

## Global determinants of prey naiveté to exotic predators

Andrea Anton, Nathan R. Geraldi, Anthony Ricciardi and Jaimie T. A. Dick

### Article citation details

*Proc. R. Soc. B* **287**: 20192978.

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### Review timeline

Original submission: 22 December 2019

1st revised submission: 18 April 2020

2nd revised submission: 28 April 2020

Final acceptance: 28 April 2020

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

## Review History

### RSPB-2019-2978.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?**

Excellent

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

Excellent

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

Excellent

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

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

No

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

**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

### **Comments to the Author**

First, I'd like to commend the authors on an incredibly thoughtful and thorough revision of their manuscript. Well done! Below I list some key, focused responses to the revisions.

1) The authors expansion of the database added a significant number of observations to the dataset. This in combination with their approach to remove treatments with fewer than 10 observations, has greatly strengthened their analyses and the conclusions that they can draw from the results. I have no further concerns with the sample sizes presented in their analyses.

2) I'm glad that the authors considered and ultimately included time since introduction as a covariate in their analyses. However, unless I overlooked, it I think the manuscript could be improved by actually including whether that covariate ended up being significant or not. If it wasn't significant, was it left in the analysis?

3) I appreciate the thought that the authors put into the organization of their hypotheses and the mechanisms that might drive variation in naivete underneath the particular eco-evolutionary theme. I think the four themes are reasonable and particularly like how there are now multiple lines of evidence for at least two of the themes (isolation and taxonomic attribute). Further, this organization has helped to improve the clarity of the goals of the analysis.

4) Discussion. Overall, I feel that the authors have greatly improved the discussion, but I do have a couple of comments on this section.

Pg. 9-10, lines 259 - 263: Please clarify the last two sentences of this paragraph. What do the authors mean by only three studies in their database addressing prey naivete "per se"? It seems like there's some relationship with distance from the nearest continental land mass that the authors aim to discuss here, but I struggled to follow what the authors were highlighting there and how this was leading to a new hypothesis.

Pg. 10, Lines 280-289: How can we be sure that the result that herpetofauna and fish have a high probability of encountering naïve prey is, indeed, due to taxonomic attribute and not just driven by ecosystem type (e.g. aquatic vs terrestrial). I guess this might be less likely to be true for herpetofauna but it'd depend on how many full or semi-aquatic species were in the database. But for fish, could this just be the result of ecosystem type (or vice versa for that matter). I'm not sure there's anyway to statistically disassociate these but I feel like the authors should consider these two results and how they may or may not just be a signature of the aquatic ecosystem (and not

taxonomic attribute).

Pg. 11-12: Lines 320 – 336: It could be interested in to examine this result a bit more. For example, can you text whether naivete erodes faster with degree of naivete (or ecosystem type, predator attribute).

## Review form: Reviewer 2

### Recommendation

Reject – article is scientifically unsound

**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?**

Marginal

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

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

No

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

**Is it accessible?**

No

**Is it clear?**

No

**Is it adequate?**

No

**Do you have any ethical concerns with this paper?**

No

### Comments to the Author

First of all, let me say that I think the topic and approach (a meta-analysis) are both timely and appropriate for the field. I would also like to commend the authors on the somewhat Herculean task of assembling the data set that such an undertaking requires. I think that meta-analytic reviews are very useful once a field's body of literature has reached a certain point, and I do think that naivety research has reached that point.

However, my overarching sense after reading this manuscript in detail is one of dissatisfaction with the degree to which the authors appear to have engaged with the existing theoretical literature on this topic. While many of the papers I am thinking of appear in the reference list, their ideas are not engaged with in the text in any meaningful way.

For example – what is naivety? Under what circumstances should we expect to find it? How does the native status of both predator and prey relate to whether we expect to see naivety in a given predator-prey pairing? In most cases it is not just enough to think about native vs exotic species, but rather important aspects of novelty (which the authors touch on briefly here in respect to archetypes, but again without much depth or consideration of other possible types of novelty). What does recognition mean in this context, and how does it differ from response? Which should we therefore measure when testing for naivety? There has been quite a lot written about these questions and their correlates, yet this discussion is barely alluded to, which I think is a shame. The knowledge base that literature provides would provide a framework around which the study could have been better designed, executed, and interpreted.

