

The environmental predictors of spatio-temporal variation in the breeding phenology of a passerine bird

Jack D. Shutt, Irene Benedicto Cabello, Katharine Keogan, Dave I. Leech, Jelmer M. Samplonius, Lorianne Whittle, Malcolm D. Burgess and Albert B. Phillimore

Article citation details

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Review timeline

Original submission: 24 April 2019
Revised submission: 10 July 2019
Final acceptance: 19 July 2019

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

Review History

RSPB-2019-0952.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?

Good

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

Good

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

No

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

No

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

Is it accessible?

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

Changes in phenology are a central feature of global warming. Shutt and coauthors provide, in my view, the most convincing dissection to date of factors that drive songbird phenology. From a great number of replicate sites, they collected data on trees, invertebrates, laying, and on the much less reported nest initiation. Unusually, they also cross-validated their findings by further data sets. I find the fit of the model extrapolated to two subsequent years spectacular. This is particularly important because a subsequent year was apparently warmer, so that predictions were outside of the value range of the study years. That predictions for expected warming fit so well, in my view, deserves more emphasis in this manuscript. For the second extrapolation (across the UK and over longer time intervals) I would like to see a supplemental figure or similar, to be able to assess the findings. Further, to be able to relate the UK patterns to other studies, could you please provide estimates of how oak phenology, which is more commonly reported, relate to birch phenology? Your sample sizes for both species give you a strong basis for doing so.

I have no major concerns with this elegant study. Smaller criticisms are as follows:

Please don't use abbreviations, unless fully unavoidable! I found this made the otherwise nicely written study very hard to read. For example, after explaining which measure you used, you could simply say lay date or bud burst, giving readers brain space to take in more interesting points.

Abstract: state here that the birch effect was additional to the temperature effect

Introduction: could you please make it more succinct? some information is duplicate, other points are interesting tangents. Perhaps a few points (e.g. on chemical cues) could be mentioned in brief in the Discussion? Long-term national data set: please give a bit more info so readers grasp the scope of it early on.

Methods: would path analysis been a valuable additional search tool for sorting out predictors? I also don't understand the rationale that sliding windows didn't work well for design reasons for bird data, but they seem to do well for similarly designed invertebrate data?

Pot: what material did you use? Sticky traps: please explain here very briefly what you did, it's one of your main predictors. In contrast, the tree methods are very detailed and take up much

space. Perhaps this detail could be moved to Supplements?

L. 179: "each measure" is unclear, especially because you talk about so many predictors

L. 201: Daytime: so this time window is the mean of sunrise and sunset times over sites and the observation window? Obviously, daylength changes fastest around the equinoxes, around the time of your study.

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L. 303: what's RMSE?

L. 307: I suppose you now talk about mean ambient temperature over 24 h? Please specify, and also specify the range of years, so that the temporal effects can be understood without consulting the appendix.

Discussion:

L. 322: earlier, not later birch?

L. 325: a supplemental figure on the UK data would be great

L. 334: here reference to oaks becomes urgent, and quantitative information (see above) would be an extra asset

L. 366, reference 59: this is important, but the reference is unclear, and so are others in the literature list (eg Perrins)

Overall, the Discussion takes up just a few points and is somewhat repetitive as it stands.

Table 1: what is "nu"?

Fig. 1, caption: variables AND two measures?

Review form: Reviewer 2

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

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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

This is a nice study, that has examined the breeding phenology of the well-studied blue tit, and arrived at some interesting novel findings with respect to the determinants of breeding time. This has been achieved using data from a transect across Scotland and a number of environmental parameters. The findings are then tested using data from the wider data from a BTO database across the UK.

The findings are timely, given the focus on animal phenology in a changing climate, and make sense in that they point to a plausible mechanism through which a link between temperature and breeding can be understood.

There are just a few edits that I believe will help to improve the paper and make it slightly more readable to the community of those working in this area.

1. I do understand that the details may well have been provided in the earlier study cited in the paper (Shutt et al 2018), but I was a little surprised at the complete lack of information regarding methodological details of the transect. Readers of this study should not have to read another paper to get even basic details about this transect, and it would be good if some basics and perhaps a map could be provided in the manuscript, or at the very least in an easily accessible supplementary materials.
2. Whilst I understand that this is one of the most well-studied avian systems in the world, the paper is currently extremely narrowly focused on the blue tit, and as such doesn't really merit publication in such a broad journal, unless the study can be set in a much broader global context. There is lots of work on avian breeding phenology in other parts of the northern hemisphere such as North America (e.g. Winkler et al 2014, *Ecography*), which is also highly similar and where bird phenology is probably vaguely similar, as well as other places like Australia, where avian breeding phenology operates quite differently (e.g. Duursma et al. 2017, *Auk*; Duursma et al. 2019, *Ecography*). I can understand why there is value in more work on the blue tit, but I think the reporting of the study would be enhanced by trying to make some contrast with other areas of the globe which may either be similar or very different.

