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A triple threat: high population density, high foraging intensity and flexible habitat preferences explain high impact of feral cats on prey

Rowena P. Hamer, Riana Z. Gardiner, Kirstin M. Proft, Christopher N. Johnson and Menna E. Jones

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Original submission:	25 May 2020
1st revised submission:	20 September 2020
2nd revised submission:	29 November 2020
Final acceptance:	30 November 2020

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

Review History

RSPB-2020-1194.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?
Excellent

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

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

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
This manuscript presents the results of a large field effort to collar and track the space use and movements of feral cats and tiger quolls in the Midlands of Tasmania, Australia. I greatly appreciate the amount of work that such a study would have required, and I commend the authors for undertaking such important work. Understanding WHY alien predators have such great impacts on native prey is imperative, and I applaud any study that attempts to get at the mechanisms behind such impacts. I immediately liked the stated aim to compare a native and introduced predator on measures that influence their impacts on native prey – this would be an excellent thing to be able to do. However, I got lost somewhere in the detail of the paper as to how the conceptual underpinnings of measuring habitat use and "foraging behaviour" (really – landscape level movements that are consistent with foraging, not foraging behaviour in the purest sense as would be used by animal behaviourists) should translate to comparable predictions of impact.

The authors develop a framework that I like in principle. I do wonder how different it is to recent other conceptual work on the topic, such as Carthey & Blumstein (2018) in TREE. It also draws directly on previous predation sequence theory (e.g. Lima and Dill 1990, Endler 1991), without really making that explicit, although as presented it seems that Sih et al 2010 draw on this same idea of a predation sequence that actually comes from these previous references. In short, I'm not too sure if the authors mean to present this as a new framework for understanding alien predator impact more broadly, in which case I don't think it is really novel enough to be considered as such, OR as a framework intended specifically for the comparison of cats and quolls, in which case it perhaps makes more sense, but is less broadly interesting. I wonder if the authors could develop it more, having looked more closely at the other frameworks it is closely related to (specifically those mentioned above), and tie it more closely to the measures (habitat domain, hunting/foraging movements/behaviour, etc) you use here to compare quolls and cats – can they be used for most native and alien predators to evaluate their likely impacts on prey? If Sih et al (2010) already have such a framework, can the two be linked together to make something new that would be very broadly applicable? Now that would be exciting! As it stands, the framework doesn't quite gel well with the rest of the paper, or with the other literature on predator-prey naivety.

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On the whole, I think this manuscript has great potential, but the theory underpinning it needs to be explained much more clearly, and the methodology clearly linked to that theory, and more clearly explained.

Specific line by line comments follow below.

INTRODUCTION

L38-39: You had me until this line. Why/how can hunting mode and habitat domain be used to predict CEs and NCEs? Also, what is your definition of hunting mode, and of habitat domain? These aren't necessarily obvious.

L41-55: I have read and reread this several times, and referred to Figure 1 whilst doing so, but I still just don't understand HOW this is meant to work. I think some of the confusion comes from the use of terms without defining them – for example, "encounter" (what counts as an encounter here? Face to face? Within potential detection distance? Overlap of home range over a certain timeframe?), "behaviour" (from telemetry? This is more "movement patterns", isn't it?), "revisitation frequency" (why? To where?), "habitat domain estimates" (meaning? habitat preferences as in, preferences for certain landuse types? Certain structural habitat components such as dense undergrowth vs open plains? Ecosystems/climate types? Woodland vs rainforest vs swamps? Etc?). There's too much variation in what these terms could mean for the reader to

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Overall – you need to ensure you don't use terms without explaining them first – particularly if you are referring to something you will calculate later, but that your reader has not yet had explained.

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L93-102: I feel like you could give (here or in the introduction) more background explanation as to the theory for why revisitation is important. For example, a predator that revisits parts of its habitat more frequently is more dangerous to prey than one that revisits less frequently. If a low frequency revisiting predator has just visited, that location should be safe for some time. On the other hand, if a predator has high revisitation rates, then seeing a predator recently does not give much information about likely immediate future risk. This incorporates temporal patterning of revisitations as well, which I'm now wondering whether and how you have or could incorporate into your analysis?
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L164: For predators, not prey, I assume.

DISCUSSION
L167: What about prey traits though? This seems to assume that prey are randomly distributed across grid cells, which they aren't... can you explicitly discuss the assumptions here and their limits, and perhaps speculate what effect it would have on your findings to incorporate them? (Or if future work could do so?)

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L181-184: So are these the findings that are being interpreted as "foraging intensity" (foraging behaviour?)? - this isn't made clear or explicit earlier on, which would really help (did you set out to measure "foraging intensity" and decide that this was the best way to do it? Or is this a post hoc interpretation of the data? Either way - I didn't understand until now what you meant when you said foraging intensity). These ideas need to be set up earlier on in the piece.

