

Visual cues of predation risk outweigh acoustic cues: a field experiment in black-capped chickadees

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Article citation details

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Review timeline

Original submission: 12 May 2020
1st revised submission: 15 August 2020
2nd revised submission: 14 September 2020
Final acceptance: 15 September 2020

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

Review History

RSPB-2020-1101.R0 (Original submission)

Review form: Reviewer 1

Recommendation

Major revision is needed (please make suggestions in comments)

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

Acceptable

General interest: Is the paper of sufficient general interest?

Acceptable

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

Good

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

No

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

No

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

Is it accessible?

Yes

Is it clear?

Yes

Is it adequate?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

Review MS RSPB-2020-1101

To the authors

In this manuscript the authors present new empirical data on predation risk assessment based on cues varying in certainty. They found that free-ranging black-capped chickadees resumed feeding later after the presentation of a predator dummy (high certainty cue) close to a feeder than after the presentation of conspecific predator mobbing calls (lower certainty cue). Interestingly, when presented with both cues together, energetic constraints modified the response: under lower risk of starvation birds resumed feeding as late as if they were presented only the high certainty cue, indicating cue redundancy; under higher risk of starvation, however, birds resumed feeding faster than when presented the high certainty cue alone. The authors interpret this unintuitive result as birds trading-off predation risk and competition for food. I really like that the study tests variation in response to multiple cues (variation in risk-safety assessment) in combination with an energetic trade-off.

The study uses a fully-crossed experimental design in the wild and is based on a good sample size. The statistical analyses are sound and the study is well presented. All conclusions are based on results and the discussion of the findings is conclusive, also acknowledging small shortcomings of the design. Overall this is a nice and technically solid behavioural case study on predation risk assessment that should be published. Since the study is presented very much with the perspective on birds' predation risk assessment and the discussion is very closely centred around the detailed results/the study system, I miss some generality. What do we learn about predation risk assessment in general that could excite people beyond behavioural ecology, e.g., interested in information theory or evolutionary biology etc.? Thus, in my view this is very good manuscript but authors might want to work out the novelty and originality of their study a bit more. Below I made some general suggestions and specific remarks to improve the presentation of the study.

General comments

(1) General background. The introduction provides a comprehensive framework of the theoretical background of the study. However, the choice of references for very general aspects (e.g., on trade-offs between risks and reward) appears rather arbitrary, ignoring classical work in the area. Also, when reviewing what is known about anti-predator behaviour, a more comprehensive literature review (including meta-analyses, reviews) would be more appropriate.

(2) Methodological issue. The study uses latency to resume feeding as the main response variable.

Since the experimental subjects are free-ranging the onset of the experiment (e.g., setting-up of a dummy or starting the playback) is not necessarily the onset perceived by an experimental subject. In other words, some bird individuals might have perceived the cue later and therefore their response latency would appear longer. Furthermore, the perception range of visual cues and acoustic cues might differ, again leading to biased “perceived onsets” of the experimental trial. I do not think that these issues would change any general results of the study and I do highly appreciate the fact that these experiments were done in the wild under ecologically relevant conditions. Nevertheless, I would ask the authors to briefly pick it up in the discussion.

(3) Novelty and originality. As mentioned by the authors themselves, there is a wealth of studies using various cues to elicit anti-predator behaviour in a variety of taxa. There is also a wealth of studies on multi-modal cues in sexual selection research. I would ask the authors to work out a bit more clearly what exactly is novel and original in their study. Moreover, I would ask the authors to elaborate a bit more what we learnt about risk assessment, information theory and how variation in risk assessment might have evolved. Albeit reasonable the conclusions of the manuscript are again very close to the study.

Specific comments

Introduction

The introduction frames the study well. The hypotheses and predictions are convincingly derived.

In the first paragraph many important aspects of risk-sensitive foraging are introduced.

However, the choice of references appears quite random. Please cite original literature and not recent case studies for the theoretical background. This part has many references related to animal personality that should be replaced by classical theoretical work on foraging under risk.

L32: Certainly this is an important question, but it has been addressed many times before. Where does your study go beyond what we know?

L36-38: Again, here are many references on anti-predator behaviour only from a personality context. This is a classical topic in behavioural ecology, with many meta-analyses and reviews written on it.

L38: Are there really no meta-analyses summarizing the work on birds?

L46: What I miss here, is a clear justification why it should be interesting (from a theoretical perspective) to combine two cues in the first place. What are the constraints and the benefits for the receiver?

L61: Again, only bird examples although there is a rich literature on this also from other taxa (e.g., primates).

L102: Certainly, the energetic trade-off is condition-dependent. A bird with a low body condition has a higher risk of starvation. Thus, ambient temperature can only serve as rough proxy of energetic constraints.

The figure visualizing the predictions is very helpful.

Methods

L175: Do these birds perceive the stationary predator dummy as a predator or “just” a novel object?

L185: Mobbing call sequences – did the sequences vary in number of birds mobbing? If so, you might want to test your competition hypothesis in a bit more detail by testing whether birds react stronger to mobbing call sequences of more birds. How far does the acoustic cue carry? What is the approximated difference in perception range between the acoustic and visual cue?

