

Environmental variability, reliability of information and the timing of migration

Silke Bauer, John M. McNamara and Zoltan Barta

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Review timeline

Original submission: 2 September 2019

1st revised submission: 18 March 2020

2nd revised submission: 7 April 2020

Final acceptance: 7 April 2020

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

Review History

RSPB-2019-2021.R0 (Original submission)

Review form: Reviewer 1

Recommendation

Accept with minor revision (please list in comments)

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

Good

General interest: Is the paper of sufficient general interest?

Excellent

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

Excellent

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

No

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

No

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

Is it accessible?

No

Is it clear?

No

Is it adequate?

No

Do you have any ethical concerns with this paper?

No

Comments to the Author

General comments

This manuscript uses a modeling approach to investigate how environmental predictability and variability are expected to influence migration behavior by identifying optimal behavior under differing environmental scenarios. Although the model focuses on migratory behavior, the authors point out how the framework is broadly applicable to an array of life history transition. The model produces some interesting results (i.e., predicted relationships), that could be tested empirically. The Discussion highlights some existing evidence in support of the model's predictions and also suggests future avenues to test predictions. The manuscript makes a novel contribution, is well-written, and aimed at a broad audience.

Specific comments

Given that this manuscript is model based, presumably there is associated code that should be made publicly available in accordance with Royal Society policy. This does not appear to be the case.

Ln 60 – It would be useful to define variability and predictability at the outset for readers.

Ln 72 – It might be useful to make the link between these decision points and stopover sites here in the Introduction (although it does come later).

Some greater discussion of empirical evidence, or lack of evidence, for autocorrelation would be useful. In the Discussion section it is suggested how this might be investigated in the future, but is there some existing literature that could be brought to bear?

Predictability is modeled as degree of autocorrelation. Might predictability take other forms?

252-258 – The relationship between migration distance and environmental correlation seems intuitively reasonable, but is there any empirical evidence for this? This would be useful to point to in light of the fact that there are clearly counter examples (as suggested in a later paragraph (268-277)).

266-7: The implication seems to be that in the case of the bar-tailed godwits that there is also very little environmental correlation. It would be useful to be clear about this point for readers that may not be familiar with the system.

273 – What about migrants that do cross barriers (e.g., the Sahara), how do they match (or fail to match) predictions from model?

334-5 – This sentence is awkwardly worded at present.

442 – Add “life history” or similar to specify what type of transitions are meant in “Diverse transitions”

448 – Would “as” be more appropriate than “by”?

Review form: Reviewer 2 (Barbara Helm)

Recommendation

Major revision is needed (please make suggestions in comments)

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

Good

General interest: Is the paper of sufficient general interest?

Good

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

Good

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

Yes

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

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?

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

The manuscript by Bauer and colleagues presents an elegant and quite simple model that weighs up potential effects of different types of information on migratory timing. The model, in my view, is very useful and contains what I see as key components that determine timing. Several findings are exciting because of the strengths of effects, which can then be tested using data from actual migration.

Thus, I think that overall the model has a lot to offer, but at present this manuscript is a bit of a hybrid. The authors aim at making a general point on life history transitions (half of the abstract and over half of the introduction is dedicated to this), and state that they use migration as an example. The model then is entirely focused on timing of migration, and the discussion merely touches on broader applicability, leaving open whether it could work at all. Perhaps it would be more useful to fully work out the model first in migration context, and try out other applications convincingly in a new paper?

The authors' wish to be broad comes at a cost of poorly embedding the model in the field of bird migration, for which much theoretical and empirical work exists. Given this body of work, the main conclusion (in the abstract) that predicability is key for migration strategies is almost trivial (and not really underestimated) – whereas I think there is so much more to gain from the model. I would expect a stronger advance in theoretical understanding if the authors connected their study to other approaches, including some of their own work. It took me a while to consider the ways this approach differs, or is complementary to, other theoretical models of migration timing. For example, can outcomes of the model for different types of environmental information be linked to the inspiring evolutionary model by McNamara et al. 2016 *Ecol Lett* (detection vs. selection)? How would the cue use of geese associated by Bauer et al. 2008 *Ecol* with environmental cues fit this model? Are outcomes of the multiple-site analysis compatible to those of Hedenstroem et al. 2007 *Clim Res*? If it is difficult for me to fully understand how this model advances our field, others might struggle even more.

Smaller points:

Please carefully check references. In some the formatting is unintelligible, in others year is missing.