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Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

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

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

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

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

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Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
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Do you have any ethical concerns with this paper?
No

Comments to the Author
This study aims to explore why feral cats have had disproportionate impacts on native prey compared to a similar native predator, the spotted-tail quoll. The authors tackle this by applying recently proposed theory on habitat domain, in combination with sound experimental design and cutting-edge statistical approaches, to compare relative impacts between the native and non-native predators. I praise the authors for their work and as a major comment, I only suggest that the discussion should include a review of the available literature on non-consumptive effects of cats and quolls on different prey to confirm the author's predictions.
Introduction
Line 30: What about movement range, assuming that individuals that move more encounter each other more frequently? Also, what about food availability and habitat complexity?
Line 40: Is it really that simple? What about the prey's habitat domain, their age, reproductive status, or the type of antipredator response that they are implementing? Briefly discuss how prey's attributes would influence this.
Results
Table S1.3: For your model selection with AIC, when you have two models that only differs in a single parameter and are within AIC difference of two, then the extra parameter of the more complex model is actually uninformative. See:
Arnold (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management 74(6):1175–1178; DOI: 10.2193/2009-367
Discussion
Line 214: Are there any previous prey studies evaluating non-consumptive effects in response to feral cats or spotted-tail quolls that could confirm your predictions here?
Line 221: And also with food availability?
References:
Note that 'doi' appears twice in several references.

Decision letter (RSPB-2020-1194.R0)

22-Jul-2020

Dear Ms Hamer:

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.

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It is a condition of publication that you make available the data and research materials supporting the results in the article. Please see our Data Sharing Policies (https://royalsociety.org/journals/authors/author-guidelines/#data). 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.

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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.

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. 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 Locke Rowe
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
This paper has been evaluated by two experts, who both see merits in this work but also have important comments on the framing of this study. There are many valuable comments by both referees on how to embed the study better in the existing theoretical framework and previous literature, which should be taken in account. In addition, referee 1 lacks clarity in many places, both in the conceptual parts and methods. Also they are unsure how the role of prey behaviour enters the analyses, or whether it is accounted for at all. In summary there are multiple places in this manuscript requiring clarification and revised conceptual framing, requiring major reworking of this paper.

Reviewer(s)' Comments to Author:
Referee: 1
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Line 40: Is it really that simple? What about the prey's habitat domain, their age, reproductive status, or the type of antipredator response that they are implementing? Briefly discuss how prey's attributes would influence this.
Results
Table S1.3: For your model selection with AIC, when you have two models that only differs in a single parameter and are within AIC difference of two, then the extra parameter of the more complex model is actually uninformative. See:
Arnold (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management 74(6):1175–1178; DOI: 10.2193/2009-367
Discussion
Line 214: Are there any previous prey studies evaluating non-consumptive effects in response to feral cats or spotted-tail quolls that could confirm your predictions here?
Line 221: And also with food availability?
References:
Note that 'doi' appears twice in several references.

Author's Response to Decision Letter for (RSPB-2020-1194.R0)

See Appendix A.

RSPB-2020-1194.R1 (Revision)

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
I congratulate the authors on an excellent job of responding to the reviewer comments. The manuscript reads really well now, and the novel contributions it makes are are now well-explained and the novelty very clear. It is a really strong and valuable contribution to the literature.

I have only a few (very minor) additional suggestions, as follows:

L133: perhaps add "available in" Appendix S1 to make it clear that the results of this analysis have been provided, if the reader wishes to look them up

L140: perhaps add a label to the top row of the Figure, to indicate that the numbers 1:6 refer to scenarios 1:6 (if I understand correctly?)

L144-147: excellent, this makes it really clear that what you have done is both novel and needed

L179: perhaps refer to a result or your figure here, to make it abundantly clear where this conclusion has come from?

Decision letter (RSPB-2020-1194.R1)

09-Nov-2020

Dear Ms Hamer

I am pleased to inform you that your manuscript RSPB-2020-1194.R1 entitled "A triple threat: high population density, high foraging intensity and flexible habitat preferences explain high impact of feral cats on prey." has been accepted for publication in Proceedings B.

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

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

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

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

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

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

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

5) Data accessibility section and data citation
It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
• DNA sequences: Genbank accessions F234391-F234402
• Phylogenetic data: TreeBASE accession number S9123
• Final DNA sequence assembly uploaded as online supplemental material
• Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311
NB. From April 1 2013, peer reviewed articles based on research funded wholly or partly by RCUK must include, if applicable, a statement on how the underlying research materials – such as data, samples or models – can be accessed. This statement should be included in the data accessibility section.

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

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

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

Sincerely,
Dr Locke Rowe
Editor, Proceedings B
mailto:proceedingsb@royalsociety.org

Associate Editor:
Board Member: 1
Comments to Author:
This paper has been sent out for review to one of the original reviewers. The reviewer and I are both satisfied with the thorough revision done by the authors. It is now much clearer what has been done and what has not been done. I still think that for making it a truly integrative approach, observations on the real effects on a number of native prey would be necessary to quantify the costs of encounters under the six (or rather 5) prey response types (as opposed to just

discussing and speculating about it), but I also understand that this would stretch the extent of the present study too much.

There are a few minor point by the referee, which need to be accounted for.

In addition, I have one minor, formal point. I suggest moving lines 149-152 up towards the end of the Methods section (rather than being at the beginning of the Results). These lines and the Tables cited therein describe what the results are based on, but they are not results themselves.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
I congratulate the authors on an excellent job of responding to the reviewer comments. The manuscript reads really well now, and the novel contributions it makes are are now well-explained and the novelty very clear. It is a really strong and valuable contribution to the literature.