L198: Since several treatments were carried out at one particular feeder location over a day, there might be some order effects of treatment presentations if certain bird individuals visited feeders over the whole day (i.e., experienced several treatments in a row). Could you please provide some information on how often it occurred that the same individual visited feeders over several treatment presentations in a sequence? How often did it occur that the same individual was present at two feeders? Etc.

L210: I guess this assumption is the best you can make but still – as described above – birds can fly and can be anywhere in the area within one hour. Since you did a full control, this aspect is cared for but the onset of the treatment for a particular individual varies.

Stats is very well described and solid.

Results

L260: Maybe you want add some descriptive stats here as well.

Discussion

Overall, the discussion includes many repetitions of results. Certainly, this is necessary to interpret results to a certain degree but my impression is that some aspects should rather be placed in the results (e.g., repeatabilities but also other verbal descriptions). Also, in the discussion some new results on feeding rates appear. Why are they not part of the predictions and results of the manuscript but only presented in the discussion?

L283: In Figure 1 you introduce alternative scenarios, I would suggest to pick these one up again. In other words you did find support for "cue redundancy".

L294: "closely related species"

L297-306: There is some descriptive stats in this discussion part that might be better placed in the results.

L303: "half of that"

L360: "more often than the"

L363: As mentioned above, I think the manuscript has a too narrow focus on birds and the study system in particular. There are also informative studies on variation in risk-taking of various mammals, for example, that used very similar response variables as in your study. The case-specific comparison with great tits is too specific, in my view. Thus lines 263-370 can be replaced by a short general discussion of among-individual differences in risk-taking.

Conclusions – see comments above.

References

The reference list needs some proof-reading (species names in italic, missing page numbers, missing journal names abbreviated or not, etc.).

Tables and Figures

Figure 1: very helpful. Legend L577: why is there "latency" twice?

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?

Acceptable

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?

Yes

Is it clear?

Yes

Is it adequate?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

The study "Visual cues of predation risk outweigh acoustic cues: a field experiment in black-capped chickadees" by Arteaga-Torres et al. explores the very interesting theme of the environmental information provided by cues detected by different sensory systems. The proximate mechanical causation of the behavioural response is connected to plasticity of the nervous system and has strong implication in learning processes. The study has been conducted in the field by recording the bird latency to resume feeding after being exposed to predatory cues: acoustic, visual or both. Results show the higher reliability of visual cue (merlin mounts) in comparison to acoustic cue (mobbing calls) and how the response change in relation to the external environmental temperature.

Overall, I think the study has been properly conducted and the results are clear. Many methodological details have been reported. Authors have done a considerable work by deeply elucidating various aspects of the study. I recommend it for the publication. However, some points need to be clarified.

Main concern

You selected individuals that were present in the hour just before the beginning of each experimental session (ll. 207-210). I wonder if this choice is appropriate or not. Birds can suddenly move among feeders in no time, or maybe this is not the case. If possible, I would add a comment further supporting your choice (and references). The same reasoning is related to definition of "latency time", indeed fig 2 shows that it reaches a maximum of about 40 min and a range from something like 5-10 to 40 min, I wonder if the results might be undermined by that choice.

Methods

If I correctly understand, you have 8 feeders and each of them has been assigned with a random combination of cues, but I only see 4 feeders for each experimental day in table S1.

Statistics. You explained almost every passage of the analysis, if you want you can also specify that random effects in your model are crossed random effects. It would be useful to have a plot of the raw data; this will provide more information on behavioural responses (it can be added to the supplementary material or included in fig 2-3).

I suppose some of the individuals have been exposed to different levels of cues more often than others, thus they may have showed sort of habituation or sensitization to the cues. It would be interesting to explore this behaviour. Moreover, you calculated repeatability and It would also be interesting to know how many observations have been recorded for each individual (possibly you excluded those with very few observations)

Results. I see the results (at ll. 266-267) are just reported in the table, I think you do not need to repeat them. You can add a comment explaining your findings, I would put evidence on the

“flat” line for the visual treatment. It would also be worth to add comments based on the unity of time used (min), which are not immediately evident from the table.

Repeatability. As reported, some individuals have very few observations (ll. 261-261), have you included them when calculating repeatability? I would add some details. Moreover, has repeatability been calculated for the different treatments? If not, explain why and possible caveats of adopting such procedure.

Discussion. Some new statistical analysis has been reported in this section, I would prefer to have all of them in the results section. Possibly, this is just a matter of opinion. This way reader is not forced to move back and forth between the main manuscript and the supplementary materials.
ll. 328. Can you provide a definition of feeding rate?

ll.351- . I am wondering if you explored the possible correlation among individuals for latency and feeding rate.

Decision letter (RSPB-2020-1101.R0)

18-Jun-2020

Dear Mr Arteaga-Torres,

I am writing to inform you that we have now received referees' reports for your manuscript RSPB-2020-1101 entitled "Visual cues of predation risk outweigh acoustic cues: a field experiment in black-capped chickadees".

The manuscript 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. In particular, the referees raised some concern as to whether the paper contains enough of a novel advance for Proc B, but please see the suggestions in the comments (including from the Associate Editor) that would add some additional interesting dimensions.

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.

Finally, I hope you and your co-authors are well in these difficult times.

Yours sincerely,
 Professor Loeske Kruuk
 Editor
 mailto: proceedingsb@royalsociety.org

Associate Editor
 Board Member: 1
 Comments to Author:

Two referees have kindly reviewed the manuscript and offer comments on the framing of the study and the methods. They indicate that the manuscript is suitable for a broad journal, but the reviews overall suggest that the findings are insufficiently novel for Proceedings B.

