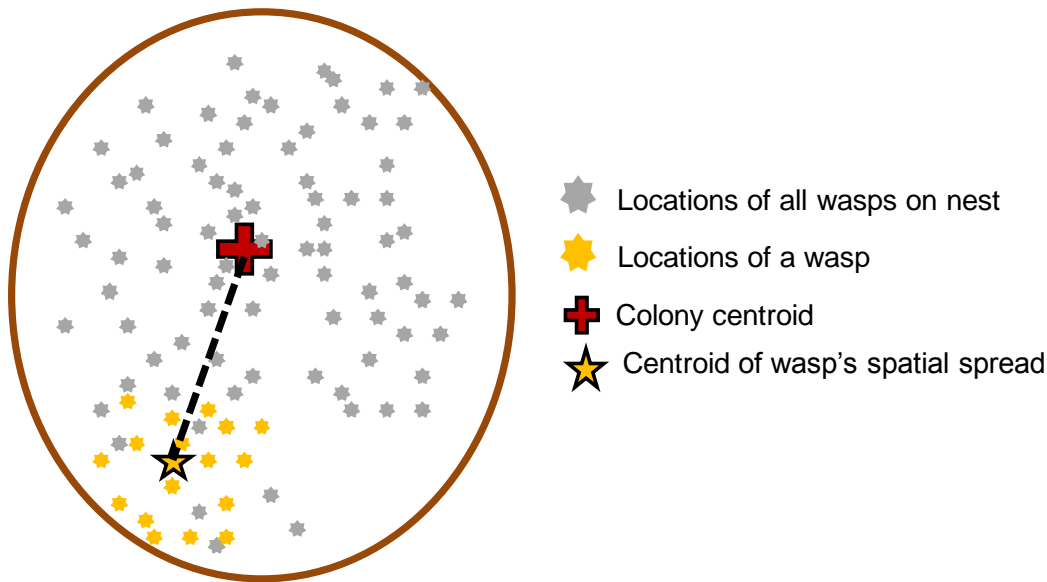
Fig. S3: Cartoon representation of the method used for quantifying distance of a wasp from colony centre. The centroid of pooled spatial locations of all wasps over all days was considered the colony centre. The Euclidean distance of the centroid of each wasp's spatial spread from the colony centre was measured as the wasp's location with respect to colony centre.

L87: consider flipping the order of this sentence and all others like it to begin with why this was done (statement that starts with 'to…')

The suggested changes have been incorporated (lines 88-110)

L88: why five and how was their positions determined?

For mixed conditional logistic regression, typically ecologists use 10 random points (Duchesne T, Fortin D, Courbin N. Mixed conditional logistic regression for habitat selection studies. Journal of Animal Ecology. 2010 May;79(3):548-55.) for making comparisons at the scale of landscapes. As the spatial scale of nests is several orders smaller, 5 randomly located circles were found to be enough to cover the nest space. Random locations were sampled from the colony distribution (as described above) as

centers for the core area and a circle around it was drawn using a radius that retained the observed core area size (using area = $\prod r^2$). Circles that crossed the nest boundary were rejected until 5 circles that lay inside the nest boundary were obtained.

L98: what research question is the information in this paragraph addressing?

This information answers the question- Was the non-random space use of workers (particularly the potential queen) related to distance from queen? – now Hypothesis 4 (lines 196-198).

L109: how is 'behavioral profile' defined?

Behavioural profile of a wasp is constituted by its degree of performance of various tasks. It is measured as the frequency per hour of feeding larvae, frequency per hour of dominance behaviour shown, frequency per hour of nest maintenance, frequency per hour of aggression received and proportion of time spent foraging (away from nest).

L112: R is the software that needs to be cited – see their help for how to cite it properly. RStudio is simply the developing environment. Also, what packages were used? Was the statistical analysis also conducted in R or in another software? If in R, what packages?

We have cited R now (ref 21), apologies for skipping this earlier. We have added two references in main text (ref 19,20) and detailed information about the packages and their citations in the supplementary material (see ESM references: 2,8,10-13). The codes for analysis involving simulations have also been added to the supplementary material (pages 17-50).

L118-120: this information already appeared in the methods

We have now removed this detail.

L121-122: This information belongs in the methods, not results.

We have now removed this detail and explained spatial fidelity in detail in the methods section (lines 77-85).

L135-139: would be helpful to report the statistics that support all these statements here. Also seems like results that could be presented in an illuminating figure.