I have only a few (very minor) additional suggestions, as follows:

L133: perhaps add "available in" Appendix S1 to make it clear that the results of this analysis have been provided, if the reader wishes to look them up

L140: perhaps add a label to the top row of the Figure, to indicate that the numbers 1:6 refer to scenarios 1:6 (if I understand correctly?)

L144-147: excellent, this makes it really clear that what you have done is both novel and needed

L179: perhaps refer to a result or your figure here, to make it abundantly clear where this conclusion has come from?

Decision letter (RSPB-2020-1194.R2)

30-Nov-2020

Dear Ms Hamer

I am pleased to inform you that your manuscript entitled "A triple threat: high population density, high foraging intensity and flexible habitat preferences explain high impact of feral cats on prey." 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 7 pages long. Our Production Office will be able to confirm the exact length at proof stage.

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

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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 handling editor

Comments to Author:

This paper has been evaluated by two experts, who both see merits in this work but also have important comments on the framing of this study. There are many valuable comments by both referees on how to embed the study better in the existing theoretical framework and previous literature, which should be taken in account. In addition, referee 1 lacks clarity in many places, both in the conceptual parts and methods. Also they are unsure how the role of prey behaviour enters the analyses, or whether it is accounted for at all. In summary there are multiple places in this manuscript requiring clarification and revised conceptual framing, requiring major reworking of this paper.

We thank the reviewers and the handling editor for their helpful comments. We have attempted to reframe the manuscript to address the concerns raised. Major changes include:

1. **Revised conceptual framing**

As requested by Reviewer 1, we have adjusted the Introduction to more clearly define the links between our approach and existing theoretical frameworks, particularly those of Carthey and Blumstein [1] and Sih, Bolnick [2]. We have also revised the layout and content of Figure 1 to strengthen these links and to distinguish between the theoretical framework (which could be used in any system) and its application to our case study.

2. **Clarifications around incorporating prey behaviour**

In our case study, we have attempted to assess the relative predation impact of a novel (feral cat) and familiar (native spotted-tailed quoll) predator on *all* shared native prey species, instead of attempting to calculate the absolute impact on a focal prey species or group of species. To do this, we have predicted relative impact of the predators across all habitats within the landscape and under 6 scenarios of prey response, as predicted by prey naïveté theory. The conceptual framework (Figure 1) allows for quantitative information on prey behaviour to be incorporated, but this would narrow the focus of the assessment to impacts on that particular prey species. We have clarified our approach within the manuscript, including by reorganising Figure 1 to distinguish between the conceptual framework in general and our case study in particular.

In the Discussion, we have also clarified how prey behaviour would influence the absolute magnitude of predation impact at each stage of the predator-prey encounter. Prey habitat

preferences and movement will affect the rate of encounter with predators, and their assessment of predation risk and types of anti-predator defences (if deployed) will affect both the consumptive and non-consumptive effects of each encounter. Nevertheless, as discussed in the manuscript, prey naïveté theory allows us to predict the relative impacts of the novel and familiar predator at each stage.

3. Increased detail in the methods section

We have reorganised and increased the amount of detail given in the Methods and ensured that we have defined terms at first use. We have also removed two analyses (behavioural state classification and diel activity analyses) to Appendix S1 to minimise confusion. These analyses were not particularly informative for our case study and their results were not included in our final calculations of encounter rate. They have been retained in the appendix, however, as they may be more informative in other systems.

4. Increased detail in the Introduction and Discussion

Both reviewers requested more detail on the theoretical link between predator behaviour and the strength of non-consumptive effects. We have attempted to strengthen and clarify this discussion both when introducing the background theory (Introduction) and when discussing how predictions were made for our case study (Discussion).

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

This manuscript presents the results of a large field effort to collar and track the space use and movements of feral cats and tiger quolls in the Midlands of Tasmania, Australia. I greatly appreciate the amount of work that such a study would have required, and I commend the authors for undertaking such important work. Understanding WHY alien predators have such great impacts on native prey is imperative, and I applaud any study that attempts to get at the mechanisms behind such impacts. I immediately liked the stated aim to compare a native and introduced predator on measures that influence their impacts on native prey – this would be an excellent thing to be able to do. However, I got lost somewhere in the detail of the paper as to how the conceptual underpinnings of measuring habitat use and "foraging behaviour" (really – landscape level movements that are consistent with foraging, not foraging behaviour in the purest sense as would be used by animal behaviourists) should translate to comparable predictions of impact.

The authors develop a framework that I like in principle. I do wonder how different it is to recent other conceptual work on the topic, such as Carthey & Blumstein (2018) in TREE. It also draws directly on previous predation sequence theory (e.g. Lima and Dill 1990, Endler 1991), without really making that explicit, although as presented it seems that Sih et al 2010 draw on this same idea of a predation sequence that actually comes from these previous references. In short, I'm not too sure if the authors mean to present this as a new framework for understanding alien predator impact more broadly, in which case I don't think it is really novel enough to be considered as such, OR as a framework intended specifically for the comparison of cats and quolls, in which case it perhaps makes more sense, but is less broadly interesting. I wonder if the authors could develop it more, having looked more closely at the other frameworks it is closely related to (specifically those mentioned above), and tie it more closely to the measures (habitat domain, hunting/foraging movements/behaviour, etc) you use here to compare quolls and cats – can they be used for most native and alien predators to evaluate their likely impacts on prey? If Sih et al (2010) already have such a framework, can the two be linked together to make something new that would be very broadly applicable? Now that would be exciting! As it stands, the framework doesn't quite gel well with the rest of the paper, or with the other literature on predator-prey naivety.