Abstract: here, the model is poorly explained. For example, intermediate steps are only mentioned as a result, without explaining at all why they are an important part of the model.

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l. 57 and ensuing paragraph: "we lack a general understanding" – do we? Please explain more precisely which gap you perceive.

l. 57 and ensuing 2 paragraphs: this entire page on the motivation for the model cites only 2 papers (of which one is very general), although much important work exists, including earlier attempts at partly overlapping ideas.

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l. 199: constant: do you mean seasonally constant, as in l. 49, i.e.: interannually similar seasonality, or no seasonality at all?

l. 248: the entire section is underreferenced, for example, no sources are given for the discussion of SO and NAO and barrier crossings.

Discussion: please critically reflect on the extent to which some strong findings might arise from assumptions, and weigh up the realism of those. For example, the penalty of arriving too early (likely mortality) explains a bias to being late (Fig. 3c) in the high variability scenario, but is this realistic? There are studies in support, but also in conflict.

Legend to Fig. 2: explain two sites, refer to the a and b in the figure

Decision letter (RSPB-2019-2021.R0)

30-Oct-2019

Dear Dr Bauer:

I am writing to inform you that your manuscript RSPB-2019-2021 entitled "The value of information for the timing of migration and other life-history transitions" has, in its current form, been rejected for publication in Proceedings B.

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

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

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

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

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

Sincerely,
Professor Gary Carvalho
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:

Both reviewers recognise the potential importance of this theoretical work on the role of information in life history transitions, but both also identify some shortcomings in the present version. Key among these are greater discussion of the results in the light of empirical evidence and other theoretical models, and, specifically, a more careful embedding of the model in the field of bird migration which, here, is its main focus. To this end, careful rewriting of parts of the text (such as Abstract and Introduction) to avoid some generalization may be needed.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

General comments

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Smaller points:

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Discussion: please critically reflect on the extent to which some strong findings might arise from assumptions, and weigh up the realism of those. For example, the penalty of arriving too early (likely mortality) explains a bias to being late (Fig. 3c) in the high variability scenario, but is this realistic? There are studies in support, but also in conflict.

Legend to Fig. 2: explain two sites, refer to the a and b in the figure

Author's Response to Decision Letter for (RSPB-2019-2021.R0)

See Appendix A.

RSPB-2020-0622.R0

Review form: Reviewer 1

Recommendation

Accept with minor revision (please list in comments)

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

Excellent

General interest: Is the paper of sufficient general interest?

Excellent

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

Excellent

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

No

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

No

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

Yes

Is it clear?

Yes

Is it adequate?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

The authors have done an excellent job addressing the comments raised by reviewers. I have only some minor suggestions.

Minor comments

Ln 172-176. This is a rather long and complex sentence, which was difficult to follow. Could this be revised?

Ln 177: "migratory systems" is a bit vague/general (and such "systems" could vary in more than the two ways identified). Could some more specific wording be used? E.g., "the relationship between locations along a migratory route"

Ln 445: Perhaps replace "first" with "the starting site"?' '

Ln 463: Wording of "on specific places" is a bit awkward.

Ln 547: I suggest editing along the lines of: "...season, but will perhaps be less pronounced in tropical or subtropical regions."

Ln 747 - 779: This sentence ("Yet, using intermediate stages is such a general strategy as well as the use of strong, reliable environmental signals before the transition that bears the strongest fitness consequences.") needs some editing for clarification. The line numbers jump from 747 to 778, so I don't know if there is perhaps something missing from the text?

Ln 1216 (Figure 1 legend): Add explanation of what dotted white lines in panel (b) indicate.

Decision letter (RSPB-2020-0622.R0)

06-Apr-2020

Dear Dr Bauer

I am pleased to inform you that your manuscript RSPB-2020-0622 entitled "Environmental variability, reliability of information and the timing of migration" has been accepted for publication in Proceedings B.

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

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

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

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

- 1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".
- 2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.
- 3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

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

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

5) Data accessibility section and data citation

It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:

- DNA sequences: Genbank accessions F234391-F234402
- Phylogenetic data: TreeBASE accession number S9123
- Final DNA sequence assembly uploaded as online supplemental material
- Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311

NB. From April 1 2013, peer reviewed articles based on research funded wholly or partly by RCUK must include, if applicable, a statement on how the underlying research materials – such as data, samples or models – can be accessed. This statement should be included in the data accessibility section.

If you wish to submit your data to Dryad (<http://datadryad.org/>) and have not already done so you can submit your data via this link

[http://datadryad.org/submit?journalID=RSPB&manu=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document%20not%20available)) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link. Please see <https://royalsociety.org/journals/ethics-policies/data-sharing-mining/> for more details.