This is a neat example of temperature-dependent risk trade-offs in a wild context. I would agree that, while the interaction is the most intriguing part, the significance is unclear. And it seems difficult to tease out the mechanism with the available data. Competition is a neat hypothesis, but the evidence is a little speculative - feeding rates in the warm conditions support your idea, but in the cold seem to contradict it. Can that mechanism be distinguished from e.g. mobbing + owl being perceived as a 'partially neutralised' owl under starvation risk?

Both referees are curious about the supplementary analyses, however. Addressing the comments would strengthen the manuscript, but expanding on these analyses may provide an opportunity to explore that interaction in more depth.

Or indeed to add novelty in another way - referee 2 suggests testing for habituation/sensitization, for example. If there is enough replication, another option that would mirror your population-level study quite nicely (and could be an extension to your existing models) would be to look at individual-level response to the cues. E.g. does average 'boldness' toward owls correlate with plasticity (random slope with temperature)? Or with propensity to use public information? However, I appreciate this would change the focus of the paper and may be limited by uncertainties about dominance effects that you have discussed.

Reviewer(s)' Comments to Author:
 Referee: 1
 Comments to the Author(s)
 Review MS RSPB-2020-1101
 To the authors

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Conclusions – see comments above.

References

The reference list needs some proof-reading (species names in italic, missing page numbers, missing journal names abbreviated or not, etc.).

Tables and Figures

Figure 1: very helpful. Legend L577: why is there “latency” twice?

Referee: 2

Comments to the Author(s)

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Overall, I think the study has been properly conducted and the results are clear. Many methodological details have been reported. Authors have done a considerable work by deeply elucidating various aspects of the study. I recommend it for the publication. However, some points need to be clarified.

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You selected individuals that were present in the hour just before the beginning of each experimental session (ll. 207-210). I wonder if this choice is appropriate or not. Birds can suddenly move among feeders in no time, or maybe this is not the case. If possible, I would add a comment further supporting your choice (and references). The same reasoning is related to definition of "latency time", indeed fig 2 shows that it reaches a maximum of about 40 min and a range from something like 5-10 to 40 min, I wonder if the results might be undermined by that choice.

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Statistics. You explained almost every passage of the analysis, if you want you can also specify that random effects in your model are crossed random effects. It would be useful to have a plot of the raw data; this will provide more information on behavioural responses (it can be added to the supplementary material or included in fig 2-3).

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Author's Response to Decision Letter for (RSPB-2020-1101.R0)

See Appendix A.

RSPB-2020-2002.R0

Review form: Reviewer 1

Recommendation

Accept as is

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?

Yes

Is it clear?

Yes

Is it adequate?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

Review MS RSPB-2020-2002 (formerly 2020-1101)

To the authors

I have reviewed the first version of this manuscript (as reviewer 1). The authors did a great job in thoroughly revising their manuscript, including adding aspects to the statistics, placing their study much better in current literature and carving out the generality of their results. All my general issues have been sufficiently dealt with. As expressed previously, I do like this study very much and think that it will be very interesting for a wide range of (behavioural) ecologists and evolutionary ecologists. I do not have any further suggestions to improve the presentation of the study and suggest to accept it as it is.

Decision letter (RSPB-2020-2002.R0)

10-Sep-2020

Dear Mr Arteaga-Torres

I am pleased to inform you that your manuscript RSPB-2020-2002 entitled "Visual cues of predation risk outweigh acoustic cues: a field experiment in black-capped chickadees" has been accepted for publication in Proceedings B.

The referee and Associate Editor have recommended publication, but the AE has requested a minor correction (see below). In addition, I found the latest version of the abstract talking about 'prey using Bayesian updating' a bit far-fetched; I don't think this was in the previous versions of the abstract? If you strongly believe it's justified, please at least change it to something like 'We suggest that this may be due to the prey effectively using 'Bayesian updating', whereby...!.

Please therefore revise your manuscript in line with these comments. 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.

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- 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 (<https://royalsociety.org/journals/authors/author-guidelines/#data>).

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:

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- 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

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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.

Yours sincerely,
Professor Loeske Kruuk
Editor
mailto: proceedingsb@royalsociety.org

Associate Editor

Comments to Author:

Thank you, one of the original referees has kindly reviewed the resubmission and is supportive of the revisions. I enjoyed the more in-depth discussion of the competing hypotheses for the intermediate response, set up well by moving the feeding rate data into the results. A minor revision only - please clarify line 400 'manipulated perceived dilution of risk benefits via the increased perceived group size'

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).

Review MS RSPB-2020-2002 (formerly 2020-1101)

To the authors

I have reviewed the first version of this manuscript (as reviewer 1). The authors did a great job in thoroughly revising their manuscript, including adding aspects to the statistics, placing their study much better in current literature and carving out the generality of their results. All my general issues have been sufficiently dealt with. As expressed previously, I do like this study very much and think that it will be very interesting for a wide range of (behavioural) ecologists and evolutionary ecologists. I do not have any further suggestions to improve the presentation of the study and suggest to accept it as it is.

Author's Response to Decision Letter for (RSPB-2020-2002.R0)

See Appendix B.