Overall, the paper suffers from not clearly defining conceptual terms, and not explicitly stating key logical links between concepts. For example, why should habitat domain and hunting behaviour "explain" high impacts of cats on prey? Many of these ideas might seem obvious to the authors, who have been thinking about them for a long time, but it is not so for your audience. We need to be led clearly through the steps from what you set out to measure and why, and how these measures can be translated to impact on (all? Certain species? Naïve or non-naïve?) prey. Perhaps the authors could consider creating a diagram that steps the reader through the process and explains the conceptual and logical links at the same time.

Another example is that, despite discussing NCEs, the analysis and interpretation of your results apparently treat prey as statically and randomly distributed throughout the landscape, such that the likelihood of encountering a cat is simply a function of the cats' habitat preferences and activity patterns (I am deducing this myself after a careful reading of the manuscript – I can't see that this is made explicit anywhere, but it should be). NCEs result from avoiding certain areas or changing behaviour in other ways in response to perceived risk, such that the actual probability of an encounter between predator and prey depends on the movements and decision-making of each in what is essentially a "game of fear". See Brown, Laundre & Gurung (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions, J Mammalogy, and other papers on the ecology of fear. Thus, as it stands, I think that most people reading your manuscript who know something about the ecology of fear between predators and prey would wonder why you have not taken into account prey risk assessment, movement, and avoidance of predators, their cues, and risky times and places (which also depends on the presence or absence of naivety, as you have identified).

Perhaps your treatment of the data can stand, if you make it much more explicit that by "encounter" between predator and prey you don't mean a literal face-to-face encounter, but rather the broader definition employed by Lima & Dill (and Sih et al?), where "encounter" can mean that prey and predator are sufficiently close as to potentially detect one another. This would allow for the game of fear to be something that happens after that point, and so not something your model needs to explicitly discuss. Then you could logically suggest that next steps for future research would be to incorporate prey's use of space and movement/activity patterns, potentially for naïve and non-naïve prey, thus better incorporating the potential effect of naivety in an assessment of alien vs native predator impacts. At the moment I am just not sure as to how prey responses (i.e., naivety or non-naivety) are actually incorporated into your comparisons of impact here (other than being "mapped onto" your Figure?).

On the whole, I think this manuscript has great potential, but the theory underpinning it needs to be explained much more clearly, and the methodology clearly linked to that theory, and more clearly explained.

We thank Referee 1 for the amount of effort they have put into providing helpful and constructive feedback on the manuscript. We think and hope that the manuscript has been significantly improved by addressing the concerns raised.

There is quite a lot to address here, so we have attempted to provide general comments on the main points raised above, as well as addressing each of the line-by-line comments in the following section. Some of these points are also discussed in the response to the handling editor, so apologies for repetition.

1. **Context of the framework presented in Figure 1.**

The aim of our framework is to understand the mechanisms underpinning differences in the impact of alien vs native predators in general, not just in this particular system (cats and quolls). We have reworded the discussion of the framework in Figure 1, which currently misrepresents it as novel – rather, it is a synthesis of existing theoretical work and frameworks into a simpler format where it can be readily applied to empirical data to make or test predictions.

The recent synthesis by Carthey and Blumstein [1] brings together a large body of theoretical work into a framework which can be used to predict how a focal prey species is likely to respond to a novel predator. We note that Carthey and Blumstein do not incorporate any information on predator behaviour within their framework. They present 11 mechanistic pathways for prey responses which are based largely on shared eco-evolutionary history. Essentially, Figure 1 can be interpreted as proposing a mechanistic link between stage 6 (antipredator response) and 7 (conservation outcome) of Carthey and Blumstein's framework, framing this in terms of relative strengths of CEs and NCEs as per Sih et al. [2].

The framework of Figure 1 is largely based on the work of Sih *et al* [2], who discuss the integration of prey naiveté theory into a framework for comparing the impact of native and invasive predators throughout the predator-prey encounter. It also incorporates predictions based on theoretical and empirical work describing the implications of predator behaviour on the relative strength of consumptive and non-consumptive effects [3, 4].

The novelty of our approach is that we use information on predator behaviour to predict the relative impact of novel vs familiar predators on the full suite of shared prey within the landscape. This should allow for a more general understanding of the devastating impact of novel predators than single-species study, however the framework can also incorporate prey behaviour to generate quantitative estimates of predator impact on focal prey species if required. The use of highly localised data (telemetry data for each predator and habitat categories defined using the range of variation observed) also helps to link the very general predictions of the framework to the specifics of the local landscape.

2. Definitions of conceptual terms

We agree that this was a major flaw in the initial submission. We have attempted to improve the consistency of terms used both in the text and the figures, and to provide more thorough information on the definition, calculation and use of each metric in the methods section.

The definition of encounter, as mentioned in referee 1's comments, has been clarified: our use of this term includes both direct interactions (where predator and/or prey are within detection distance of the other) which may result in either CEs or NCEs, as well as indirect interactions between prey and indirect cues to a predator's presence (in which case the cues, but not the predator, are within detection distance of prey) which result in NCEs only.