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

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

Sincerely,
 Professor Gary Carvalho
 mailto: proceedingsb@royalsociety.org

Associate Editor
 Board Member

Comments to Author:

An original reviewer was very positive about this resubmission, raising only a few suggested changes. I too found the revised manuscript to be clearly written and to develop articulately a set of broad conclusions. I noticed a few minor grammatical or spelling issues:

Line 210 - "were" should be "was", insert "the" before "first"

Line 221 - "sources"

Line 246 - "averages"

Line 282 - "as an information source" OR "as information sources"

Line 302 - "such a pattern"

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).

The authors have done an excellent job addressing the comments raised by reviewers. I have only some minor suggestions.

Minor comments

Ln 172-176. This is a rather long and complex sentence, which was difficult to follow. Could this be revised?

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Ln 1216 (Figure 1 legend): Add explanation of what dotted white lines in panel (b) indicate.

Decision letter (RSPB-2020-0622.R1)

07-Apr-2020

Dear Dr Bauer

I am pleased to inform you that your manuscript entitled "Environmental variability, reliability of information and the timing of migration" 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.

You are allowed to post any version of your manuscript on a personal website, repository or preprint server. However, the work remains under media embargo and you should not discuss it with the press until the date of publication. Please visit <https://royalsociety.org/journals/ethics-policies/media-embargo> for more information.

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

Dear Prof Carvalho, dear Associate Editor,

Thank you very much for giving us the opportunity to submit a revised version of our manuscript.

Editor and reviewers generally appreciated our work but identified some weak or unclear points in the original version of our manuscript, of which the most important were that the manuscript attempted to be too general and thus, lost specificity on migration; it needed better embedding of existing theory on migration and evidence (or lack thereof) for autocorrelation; and the addition of more specific references at several places.

We really appreciated this feedback and changed our manuscript accordingly. In particular, we have rewritten major parts of the ms to clearly focus on migration and the theory behind. These changes concern the general parts like abstract, introduction and discussion, which now focus on migration and outline the relevance of our findings to the timing of migration. In revising our manuscript, we have also embedded our model, its approach and major results better into existing theory as well as added the relevant references. To still point out the conceptual similarity of migration with other life-history transitions, we kept a brief paragraph in the discussion outlining how our model results could apply to such transitions as well.

Please find our detailed responses to the reviewers' comments below.

We think that the revisions have strengthened our ms and made it much clearer, and we hope it achieves the high quality required for publication in the Proceedings of the Royal Society.

Yours, sincerely,
Silke Bauer on behalf of the co-authors

Referee: 1

General comments

This manuscript uses a modeling approach to investigate how environmental predictability and variability are expected to influence migration behavior by identifying optimal behavior under differing environmental scenarios. Although the model focuses on migratory behavior, the authors point out how the framework is broadly applicable to an array of life history transition. The model produces some interesting results (i.e., predicted relationships), that could be tested empirically. The Discussion highlights some existing evidence in support of the model's predictions and also suggests future avenues to test predictions. The manuscript makes a novel contribution, is well-written, and aimed at a broad audience.

Reply: We thank the reviewer for this encouraging feedback!

Specific comments

Given that this manuscript is model based, presumably there is associated code that should be made publicly available in accordance with Royal Society policy. This does not appear to be the case.

Reply: We thank the reviewer for reminding us! We have uploaded the R-code of our model on GitHub and provide the corresponding information for accessing it in the ms. Once the manuscript is accepted, we will make the code permanently available on Zenodo, where it will also receive a DOI.

Ln 60 – It would be useful to define variability and predictability at the outset for readers.

Reply: We have substantially re-written the introduction and improved the explanation of variability and predictability at the place where they are first mentioned.

Ln 72 – It might be useful to make the link between these decision points and stopover sites here in the Introduction (although it does come later).

Reply: Done.

Some **greater discussion of empirical evidence, or lack of evidence, for autocorrelation** would be useful. In the Discussion section it is suggested how this might be investigated in the future, but is there some existing literature that could be brought to bear?