We had earlier added statistics in the form of a table in the supplementary owing to the journal's 6 pages constraint. However, we have now added Fig.2 and statistics as part of the main text, as per the reviewer's suggestion (lines 142-144 and thereafter).

L212-219: these findings seem very interesting – it would have been nice to have some idea on what might drive this relationship building up to this.

We are not yet sure what this relationship might mean biologically. It is possible that feeders have better developed ovaries and need to patrol the entire nest to keep track of the dynamic nest landscape.

L238-242: Belong in the introduction
L250-252: Belong in the introduction
L259: other tasks? Not clear
L268: this paragraph belongs with the previous one
L271-272: introduce this hypothesis in the introduction!
L276-277: introduce this hypothesis in the introduction!
L281: introduce this hypothesis in the introduction!
L283-285: Belong in the introduction
L294-295: Belong in the introduction

We have edited the manuscript to incorporate all these suggestions.

L302-305: are there implications of this work beyond wasps?

We have now briefly discussed this in the manuscript (lines 321-330).

Appendix C

Authors' responses to editor's and reviewers' comments

(responses in **bold**)

Associate Editor Board Member, Comments to Author:

This paper has been reviewed by the two experts who already commented on the original version of this resubmission. While referee 2 (previously referee1) sees improvement, both referees feel that quite a number of their comments was not incorporated (at least not in the text; some questions were answered in the letter but these questioned aimed at pointing out gaps in the text).

We found the suggestions of the reviewers very useful and have extensively revised our manuscript in accordance with their recommendations. In particular, we have extensively revised text in the introduction and discussion as suggested by the reviewers. In addition, we have now incorporated all the comments in the manuscript rather than giving them in the response to the reviewers.

Both feel that the introduction still lacks essential elements, including a clear identification of the gap in our knowledge (note that the lack of research in a particular organism as mentioned in line 42 is not the type of gap I am talking about but rather a conceptual gap) as well as an explanation and justification of the tested hypotheses, which should also be expanded in the discussion. After my own reading, I found that the little information about the hypotheses that was present in the original introduction has even been deleted. Just listing them, together with a reference, as it is now is clearly not sufficient. Referee 1 gives an example for one of the hypotheses illustrating what kind of information would be needed for all 5 hypotheses. Furthermore there are still questions about the metrics used to analyze space use. Moreover, there are many detailed comments of both referees to be taken into account. Although both referees were not fully satisfied with the revision, their general tenor was to give the authors a second chance to solve the highlighted issues. It is the policy of PRSB to allow only up to two major changes to a manuscript, so I would like to urge the authors to closely adhere to the advice and comments by both referees when revising this manuscript and to fully satisfy all concerns. If the authors feel

that this is not possible given the length restrictions of the journal then they may consider submitting to a journal that does not have such restrictions.

Thank you for giving us the opportunity to improve our manuscript further. We have reinstated and elaborated the information given in our first submission that you have pointed out would benefit understanding by reader (lines 43-64). We have additionally highlighted the existing gap in our knowledge more clearly (lines 66-90).

In response to the comment of reviewer 1 (see below), which you have reiterated, we have explained in the manuscript that smoothing parameter may overestimate core area size (lines 118-121). We have also explained in the manuscript why we think it is better to use the test ratio rather than the core areas (lines 117-129). Additionally, we have clarified what it means to have a test ratio = 1 (lines 124-127). Please see our detailed response to referee 1 below, on this matter.

=====
Reviewers' Comments to Author:

Referee: 2

While I'm happy with the answers provided in the response letter to my previous comments, many of the answers were not incorporated into the text. The reason I raised those questions was because the text was not clear about these points and should be revised so that other readers won't have the same questions come up. However, much of the reasoning provided in the response letter is not presented in the paper for other readers to see.

We apologize and as suggested now, all our clarification provided in this document has been incorporated in the manuscript, at the appropriate places.

The introduction still does not do a good enough job at introducing the questions the paper set out to study. While I appreciate that the hypotheses were moved to the introduction, the reader is not provided with the justification for why these questions are addressed. What are the broader knowledge gaps the paper is set out to address? Background for each of the 5 hypotheses you set out to test is still missing - why you asked them and what is already known and not known for each particular questions should be presented in the introduction. For example, the way the introduction is currently written, there is no way for a reader to know what you mean by 'organizational immunity'. What is organizational immunity? What spatial patterns would be expected if there was organizational immunity? What is already known about the link between space use and organizational immunity? Similar questions need to be addressed for each of the 5 hypotheses in the introduction, otherwise, it is not clear why you chose to study these hypotheses.