3. Key logical links

We have also extended the discussion of the link between predator behaviour and the strength of non-consumptive effects in particular. This can be split into two aspects: the effect of predator behaviour on:

- *if* prey are likely to employ antipredator responses, i.e. their assessment of imminent predation risk; and
- *what type* of anti-predator responses are likely to be employed, and their associated costs.

Briefly: predator behaviour, particularly hunting mode, determines how closely associated the predator is with indirect cues to its presence (e.g. odour), and therefore how reliable these cues are for prey as a signal of imminent predation risk [3-5]. Hunting mode is usually defined qualitatively (e.g. actively hunting, sit and pursue, sit and wait). By using quantitative estimates of revisitation frequency, we aim to tease out finer differences in cue reliability between cats and quolls based on the way they use the landscape. For clarity, we have adjusted the wording throughout the report to

place more emphasis on the underlying mechanism (cue reliability) rather than the term hunting mode.

Predator habitat domain (defined as the subset of available habitats used by the organism, and their spatial movement within those habitats [3]) should, theoretically, influence the type and cost of anti-predator responses deployed. Narrow domain predators (i.e. those with strong habitat preferences, and those which are spatially restricted within their chosen habitats) are more predictable in time and space, and are more likely to invoke costly shifts in habitat type or activity time by prey. For broad-domain predators, however, there are less 'safe' alternative times or habitats available, and such chronic (and costly) avoidance responses are therefore less effective, so prey are predicted to respond only to imminent predation risk from these predators [3, 4]. We note, here and in the manuscript, that this link is yet to be theoretically tested.

4. Incorporating prey behaviour

See point 2 in response to the comments of the handling editor (previous section). We have (hopefully) clarified the question of prey attributes throughout the manuscript. Rather than assessing the impact of a novel and familiar predator on a focal species of prey, we aimed to show that data on predator behaviour can be used to predict relative predation impacts on shared prey across the landscape, using prey naivete theory to predict a range of prey response scenarios. The absolute predation impact can then be estimated by incorporating information on prey attributes, however this is not part of our analysis.

Introduction

L38-39: You had me until this line. Why/how can hunting mode and habitat domain be used to predict CEs and NCEs? Also, what is your definition of hunting mode, and of habitat domain? These aren't necessarily obvious.

We have expanded this section to step through the logic behind using hunting mode/ habitat domain to predict relative NCE strength and explain these terms. See point 3 in the general comments section, above, for more detail.

L41-55: I have read and reread this several times, and referred to Figure 1 whilst doing so, but I still just don't understand HOW this is meant to work. I think some of the confusion comes from the use of terms without defining them – for example, "encounter" (what counts as an encounter here? Face to face? Within potential detection distance? Overlap of home range over a certain timeframe?), "behaviour" (from telemetry? This is more "movement patterns", isn't it?), "revisitation frequency"

(why? To where?), "habitat domain estimates" (meaning? habitat preferences as in, preferences for certain landuse types? Certain structural habitat components such as dense undergrowth vs open plains? Ecosystems/climate types? Woodland vs rainforest vs swamps? Etc?). There's too much variation in what these terms could mean for the reader to understand what you have actually done and the basis for it. For a specific example, in L49 you say that cats and quolls have similar hunting modes but then in the second half of the sentence you say you hypothesize sufficiently different foraging behaviour… what is the distinction between hunting mode and foraging behaviour here? I know what I think these terms mean, but it's not clear how you are using them. In short, I think you need to be much more specific about defining your terms and explaining how you've used the different concepts here to build your case for how you've measured various things and used them to compare cats and quolls to conclude that cats have greater impacts than quolls (which I completely believe to be true, I just need you to explain it better).

We have reworked Figure 1 and the introduction to give a more thorough introduction to the terms and concepts used, and have added detail to the methods section on why metrics were chosen and how they were calculated. We have also removed all references to foraging behaviour, and moved the behavioural classification of movement analysis (which is why some of these terms were included) into the appendix to avoid confusion.

For reasons of space, we have not included a glossary inset in the manuscript. The following table (or an expanded version) can be incorporated into the manuscript if thought necessary by the referees and/or handling editor.

Term	**Definition**
Habitat domain	The subset of available habitats used by the organism, and their spatial movement range within those habitats [3]. Narrow-domain predators use only a subset of available microhabitat: this may include having very strong habitat preferences or being spatially restricted to a very small area within preferred microhabitats.
Hunting mode	Usually defined qualitatively as "active" – continuously patrol for prey, "sit-and-pursue" – remain at a fixed location but actively pursue prey which move within a certain distance, and "sit-and-wait" – remain at fixed locations for prolonged periods [3].
Encounter	Occurs whenever the distance between a predator and prey is less than the detection radius of either animal [6]. Note that in this paper we include both direct encounters, where both predator and prey are physically present at the same time; and indirect encounters, where prey interact with cues (visual, auditory or olfactory) to a predator's presence.

Methods

Overall – you need to ensure you don't use terms without explaining them first – particularly if you are referring to something you will calculate later, but that your reader has not yet had explained.
We have attempted to define each term at first use.

