

## Mesocarnivore community structuring in the presence of Africa's apex predator

Gonçalo Curveira-Santos, Chris Sutherland, Simone Tenan, Albert Fernández-Chacón, Gareth K. H. Mann, Ross T. Pitman and Lourens H. Swanepoel

### Article citation details

*Proc. R. Soc. B* **288**: 20202379.  
<http://dx.doi.org/10.1098/rspb.2020.2379>

### Review timeline

Original submission: 24 September 2020  
1st revised submission: 12 January 2021  
2nd revised submission: 15 February 2021  
Final acceptance: 15 February 2021

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

## Review History

### RSPB-2020-2379.R0 (Original submission)

Review form: Reviewer 1 (Marion Valeix)

#### Recommendation

Accept as is

**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?**

N/A

**Is it adequate?**

N/A

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

No

### **Comments to the Author**

I have really enjoyed reading the manuscript "Mesocarnivore community structuring in the presence of Africa' apex carnivore", which I have found highly interesting.

I congratulate the Authors for an excellent piece of work.

It is extremely well written, based a large dataset (congratulations for the fieldwork), perfectly clear and highly relevant for both theoretical and applied questions.

I think it is the first time in my "career as a reviewer" (71 reviews of articles so far) that I do not find anything to comment on...

I have managed to find just a few very minor comments to make ;-)

(1) Line 139: the authors mention 61360 effective trap days while there seem to be 61019 in the Appendix. Could the Authors check which number is the correct one?

(2) Line 177: maybe the following reference is relevant for this sentence: Loveridge et al. (2020) Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. *Biological Conservation* 244: 108504.

(3) Lines 179-182: the exact structure of the model is not totally clear from this sentence. What about AREA and HDIV? I would suggest including the mathematical writing of the model for perfect clarity.

(4) Line 198: "q" should be defined at its first appearance in the text.

(5) Lines 322-end of the paragraph: I think it would be also important that similar studies are carried out in large open protected areas so that findings between small fenced areas and large open areas can be compared and discussed. This line of future research could be included I think.

(6) Overall, the discussion would benefit from being slightly shorter.

(7) Line 494: journal?

(8) Line 505: "Andrew" should be "A"

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(10) Line 577: "*Panthera leo*" should be in italic.

(11) In figure 1, I would suggest adding mesocarnivore for "mesocarnivore species richness" in the axis legends.

(12) Line 594: (Nr) should be omitted.

Again, my congratulations to the Authors for their work, which will be, undoubtedly, a definitive contribution to the literature on these questions!

Marion Valeix.

## Review form: Reviewer 2

### **Recommendation**

Accept with minor revision (please list in comments)

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

Acceptable

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

Acceptable

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

Good

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

Yes

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

No

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

No

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**Is it accessible?**

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**Is it clear?**

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**Is it adequate?**

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

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This study is not novel and just provided additional information with more sample size from the ancillary camera-trap data. Already the effect of top down on mesopredator in terms of probability detection through occupancy model has been tested in other studies such as Staying safe from top predators: patterns of co-occurrence and inter-predator interactions in South Africa. However, this paper has been relatively well written from introduction - discussion by authors. They have used appropriate methods to analyse the large camera trapping data. The provided information has conservation implication for biodiversity management. My major concern is that the effect of other co-occurring large predators such as leopard cannot be ruled out on its influence on mesopredators since leopard is widely distributed across all the study areas. Their abundance/occupancy could play a major role in determining the occupancy/detection

probability of mesopredators. Hence, I would strongly suggest that abundance/occupancy of leopard should be taken into the modelling process to ascertain whether lion solely is having the effect or with the combination of leopard abundance on mesopredators. Spotted hyena may also exert competition with mesopredators like jackals. Maybe you could also include the effect of spotted hyena and leopard along with lion.

Another concern is by looking at Fig 2. It doesn't seem that there is a major difference in the mesopredator richness between both scenarios so one cannot make a statement on positive correlation between lion presence and richness and generalise this relationship to the entire discussion. Such generalised discussions should be avoided throughout the manuscript.