Decision letter (RSPB-2020-2002.R1)

15-Sep-2020

Dear Mr Arteaga-Torres

I am pleased to inform you that your manuscript entitled "Visual cues of predation risk outweigh acoustic cues: a field experiment in black-capped chickadees" 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 10 pages long. Our Production Office will be able to confirm the exact length at proof stage.

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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,
Editor, Proceedings B
<mailto:proceedingsb@royalsociety.org>

Appendix A

Response to comments from Associate Editor and referees

Associate Editor

1. Two referees have kindly reviewed the manuscript and offer comments on the framing of the study and the methods. They indicate that the manuscript is suitable for a broad journal, but the reviews overall suggest that the findings are insufficiently novel for Proceedings B.

Response: Thank you for your comments. In reading the comments provided by the two referees, we agree that we were not explicit enough in the discussion about the novelty of this work, both from a food-safety trade-off perspective, and in terms of the broader contributions to empirical work on uncertainty reduction and multi-modal information. We have revised the discussion significantly to address this point (Lines 379-831, 407-433, 457-458). Please see also our response to point 6.

2. This is a neat example of temperature-dependent risk trade-offs in a wild context. I would agree that, while the interaction is the most intriguing part, the significance is unclear. And it seems difficult to tease out the mechanism with the available data. Competition is a neat hypothesis, but the evidence is a little speculative - feeding rates in the warm conditions support your idea, but in the cold seem to contradict it. Can that mechanism be distinguished from e.g. mobbing + owl being perceived as a 'partially neutralised' owl under starvation risk?

Response: We were also intrigued by the observed interactions between temperature and cue type on risk-taking. This was not an anticipated result, and thus, our interpretation of the result is entirely speculative. However, these interactions were estimated with large sample sizes (both in terms of number of individuals and number of replicates per individual), and the magnitude of the effects are quite large. Thus, we are confident that this reflects a biologically real phenomenon in our population of chickadees. The associated editor also raises another potential post-hoc interpretation, that the presence of mobbing calls actually mitigates perceived risk because the threat is already being 'dealt' with by other conspecifics. This is a really interesting suggestion, and we have now included it in our post-hoc interpretations (lines 410-416). We also provide more clear details on the types of studies that would be needed to thoroughly address these post-hoc explanations (lines 404-406, 431-433, 451-452).

3. Both referees are curious about the supplementary analyses, however. Addressing the comments would strengthen the manuscript, but expanding on these analyses may provide an opportunity to explore that interaction in more depth.

Response: Done. Our responses to the referees relating to the supplementary analyses are found directly following each of their points.

4. Or indeed to add novelty in another way - referee 2 suggests testing for habituation/sensitization, for example. If there is enough replication, another option that would mirror your population-level study quite nicely (and could be an extension to your existing models) would be to look at individual-level response to the cues. E.g. does average 'boldness' toward owls correlate with plasticity (random slope with temperature)? Or with propensity to use public information? However, I appreciate this would change the focus of the paper and may be limited by uncertainties about dominance effects that you have discussed.

Response: The Associate editor raises two separate points: 1) whether we could look at evidence of habituation to cues, and 2) whether we could expand our analyses by looking at individual reaction norms. We address each of these points in turn.

Habituation: Done. We designed the experiment specifically to avoid habituation (e.g., 4 replicates spread over >3 months, multiple unique playback sequences used, and multiple predator mounts). We have now added text to the manuscript to clarify that these decisions were all taken in part to minimize the risk of habituation to our treatments over the course of the experiments (see line 199). Given that we took great care to mitigate habituation, we do not feel testing for habituation would be appropriate as a central question in the analysis, however, we agree that it would be prudent to confirm that these steps were successful. We now address this notion of habituation directly by including "replicate" as a random effect in our models. If there was significant habituation across replicates, we would have observed large among-replicate variance in risk-taking. Note however, that large among-replicate variance in risk-taking could also arise via mechanisms other than habituation. However, neither for latency to resume feeding nor for foraging rates after returning to feed, was there support for an important contribution of replicate to the total variance. We have added this detail to the results, including its implication for ruling out habituation (lines 239-242).

Individual reaction norms: We agree that looking at individual reaction norms within the framework of uncertainty reduction and energetic constraints would be very interesting. Indeed, we hope to conduct studies that would allow us to do this in the future. Unfortunately, the current experiment is not suited for this analytical approach because we have four categorical treatment levels for our manipulations of perceived predation risk. Random slope analyses require minimum sample sizes of 200 for each estimated reaction norm, with an ideal balance of 10 observations for each 20 individuals [1] to have moderate power. Due to the categorical nature of the treatments used in the current study, reaction norms would need to be calculated across environmental gradients of pair-wise treatments (e.g., control vs. acoustic, control versus visual, control versus combined cues, etc.). As we carried out a total of 4 replicates per treatment, we have at most 8 replicates per individual for a given reaction norm, but very often less due to the fact that birds were not present for all treatments (see lines 289-296 for descriptive statistics). Additionally, we feel that given our study design, such analyses would be overly complex due to the number of reaction norms that could be estimated across the four categorical treatments (N = 6 reaction norms). We have not made any changes to the text in response to this point.