L85-91: So, I don't really understand this, despite re-reading it several times. What is "any one location", and how far apart do two points need to be to be considered separate locations? What spatial scale are you working at? This is also the section where it becomes clear that prey occupancy and movement patterns will not be considered – rather than letting the reader deduce this, you should state it explicitly, along with the reasons for doing so. You are also referring to "log-odds habitat selection ratios", which we have not heard mention of until now, and so can only guess at what they are. After rereading again – are the 30m grid cells of the Landsat mapping your "locations"? If so, what implications does an assessment at that scale have for the interpretation of your data? How does a 30 x 30m spatial scale related to the ecology of the species under study? Many spatial analyses are highly sensitive to the scale of assessment, meaning that this is not an unimportant consideration.

Consideration of prey attributes:

We have made it explicit in the introduction that we have not incorporated the attributes of specific prey species, but are rather predicting the relative predation impacts of the predators under all scenarios of prey response (see comments above and Figure 1).

Habitat ratios:

Wording adjusted.

Scale:

We agree that spatial scale is important. We are constrained by the availability of broad-scale habitat data and the error (approx. +/- 20m) implicit in the GPS data. We have used the finest possible spatial scale (30m resolution) for these analyses because many of their prey species (such as rodents and other small mammals, reptiles, frogs etc) are likely to respond to their environment at very fine spatial scales. (i.e. yes, the 30m grid cells are the 'locations' referred to – wording has been adjusted). This is also a very fine spatial scale relative to the home-ranges of the two predators (average home range in this region 660ha for quolls and 370ha for cats), meaning that we can hopefully tease out fine-scale differences in the habitat selection and movement behaviour of the

two species. For some prey species, this may mean that we have quantified risk of encounter with a predator at their home range scale of the prey, while for others it may be at the movement step scale. We have added a statement to this effect to the habitat domain section.

L93-102: I feel like you could give (here or in the introduction) more background explanation as to the theory for why revisitation is important. For example, a predator that revisits parts of its habitat more frequently is more dangerous to prey than one that revisits less frequently. If a low frequency revisiting predator has just visited, that location should be safe for some time. On the other hand, if a predator has high revisitation rates, then seeing a predator recently does not give much information about likely immediate future risk. This incorporates temporal patterning of revisitations as well, which I'm now wondering whether and how you have or could incorporate into your analysis?
Also, how does the theory on revisitation translate to how you are using the concept here? Are you suggesting that a prey animal at a certain location (a 30 x 30 m grid cell?) is "X" amount more likely to encounter a predator within a "Y" timeframe, if that predator revisits sites with a frequency of "X"? Please state this explicitly… For that matter, are you in fact (as best I can work out) calculating the likelihood of prey encountering the predator in a particular location (how do you define a location in this context?) and within a certain timeframe (over the course of one night?)?
I am left wondering "where" the prey are in this scenario…?

Importance of revisitation

We have added more explanation of the relevance of revisitation to the methods as suggested. Essentially we have used revisitation (the number of visits made by an animal to each raster cell within its home range) as an empirical estimate of encounter rate (more accurately encounter risk, as we are not incorporating prey behaviour, as discussed below). As described, this approach was taken rather than using a variation on the ideal gas equation (i.e. encounter rate ~ density + velocity) because of the limitations of this approach when dealing with animals that move non-randomly. Because these behavioural differences between the two species are what we are really interested in, we decided that an empirical approach would give a better indication of the relative likelihood of encountering each of these predators.

Note that revisitation frequency is also used as a quantitative comparison of cue reliability between the two predators (we have expanded the discussion on this in the methods also) – we would have preferred to use revisitation interval but decided this was impractical with our dataset (see below).

Temporal patterning of revisitation

We would have liked to tease this out for exactly this reason – to provide more information about predictability and therefore likely NCE strength. Generally speaking, our data suggested that differences in cat and quoll movement behaviours were a bit like the differences between set stocking vs cell grazing regimes. Cats were more static in their home range use, revisiting areas much more frequently and consistently (some cats would visit the same foraging areas every night during the tracking period). Quolls, in contrast, would typically spend a few days in an area before moving on, usually moving den sites and foraging areas every few nights.

We did try calculating the length and predictability of revisitation intervals as well as the number of visits/month. However, our tracking period was only ~30 days and average revisitation rate for quolls was only ~3.5 revisits per month. Coupled with the small number of animals tracked, we just didn't feel confident in our sample sizes – we have added a sentence in the text to indicate this.

Our calculations of revisitation

As discussed, we have made explicit in the introduction that we are not incorporating prey attributes in these calculations. For each cell within the landscape we are calculating the likelihood of a predator being present. This can then be combined with prey distribution data for focal species of interest, but this is not part of our analysis.

Within our analysis, we are calculating the average frequency with which each predator revisits each 30m raster cell (i.e. at the same scale as we quantified habitat preferences). This is expressed as the number of visits/ tracking night (as each animal is tracked for a slightly different length of time – note that we discarded any animals tracked for less than 2 weeks for this analysis).

L104: What is a habitat selection ratio? What is a Design III analysis?

We have clarified this in the text. Briefly:

- Habitat selection ratios as defined by Manly et al [7] are calculated by comparing habitat use to availability. A log-odds ratio of >1 indicates positive selection for a habitat (i.e. it is used more often that would be expected based on its distribution in the landscape), whereas a log-odds ratio of <1 indicates negative selection.
- Design III analyses measure both habitat use and availability at the scale of the individual (as in this study). This differs from design I analyses where use and availability are measured at the population level, and design II measure use for individual animals but availability is kept constant for all individuals [7, 8].