Decision letter (RSPB-2019-0952.R0)

19-Jun-2019

Dear Dr Shutt:

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

We 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:

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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=\(Document not available\)](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.

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

Professor V A Braithwaite
mailto:proceedingsb@royalsociety.org

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Associate Editor, Comments to Author:

The manuscript has received highly positive reviews, and the reviewers have no doubt that the manuscript is a meaningful contribution to the field. Please address all reviewers comments; the interesting additional analyses requested by reviewer 1 can be added as supplementary material or, depending on space availability, directly in the manuscript. In particular, I would highly

encourage the authors to include the analysis testing for relationships between oak and birch phenology directly in the manuscript.

===

Reviewers' Comments to Author:

Referee: 1

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Overall, the Discussion takes up just a few points and is somewhat repetitive as it stands.

Table 1: what is “nu”?

Fig. 1, caption: variables AND two measures?

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Referee: 2

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2. Whilst I understand that this is one of the most well-studied avian systems in the world, the paper is currently extremely narrowly focused on the blue tit, and as such doesn't really merit publication in such a broad journal, unless the study can be set in a much broader global context. There is lots of work on avian breeding phenology in other parts of the northern hemisphere such as North America (e.g. Winkler et al 2014, *Ecography*), which is also highly similar and where bird phenology is probably vaguely similar, as well as other places like Australia, where avian breeding phenology operates quite differently (e.g. Duursma et al. 2017, *Auk*; Duursma et al. 2019, *Ecography*). I can understand why there is value in more work on the blue tit, but I think the reporting of the study would be enhanced by trying to make some contrast with other areas of the globe which may either be similar or very different.

Author's Response to Decision Letter for (RSPB-2019-0952.R0)

See Appendix A.

Decision letter (RSPB-2019-0952.R1)

19-Jul-2019

Dear Dr Shutt

I am pleased to inform you that your manuscript entitled "The environmental predictors of spatiotemporal variation in the breeding phenology of a passerine bird" 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

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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,
Victoria Braithwaite

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

Appendix A

Dear Editor,

We wish to thank the editor and both reviewers for the insightful comments and suggestions that have improved the manuscript. We have addressed each of the comments and the major changes that have been made to the manuscript during this revision are:

a) The methods section, particularly relating to the cross-validations and the basic details of the transect, has been bolstered significantly in the main manuscript in response to comments by both reviewers. A new figure showing the relationships captured by the nationwide analysis has also been added to the supplementary material, as requested by reviewer 1.

b) An analysis of the correlation between birch and oak phenology across the UK has been made, as suggested by reviewer 1, and the results of this have been placed directly in the manuscript as requested by the associate editor.

c) A new discussion paragraph has been written comparing and contrasting avian phenology in our study with other systems worldwide in response to a comment from reviewer 2.

d) The terminology in the paper has been simplified and unnecessary abbreviations have been removed, as suggested by reviewer 1.

Below in this document we respond to each of the comments in turn. This is followed by the 'track changes' version of the revised manuscript. We thank you for the opportunity to revise our paper.

Yours faithfully,

The authors.

Associate Editor, Comments to Author:

The manuscript has received highly positive reviews, and the reviewers have no doubt that the manuscript is a meaningful contribution to the field. Please address all reviewers comments; the interesting additional analyses requested by reviewer 1 can be added as supplementary material or, depending on space availability, directly in the manuscript. In particular, I would highly encourage the authors to include the analysis testing for relationships between oak and birch phenology directly in the manuscript.

** We thank the editor and reviewers for their positive and constructive comments. We have addressed all of the suggestions in this revision and feel that they have improved the manuscript. We have included the results of the specific analysis mentioned above directly in the manuscript as suggested (in the discussion when discussing the early phenology of birch, lines 349-52).

XX

Reviewers' Comments to Author:

Referee: 1

Changes in phenology are a central feature of global warming. Shutt and coauthors provide, in my view, the most convincing dissection to date of factors that drive songbird phenology. From a great number of replicate sites, they collected data on trees, invertebrates, laying, and on the much less reported nest initiation. Unusually, they also cross-validated their findings by further data sets. I find the fit of the model extrapolated to two subsequent years spectacular. This is particularly important because a subsequent year was apparently warmer, so that predictions were outside of the value range of the study years. That predictions for expected warming fit so well, in my view, deserves more emphasis in this manuscript.