For example, the decision-making process around selection of studies to include is not clearly justified, but I'm also not certain it makes sense. Does not any kind of response by prey indicate recognition of the predator? I'm aware that some of the theory papers address exactly this question (and would therefore be a useful thing to reference. Why then, choose to exclude studies showing physiological responses to predators, for example? While the authors may disagree with me on this point (which is fine), the reasoning for such decisions is not discussed in sufficient detail for me to understand why this choice was made.

Another example - why was it considered essential that there be a native predator treatment as a control (rather than, for example, no predator or predator absence)? This is not explained in the text, yet it clearly excluded a lot of studies from being considered.

My overall feeling is that the authors have not spent sufficient time reading and thinking critically about the ecological and evolutionary theory underpinning the field. This comes through in the introduction, where the hypotheses are not well explained or aligned with previous conceptual work in the field of antipredator recognition and antipredator responses more generally, and in the discussion, where the results are not related back to theory in any deep way. It also comes through in the way that big statements are made about the meaning of results without critical appraisal of whether such results make sense in light of the proximal mechanisms that could be assumed to be operating. For example, I do not feel there is an appropriate discussion of the (important) differences between learning, adaptation, and more general “acquisition” of antipredator responses.

Finally, I have included a marked-up proof with detailed comments and highlighted examples of my concerns as outlined above. I hope these prove useful in a substantial reworking of the study and manuscript.

## Decision letter (RSPB-2019-2978.R0)

14-Feb-2020

Dear Dr Anton:

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 not available)), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy <http://royalsocietypublishing.org/data-sharing>.

Electronic supplementary material:

All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

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

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,  
Dr Sasha Dall  
mailto:proceedingsb@royalsociety.org

Associate Editor  
Board Member: 1  
Comments to Author:

I have now received reviews from two experts, one of whom reviewed the initial submission. Both reviewers were positive about the topic and the potential of this meta-analysis to be a timely contribution to the field. However, both reviewers also had concerns pertaining to the general framework, the inclusion criteria and justifications, and the interpretations and depth of discussion. From my own reading of the manuscript, I am in agreement with the reviewer comments and concerns.

Both reviewers highlighted that many results and interpretations are not discussed in a meaningful way and how the conclusions fit into a broader framework and what is currently understood in the field is not clear. Without tying the results more clearly to the current state of the field and exploring the literature (and interpretations) in sufficient depth, the authors are missing an opportunity to increase the impact of their meta-analysis. Reviewer #2 provides many detailed comments directly on the PDF of the manuscript about particular aspects that are unclear or vague. Additionally, justifications for particular approaches, such as the criteria for inclusion, need to be stated explicitly and in more detail. I do not have concerns about studies only being included if they test the response to both native and exotic predators, however the justification for this approach (which clearly excludes many studies) needs to be clear.

Overall, I feel this study has the potential to be of interest to a broad audience, particularly if the results are set more solidly in a discussion of the current state of the field. This version is substantially improved compared to the initial submission and I look forward to an even better

revision. I encourage the authors to pay careful attention to the helpful comments so thoughtfully provided by the reviewers in their reviews and on the PDF of the manuscript.

Katie McGhee  
Associate Editor

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

First, I'd like to commend the authors on an incredibly thoughtful and thorough revision of their manuscript. Well done! Below I list some key, focused responses to the revisions.

1) The authors expansion of the database added a significant number of observations to the dataset. This in combination with their approach to remove treatments with fewer than 10 observations, has greatly strengthened their analyses and the conclusions that they can draw from the results. I have no further concerns with the sample sizes presented in their analyses.

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4) Discussion. Overall, I feel that the authors have greatly improved the discussion, but I do have a couple of comments on this section.