Minor comments

L24-26: Delete this part of the sentence "a striking knowledge gap ..... over Africa's diverse mesocarnivore communities".

The impact of lions on mesopredator community is a known pattern. Please modify the statement Line 33: "Distributional contractions of xxxxxx ....within lion reserves??" Is it mesocarnivore community? Its not clear in the beginning of the statement

Considering above comments, line 242-243 should be reworded.

Line 124: Suggest delete "spanning a region of approximately 220,000 km<sup>2</sup>".

Line 129-131: Provide citation for the climatic gradient

## Decision letter (RSPB-2020-2379.R0)

30-Dec-2020

Dear Mr Curveira-Santos:

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:

**Research ethics:**

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. 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.

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 Maurine Neiman  
mailto: proceedingsb@royalsociety.org

Associate Editor  
Board Member: 1  
Comments to Author:

Thank you for your paper submission and interesting work. Two reviewers evaluated the paper and have a favorable opinion of it. But one reviewer has an important concern that needs to be addressed – that apex predators other than lions (leopard) could affect the results and interpretation. Please consider if additional analyses are needed to address this concern and submit a response to reviewers document with your revision.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

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Again, my congratulations to the Authors for their work, which will be, undoubtedly, a definitive contribution to the literature on these questions!

Marion Valeix.

Referee: 2

#### Comments to the Author(s)

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Considering above comments, line 242-243 should be reworded.

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Line 129-131: Provide citation for the climatic gradient

## Author's Response to Decision Letter for (RSPB-2020-2379.R0)

See Appendix A.

## RSPB-2020-2379.R1 (Revision)

### 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?**

Good

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

Good

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

Good

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

Yes

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

No

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

Yes

**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 see some improvements in the revised manuscript but it is incomplete. Please see my comments below.

I am not satisfied completely with author's response in response to point no. 15. as their data also used as simple lion presence from ancillary camera-trap data but not tested directly. Please also remember that either detection probability/occupancy are abundance measures only. Richness and multispecies occupancy have been also already explained across reserves including reserve with lion (see: Native habitat and protected area size matters: Preserving mammalian assemblages in the Maputaland Conservation Unit of South Africa). It can be only an extension of existing one with larger geographical focus. So, the authors should be cautious with their "first ever study" statement and again suggest make changes throughout the manuscript.

Again, see the comments with the reference to point no. 17. Since you have not found any significant variation reserve-scale average leopard density and insignificant variation in species richness among sites with lion or without lion, and known fact that reserve-scale average leopard density will not have any differences. It should be tested at site level like how lion abundance indices/presence used in the modelling process using the information recorded from the same camera trap sites which doesn't require any extra research projects. Another point If you haven't used lion presence already at camera site level then suggested to use at individual camera site level. I don't see anywhere reserve-scale average leopard density in your manuscript. It is suggested to give it in the supplementary. Leopard play a major role as an apex predator in the absence of lion in several landscapes/countries in particular their abundance/occupancy play a major role in determining the occupancy/detection probability of mesopredators. The carnivore



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With reference to point no. 18., I think it is not advisable to conclude anything solid from insignificant positive relationship. Just addition of one species may not make much sense to me. It can be the artifact of microclimatic, micro habitat condition and other local parameters which you couldn't use in the modelling process.

Reference to point no. actually 19 (minor comments), There are too many literatures available and the presented information is not novel. Better to delete the statement.

## Decision letter (RSPB-2020-2379.R1)

02-Feb-2021

Dear Mr Curveira-Santos:

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.

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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.

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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 Maurine Neiman

Editor, Proceedings B

mailto:proceedingsb@royalsociety.org

Associate Editor

Board Member: 1

Comments to Author:

We appreciate that effort was made to address the import of leopards in the study region, but the reviewer raises legitimate concerns that analyses involving leopards can and should go further.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s)

I see some improvements in the revised manuscript but it is incomplete. Please see my comments below.