** We thank the reviewer for their positive comments and help in producing a better manuscript. We appreciate the idea that predicting warming so well would deserve extra emphasis, however the warmest year on the transect was 2014 (mean night-time temperature on days 75-128 across sites monitored in all years = 6.29°C) and the coolest was 2016 (4.36°C), so the subsequent years (2017 (5.41°C) and 2018 (4.76°C)) used in the cross-validation are within the temperature value range of the study years (with the remaining year, 2015 = 4.49°C).

For the second extrapolation (across the UK and over longer time intervals) I would like to see a supplemental figure or similar, to be able to assess the findings. Further, to be able to relate the UK patterns to other studies, could you please provide estimates of how oak phenology, which is more commonly reported, relate to birch phenology? Your sample sizes for both species give you a strong basis for doing so.

** We agree that these suggestions improve the manuscript and have now incorporated Fig A3 in the supplementary material to illustrate the second (UK-wide) cross-validation and incorporated a new analysis (with the results reported in the discussion on lines 349-52 and the methods placed in the supplementary material) to estimate how oak and birch phenology relate across the UK using the national datasets. On average, oak phenology occurs 13.8 days later than birch phenology and the two are strongly positively correlated across both space and time.

I have no major concerns with this elegant study. Smaller criticisms are as follows:

Please don't use abbreviations, unless fully unavoidable! I found this made the otherwise nicely written study very hard to read. For example, after explaining which measure you used, you could simply say lay date or bud burst, giving readers brain space to take in more interesting points.

** We see the reviewer's point that these abbreviations were confusing and avoidable and have removed all possible and replaced them throughout with more descriptive terminology as requested.

Abstract: state here that the birch effect was additional to the temperature effect

** We thank the reviewer for bringing to our attention that we had not stated this explicitly, and we have rectified this.

Introduction: could you please make it more succinct? some information is duplicate, other points are interesting tangents. Perhaps a few points (e.g. on chemical cues) could be mentioned in brief in the Discussion? Long-term national data set: please give a bit more info so readers grasp the scope of it early on.

** We have streamlined several sections of the introduction as requested, removing duplicated information, and also added extra lines explaining the long-term national data sets on lines 122-25.

Methods: would path analysis been a valuable additional search tool for sorting out predictors?

** This is an interesting suggestion. In this study we are most interested in evaluating predictors as proximate causal drivers of breeding times, and this is what multiple regression is designed to do. If we were interested in also identifying causal pathways then path analysis would be excellent, however, given the space constraints of a Proc B article, we consider this beyond the scope of this study.

I also don't understand the rationale that sliding windows didn't work well for design reasons for bird data, but they seem to do well for similarly designed invertebrate data?

** The issue with sliding windows surprised us initially and took us a while to understand. The problem with temperature data is that the correlation between temperatures on different days (even weeks apart) assessed across sites is very high. This arises because the high elevation sites are almost always colder than the low elevation sites. Therefore when we applied the sliding window method there is very little difference of the predictive power of temperatures over different time windows. In the case of the invertebrate data there is less evidence for a consistent spatial gradient in abundance which means that the abundances in two different time windows are much less correlated with each other. The result is that the sliding window approach can be much more effectively applied to the invertebrate data. We have included some extra information regarding this issue in the manuscript on lines 178-81.

Pot: what material did you use? Sticky traps: please explain here very briefly what you did, it's one of your main predictors. In contrast, the tree methods are very detailed and take up much space. Perhaps this detail could be moved to Supplements?

** Plastic film cartridges were used as the pots (now included in the text on lines 136-7) and we have added extra details for the sticky trap protocol on line 138-41. To accommodate this and the extra cross-validation methods from a later comment, the focal tree selection protocol has been moved to the supplementary material as suggested by the reviewer.

L. 179: "each measure" is unclear, especially because you talk about so many predictors

** This has been reworded to be "each measure of each predictor (detailed below)", as the measures in question are the subject of the following few paragraphs (e.g. night-time temperature, day-time temperature are measures within the temperature predictor block) and we can see why this terminology here was unclear and only explained later, and we hope that the new wording is clearer.

L. 201: Daytime: so this time window is the mean of sunrise and sunset times over sites and the observation window? Obviously, daylength changes fastest around the equinoxes, around the time of your study.

** The daytime hours are slightly different to those understood by the reviewer. We included in daytime all hourly temperature recordings (temperature recordings on the hour, every hour) that would be between sunrise and sunset throughout the entire period in question along the whole transect, as this gave us an equal daily sample size. So, for the time period 24th February – 18th April (the thermal sensitivity period for nest initiation), the hours between 0800-1700 were always daytime hours and the temperature recordings at each hour within this period classed as daytime temperature recordings. This is explained in the manuscript on lines 185-8 now.