Pg. 9-10, lines 259 - 263: Please clarify the last two sentences of this paragraph. What do the authors mean by only three studies in their database addressing prey naivete "per se"? It seems like there's some relationship with distance from the nearest continental land mass that the authors aim to discuss here, but I struggled to follow what the authors were highlighting there and how this was leading to a new hypothesis.

Pg. 10, Lines 280-289: How can we be sure that the result that herpetofauna and fish have a high probability of encountering naïve prey is, indeed, due to taxonomic attribute and not just driven by ecosystem type (e.g. aquatic vs terrestrial). I guess this might be less likely to be true for herpetofauna but it'd depend on how many full or semi-aquatic species were in the database. But for fish, could this just be the result of ecosystem type (or vice versa for that matter). I'm not sure there's anyway to statistically disassociate these but I feel like the authors should consider these two results and how they may or may not just be a signature of the aquatic ecosystem (and not taxonomic attribute).

Pg. 11-12: Lines 320 - 336: It could be interested in to examine this result a bit more. For example, can you text whether naivete erodes faster with degree of naivete (or ecosystem type, predator attribute).

Referee: 2

#### Comments to the Author(s)

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Finally, I have included a marked-up proof with detailed comments and highlighted examples of my concerns as outlined above. I hope these prove useful in a substantial reworking of the study and manuscript.



## Author's Response to Decision Letter for (RSPB-2019-2978.R0)

See Appendix A.

### Decision letter (RSPB-2019-2978.R1)

24-Apr-2020

Dear Dr Anton

I am pleased to inform you that your Review manuscript RSPB-2019-2978.R1 entitled "Global determinants of prey naiveté to exotic predators" has been accepted for publication in Proceedings B.

The referee(s) do not recommend any further changes. Therefore, please proof-read your manuscript carefully and upload your final files for publication. 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 me know immediately.

To upload your 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 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, upload a new version through your Author Centre.

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

- 1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".
- 2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. Please note that PowerPoint files are not accepted.
- 3) Electronic supplementary material: this should be contained in a separate file from the main text and the file name should contain the author's name and journal name, e.g. `authorname_procb_ESM_figures.pdf`

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 see: <https://royalsociety.org/journals/authors/author-guidelines/>

#### 4) Data-Sharing and data citation

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

repository. Details of how to access data should be included in your paper. Please see <https://royalsociety.org/journals/ethics-policies/data-sharing-mining/> for more details.

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=RSPB-2019-2978.R1> 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.

5) 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 final version. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,  
Dr Sasha Dall  
Editor, Proceedings B  
<mailto:proceedingsb@royalsociety.org>

Associate Editor Board Member

Comments to Author:

Thank you for your careful attention to the comments of the reviewers. It is much appreciated. The revised manuscript is clearer, set more solidly in the field, and provides key justifications and details. I feel that the revised version of the manuscript will be of broad interest and an excellent contribution to Proc B!

Minor comments

1. Line 29: "... A major cause of..."
2. Line 355: "...lack of A comparative treatment..."
3. Line 395: "...regardless OF if it is..."
4. Line 407: replace "enhanced mortality" with "increased mortality"
5. Line 419: prioritize
6. Change spellings of "mollusk" to UK spelling "mollusc" throughout - there are currently both spellings (line 341, 167 vs 245, 194)

Best,  
Katie McGhee  
Associate Editor

## Decision letter (RSPB-2019-2978.R2)

28-Apr-2020

Dear Dr Anton

I am pleased to inform you that your manuscript entitled "Global determinants of prey naiveté to exotic predators" 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.

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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.

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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,

Proceedings B

<mailto:proceedingsb@royalsociety.org>

## Appendix A

### Revision of Manuscript ID RSPB-2019-2978 Proceedings of Royal Society B

#### Referee: 1

First, I'd like to commend the authors on an incredibly thoughtful and thorough revision of their manuscript. Well done! Below I list some key, focused responses to the revisions.

*Comment: We thank the reviewer for the encouraging comments.*

1) The authors expansion of the database added a significant number of observations to the dataset. This in combination with their approach to remove treatments with fewer than 10 observations, has greatly strengthened their analyses and the conclusions that they can draw from the results. I have no further concerns with the sample sizes presented in their analyses.

