Computational model of collective nest selection by ants with heterogeneous acceptance thresholds

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Review form: Reviewer 1 (Mathieu Lihoreau)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
Yes

Do you have any ethical concerns with this paper?
No
Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
The authors use computational models to examine the implications of heterogeneous acceptance thresholds in collective nest choice by ants. The study elaborates on a previous model by the same group (Robinson et al. 2011 PLoS One 6:e19981). Their new (simpler) approach reproduces a number of empirical observations such as speed-accuracy and speed-cohesion trade-offs, and thus provides a parsimonious mechanism.

I enjoyed reading this clear and well-written paper. The new ABM is a promising tool for generating new empirically testable predictions in ants, with potential implications for other complex biological systems.

My main concern is the almost exclusive focus on the problem of nest selection in ants, specifically Temnothorax albipennis, with few parallels to honeybees. The relatively narrow scope is reflected by the very short introduction (half a page) and the reference list in which > 50% of the articles are from the same group. Although I realise that most work on collective emigration has been conducted on this particular ant species, similar mechanisms are at play in several other organisms and models already exists. The article could generate broader interest if it discussed more explicitly the relevance of heterogeneous threshold models to other species and types of collective decisions. The discussion at lines 386-390 is a good start.

Specific comments:
1. L22: to develop “an” analytical …
2. L27: remove “extant”
3. L50: Please define what you mean by “scouts”.
5. L53: Some basic information about collective migration in ants is needed for non specialists. For instance what is a good site and a poor site for the ants etc...
7. L126: Please explain the recruitment latency hypothesis in more details.
8. L129: typo -> hypothxesis
9. L182: typo -> numeical
10. Figure 1: Why are thick solid lines green and the others black? This is confusing. Also indicate “current nest site” above the left hand box.
11. Figure 2: I don’t understand how the number of recruiters for the poor nest sites (blue dotted line) can become higher than the total number at the poor nest site. Did I miss something?
12. Figure 3: Indicate the number of simulation runs. Same comment for figures 5, 7.
13. Figure 4: Re-explain T, P and H in the legend. Same comment for figure 6.

14. Supplementary figure S1: The figure legend should be moved below panel (k). On my PDF version it is in the middle. Same comment for fig. S6.

Well done to the authors for this nice study.

Mathieu Lihoreau
Research Center on Animal Cognition
University Paul Sabatier, Toulouse

Review form: Reviewer 2 (Ana Duarte)

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I enjoyed reading this paper on collective nest choice in individuals with heterogeneous thresholds. The authors build on previous work that showed a simple threshold mechanism (where individuals differ in their acceptance thresholds for nest quality) can explain how ant colonies may be able to accurately select between nests of different quality. Here, the authors present a thorough analysis of a mathematical model and individual based simulations, showing that a threshold mechanism can also lead to the speed-accuracy and speed-cohesion trade-offs observed empirically.

However, I have a few concerns:

1) The authors model individuals as being either high or low-threshold individuals. This is unlikely to be the case in real colonies. I understand that this approach is used for simplicity and tractability of the mathematical model, and when the choice is only between two nests of differing quality, having high vs low thresholds is effectively the same as having thresholds drawn from a normal distribution. But I still wonder whether normally distributed thresholds would change the results on trade-offs, at least for some parts of the parameter space. It would
strengthen the paper to show that results are robust even when you consider a less structured colony. It should be at least justified why the authors depart from Robinson et al 2011 in their approach.

2) Authors should justify better why space is not important in this case. Since the model concerns nest choice, which is a process that must depend on spatial exploration, why have the authors chosen to ignore space in this case?

3) The explanation and presentation of the trade-off results is very confusing, and detracts from the overall quality of the paper. It took me quite a while to figure out what was actually being shown in the heatplots (figs 4, 6, and similar figures in the supplement). When I read in the legend of fig.4: “Correlation coefficient between T and P when we varied H”, I expected to see H as an independent variable in the graph, and only after some effort I understood that the correlation coefficient shown takes pairs of T and P values, across a range of H. I don’t agree with the use of a Pearson correlation coefficient on the points obtained like this, because this ignores the effect of H on those values. I believe this is statistically incorrect. Why have the authors not used a coefficient of multiple correlation? That would be more correct, in my opinion. Also, the explanation of how the correlations were calculated and effectively how to interpret these graphs appears much later in Appendix B, whereas it should be in the main text, since this is crucial to understand the main results.

Minor comments:
4) Overall the paper would benefit from checking the grammar and spelling, I found quite a few mistakes and typos.