Thank you for your suggestions on improving the introduction. We have extensively re-written the introduction to incorporate your suggestion. We have given a detailed background for non-random space use and introduced each hypothesis elaborately (lines 24-64). We have highlighted the gap in our knowledge and provided a justification for why we posed these questions and tested all the major hypotheses proposed to explain non-random space use in *Ropalidia marginata* (lines 66-90).

The sub headings in the results section all imply causation when only correlations can be inferred.

The sub-headings have been edited as suggested (see lines 214, 224, 236, 244 and 267).

Line by line comments:

Line 4: the transition to the second sentence of the abstract is not clear. Why is this 'Although'? seems like the same line of reasoning as the first sentence.

Thank you for pointing out that the abstract is not very clear. We have now edited it substantially for better clarity (lines 3-6).

Line 11: list these hypotheses

We have listed them in the abstract now (lines 6-9).

Line 30: The topic sentence here is not a stand alone. I would suggest not opening it with a contrasting phrase, rather write it as a statement that does not depend on the previous paragraph. E.g. start on 'non-random' and replace 'similar' with something along the lines of 'important'.

We have now extensively re-written the introduction and this line has been deleted.

Line 39: what are the fitness consequences of this organization? you state in the topic sentence that there are fitness consequences but those are not referred back to in this paragraph.

Thank you for pointing this out. We have now re-written the introduction to explicitly outline the benefits of non-random space use both outside the nests of social insects (lines 27-28) as well as inside (lines 33-36).

Line 40: what does non-random distribution of tasks have to do with being highly eusocial? The logic of this sentence is not clear.

Thank you for pointing out the lack of connection. We have now explicitly explained why highly eusocial insect nests are more likely to have non-random distribution of tasks (see lines 72-77).

Line 42: not clear how wasps provide these opportunities, or why these opportunities would be important to address.

This has now been clarified (see lines 66-90).

Line 55: the link between space use and the earlier parts of this paragraph is not clear. You start by telling us about the wasps and then go on to telling us about your hypotheses, but why study these hypotheses in this system, is not clear. What are the gaps your study addresses?

After extensively re-writing the introduction, we have highlighted the gap in our knowledge and the reason for studying space use and testing hypotheses in _Ropalidia marginata_ in detail now (see lines 66-90).

In addition, each of these hypotheses requires a much more detailed introduction. So for example, instead of talking about a specific study system (elk and wolves) in the first paragraph, introducing the mechanisms that underlie spatial fidelity in more general terms would be more appropriate for this study.

We have removed the elk and wolves example and described the mechanisms underlying space use in general terms (see lines 24-64).

While it is great to have the hypotheses listed here in the introduction the goal of the introduction is to provide background and justification for why you asked the questions and not just list them.

We have now included a detailed background and justification for posing the question in the wasp _Ropalidia marginata_ (see lines 24-90).

Line 126: not clear from the structure of the sentences if the pooling is of all 155 wasps or of 3 days for each wasp.

Edited to "When the core areas of each of the 155 wasps were determined by pooling data for each wasp over three days.." as now stated in lines 176-177.

Line 131: why is this 'as expected'?

This has now been clarified in the manuscript. (see lines 186-190).

Line 151: grammar of the sentence needs fixing

This has now been edited to "The respective distances of different wasps from the colony centre were strongly positively correlated with the proportion of time that they spent in foraging." (see lines 204-205).

Figures 1 and 2: I appreciate the addition of these figures to the main text and would suggest having the same y axis on all subplots in each of these figures. It would also be helpful to plot the actual data and not just the model fits (on figure 3 as well). In addition, the text size on the labels could be larger.

Thank you for this suggestion. We have now used the same y-axis for the subplots, increased the font size of the labels and plotted the actual data in figures 1-4.

Line 161: the phrasing of this suggests causation, but you are only showing correlation. Please edit this, for example to something along the lines of: 'relationship between dominance interactions and spatial distance'.

Thank you for pointing this out. We have now re-worded all sub-headings so as to avoid suggesting causation (see lines 214, 224, 236, 244 and 267).

Line 166: what do you mean by 'trophic interactions'? trophallactic?

To avoid confusion, we have now used the phrase 'dyadic food exchange' (see lines 143, 220, 300).