Referee 1

5. In this manuscript the authors present new empirical data on predation risk assessment based on cues varying in certainty. They found that free-ranging black-capped chickadees resumed feeding later after the presentation of a predator dummy (high certainty cue) close to a feeder than after the presentation of conspecific predator mobbing calls (lower certainty cue). Interestingly, when presented with both cues together, energetic constraints modified the response: under lower risk of starvation birds resumed feeding as late as if they were presented only the high certainty cue, indicating cue redundancy; under higher risk of starvation, however, birds resumed feeding faster than when presented the high certainty cue alone. The authors interpret this unintuitive result as birds trading-off predation risk and competition for food. I really like that the study tests variation in response to multiple cues (variation in risk-safety assessment) in combination with an energetic trade-off.

Response: Thank you.

6. The study uses a fully-crossed experimental design in the wild and is based on a good sample size. The statistical analyses are sound and the study is well presented. All conclusions are based on results and the discussion of the findings is conclusive, also acknowledging small shortcomings of the design. Overall this is a nice and technically solid behavioural case study on predation risk assessment that should be published. Since the study is presented very much with the perspective on birds' predation risk assessment and the discussion is very closely centred around the detailed results/the study system, I miss some generality. What do we learn about predation risk assessment in general that could excite people beyond behavioural ecology, e.g., interested in information theory or evolutionary biology etc.? Thus, in my view this is very good manuscript but authors might want to work out the novelty and originality of their study a bit more.

Response: Thank you for these comments. In re-reading our discussion, we agree that the scope was overly narrow. We have now expanded the discussion in several areas to discuss the results more generally. Specifically, we have broadened the scope of the discussion in terms of the range of taxa, and we discuss the phenomenon of multimodal cue integration more broadly (lines 338-340, 371-378, 407-433, 447, 457-458).

Below I made some general suggestions and specific remarks to improve the presentation of the study.

7. (formerly general comment 1) General background. The introduction provides a comprehensive framework of the theoretical background of the study. However, the choice of references for very general aspects (e.g., on trade-offs between risks and reward) appears rather arbitrary, ignoring classical work in the area. Also, when reviewing what is known about anti-predator behaviour, a more comprehensive literature review (including meta-analyses, reviews) would be more appropriate.

Response: Thank you for pointing this out. We have made numerous changes to the literature that is cited in the introduction to favour more classic works and/or synthetic work when possible.

8. (formerly general comment 2) Methodological issue. The study uses latency to resume feeding as the main response variable. Since the experimental subjects are free-ranging the

onset of the experiment (e.g., setting-up of a dummy or starting the playback) is not necessarily the onset perceived by an experimental subject. In other words, some bird individuals might have perceived the cue later and therefore their response latency would appear longer. Furthermore, the perception range of visual cues and acoustic cues might differ, again leading to biased “perceived onsets” of the experimental trial. I do not think that these issues would change any general results of the study and I do highly appreciate the fact that these experiments were done in the wild under ecologically relevant conditions. Nevertheless, I would ask the authors to briefly pick it up in the discussion.

Response: These are both good points. The referee is correct in pointing out that the timing of perception of cues across individuals may have differed (or across replicates for the same individual). We have no way of evaluating this, as the automated detection of individual via the RFID system has a very small detection radius, and thus, could only detect birds present at the feeder (see line 150). We attempted to address this by limiting our analyses to birds that were present in the vicinity of a feeder in the 1-hour interval preceding the onset of a given treatment. However, stochastic differences in the timing of perception of cues within-individuals, or repeatable among-individual differences in cue perception would add noise to the results (i.e., hinder our ability to detect treatment effects). Thus, our findings are likely conservative. We have added detail to the text to clarify this point (lines 211-220).

However, the referee points out another very important point; that the spatial range at which cues could be perceived would differ across treatments (i.e., the acoustic cue could be perceived at greater distance, and therefore, might be perceived sooner). Indeed, we now explicitly address this in the discussion and consider how such differences in detection may have contributed to the observed results (lines 165-167, 182, 407-433).

9. (formerly general comment 3) Novelty and originality. As mentioned by the authors themselves, there is a wealth of studies using various cues to elicit anti-predator behaviour in a variety of taxa. There is also a wealth of studies on multi-modal cues in sexual selection research. I would ask the authors to work out a bit more clearly what exactly is novel and original in their study. Moreover, I would ask the authors to elaborate a bit more what we learnt about risk assessment, information theory and how variation in risk assessment might have evolved. Albeit reasonable the conclusions of the manuscript are again very close to the study.

Response: We thank the referee for this comment. We agree that the initial submission did not go far enough to place this study within the broader context of information theory and risk assessment, nor in highlighting the novelty of our work. We have significantly revised sections of the abstract (lines 12-16) introduction (lines 35-46, 53-55), and discussion (lines 407-433, 447-452) to address this point.

10. The introduction frames the study well. The hypotheses and predictions are convincingly derived.

Response: Thank you.

11. In the first paragraph many important aspects of risk-sensitive foraging are introduced. However, the choice of references appears quite random. Please cite original literature and not recent case studies for the theoretical background. This part has many references related to animal personality that should be replaced by classical theoretical work on foraging under risk.

Response: Done. We have increased the citation of more classic works that relate to our study.

12. L32: Certainly this is an important question, but it has been addressed many times before. Where does your study go beyond what we know?

Response: This point has been addressed in response to point 9 by the same referee.