5) when showing averages, please show error bars as well or explain if error bars are too small to be seen (e.g., fig 3)

6) Explanation of x_h,p,vis should come where it first appears (when leakage is explained, lines 88-92)

7) Line 178: “the vote for the good nest site and the corresponding number of recruiter are larger than those for the poor site”. But in fig. 2 the legend indicates the blue dotted line as ‘poor, recruiter’, and this line stays above the red dotted line (‘good, recruiter’). Probably a mistake in the legend?

8) Line 374: \( \alpha = \infty \), shouldn't it be zero?

9) Appendix B: line 431, “H = 0, 0.667,...”. Should be 0.0667, probably.

10) Please change axis titles in graphs throughout the paper to include a short description of variables to make them clear without the reader having to go back to the main text to remind themselves of what the variable is. For example, in fig 4, the x-axes could read: \( \alpha \), rate at which ants become recruiters. Even when it's explained in the legend (as in fig. 5) it helps the reader a lot to see the variable description immediately in the graph.
Dear Miss Masuda,

The Subject Editor assigned to your paper ("Computational model of collective nest selection by ants with heterogeneous acceptance thresholds") has now received comments from reviewers. We would like you to revise your paper in accordance with the referee and Subject Editor suggestions which can be found below (not including confidential reports to the Editor). Please note this decision does not guarantee eventual acceptance.

Please submit a copy of your revised paper within three weeks (i.e. by the 30-Apr-2015). If we do not hear from you within this time then it will be assumed that the paper has been withdrawn. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office in advance. 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 Editors, 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.

To revise your manuscript, log into http://mc.manuscriptcentral.com/rsos 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. Revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you must respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". Please use this to document how you have responded to the comments, and the adjustments you have made. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response.

In addition to addressing all of the reviewers' and editor's comments please also ensure that your revised manuscript contains the following sections before the reference list:

- Ethics statement
  If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

- Data accessibility
  It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.
• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.

• Authors’ contributions
All submissions, other than those with a single author, must include an Authors’ Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria: 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:
AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

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

Yours sincerely,
Emilie Aimé
Senior Publishing Editor, Royal Society Open Science
openscience@royalsociety.org

Author's Response to Decision Letter for (RSOS-140533)
See Appendix A.

RSOS-140533.R1 (Revision)

Review form: Reviewer 1 (Mathieu Lihoreau)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes
Is the language acceptable?
Yes

Is it clear how to access all supporting data?
All supporting data are available and clear.

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept as is

Comments to the Author(s)
The authors have successfully addressed my comments. I can now fully endorse the manuscript for publication in Royal Society Open Science.

Well done!

Review form: Reviewer 2 (Ana Duarte)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept as is

Comments to the Author(s)
The paper has improved substantially, it is now much clearer. I understand and accept your justification for using a Pearson correlation. I would still perform a more thorough proof-reading of the ms, as there are still a few typos (eg 'Finding statement', instead of 'Funding statement').
14-May-2015

Dear Miss Masuda,

I am pleased to inform you that your manuscript entitled "Computational model of collective nest selection by ants with heterogeneous acceptance thresholds" is now accepted for publication in Royal Society Open Science.

You can expect to receive a proof of your article within approximately 10 days. Please contact the editorial office (emilie.aime@royalsociety.org) to let us know if you are likely to be away from e-mail contact during that period. Due to rapid publication and an extremely tight schedule, if comments are not received, your paper may experience a delay in publication.

Royal Society Open Science operates under a continuous publication model (http://bit.ly/cpFAQ). Your article will be published straight into the next open issue and this will be the final version of the paper. As such, it can be cited immediately by other researchers. As the issue version of your paper will be the only version to be published I would advise you to check your proofs thoroughly as changes cannot be made once the paper is published.

In order to raise the profile of your paper once it is published, we can send through a PDF of your paper to selected colleagues. If you wish to take advantage of this, please reply to this email with the name and email addresses of up to 10 people who you feel would wish to read your article.

On behalf of the Editors of Royal Society Open Science, we look forward to your continued contributions to the Journal.

Best wishes,

Emilie Aime
emilie.aime@royalsociety.org
http://rsos.royalsocietypublishing.org/
Response to Reviewer 1

In response to the valuable comments of the referee we have modified our paper appropriately to address her/his concerns. Below we give a point-by-point reply to each criticism.

The authors use computational models to examine the implications of heterogeneous acceptance thresholds in collective nest choice by ants. The study elaborates on a previous model by the same group (Robinson et al. 2011 PLoS One 6:e19981). Their new (simpler) approach reproduces a number of empirical observations such as speed-accuracy and speed-cohesion trade-offs, and thus provides a parsimonious mechanism.

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Thank you for reviewing. We are glad to hear overall positive evaluations.