Lines 171-172: again stated as a causative statement when what you show is correlative.

We have now re-worded all sub-headings so as to avoid suggesting causation (see lines 214, 224, 236, 244 and 267).

Line 185: not clear what you mean by 'inherent'. Do you mean individual variation?

Yes, this has now been clarified (see lines 54 and 236).

Line 196: 'in order to' suggests causation again when only correlation can be inferred.

We have edited our question (sub-heading) to rule out causation and only stress on correlation (see lines 244-245).

Line 223: again, causation vs correlation, could it be that the workers are avoiding the queen rather than the queen avoiding the workers?

While we have re-worded the result on spatial avoidance to avoid invoking causation (see lines 270-272), we have retained the question (lines 267-268) because behavioural observations indeed help us to understand the direction of avoidance (see lines 342-346).

Line 232: how could you distinguish who avoided whom?

We have observed from the videos that the queens in all six nests moved away from approaching workers rather than the other way round. This has been clarified in the manuscript (see lines 272-275 and lines 344-346).

239-247: this information belongs in the introduction.

We have now deleted this from the discussion and paraphrased it differently in the introduction.

255-257: this information belongs in the introduction to justify one of your hypotheses.

This has been removed from the discussion and re-written in the introduction (see lines 46-50 and 72-77).

Paragraph on 274: the logic of the paragraph seems to move from one topic to another. In addition, it is not clear why you use 'also' in the topic sentence.

This section has been re-written (see lines 326-331).

Line 297: you did not look at pheromones so this is an odd way to start a discussion on this topic.

Re-written as suggested (see lines 331-339).

Lines 323-327: considering disease transmission was not examined explicitly, this part of the discussion doesn't seem to directly follow from this study.

This has been deleted as suggested and the discussion for this hypothesis has been re-written (341-374).

Conclusions should be more forward looking and broaden the discussion beyond the study system.

We have attempted to re-write the conclusion as suggested.

===
Referee: 1
Overall, I believe the manuscript is substantially improved.
However, I do have some remaining concerns that I think should still be addressed. I think many of the overall issues highlighted by Reviewer 2 on organization
and structure remain, and the paper could be improved by expanding and clarifying the discussion of motivating hypotheses in the introduction, and discussion.

Thank you for your suggestions on improving the introduction. We have now given a detailed background for each hypotheses (lines 43-63) and indicated the gaps in our knowledge (see lines 66-77). We have also clarified the reasons behind testing of all major hypotheses in _Ropalidia marginata_ (see lines 66-90). We have also discussed each hypothesis in great detail in the discussion (see lines 296-363).

There also remain some issues on the definition of metrics for spatial fidelity, I believe. In particular, in regards to the test statistic, the authors' response has sufficiently addressed my previous concerns about why the core area is, on average, greater than 50% (although I think it's worth making it more explicit in the manuscript that the "core area" statistic differs from 50%, see note below). However, the response has not sufficiently addressed my other concern about the test statistic. In particular, variation in the test statistic is almost entirely explained by variation in core area size, rather than occupancy rate of the core area (see my previous comments). In addition, I find the occupancy rate to the be slightly confusing to interpret (i.e., what does it mean that some individuals have an occupancy rate of 1 of their core area, given that core area is intended to estimate 50% occupancy?). My suspicion, in light of the additional and informative information the authors have provided in terms of the biased KDE estimator they use (href), is that variation in occupancy rate is primarily driven by variance in the bias of this estimator across different datasets, and I find the interpretation of this metric fairly unintuitive.

Given this, would it not be more straightforward and facilitate ease of interpretation to simply report the core area size, and then perform statistical test directly on core area, rather than the test statistic? This would still allow for an explicit statistical test of whether individual wasps display "spatial fidelity" (i.e., has a core area smaller than expected by chance). If not, I think the authors should provide a clearer explanation of why the test statistic is preferable over simply performing statistical tests on core area, and how to interpret the occupancy rate component of the test statistic.

We have re-written this section to clarify that the smoothing parameter may overestimate core area size (lines 118-121). We have also explained the need for test ratio instead of core

areas in detail now (lines 117-129) and explained what it means to have a test ratio = 1 (lines 124-127).