Reply: Many earlier publications, e.g. on the consequences of climatic changes on migration phenology, implicitly assume a relation between migration distance and environmental correlation (e.g. [1]) but to our knowledge a systematic test is still missing (as we point out in the discussion). Such test would require quantifying the correlation of various environmental variables across increasing spatial scales and across major migration systems and, ideally, also over various time-lags. We acknowledge that this is a major endeavour, which is not only computationally intensive but has so far failed because the relevant variables (cues) are often not identified. Nevertheless, auto- and cross-correlations in meteorological variables are commonly known as are their variations across the globe. These are often summarized through large-scale indices, e.g. the North-Atlantic Oscillation [2], the El Niño Southern Oscillation [3] or the Indian Ocean Dipole [4]. The reviewer might be aware of the long research history in another research field namely that of the relation between spatial autocorrelation in weather (or other environmental conditions) and the synchrony in the dynamics of spatially separated populations – the “Moran-effect”, e.g. [5][6][7] and numerous other publications. Thus, spatial autocorrelation indeed exists globally but the distances over which conditions are correlated vary such that migratory animals might be influenced by several of these large-scale patterns, e.g. [8].

Predictability is modeled as degree of autocorrelation. Might predictability take other forms?

Reply: Yes, the reviewer is right that predictability might also arise through cross-correlation, i.e. the correlation between two (or more) relevant variables and not only from the correlation of the same variable across time or space. We added this aspect to the sentence.

We also added a more elaborate discussion on the more technical side of how we incorporated predictability, which is equivalent to how it was incorporated in [9], namely that “if the onset of spring in one site is predictive of that on the next site, then the relationship between the onsets of spring on the sites is specified by the joint probability distribution. For simplicity, we assumed that this joint distribution is bivariate normal and thus, specified by the mean, variances and correlation but, of course, other joint distributions are possible”.

252-258 – The relationship between migration distance and environmental correlation seems intuitively reasonable, but is there any empirical evidence for this? This would be useful to point to in light of the fact that there are clearly counter examples (as suggested in a later paragraph (268-277)).

Reply: Please see response to comment before previous.

266-7: The implication seems to be that in the case of the bar-tailed godwits that there is also very little environmental correlation. It would be useful to be clear about this point for readers that may not be familiar with the system.

Reply: Indeed, we implied that across the distances bar-tailed godwits migrate, there will be no or very little correlation and thus, we expected the results for no correlation to apply here. We changed the sentence to make this clear.

273 – What about migrants that do cross barriers (e.g., the Sahara), how do they match (or fail to match) predictions from model?

Reply: For migrants crossing barriers such as the Sahara, we would expect them to have no information as to the conditions behind the barrier and thus, we would expect migrants to depart on a fixed day, irrespective of the actual onset of spring, and to use an invariable cue such as daylength to time migrations. We have clarified the respective part in the ms.

334-5 – This sentence is awkwardly worded at present.

Reply: Sentence re-phrased.

442 – Add “life history” or similar to specify what type of transitions are meant in “Diverse transitions”

Reply: Sentence has been omitted as figure was changed.

448 – Would “as” be more appropriate than “by”?

Reply: Figure and legend changed.

Referee: 2

Comments to the Author(s)

The manuscript by Bauer and colleagues presents an elegant and quite simple model that weighs up potential effects of different types of information on migratory timing. The model, in my view, is very useful and contains what I see as key components that determine timing. Several findings are exciting because of the strengths of effects, which can then be tested using data from actual migration.

Thus, I think that overall the model has a lot to offer, but at present this manuscript is a bit of a hybrid. The authors aim at making a general point on life history transitions (half of the abstract and over half of the introduction is dedicated to this), and state that they use migration as an example. The model then is entirely focused on timing of migration, and the discussion merely touches on broader applicability, leaving open whether it could work at all. **Perhaps it would be more useful to fully work out the model first in migration context, and try out other applications convincingly in a new paper?**

The authors' wish to be broad comes at a cost of poorly embedding the model in the field of bird migration, for which much theoretical and empirical work exists. Given this body of work, the main conclusion (in the abstract) that predicability is key for migration strategies is almost trivial (and not really underestimated) – whereas I think there is so much more to gain from the model. I would expect **a stronger advance in theoretical understanding if the authors connected their study to other approaches**, including some of their own work. It took me a while to consider **the ways this approach differs, or is complementary to, other theoretical models of migration timing**. For example, can outcomes of the model for different types of environmental information be linked to the inspiring evolutionary model by McNamara et al. 2016Ecol Lett (detection vs. selection)? How would the cue use of geese associated by Bauer et al. 2008Ecol with environmental cues fit this model? Are **outcomes of the multiple-site analysis compatible to those of Hedenstroem et al. 2007ClimRes?** If it is difficult for me to fully understand how this model advances our field, others might struggle even more.