My main concern is the almost exclusive focus on the problem of nest selection in ants, specifically Temnothorax albipennis, with few parallels to honeybees. The relatively narrow scope is reflected by the very short introduction (half a page) and the reference list in which > 50% of the articles are from the same group. Although I realise that most work on collective emigration has been conducted on this particular ant species, similar mechanisms are at play in several other organisms and models already exists. The article could generate broader interest if it discussed more explicitly the relevance of heterogeneous threshold models to other species and types of collective decisions. The discussion at lines 386-390 is a good start.

We substantially expanded Introduction as follows:

- In the first paragraph, which was almost entirely renewed, we explained consensus decision making and quorum sensing by other animals, citing more than ten papers by other research groups.

- In the third paragraph, we added short discussion on empirical evidence of heterogeneous thresholds in other species (lines 61–67).
In the fourth paragraph, we expanded on the goal of the present study (lines 74–76).

In the fourth paragraph, we also explained speed-accuracy and speed-cohesion trade-offs with examples (lines 77–85).

In discussion, we added two references on heterogeneous thresholds in bees (line 449).

Specific comments: 1. L22: to develop “an” analytical …

Corrected.

2. L27: remove “extant”

Replaced by “existing”.

3. L50: Please define what you mean by “scouts”.

We added the following text (line 93):

“(i.e., ants that proactively search for suitable sites)”


We expanded the last paragraph of Introduction to explain the speed-accuracy and speed-cohesion trade-offs with examples (lines 77–85).

5. L53: Some basic information about collective migration in ants is needed for non specialists. For instance what is a good site and a poor site for the ants etc...

We added the following text (lines 88–91):

“Experimentally, two (or more) nests of different qualities are presented to a colony, with the quality of each nest as the ants perceive it depending on floor area, ceiling height, darkness and entrance size [31]. Even if the current nest is kept intact, as we assume in the following models, colonies emigrate if a sufficiently better nest site is presented [32].”
6. L74: Explain $x_l$ and $x_h$ first.

We moved the explanation before equations (1) and (2). We also slightly expanded the explanation of $x_{h,c}$, $x_{l,g,rec}$, $x_{h,g,rec}$, $x_{l,g,com}$, and $x_{h,g,com}$ in the same place.

7. L126: Please explain the recruitment latency hypothesis in more details.

We expanded this part as follows (lines 177–178):

“recruitment latency hypothesis, according to which ants visiting a nest site hesitate for longer before recruiting nest mates if the site is of low quality.”

8. L129: typo → hypothxesis

Corrected.

9. L182: typo → numeical

Corrected.

10. Figure 1: Why are thick solid lines green and the others black? This is confusing. Also indicate “current nest site” above the left hand box.

We changed the colour from green to black. We also indicated “the current nest site” as suggested by the referee.

11. Figure 2: I don’t understand how the number of recruiters for the poor nest sites (blue dotted line) can become higher than the total number at the poor nest site. Did I miss something?

Sorry for the mistake. The thin solid (red) line and the thin dotted (blue) line should have been swapped. We corrected it.

12. Figure 3: Indicate the number of simulation runs. Same comment for figures 5, 7.
We added “The results shown in this and the following figures are calculated on the basis of $10^4$ runs.” to the caption of the former figure 3 (figure 4 in the revised version). We did not add the explanation to each figure because all the figures (not only the former figures 3, 5, and 7 as pointed out by the referee) were based on the same number of runs. The number of runs is also explained in the main text.

13. Figure 4: Re-explain T, P and H in the legend. Same comment for figure 6.

Done (figure 6 and 8 in the revised version). We did the same amendment to Figures S1, S3, S4, S5, S6 and S7.

14. Supplementary figure S1: The figure legend should be moved below panel (k). On my PDF version it is in the middle. Same comment for fig. S6.

Corrected.
Response to Reviewer 2

In response to the valuable comments of the referee we have modified our paper appropriately to address her/his concerns. Below we give a point-by-point reply to each criticism.

I enjoyed reading this paper on collective nest choice in individuals with heterogeneous thresholds. The authors build on previous work that showed a simple threshold mechanism (where individuals differ in their acceptance thresholds for nest quality) can explain how ant colonies may be able to accurately select between nests of different quality. Here, the authors present a thorough analysis of a mathematical model and individual based simulations, showing that a threshold mechanism can also lead to the speed-accuracy and speed-cohesion trade-offs observed empirically.

Thank you for reviewing. We are glad to hear overall positive evaluations.