*Comment: We agree with the reviewer that the dataset and analyses are now more robust.*

2) I'm glad that the authors considered and ultimately included time since introduction as a covariate in their analyses. However, unless I overlooked, it I think the manuscript could be improved by actually including whether that covariate ended up being significant or not. If it wasn't significant, was it left in the analysis?

*Comment: We agree that this was not clear in the previous version. The covariate 'number of generations since introduction' was significant or marginally significant in most cases. But most importantly, the AIC in all the analyses was lower when including 'number of prey generations' as a covariate. Therefore, it was always retained in the models.*

*Action: We have now included this information in lines 223-225: "The models that included 'number of prey generations' had lower AICs than those that excluded this variable, so the variable was kept in the models, regardless of its significance."*

3) I appreciate the thought that the authors put into the organization of their hypotheses and the mechanisms that might drive variation in naivete underneath the particular eco-evolutionary theme. I think the four themes are reasonable and particularly like how there are now multiple lines of evidence for at least two of the themes (isolation and taxonomic attribute). Further, this organization has helped to improve the clarity of the goals of the analysis.

*Comment: We are also satisfied with the current succinct presentation of the hypotheses and mechanisms. We thank the reviewer for this suggestion.*

4) Discussion. Overall, I feel that the authors have greatly improved the discussion, but I do have a couple of comments on this section.

Pg. 9-10, lines 259 – 263: Please clarify the last two sentences of this paragraph. What do the authors mean by only three studies in their database addressing prey naivete “per se”? It seems like there’s some relationship with distance from the nearest continental land mass that the authors aim to discuss here, but I struggled to follow what the authors were highlighting there and how this was leading to a new hypothesis.

*Comment: We agree with the reviewer that the sentence was unclear. By “per se” we meant that only a few studies have assessed prey naiveté on islands explicitly and quantitatively using experiments.*

*Action: We have now edited and clarified the entire paragraph, including that specific sentence. The paragraph now reads as follows (lines 277-294): “Evidence from this study supports the hypothesis that terrestrial animals on islands are generally naïve towards exotic predators, representing the first global quantification of prey naiveté on islands. When isolated from predators, prey on islands can experience a rapid loss of no longer functional antipredator behaviour through relaxed selection [53–56]. Indeed, some prey species lack predators in the isolated Galapagos Islands, which are often described as being naïve to predatory risk [57]. Similar examples exist on less remote islands, such as snake-free Balearic Islands in the Mediterranean, where wall-lizards show a lack of antipredator behaviours such as tail-waiving or slow-motion movement when exposed to introduced snakes [58]. Prey naiveté is a primary explanation for the more devastating impacts of introduced predators on oceanic islands compared with continental terrestrial systems [10]. However, only three studies in our database addressed prey naiveté on islands and two of those were coastal islands (the exception was New Zealand). We hypothesize that the degree of prey naiveté on remote oceanic islands likely exceeds that reported in this meta-analysis. Australia was included as a continental mainland in our study owing to its large size; we performed an additional test by including Australia in the island category, which did not change our findings ( $g = -0.16 \pm 0.15$ ;  $p=0.039$  and  $g = -0.04 \pm 0.15$ ;  $p=0.853$  for island and mainland respectively), suggesting that our results robustly support the hypothesis that terrestrial species on islands display pronounced levels of prey naiveté.”*

Pg. 10, Lines 280-289: How can we be sure that the result that herpetofauna and fish have a high probability of encountering naïve prey is, indeed, due to taxonomic attribute and not just driven by ecosystem type (e.g. aquatic vs terrestrial). I guess this might be less likely to be true for herpetofauna but it’d depend on how many full or semi-aquatic species were in the database. But for fish, could this just be the result of ecosystem type (or vice versa for that matter). I’m not sure there’s anyway to statistically disassociate these but I feel like the authors should consider these two results and how they may or may not just be a signature of the aquatic ecosystem (and not taxonomic attribute).