Reply: We thank the reviewer very much for these insightful and encouraging comments and constructive criticism. We agree that the earlier version had been a bit of a hybrid that emphasized general transitions at the cost of becoming perhaps too vague for migration. Following the suggestions and advice of the reviewer, we substantially changed the general sections of the manuscript – namely abstract, introduction and discussion - to unambiguously focus on (bird) migration as the broader framework and better embed the ms into existing theory. We also agree that the ms in general could be better embedded into existing theory of migration and have incorporated this in the general parts of the ms, namely introduction and discussion.

Smaller points:

Please carefully **check references**. In some the formatting is unintelligible, in others year is missing.

Reply: We have carefully checked and updated the references and hope that they are complete and clear now.

Abstract: here, the model is poorly explained. For example, intermediate steps are only mentioned as a result, without explaining at all why they are an important part of the model.

Reply: We have almost entirely rewritten the abstract and hope that the reviewer agrees that it now better reflects the focal points of the ms.

I. 42: reference 1 is odd for such a broad point; some other references also don't fully reflect the background

Reply: Since we revised the manuscript with the focus on migration, we replaced this and several other general references with more specific ones and also included additional references.

I. 49: what are stable seasonal environments?

Reply: We meant seasonal environments with little variability between years, i.e. the environment is seasonal but seasonality (e.g. the onset of spring) is almost the same in every year. We changed the sentence to make this meaning clear.

I. 59: something wrong

Reply: Introduction significantly revised, including this sentence.

I. 57 and ensuing paragraph: "we lack a general understanding" – do we? Please explain more precisely which gap you perceive.

Reply: We rewrote most of the introduction and explain more specifically where we perceived the knowledge gap to be. This included also incorporating recent syntheses/reviews that explicitly address the link between movement and availability/ reliability of information that is still largely missing.

I. 57 and ensuing 2 paragraphs: this entire page on the motivation for the model cites only 2 papers (of which one is very general), although much important work exists, including earlier attempts at partly overlapping ideas.

Reply: Again, in the original version, we had only very limited scope for additional references but since we revised the ms, we have also added several specific references.

I. 115 "terminal award" is obviously crucial for the model, but it's not explained, making it hard to understand the model. Later (I. 130) it sounds as if several rewards existed?

Reply: We added the explicit (mathematical) expression for the terminal reward, which consists of two terms for present and future expected reproductive success.

I. 173: I'm confused about the timing. If birds started when spring already began at the destination, would they not by definition arrive too late?

Reply: Rephrased to make meaning clear.

I. 182: so if under full variability the best solution is a fixed day – would this be the same strategy as under full determination (no variability at all)? Does certainty of the long-term average matter? This seems touched on in Fig. 5, but not in the text.

Reply: This phrase was probably misleading. We meant that migrants would depart on a fixed day when there is no information as to when spring starts in the destination, irrespective of how much spring is advanced or delayed. In case of little environmental variability (Fig. 2a), this is day 70 – the long-term average for the onset of spring and thus, too late for earlier springs and too early for late springs. When environmental variability is higher (Fig. 2b and 2c), migrants still depart on a fixed day when they have no information but this day is somewhat later than the long-term average for the onset of spring.

We changed the paragraph to clarify.

I. 199: constant: do you mean seasonally constant, as in I. 49, i.e.: interannually similar seasonality, or no seasonality at all?

Reply: Similar to the comment above, we meant little variability in seasonality between years, e.g., a similar onset of spring between years. We changed the sentence to make this clear.

I. 248: the entire section is underreferenced, for example, no sources are given for the discussion of SO and NAO and barrier crossings.

Reply: We added several references to these statements. Nevertheless, as the reviewer certainly knows there are numerous studies in the realm of bird migration and therefore, many more relevant references could have been added but adherence to the space and word limit required us to make a selection of references.

Discussion: please critically reflect on the extent to which some strong findings might arise from assumptions, and weigh up the realism of those. For example, the penalty of arriving too early (likely mortality) explains a bias to being late (Fig. 3c) in the high variability scenario, but is this realistic? There are studies in support, but also in conflict.

Reply: We have added a section to discuss two important assumptions in our model – the joint probability distribution as the basis for predictability and the mortality function that penalizes early arrival. We think both are justified as a first approximation but can be adjusted once more specific empirical evidence is available.

Legend to Fig. 2: explain two sites, refer to the a and b in the figure

Reply: We have combined the earlier figures 1 and 2, added the missing sub-plot labels and revised the figure legend.

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