13. L36-38: Again, here are many references on anti-predator behaviour only from a personality context. This is a classical topic in behavioural ecology, with many meta-analyses and reviews written on it.

Response: Done. We have updated the citations.

14. L38: Are there really no meta-analyses summarizing the work on birds?

Response: We were also surprised that given the vast amount of work that has been done in this area, no systematic quantitative review has yet been conducted. We agree

that this is a major knowledge gap given the number of studies published in this area on birds, and we are currently working on a meta-analysis of this very topic.

15. L46: What I miss here, is a clear justification why it should be interesting (from a theoretical perspective) to combine two cues in the first place. What are the constraints and the benefits for the receiver?

Response: Done. We have added details from both a biological and theoretical perspective on why cues may be combined in the first place (lines 40-46).

16. L61: Again, only bird examples although there is a rich literature on this also from other taxa (e.g., primates).

Response: Done. We have broadened the range of taxa represented in the citations, including greater citation of reviews.

17. L102: Certainly, the energetic trade-off is condition-dependent. A bird with a low body condition has a higher risk of starvation. Thus, ambient temperature can only serve as rough proxy of energetic constraints.

Response: We fully agree. Energetic constraints are shaped by multiple factors simultaneously, including current energy reserves, temperature, food availability, time available for feeding (e.g., daylength). We have added text to the manuscript to clarify that temperature is one proxy of energetic constraint, all else being equal (line 90).

18. The figure visualizing the predictions is very helpful.

Response: Thank you.

19. L175: Do these birds perceive the stationary predator dummy as a predator or “just” a novel object?

Response: Chickadees are known for being relatively neophilic [2], thus, we would not expect them to demonstrate an aversion to feeding in response to the presence of a

novel object in the vicinity of the feeder. Furthermore, there is substantial work demonstrating that birds, including chickadees, are able to recognize different types of predators [e.g., 3]. Given this body of work, we find it unlikely that the merlin mounts were perceived as novel objects rather than as predators. Nonetheless, we included control treatments in our experimental design in which all the non-biological components of the treatments that were manipulated during the treatment were presented (e.g., wooden post, speaker). We have added detail to the text to clarify this point (lines 183-186).

20. L185: Mobbing call sequences – did the sequences vary in number of birds mobbing? If so, you might want to test your competition hypothesis in a bit more detail by testing whether birds react stronger to mobbing call sequences of more birds. How far does the acoustic cue carry? What is the approximated difference in perception range between the acoustic and visual cue?

Response: The referee raises two points. The first is a suggested test of the competition hypothesis we develop in the discussion. This is a really good suggestion. We actually considered a priori that the number of chickadees vocalizing during mobbing calls might influence the level of information the playbacks provided, and consequently, took care to standardizing the acoustic features of the playbacks. Consequently, the playbacks used in this study do not vary in the number of individuals present during mobbing sequences (each 1-hour playback includes sequences with 1 to 4 chickadees), and therefore are not suitable for testing the competition hypothesis. We have added this detail to the methods (lines 177-179). However, this would make an excellent follow up experiment, and we have added this suggestion to the discussion (lines 404-406).

The second point is about the perception range of the different cues. As the experiments were conducted in winter, after the foliage from deciduous trees had fallen, the range at which the predator mounts were visible to human observers was circa 20 to 50 meters depending on the specific feeder and the bearing (the amount of trees obstructing views varied, JAT personal observation). The acoustic cues were broadcast so that they could be heard at distances of 80-90 meters, similar to natural chickadee mobbing calls. We have added these details to the methods (lines 165-166 and 182), as well as discussed how these differences in perception distance may have contributed to our results (lines 350 and 407-433).

Note that a model on multimodal integration was recently developed [4] which makes specific predictions about how cue integration in a food-safety trade-off context might be mitigated by energetic constraints. We have revised the discussion substantially to allow for interpretation of our results in light of this new model (lines 407-433).

21. L198: Since several treatments were carried out at one particular feeder location over a day, there might be some order effects of treatment presentations if certain bird individuals visited feeders over the whole day (i.e., experienced several treatments in a row). Could you please provide some information on how often it occurred that the same individual visited feeders over several treatment presentations in a sequence? How often did it occur that the same individual was present at two feeders? Etc.

Response: The referee has misunderstood the experimental design. A single treatment was carried out at a given feeder per day, with at least one day break between successive treatments at the same feeder. There were 4 treatments carried out across the entire study area on a given day – each at different feeders. We have revised the text clarify the experimental design (lines 192-198 and 201-204). As discussed above in response to point 4, we did not want to have frequent treatments as we were trying to minimize the likelihood of birds habituating to the stimuli. Most birds were observed at a single feeder, though a small number of birds used more than one feeder. This information is now provided in the descriptive statistics (lines 289-290).

22. L210: I guess this assumption is the best you can make but still – as described above – birds can fly and can be anywhere in the area within one hour. Since you did a full control, this aspect is cared for but the onset of the treatment for a particular individual varies.

Response: Absolutely, the timing when birds may have perceived the cues presented in our experiment were out of our control, and we had no way of recording them. Please see point 8 for a detailed response to this concern.

23. Stats is very well described and solid.

Response: Thank you.

24. L260: Maybe you want add some descriptive stats here as well.

Response: Done. We have added more descriptive statistics to the results section (lines 290-296, 298-300, 315-318, 333-336).