*Comment: We agree with the reviewer that there could be a confounding factor in these results.*

*Action:* We performed an additional analysis to test whether the high probability of herpetofauna and fish to encounter naïve prey was, indeed, due to taxonomic attribute and not just driven by ecosystem type (e.g. freshwater vs terrestrial vs marine). This information has been added in lines 321-328 as follows: “We performed an additional analysis to ascertain whether the high probability of herpetofauna and fish to encounter naïve prey was due to taxonomic affiliation and not simply driven by ecosystem type (freshwater, terrestrial, marine). We found similar results for these two taxonomic groups, regardless of the ecosystem type ( $g = -0.39 \pm 0.27$ ;  $p=0.005$  and  $g = -1.07 \pm 0.44$ ;  $p<0.001$  for freshwater and marine fishes, respectively, and  $g = -0.39 \pm 0.41$ ;  $p=0.060$  and  $g = -1.29 \pm 1.11$ ;  $p=0.022$  for freshwater and terrestrial herpetofauna, respectively), supporting our findings of likelihood of prey naiveté towards fish and herpetofauna.”

Pg. 11-12: Lines 320 – 336: It could be interested in to examine this result a bit more. For example, can you text whether naivete erodes faster with degree of naivete (or ecosystem type, predator attribute).

*Comment:* Such analyses should be done at many levels (e.g., changes through time by ecosystem type, the taxonomic level of the prey, across taxonomic levels of the predator, islands vs continents, etc). Running only a few of these would present an inconsistent and potentially misleading picture, whereas a full analysis of these results is beyond the scope of this project. We agree that the result is intriguing and we hope it inspires other researchers to explore the concept further.

*Action:* We encouraged further exploration of the dataset in the discussion, lines 412-416: “The relationship between overall prey naiveté and the number of prey generations suggests that long-lived species could be particularly vulnerable to introduced predators. It remains to be determined how other eco-evolutionary factors influence the loss of prey naiveté through time – e.g., how does this rate differ across taxa groups and ecosystem types?”.

## Referee: 2

Comments to the Author(s)

First of all, let me say that I think the topic and approach (a meta-analysis) are both timely and appropriate for the field. I would also like to commend the authors on the somewhat Herculean task of assembling the data set that such an undertaking requires. I think that meta-analytic reviews are very useful once a field’s body of literature has reached a certain point, and I do think that naivety research has reached that point.

*Comment:* We thank the reviewer for the support.

However, my overarching sense after reading this manuscript in detail is one of dissatisfaction with the degree to which the authors appear to have engaged with the existing theoretical literature on this topic. While many of the papers I am thinking of

appear in the reference list, their ideas are not engaged with in the text in any meaningful way.

***Comment:** We understand and appreciate the reviewer's concern with regard to our engagement with the theoretical literature in our previous draft. We have now revised the manuscript following the referee's suggestions, including the addition of a paragraph in the introduction and substantial editing of many sections in the discussion.*