I am not satisfied completely with author's response in response to point no. 15. as their data also used as simple lion presence from ancillary camera-trap data but not tested directly. Please also remember that either detection probability/occupancy are abundance measures only. Richness and multispecies occupancy have been also already explained across reserves including reserve with lion (see: Native habitat and protected area size matters: Preserving mammalian assemblages in the Maputaland Conservation Unit of South Africa). It can be only an extension of existing one with larger geographical focus. So, the authors should be cautious with their "first ever study" statement and again suggest make changes throughout the manuscript.

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With reference to point no. 18., I think it is not advisable to conclude anything solid from insignificant positive relationship. Just addition of one species may not make much sense to me. It can be the artifact of microclimatic, micro habitat condition and other local parameters which you couldn't use in the modelling process.

Reference to point no. actually 19 (minor comments), There are too many literatures available and the presented information is not novel. Better to delete the statement.

## Author's Response to Decision Letter for (RSPB-2020-2379.R1)

See Appendix B.

## Decision letter (RSPB-2020-2379.R2)

15-Feb-2021

Dear Mr Curveira-Santos

I am pleased to inform you that your manuscript entitled "Mesocarnivore community structuring in the presence of Africa's apex predator" 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](mailto:procb_proofs@royalsociety.org)

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#### Electronic supplementary material:

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

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Dr Maurine Neiman

Editor, Proceedings B

<mailto:proceedingsb@royalsociety.org>

## Appendix A

Proceedings of the Royal Society B: Biological Sciences

Editor-in-Chief

Lisbon, 12<sup>th</sup> of January 2021

Re: Mesocarnivore community structuring in the presence of Africa' apex carnivore (Manuscript ID RSPB-2020-2379)

Dear Editor,

Thank you very much for your decision and the invitation to resubmit our manuscript RSPB-2020-2379 after revisions. We greatly appreciate the time invested by the Associate Editor and the Reviewers to provide detailed and constructive feedback on this manuscript, and were delighted with the positive responses. We have now acted on all comments provided by each reviewer, which are outlined in detail below.

The major concern, raised by Reviewer 2, was of the potential effect of other large carnivores and, in particular, whether observed associations with lion presence could be confounded by a collective effect of other large carnivores. We have provided a detailed discussion in support of our lion-focused approach but acknowledge that this could be more clearly stated in the manuscript itself. As such, we have also revised the manuscript to ensure that our assertions, and associated caveats, are more explicit. We strongly considered whether additional analyses were necessary, but unfortunately, we don't have the data to model these effects robustly and comprehensively, and feel such overview would be beyond the scope of what we try to achieve in this manuscript. Notwithstanding, we provide statistical support for why our results are likely not an artefact of leopard densities covarying with lion presence. We believe that our approach of being more explicit about potential effects of co-occurring large carnivores and of the justifications of our conclusions goes a long way towards satisfying the concerns of reviewer 2.

Thank you for the opportunity to make these revisions. We eagerly await your judgment of the paper and hope you will agree the manuscript is now significantly improved and suitable for publication.

Yours sincerely,

Gonçalo Curveira-Santos, on behalf of all authors

### **Associate Editor's Comments to Author:**

Thank you for your paper submission and interesting work. Two reviewers evaluated the paper and have a favorable opinion of it. But one reviewer has an important concern that needs to be addressed — that apex predators other than lions (leopard) could affect the results and interpretation. Please consider if additional analyses are needed to address this concern and submit a response to reviewers document with your revision

*Author's Response:* Thank you for your positive assessment of our work and the specific comments made by the reviewers.

We would like to thank Reviewer 2 for the suggestion to include other large carnivores (leopard) in the analysis. We certainly agree that further research is needed to elucidate net effects of the complete large carnivore guild over South African mesocarnivore communities. Indeed, this is something we highlight in the manuscript (lines 288-290 [version with tracked changes]), now in greater detail (lines 290-292). Nevertheless, we believe that specificities of apex predator's ecological effects and lion-oriented management and umbrella species conservation concepts (e.g., lines 54-60), justify a focused approach. In our response below, we provide a detailed overview of our extensive thinking about this concern.