L. 247: more info here! This is far more important than details of tree selection.

** We agree with the reviewer that this is important information to have in the manuscript itself and have now included the cross-validation protocol from the supplementary material in the main manuscript, now occupying lines 226-52.

Results:

L. 282 and following: I can't follow, please rewrite

** This section has been rewritten in a way we feel is easier to follow, now lines 281-3.

L. 303: what's RMSE?

** We thank the reviewer for highlighting that we had not explained this. RMSE is the abbreviation for root-mean-square-error and this has been written in full now in the manuscript (now line 301).

L. 307: I suppose you now talk about mean ambient temperature over 24 h? Please specify, and also specify the range of years, so that the temporal effects can be understood without consulting the appendix.

** We thank the reviewer for highlighting these gaps in the main manuscript. These details are now both in the longer cross-validation methodology on lines 226-52 as well as in the results section stated above (now line 304).

Discussion:

L. 322: earlier, not later birch?

** The reviewer is correct and we apologise for this error, which has now been fixed.

L. 325: a supplemental figure on the UK data would be great

** We agree that this is a useful addition and has now been added as Fig A3.

L. 334: here reference to oaks becomes urgent, and quantitative information (see above) would be an extra asset

** We have included the extra analysis suggested by the reviewer above in the supplementary material and note the results in the discussion here as suggested (lines 349-52).

L. 366, reference 59: this is important, but the reference is unclear, and so are others in the literature list (eg Perrins)

** The reference in question is the PhD thesis of the first author (now reference 45) wherein it is shown genetically via faecal metabarcoding approaches that Scottish blue tits in early spring rely heavily on prey associated with birch buds and catkins. The paper from this chapter of the thesis is ready to be submitted to a peer reviewed journal imminently but is not currently published, however the dietary species list and association of key items with birch in the spring are shown in Chapter 4 and Appendix D of the thesis, which has been published for nearly a year and is freely available to view online from the 9th July 2019.

Overall, the Discussion takes up just a few points and is somewhat repetitive as it stands.

**** We have modified sections of the discussion to avoid repetition, for example by removing the old second to last paragraph, and explore more points comparing and contrasting to other avian systems worldwide on lines 384-90.**

Table 1: what is “nu”?

**** Nu is a parameter in the Matern covariance function. Setting nu at 0.5 in spaMM constrains the spatial autocorrelation to follow an exponential. This is now explained in the table legend as suggested, as well as in the main body (lines 220-21).**

Fig. 1, caption: variables AND two measures?

**** The reviewer is correct and we apologise for this error, which has been corrected.**

XX

Referee: 2

This is a nice study, that has examined the breeding phenology of the well-studied blue tit, and arrived at some interesting novel findings with respect to the determinants of breeding time. This has been achieved using data from a transect across Scotland and a number of environmental parameters. The findings are then tested using data from the wider data from a BTO database across the UK.

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**** We thank the reviewer for their positive and constructive comments.**

1. I do understand that the details may well have been provided in the earlier study cited in the paper (Shutt et al 2018), but I was a little surprised at the complete lack of information regarding methodological details of the transect. Readers of this study should not have to read another paper to get even basic details about this transect, and it would be good if some basics and perhaps a map could be provided in the manuscript, or at the very least in an easily accessible supplementary materials.

** We agree with the reviewer that we should have incorporated more methodological detail of the transect rather than purely citing previous work. To this end, we have included more basics of the transect design on lines 130-3, a map in the supplementary materials (Fig A1) and extra background to the cross-validating datasets on lines 226-52.

2. Whilst I understand that this is one of the most well-studied avian systems in the world, the paper is currently extremely narrowly focused on the blue tit, and as such doesn't really merit publication in such a broad journal, unless the study can be set in a much broader global context. There is lots of work on avian breeding phenology in other parts of the northern hemisphere such as North America (e.g. Winkler et al 2014, *Ecography*), which is also highly similar and where bird phenology is probably vaguely similar, as well as other places like Australia, where avian breeding phenology operates quite differently (e.g. Duursma et al. 2017, *Auk*; Duursma et al. 2019, *Ecography*). I can understand why there is value in more work on the blue tit, but I think the reporting of the study would be enhanced by trying to make some contrast with other areas of the globe which may either be similar or very different.

** We thank the reviewer for their guidance in this regard, agree that this was necessary and have incorporated an extra discussion paragraph addressing this by comparing and contrasting with phenology in other avian systems worldwide on lines 384-90.