25. Overall, the discussion includes many repetitions of results. Certainly, this is necessary to interpret results to a certain degree but my impression is that some aspects should rather be placed in the results (e.g., repeatabilities but also other verbal descriptions). Also, in the discussion some new results on feeding rates appear. Why are they not part of the predictions and results of the manuscript but only presented in the discussion?

Response: We have revised the discussion substantially in response to comments 6, 8, 9 and 20, including editing to reduce the amount of repetition. The reporting repeatabilities (but not their discussion), have been moved to the results (lines 313-315, and lines 331-333). The post-hoc analyses of feeding rates were presented in the discussion because these analyses and predictions were not conceived of *a priori*, but were devised in light of the unanticipated result we found related to the interaction between treatment and temperature on latency to resume feeding. We have moved the description of these analyses to the methods (lines 276-286), and present model output in the results (lines 319-336), while being clear that these are *post-hoc* analyses.

26. L283: In Figure 1 you introduce alternative scenarios, I would suggest to pick these one up again. In other words you did find support for “cue redundancy”.

Response: Done. We have revised the text so that we more clearly articulate how the results do (and do not) align with the scenarios presented in Figure 1 (lines 345-348)

27. L294: “closely related species”

Response: Done. We have corrected this typo.

28. L297-306: There is some descriptive stats in this discussion part that might be better placed in the results.

Response: Done. We have moved the descriptive statistics to the results section (lines xx).

29. L303: “half of that”

Response: Done.

30. L360: “more often than the”

Response: Done.

31. L363: As mentioned above, I think the manuscript has a too narrow focus on birds and the study system in particular. There are also informative studies on variation in risk-taking of various mammals, for example, that used very similar response variables as in your study. The case-specific comparison with great tits is too specific, in my view. Thus lines 263-370 can be replaced by a short general discussion of among-individual differences in risk-taking.

Response: Done. We have revised the text to broaden the scope of the discussion, including references to similar studies in other taxa (lines 407-433).

32. Conclusions – see comments above.

Response: Done. See also above.

33. References. The reference list needs some proof-reading (species names in italic, missing page numbers, missing journal names abbreviated or not, etc.).

Response: Done.

34. Figure 1: very helpful.

Response: Thank you.

35. Legend L577: why is there “latency” twice?

Response: Corrected.

Referee 2

36. The study “Visual cues of predation risk outweigh acoustic cues: a field experiment in black-capped chickadees” by Arteaga-Torres et al. explores the very interesting theme of the environmental information provided by cues detected by different sensory systems. The proximate mechanical causation of the behavioural response is connected to plasticity of the nervous system and has strong implication in learning processes. The study has been conducted in the field by recording the bird latency to resume feeding after being exposed to predatory cues: acoustic, visual or both. Results show the higher reliability of visual cue (merlin mounts) in comparison to acoustic cue (mobbing calls) and how the response change in relation to the external environmental temperature.

Overall, I think the study has been properly conducted and the results are clear. Many methodological details have been reported. Authors have done a considerable work by deeply elucidating various aspects of the study. I recommend it for the publication. However, some points need to be clarified.

Response: Thank you for your comments. We address your specific points below.

37. Main concern. You selected individuals that were present in the hour just before the beginning of each experimental session (ll. 207-210). I wonder if this choice is appropriate or not. Birds can suddenly move among feeders in no time, or maybe this is not the case. If possible, I would add a comment further supporting your choice (and references). The same reasoning is related to definition of “latency time”, indeed fig 2 shows that it reaches a maximum of about 40 min and a range from something like 5-10 to 40 min, I wonder if the results might be undermined by that choice.

Response: The data presented in the figures do not represent maximum latencies, but rather are estimates derived from the model and their 95% confidence intervals. The observed latency to resume feeding varied from <1 min to > 370 min after the presentation of the treatments. We now provide these summary statistics in the results in response to comment 24. Additionally, reanalysis of the latency to resume feeding data

without filtering based on whether or not birds were present in the 1 hour before the treatment do not change the results either qualitatively or quantitatively. We provide these results in the ESM (Table S2), and the data required for the analyses have been deposited on Open Science Framework.

38. If I correctly understand, you have 8 feeders and each of them has been assigned with a random combination of cues, but I only see 4 feeders for each experimental day in table S1.

Response: That is correct. Due to logistical constraints, we only conducted 4 treatments per day, and these were each done at separate feeders. We have also clarified the methods in response to point 21 by referee 1.

39. Statistics. You explained almost every passage of the analysis, if you want you can also specify that random effects in your model are crossed random effects. It would be useful to have a plot of the raw data; this will provide more information on behavioural responses (it can be added to the supplementary material or included in fig 2-3).

Response: Done, we have now explicitly stated that the random effects are crossed (lines 242-244). Although we appreciate the suggestion to plot raw data (we also prefer to illustrate with raw data whenever possible), the raw data do not account for the important random effects structure, or the additional important fixed effects (e.g., sex, or latency to resume feeding for the feeding rate analyses). Consequently, we feel that are not easily interpretable, and prefer not to include them in the manuscript. However, we could add them to the supplementary material if the referee and/or editor feel strongly about this.