L106: Why 14 categories, why those 14 categories and not others, and based on what characteristics? I've looked in the supp material and this information is not there either.

We have added information on the derivation and choice of habitat categories to Appendix S1. Briefly, habitat categories were selected to reflect features known or thought to be significant to these carnivores (e.g. linear habitat features such as woodland edges, roads and creeklines) as well as variation in habitat complexity (and therefore availability of niches and refuge sites for both predators and their prey).

Results

L121: What were the final numbers of quolls and cats used?

We have added Table S1.2 to clarify this for each analysis. 25 cats and 10 quolls were used in most analyses (behavioural classification of movement paths, habitat domain and diel activity). Two cat and two quoll collars with were discarded for revisitation analyses as data from these animals did not represent a true home range (i.e. animals were tracked for <2 weeks due to collar malfunctions, or underwent a range shift during the tracking period).

L159: I'm not clear on how this differs from what you'd expect based on random chance of prey and predator encountering one another, based only on their relative densities in each habitat? I assume it incorporates activity patterns and movement states, etc, but I'm just not clear on how you've done the calculations.

See response to comment L93-102, above. Revisitation frequency is included to account for activity patterns as suggested. The methods have been expanded to make the calculation process clearer.

L164: For predators, not prey, I assume.

Line removed during rewrite.

Discussion

L167: What about prey traits though? This seems to assume that prey are randomly distributed across grid cells, which they aren't... can you explicitly discuss the assumptions here and their limits, and perhaps speculate what effect it would have on your findings to incorporate them? (Or if future work could do so?)

L172: I'm afraid I'm just not convinced that this is true... (1) I need to understand better how it's calculated, (2) prey are not randomly distributed and also make decisions that balance costs against benefits of behaviour, so they may adjust these decisions dynamically according to risk (perhaps this

is all better couched in terms of risk at certain grid cells of the map?), (3) what do you mean, "regardless of"... surely these matter a great deal (see points 1 & 2)?

These comments are related so we have addressed them together (out of order). We have reworked the first paragraph of the discussion to address both comments. As per comments in the Methods section (L93-102), we have attempted to:

- quantitatively predict *relative* risk of encounter rate with an invasive vs native predator (i.e. cats vs quolls) across all habitats in the landscape (Figure 3 – now adjusted to show relative encounter risk rather than estimates for each species); and
- qualitatively predict the *relative* cost per encounter under 6 scenarios of prey response with regards to both consumptive and non-consumptive effects.

We have amended the Introduction and Discussion sections to explicitly state that the absolute magnitude of predation impact (i.e rate of encounter * cost per encounter) cannot be calculated without information on prey behaviours (habitat preferences, efficacy and cost of antipredator behaviours). What we can predict, however, is the relative predation impact of an invasive vs native predator across all habitats in the landscape (Figure 4) and under all scenarios of prey response (Figure 1).

Within our case study (cats v quolls), we are able to clearly show that the rate of encounter with cats is much higher across all habitats (i.e. prey are more likely to encounter cats more frequently regardless of prey habitat preferences). We also predict that the cost to prey per encounter will be equivalent or higher when encountering a cat rather than a quoll for all prey response scenarios. These predictions are based in prey naivete theory (for predicting consumptive effects) and empirical and theoretical work describing the influence of predator hunting mode/habitat domain on the strength of non-consumptive effects, as shown in Figure 1. We have amended subsequent paragraphs (see response to comments re: L209 - 215) to clarify the basis for these predictions and make our assumptions clearer.

L169: I don't remember seeing an explanation of what was measured to estimate "foraging intensity"?

Changed to "revisitation frequency".

L181-184: So are these the findings that are being interpreted as "foraging intensity" (foraging behaviour?)? - this isn't made clear or explicit earlier on, which would really help (did you set out to measure "foraging intensity" and decide that this was the best way to do it? Or is this a post hoc

interpretation of the data? Either way - I didn't understand until now what you meant when you said foraging intensity). These ideas need to be set up earlier on in the piece.

Altered to movement behaviour (rather than foraging behaviour).

These references reflect earlier analyses which were subsequently removed. The HMM analysis (which split movement paths into foraging, travelling and resting states) has been completely moved into the appendix, and all references to foraging intensity/behaviour (hopefully) removed to avoid confusion.

L204: expected by whom? Slightly odd turn of phrase there.

Sentence rewritten.

L207-208: This sounds like the cues have home ranges and revisitation rates – reword

Paragraph rewritten to address next two comments (below) – sentence removed.

L209-210: It's not clear here why this should be more likely? Can you make the logical links more explicit please?

Discussion has been extended to provide more context and make the progression of arguments clearer. See Point 3 in the general comments section (above).

L210-212: Could do with being split into smaller sentences and the logical links made more explicit. WHY could it imply that?

As above – paragraph rewritten. See Point 3 in the general comments section (above).

L213: Which relationship?

This refers to the relationship between habitat domain and NCE strength. Paragraph rewritten as above and sentence no longer present.

L214-215: This needs to be expanded upon and spelled out more clearly – the conceptual/logical links behind these assumptions are not clear.

As above – paragraph rewritten. See Point 3 in the general comments section (above).