***Action:** Examples of these modified sections are:*

- *The addition of a paragraph in the introduction that reads as follows (lines 50-64): "Prey naiveté was originally conceived as a simplistic phenomenon where native animals become 'easy prey' to exotic predators owing to naïve behaviour [11]. However, prey naiveté is now recognized as a more complex phenomenon and four levels of prey naiveté have been proposed [15,16,19]. Level-1 naïve prey do not recognize the exotic predator as a threat, which precludes any antipredator behavioural responses [19]. Native animals experience level-2 naiveté if they recognize the exotic predator but show an inappropriate antipredator behaviour [19]. Level-3 naïve prey display an appropriate but ineffective behavioural response towards an exotic predator [19]. Lastly, level-4 naïve prey over-responds to the exotic predator after experiencing excessive sublethal costs of predation [16]. In addition to exhibiting inadequate antipredator behaviour, prey species that lack evolutionary experience to exotic predation may also possess other morphological or physiological traits that make them susceptible to exotic predators such as insufficient armature, flightlessness, conspicuous scent, or inadequate camouflage [20]. Although prey naiveté is a well-accepted phenomenon [16], it varies under the influence of eco-evolutionary factors [14,15,21] whose relative importance and generality have yet to be quantified."*
- *A deeply edited paragraph in the discussion linking the ecological theory presented on our study with the applications to real-world problems. See lines 406 – 423 as follows: "Our meta-analysis identifies some global drivers of prey naiveté, paving the way for testing these drivers in different contexts. Assuming that prey naiveté results in enhanced mortality [14], our results point to several animal groups as being disproportionately sensitive to introduced predators. Some of these vulnerable cases were expected, such insular terrestrial and freshwater fauna; whereas other case were unpredicted, such as the high susceptibility of native prey to exotic predators in marine systems, or the vulnerability of specific prey taxa, including fishes and amphibians. The relationship between overall prey naiveté and the number of prey generations suggests that long-lived species could be particularly vulnerable to introduced predators. It remains to be determined how other eco-evolutionary factors influence the loss of prey naiveté through time – e.g., how does this rate differ across taxa groups and ecosystem types? Additionally, the most damaging groups of exotic predators were found to be animals that originate from a foreign biogeographical realm or that represent a new generic archetype. Particular attention should be given to the introduction of*

predatory fishes, reptiles and mammals (perhaps with the exception of canids). This information could guide efforts to prioritise invasion threats to biodiversity and inform risk assessments of conservation schemes involving assisted colonization. Finally, we identified several areas in which the quantification of prey naiveté is notably scant (e.g., marine ecosystems, remote oceanic islands, and many taxa of prey species) and these should be prioritized to clarify predictive patterns of prey naiveté.”

For example – what is naivety?

**Action:** *We included an explicit definition of prey naiveté in lines 40-43: “The disproportionate impact of exotic predators on native communities is often attributed to prey naiveté – the failure of prey to recognize (or respond appropriately) to a novel predator species and/or the lack of an appropriate defense (sensu [10]).”*

Under what circumstances should we expect to find it?

**Comment and action:** *We discuss in lines 65-89 several eco-evolutionary factors that have been tested or hypothesized to shape the degree of prey naiveté as follows: “We hypothesize that the occurrence and strength of prey naiveté stems from several, non-exclusive factors that can be clustered into four themes (Table 1). First, prey naiveté can be promoted by persistent biogeographic (hence evolutionary) isolation between predator and prey [13]. The pronounced isolation of freshwater biota has been hypothesized to render prey more sensitive to introduced predators compared with terrestrial or marine biota [10,22] (Hypothesis 1 in Table 1). Prey naiveté is also presumed to be more prevalent on islands than on mainlands [23–25], owing to lack of eco-evolutionary experience with exotic predators – or even native ones on predator-free islands (Hypothesis 2 in Table 1). Likewise, predators introduced to geographically isolated or species-poor biotas are more likely to represent a novel archetype – that is, prey will not display antipredator responses towards exotic predators that are unfamiliar, where a practical proxy for ‘archetype’ distinction has been proposed at the taxonomic level of genus or family [10,16,26,27] (Hypothesis 3 in Table 1). The introduction of a predator from a different biogeographic realm enhances the probability that the predator will be distinct from those of the recipient biota and thus unfamiliar [10] (Hypothesis 4 in Table 1). The second theme is related to the way animals acquire antipredator responses (and lose prey naiveté) over time through adaptation, which could be a function of the number of prey generations since the introduction of a predator [28–30] (Hypothesis 5 in Table 1). The third theme is related to the mediating role of latitude on prey naiveté, as novel predator recognition could be higher in low latitude communities, which generally experience greater and more diverse predation pressure [31–33] and thus whose prey may display antipredator behaviours to a broader variety of predator archetypes (Hypothesis 6 in Table 1). Finally, the fourth theme is related to taxonomic specificity, as the recognition of introduced predators might vary across taxa [34], such that certain predators are more recognizable than others and certain prey are better adapted to recognize certain predators or entire suites of predatory taxa [Hypotheses 7 and 8 respectively in Table 1].”*



How does the native status of both predator and prey relate to whether we expect to see naivety in a given predator-prey pairing? In most cases it is not just enough to think about native vs exotic species, but rather important aspects of novelty (which the authors touch on briefly here in respect to archetypes, but again without much depth or consideration of other possible types of novelty).