While we agree that it would be more straightforward to check if wasps were using significantly more than 50% of the nest area, this would be possible only if the KDE smoothing parameter uniformly delineated core areas for all individuals as including 50% occurrence. But as you also note, the occupancy varies and often contains more than 50% locations, this wouldn't be an ideal method because the delineated core area would vary from individual to individual in terms of the locations within it. The metric used in our analysis of spatial fidelity called "test ratio" helps us standardize the space use of each individual given the knowledge of the tendency of the smoothing parameter (href) to overestimate the core area boundary. Considering that the degree of such overestimation varies from individual to individual, the way to standardizing the metric for spatial fidelity is to test if individuals are sighted in the core area merely proportional to the core area size (no spatial fidelity) or more than proportionally (spatial fidelity). For example, we cannot merely rule out spatial fidelity because the observed core area size of a wasp is 50% because it may have been sighted more than 50% of the times within this core area. Hence, hypothesis testing using test ratios instead of core areas, helps us overcome the limitation of overestimation by the smoothing parameter. Even if a wasp is sighted in a 50% core area, it might in fact be using it more intensively, meaning using 50% of the nest area more than 50% of the time (hence, the test ratio is greater than 1). To illustrate our argument, we have re-done the analysis for each of 155 wasps using core areas as suggested by the reviewer instead of test ratios and found that 53% of the wasps show spatial fidelity. The difference in this proportion is because of the 9% cases where href overestimated the core area boundary and therefore included much more than 50% datapoints.

In the example below for instance, we have used both the core area and the test ratio. The figure in the left panel (using core area) below suggests lack of spatial fidelity while the figure on the right panel (using test ratios) shows fidelity for the same wasp. The reason for this discrepancy is the overestimation of the core area by the smoothing parameter. If there was no such overestimation, both methods should give the same results for all wasps.

Thus, by correcting for the overestimation we are detecting true spatial fidelity in an additional 9% of the wasps, taking the proportion of wasps showing spatial fidelity up from 53% to 62%.
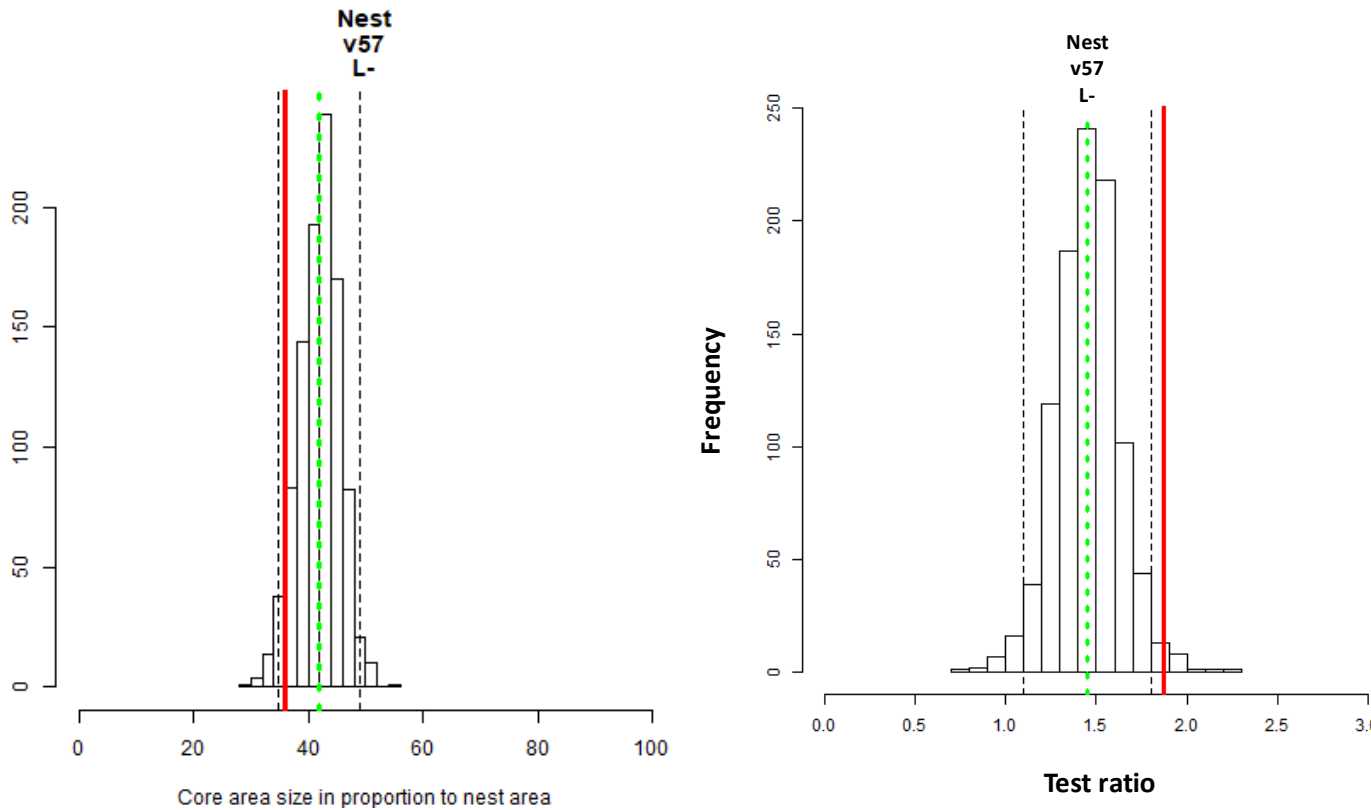
Fig 1: Spatial fidelity measured using core area for a wasp 'L-' in one of the nests (left) and spatial fidelity measured using test ratio for the same wasp (right).