40. I suppose some of the individuals have been exposed to different levels of cues more often than others, thus they may have showed sort of habituation or sensitization to the cues. It would be interesting to explore this behaviour. Moreover, you calculated repeatability and It would also be interesting to know how many observations have been recorded for each individual (possibly you excluded those with very few observations)

Response: We have partially addressed the point regarding habituation in response to point 4 above. We have no way of assessing whether or not an individual was exposed to cues. A bird that is not observed at the feeder on the day of a treatment may have been elsewhere that day and not encountered the cue(s), or, may have encountered them and chosen to avoid using that feeder for the remainder of the day. Therefore, we do not feel we can use number of observation session with feeder visits tests as a proxy for exposure to cues. However, we have now added descriptive statistics describing the number of observations per individual (lines 289-290). Additionally, all individuals were included in the analyses regardless of the number of observations for which they were present, which we believe should be clear now that we explicitly state the range of observations per individual.

41. Results. I see the results (at ll. 266-267) are just reported in the table, I think you do not need to repeat them. You can add a comment explaining your findings, I would put evidence on the “flat” line for the visual treatment. It would also be worth to add comments based on the unity of time used (min), which are not immediately evident from the table.

Response: Done. We now only report the estimated effect sizes and 95% CI's in Table 1, and do not duplicate them in the results text. We also clarify the units of measurement.

42. Repeatability. As reported, some individuals have very few observations (ll. 261-261), have you included them when calculating repeatability? I would add some details. Moreover, has repeatability been calculated for the different treatments? If not, explain why and possible caveats of adopting such procedure.

Response: Done. All individuals were included regardless of the number of observations we had for them because keeping these individuals in the analysis helps estimate the fixed effects, even if they do not contribute much power to the estimation of random effects [1]. We have added this detail and reference to the main text (lines 289-296). A key caveat is that if the individuals for which we have few observations are both a non-random subset of birds with respect to risk-taking, and also more likely to be observed following specific treatment types (e.g., they are very risk-avoiding, and we only detect them after the control), this could result in biased parameter estimates. However, this

was not the case. Equal numbers of birds were observed following each treatment type. We have added this detail to the text (lines 293-296).

43. Discussion. Some new statistical analysis has been reported in this section, I would prefer to have all of them in the results section. Possibly, this is just a matter of opinion. This way reader is not forced to move back and forth between the main manuscript and the supplementary materials.

Response: We actually struggled a lot with the decision of where to report these results. These analyses were not planned *a priori*, but were conducted post hoc to aid in our interpretation of the surprising result (the strong interaction between treatment and temperature). Our concern was that if we presented these analyses in the methods and results section, some readers may not appreciate that these are post hoc, exploratory analyses. However, we agree that presenting these analyses with the methods and results may allow for a more streamlined presentation, which we have now done, while taken care to articulate that these are *post hoc* analyses.

44. II. 328. Can you provide a definition of feeding rate?

Response: Done (lines 280-281).

45. II.351- . I am wondering if you explored the possible correlation among individuals for latency and feeding rate.

Response: No, we had not, but this is a good suggestion. Logically, longer latency to resume feeding may necessitate higher feeding rates once foraging resumes. We now address this by including latency to resume feeding as a covariate in our *post hoc* analyses of feeding rates (lines 281-286). As expected, greater latency is associated with higher subsequent feeding rates (lines 320-323). Inclusion of this covariate has also aided in the interpretation of these analyses relative to the competition hypothesis and dilution of risk hypothesis (lines 389-406).

References cited in the responses to Associate Editor and referees:

1. Martin J.G.A., Nussey D.H., Wilson A.J., Réale D. 2011 Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models. *Methods in Ecology and Evolution* **2**, 362-374.
2. Smith S.M. 1992 *The black-capped chickadee: behavioral ecology and natural history*. Ithaca, NY, Cornell University Press.
3. Templeton C.N., Greene E., Davis K. 2005 Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science* **308**, 1934-1937.
4. Munoz N.E., Blumstein D.T. 2019 Optimal multisensory integration. *Behavioral Ecology*. (doi:10.1093/beheco/arz175).

Appendix B

Response to comments from Associate Editor and referee

Associate Editor

1. The referee and Associate Editor have recommended publication, but the AE has requested a minor correction (see below). In addition, I found the latest version of the abstract talking about 'prey using Bayesian updating' a bit far-fetched; I don't think this was in the previous versions of the abstract? If you strongly believe it's justified, please at least change it to something like 'We suggest that this may be due to the prey effectively using 'Bayesian updating', whereby...'.

Response: Done. We have rephrased the sentence to remove the term 'Bayesian updating'. (see line 12)

2. Thank you, one of the original referees has kindly reviewed the resubmission and is supportive of the revisions. I enjoyed the more in-depth discussion of the competing hypotheses for the intermediate response, set up well by moving the feeding rate data into the results. A minor revision only - please clarify line 400 'manipulated perceived dilution of risk benefits via the increased perceived group size'

Response: Done. We have added information to make our interpretation easier to understand (see lines 400-405).

Referee: 1

1. I have reviewed the first version of this manuscript (as reviewer 1). The authors did a great job in thoroughly revising their manuscript, including adding aspects to the statistics, placing their study much better in current literature and carving out the generality of their results. All my general issues have been sufficiently dealt with. As expressed previously, I do like this study very much and think that it will be very interesting for a wide range of (behavioural) ecologists and evolutionary ecologists. I do not have any further suggestions to improve the presentation of the study and suggest to accept it as it is.

Response: Thank you.