*Comment:* We agree with the reviewer that within a predator-prey pairing there are many aspects of novelty that are not considered in this study, such as the assessment of the eco-evolutionary experience of native prey with their extant (and extinct) cohort of predatory species, which can influence their antipredator responses.

*Action:* We have edited many sections of the Introduction and Discussion to address this concern. See, for instance:

- In lines 72 -78 as follows: “Likewise, predators introduced to geographically isolated or species-poor biotas are more likely to represent a novel archetype – that is, prey will not display antipredator responses towards exotic predators that are unfamiliar, where a practical proxy for ‘archetype’ distinction has been proposed at the taxonomic level of genus or family [10,16,26,27] (Hypothesis 3 in Table 1). The introduction of a predator from a different biogeographic realm enhances the probability that the predator will be distinct from those of the recipient biota and thus unfamiliar [10] (Hypothesis 4 in Table 1).”

What does recognition mean in this context, and how does it differ from response? Which should we therefore measure when testing for naivety? There has been quite a lot written about these questions and their correlates, yet this discussion is barely alluded to, which I think is a shame. The knowledge base that literature provides would provide a framework around which the study could have been better designed, executed, and interpreted. For example, the decision-making process around selection of studies to include is not clearly justified, but I’m also not certain it makes sense. Does not any kind of response by prey indicate recognition of the predator? I’m aware that some of the theory papers address exactly this question (and would therefore be a useful thing to reference).

*Comment:* In our study we have assessed antipredator response of prey assuming that a significant lack of response to an exotic predator (as compared to a native predator) indicates a lack of recognition of the exotic predator as a predatory threat (Level 1 prey naiveté). However, we agree that an antipredator response towards an exotic predator does not necessarily imply a lack of naiveté, as the response can be inappropriate (level 2 prey naiveté), ineffective (level 3 prey naiveté), or excessive (level 4 prey naiveté).

*Action:* We have added this information in the Introduction and Discussion:

- The addition of a paragraph in the Introduction that reads as follows (lines 50-64): “Prey naiveté was originally conceived as a simplistic phenomenon where

native animals become ‘easy prey’ to exotic predators owing to naïve behaviour [11]. However, prey naiveté is now recognized as a more complex phenomenon and four levels of prey naiveté have been proposed [15,16,19]. Level-1 naïve prey do not recognize the exotic predator as a threat, which precludes any antipredator behavioural responses [19]. Native animals experience level-2 naiveté if they recognize the exotic predator but show an inappropriate antipredator behaviour [19]. Level-3 naïve prey display an appropriate but ineffective behavioural response towards an exotic predator [19]. Lastly, level-4 naïve prey over-responds to the exotic predator after experiencing excessive sublethal costs of predation [16]. In addition to exhibiting inadequate antipredator behaviour, prey species that lack evolutionary experience to exotic predation may also possess other morphological or physiological traits that make them susceptible to exotic predators such as insufficient armature, flightlessness, conspicuous scent, or inadequate camouflage [20]. Although prey naiveté is a well-accepted phenomenon [16], it varies under the influence of eco-evolutionary factors [14,15,21] whose relative importance and generality have yet to be quantified.”

*- In the Discussion as follows (lines 396 - 403):* “Second, our study only included measurements of level-1 prey naiveté (sensu [16,19]), which interprets a lack of response to an exotic predator (as compared to a native predator) as a lack of recognition of the exotic predator as a threat. However, native animals experience additional levels of naiveté (level-2, -3, and -4), which relate to appropriate, effective and/or commensurate responses to exotic predators, respectively. Therefore, wildlife might still experience heavy predation by exotic predators despite low level-1 naiveté. By focusing on level-1 naiveté, our study did not consider physiological responses to the presence of predators [76], which can be considered another important form of prey naiveté.”