Specific comments:

L8: Should modify here to clarify that the core area does not actually contain, on average, 50% of observations

This has now been clarified (lines 118-121).

L53-55: I think the background for these multiple potential hypothesis should be introduced and motivated more fully, given the centrality for the manuscript.

This has now been re-written as suggested (see lines 24-64).

L77-79: Given the points raised above, I don't think this description accurately conveys what the metric tests. As quantified, a wasp would be scored as displaying significant "spatial fidelity" just by having a small core area, and not exclusively by "using its core area more intensively than expected by chance alone," given that most of the variation in the test statistic comes from variation in core area size, not from occupancy rate.

Please see our response above and clarification in the manuscript (see lines 117-129).

L185: What is the relationship between activity and core area size?

We have removed this detail from this section now as it is not directly related to testing the 'activity levels' hypothesis.

L336-337: Not totally clear to me why the specific result on organizational immunity and no other positive, significant results found are emphasized here.

Thank you for pointing this out. We have now also highlighted the other positive result namely that non-random space use facilitates efficient food exchange among wasps (see lines 12-14, lines 301-306 and 367-369).

Figs 2-4: For all figures, I would suggest clarifying what is being plotted (presumably these are effect plots?), and in particular including specifically indicating with the dotted lines and shaded regions (95% CI?) indicate.

As suggested, we have now clarified in the description of the figures that these are effect plots and that the shaded regions are 95% CI (see figure legends lines 493 to 513).

Appendix D

Authors' responses to editor's comments

(responses in **bold**)

Associate Editor, Comments to Author:

I am by and large satisfied with the revision. The introduction reads well now, also the abstract is much clearer, and the points by the referees have been well incorporated. So I am happy to recommend acceptance pending the minor revisions outlined below.

We are immensely grateful to you for your patience and dedication for improving this manuscript as well as for accepting it. We have further incorporated all your valuable suggestions for revision in this version of the manuscript.

1) Abstract: reads well now but ends sort of without end, with the results. What is the general conclusion of this study?

We have added a line with general conclusion in the abstract now (see lines 16-17).

2) Line 82: unenveloped? This does not seem to be an English word. Is this a terminus technicus? It needs some explanation

We have used a technical term now i.e. 'gymnodomous' and explained it means an unenveloped nest (see line 81).

3) Re the new text: "This is to be expected because wasps that show spatial fidelity spend more time in their core areas than expected by chance alone, while wasps that do not show spatial fidelity spend no more time in their core areas than expected by chance alone, thus it follows that the core areas of wasps showing spatial fidelity should be smaller than those of wasps who do not show spatial fidelity."

This is a lengthy explanation for something not really important (i.e., to explain the "as expected" from the previous version. I understand what you mean, because I worked with kernels previously myself, but for someone who has not, it may sound tautological. I suggest to delete these lines completely.

We have deleted these sentences as suggested.

4) line 362: It is not possible to start this sentence with "Nor". See my suggestion in text file

Edited as suggested (line 322).

5) line 353: "in den-sharing possums (***give latin name in brackets***)

Added the scientific name as suggested (see line 351).

6) For a better read, I made a number of very small edits in the text (I used the track-changes word document, which I attach here), taking care not to change the content. In case I may still have changed the content feel free to ignore that edit.

We have incorporated all the edits that you suggested.