However, I have a few concerns:

1) The authors model individuals as being either high or low-threshold individuals. This is unlikely to be the case in real colonies. I understand that this approach is used for simplicity and tractability of the mathematical model, and when the choice is only between two nests of differing quality, having high vs low thresholds is effectively the same as having thresholds drawn from a normal distribution. But I still wonder whether normally distributed thresholds would change the results on trade-offs, at least for some parts of the parameter space. It would strengthen the paper to show that results are robust even when you consider a less structured colony. It should be at least justified why the authors depart from Robinson et al 2011 in their approach.

As long as the number of new nest sites is two, the results will stay exactly the same if we employ a normal distribution as we did in Robinson et al. PLOS ONE (2011). To illustrate this point to guide readers, we inserted a paragraph (second paragraph in section 2.1; lines 112–119) and a schematic figure (Fig. 1). Similarly, we added text (lines 440–442) and a schematic figure (Fig. S8) when we briefly discussed the three-nest case in the discussion section.
2) authors should justify better why space is not important in this case. Since the model concerns nest choice, which is a process that must depend on spatial exploration, why have the authors chosen to ignore space in this case?

There is a trade-off between the complexity of the model and its analytical tractability. In this paper, we chose to neglect the space. This choice enables us to gain a deeper analytical insight into the phenomenon, while keeping main features of the collective nest choice behaviour (e.g., threshold response and speed-accuracy trade-offs). We are not saying space is not important. Neglect of the space is our choice. This point is stated in Introduction as follows (lines 71–73): “The goal of the present study is to explore this mechanism further, by introducing non-spatial mathematical models taking a minimalist approach (i.e., with a relatively small number of variables and parameters)”.

3) the explanation and presentation of the trade-off results is very confusing, and detracts from the overall quality of the paper. It took me quite a while to figure out what was actually being shown in the heatplots (figs 4, 6, and similar figures in the supplement). When I read in the legend of fig.4: “Correlation coefficient between T and P when we varied H”, I expected to see H as an independent variable in the graph, and only after some effort I understood that the correlation coefficient shown takes pairs of T and P values, across a range of H. I don’t agree with the use of a Pearson correlation coefficient on the points obtained like this, because this ignores the effect of H on those values. I believe this is statistically incorrect. Why have the authors not used a coefficient of multiple correlation? That would be more correct, in my opinion. Also, the explanation of how the correlations were calculated and effectively how to interpret these graphs appears much later in Appendix B, whereas it should be in the main text, since this is crucial to understand the main results.

We admit that the presentation was confusing. To help understanding Figs. 6 and 8 (Figs. 4 and 6 in the previous version) and similar supplementary figures, we added a schematic figure (Fig. 5) and a paragraph (third paragraph in section 3.2; lines 249–259) to explain what we did there.

In Fig. 6 (Fig. 4 in the previous version), $H$ is not an independent variable. It controls trade-offs between the speed and accuracy
(when the other parameters are set such that the speed-accuracy trade-offs do occur, which is not the case for the particular parameter values used in Fig. 4 though). We measured the correlation coefficient to succinctly assess the existence and extent of speed-accuracy trade-offs. Therefore, we do not believe that a multiple correlation coefficient is required. We believe that Fig. 5 and the added text make this point clear.

Minor comments: 4) overall the paper would benefit from checking the grammar and spelling, I found quite a few mistakes and typos.

We checked throughout the manuscript and ran a spell checker to correct mistakes.

5) when showing averages, please show error bars as well or explain if error bars are too small to be seen (e.g., fig 3)

We added error bars to Figs. 4, 7, 9, S2, S4, S6, and S7 with the explanation in the captions of these figures.

6) explanation of $x_{h,p,vis}$ should come where it first appears (when leakage is explained, lines 88-92)

We moved the explanation to lines 125–127.

7) Line 178: “the vote for the good nest site and the corresponding number of recruiter are larger than those for the poor site”. But in fig. 2 the legend indicates the blue dotted line as ‘poor, recruiter’, and this line stays above the red dotted line (‘good, recruiter’). Probably a mistake in the legend?

Sorry for the mistake. The thin solid (red) line and the thin dotted (blue) line should have been swapped. We corrected it.

8) line 374: $\alpha = \infty$, shouldn’t it be zero?

Indeed, it should be $\alpha = 0$. Corrected. Thank you for careful reading.
9) Appendix B: line 431, “\( H = 0, 0.667, \ldots \)”.
   Should be 0.0667, probably.
   Corrected.

10) please change axis titles in graphs throughout the paper to include a short description of variables to make them clear without the reader having to go back to the main text to remind themselves of what the variable is. For example, in fig 4, the x-axes could read: \( \alpha \), rate at which ants become recruiters. Even when it’s explained in the legend (as in fig. 5) it helps the reader a lot to see the variable description immediately in the graph.
   Done (Figs. 4, 6, 7, 8, 9, and S1–S7).