Referee: 2

Comments to the Author(s)

This study aims to explore why feral cats have had disproportionate impacts on native prey compared to a similar native predator, the spotted-tail quoll. The authors tackle this by applying recently proposed theory on habitat domain, in combination with sound experimental design and

cutting-edge statistical approaches, to compare relative impacts between the native and non-native predators. I praise the authors for their work and as a major comment, I only suggest that the discussion should include a review of the available literature on non-consumptive effects of cats and quolls on different prey to confirm the author's predictions.

We thank referee 2 for their kind comments. We have added reference to available literature to the discussion as suggested, though note extrapolating these results to support our predictions is problematic given the difficulty of teasing apart the effects of prey naivete vs signal fatigue (see comments below).

Introduction

Line 30: What about movement range, assuming that individuals that move more encounter each other more frequently? Also, what about food availability and habitat complexity?

These factors are incorporated into the idea of habitat domain, which accounts not only for the species' habitat preferences but also their movement range within their preferred habitats. We have defined this term in the introduction, and altered the methods section to more clearly explain that revisitation frequency has been incorporated into calculations of encounter risk to account for differences in movement activity. We have also added descriptions of how habitat categories are defined to Appendix S1, to show that habitat complexity has been included in their definition.

Line 40: Is it really *that simple? What about the prey's habitat domain, their age, reproductive status, or the type of antipredator response that they are implementing? Briefly discuss how prey's attributes would influence this.*

We have rewritten large sections of the introduction, methods and discussion to clarify that we have not attempted to incorporate the attributes of prey species (see point 2 in the response to the handling editor section, above). Instead, we provide an assessment of relative predation impact of a novel (cats) vs familiar (quolls) predator, under scenarios of differing prey response as predicted by prey naïveté theory. We are able to demonstrate that, for our case study, prey are more likely to encounter cats than quolls in all habitat types, and that the cost per encounter is likely to be higher for all scenarios of prey response. We have added statements throughout to highlight that information on prey behaviour and responses is required to calculate the absolute rate of encounter and cost per encounter, but that this is not part of the current analysis.

Results

Table S1.3: For your model selection with AIC, when you have two models that only differs in a single parameter and are within AIC difference of two, then the extra parameter of the more complex model is actually uninformative. See:
Arnold (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management 74(6):1175–1178; DOI: 10.2193/2009-367

We have highlighted the top model for each set in Table S1.3 (now S1.4) and adjusted the discussion to remove the implication that the extra parameter is informative. We thank referee 2 for picking this up (and for going above and beyond and checking the appendix!).

Discussion

Line 214: Are there any previous prey studies evaluating non-consumptive effects in response to feral cats or spotted-tail quolls that could confirm your predictions here?

There are a few relevant studies, however it is difficult to separate out whether differences in response, if present, are due to prey naïveté (e.g. lack of recognition of cats as a predator or inappropriate response to cat presence) or to differing investment in avoidance behaviours due to differences in predator behaviour.

There are only a few studies where native prey responses to feral cats and spotted-tailed quolls have been directly compared, and the results are inconsistent. In comparative trials undertaken by Carthey and Banks [9], for example, native bush rats (*Rattus fuscipes*) did not show measurable responses (giving-up density, vigilance or foraging time) to spotted-tailed quoll odour, possibly due to small sample sizes and insufficient statistical power. In the same study, rats increased vigilance and decreased foraging time, but also decreased giving-up density (i.e. continued foraging for longer as rewards decreased) in the presence of feral cat odour compared to controls. This inconsistent behaviour may be partially explained by *Toxoplasma gondii* infection, which was present but rare in the study area, as infection with this parasite can increase risk-taking behaviour and attraction to cats [10]. In a Tasmanian study, swamp rats (*Rattus lutreolus velutinus*) showed increased 'risk assessment' responses to spotted-tailed quoll odour but no significant response to feral cat odour, though these differences were only distinguishable with aggregate response indices [11]. In this study, the lack of response to cats was interpreted as indicating naïveté (i.e. lack of cue recognition) rather than differential investment in anti-predator defences. It is therefore difficult to use these to confirm our predictions about relative NCE strength.

We have added reference in the discussion to what we can conclude from previous studies. Briefly: most native prey species studied to date have shown recognition and/or antipredator responses to

cues of spotted-tailed quoll, provided they came from a region which naturally supported spotted-tailed quolls ([12-14], but see [9]). In addition, most studies of native prey responding to cats have shown non-zero responses, indicating a general lack of level 1 naïveté, but more than half of prey studied actually showed increased risk-taking behaviour, possibly due to *Toxoplasma gondii* infection [15].

Line 221: And also with food availability?

Added "with factors such as" to sentence. We didn't have space to go into all factors which may influence the absolute magnitude of cat impact on prey, so have focused on habitat complexity as recent research suggests that manipulating understorey structure offers promising mechanism of reducing cat impact at a landscape scale. As an aside, we note that food availability per se may not have such a great impact on cat predation impacts as might be expected, given the prevalence of 'surplus killing' by cats [e.g. 16]. It may, however, influence the willingness of cats to hunt non-preferred prey (particularly larger species) if preferred prey are not present (i.e. prey switching [e.g. 17]). Unfortunately, we simply ran out of space to address this in the paper.

References:

Note that 'doi' appears twice in several references.

Corrected- thanks!

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