Why then, choose to exclude studies showing physiological responses to predators, for example? While the authors may disagree with me on this point (which is fine), the reasoning for such decisions is not discussed in sufficient detail for me to understand why this choice was made.

***Comment:*** *Prey naiveté is a complex phenomenon that may comprise morphological and/or physiological defenses, even though it most often described in terms of behavior (see, for example, the meta-analysis of prey naiveté in Australian mammals, by Banks and colleagues in Proc Roy Soc B, 2018).*

***Action:*** *We have included this statement in lines 58-61 as follows: “In addition to exhibiting inadequate antipredator behaviour, prey species that lack evolutionary experience to exotic predation may also possess other morphological or physiological traits that make them susceptible to exotic predators such as insufficient armature, flightlessness, conspicuous scent, or inadequate camouflage [20].”*

Another example - why was it considered essential that there be a native predator treatment as a control (rather than, for example, no predator or predator absence)? This is not explained in the text, yet it clearly excluded a lot of studies from being considered.

***Comment:** We considered only experimental designs that included empirical comparisons between native and exotic predators, to ensure a direct and consistent method of quantifying the perceived risk threat of an exotic predator.*

***Action:** This information has been included in lines 387-396: “First, studies were excluded unless they met several criteria, with the disadvantage of not considering the totality of evidence generated globally on prey naiveté. We only considered experimental designs that included empirical comparisons between native and exotic predators, to ensure a direct and consistent way to quantify the perceived risk threat of an exotic predator. Consequently, we excluded studies with controls such as ‘absence of exotic predator’, as those comparisons often require cautious interpretation (e.g., does the behavioural response of prey towards the exotic predator as compared with an empty control indicate predator recognition or simply a response to the presence of an organism, regardless if it is perceived as a predatory threat?).”*

My overall feeling is that the authors have not spent sufficient time reading and thinking critically about the ecological and evolutionary theory underpinning the field. This comes through in the introduction, where the hypotheses are not well explained or aligned with previous conceptual work in the field of antipredator recognition and antipredator responses more generally, and in the discussion, where the results are not related back to theory in any deep way. It also comes through in the way that big statements are made about the meaning of results without critical appraisal of whether such results make sense in light of the proximal mechanisms that could be assumed to be operating.

***Comment:** We have heavily edited our manuscript to accommodate these concerns, including the general and specific comments marked on the PDF copy. We hope that these concerns are now largely addressed by the revised description of the hypotheses and the interpretation of results within the theoretical eco-evolutionary framework of biological invasions.*

For example, I do not feel there is an appropriate discussion of the (important) differences between learning, adaptation, and more general “acquisition” of antipredator responses.

***Action:** There is a vast literature documenting the debate about the mechanisms and extent to which learning (and instinctual behaviour) is an evolved trait, and we do not feel our paper is the appropriate place to summarize these arguments. Our premise, supported by published studies such as Juliano & Gravel (2002), is that predator recognition, vigilance, and other behaviours that determine the survival of individuals facing a novel predation threat can vary substantively across a population and can be subject to strong selection in the persistent presence of a predator. Learning and social transmission of anti-predatory behaviour can begin the process, but time (number of*

*generations) is needed for selection and adaptation, presuming the prey is not extirpated before the process can play out.*

*We have now expanded on the discussion to clarify this specific concern in lines 358-362: “The antipredator response of native prey to novel predators can evolve through time, if predation selects for predator recognition and avoidance behaviour [28]. Behaviours that determine the survival of individuals facing a novel predation threat can be subject to strong selection in the persistent presence of a predator [67]. If extinction is averted, evolutionary adaptation can be achieved in a small number of generations.”*

Finally, I have included a marked-up proof with detailed comments and highlighted examples of my concerns as outlined above. I hope these prove useful in a substantial reworking of the study and manuscript.

***Comment:*** *We have followed and implemented all the comments and concerns of the reviewer, which can be assessed in the tracked-changes version of the manuscript.*