### **Reviewer(s)' Comments to Author:**

#### **Referee: 1**

1) I have really enjoyed reading the manuscript “Mesocarnivore community structuring in the presence of Africa’ apex carnivore”, which I have found highly interesting. I congratulate the Authors for an excellent piece of work. It is extremely well written, based a large dataset (congratulations for the fieldwork), perfectly clear and highly relevant for both theoretical and applied questions. I think it is the first time in my “career as a reviewer” (71 reviews of articles so far) that I do not find anything to comment on...

*Author's Response:* Thank you very much for your careful attention to our manuscript and positive feedback! We are delighted that you consider our findings to make a highly relevant theoretical and applied contribution. As a Ph.D. candidate and early career researcher, these comments are very encouraging, and are deeply appreciated.

2) Line 139: the authors mention 61360 effective trap days while there seem to 61019 in the Appendix. Could the Authors check which number is the correct one?

*Author's Response:* The correct number is the one in the Appendix (61019 effective trap days). We have changed the main text accordingly.

3) Line 177: maybe the following reference is relevant for this sentence: Loveridge et al. (2020) Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. *Biological Conservation* 244: 108504.

*Author's Response:* Thank you, this is an interesting paper we had not come across before, highlighting bush-meat poaching as a crucial threat to carnivore species associated with human presence in the vicinity of conservation areas - our broad proxy for human-wildlife conflicts. We have now included this reference (line 177).

4) Lines 179-182: the exact structure of the model is not totally clear from this sentence. What about AREA and HDIV? I would suggest including the mathematical writing of the model for perfect clarity.

*Author's Response:* We clarified that we modelled response variables (species richness and occupancy probability) as a linear function of different covariates specifically listed for each (lines 174-178, 179-181). This should make explicit the type of the relationship and ease readability without the inclusion of equations that remain in Appendix.

5) Line 198: "q" should be defined at its first appearance in the text.

*Author's Response:* Hill numbers are a mathematically unified family of diversity indices differing among themselves only by the  $q$  exponent. We added this simplified definition  $q$  in lines 198-199, as suggested.

6) Lines 322-end of the paragraph: I think it would be also important that similar studies are carried out in large open protected areas so that findings between small fenced areas and large open areas can be compared and discussed. This line of future research could be included I think.

*Author's Response:* Thank you for this nice suggestion. We fully agree and have added explicit mention to this future research line where we refer to the need for adequate benchmarks to fully understand the ecological relevance of changes in mesocarnivores communities associated with lion reintroductions: "In this context, the comparison of our results with similar studies carried out in large and unfenced protected areas, home to remaining free-ranging lion populations, could produce valuable insights." (lines 384-386).

7) Overall, the discussion would benefit from being slightly shorter.

*Author's Response:* Without specific suggestions it is difficult to know what material could/should be removed (this paper has been two years in the making and we are perhaps suffering from an inability to 'Kill our darlings'). That said, we have strived to streamline the discussion by shortening some passages (e.g., lines 265-267, 338-341, 372-373) or removing non-crucial ideas (e.g., lines 350-352).

8) Line 494: journal?

*Author's Response:* Changed to "Kays R et al. 2020 An empirical evaluation of camera trap study design: How many, how long and when? *Methods Ecol. Evol.* 11, 700–713. (doi:10.1111/2041-210X.13370)".

9) Line 505: "Andrew" should be "A"

*Author's Response:* Corrected.

10) Line 547: "(cop.)" is not needed.

*Author's Response:* Deleted.

11) Line 577: "Panthera leo" should be in italic.

*Author's Response:* Corrected.

12) In figure 1, I would suggest adding mesocarnivore for "mesocarnivore species richness" in the axis legends.

*Author's Response:* Changed as suggested.

13) Line 594: (Nr) should be omitted.

*Author's Response:* Omitted as suggested.

14) Again, my congratulations to the Authors for their work, which will be, undoubtedly, a definitive contribution to the literature on these questions!

*Author's Response:* Thank you very much!

**Referee: 2**



15) This study is not novel and just provided additional information with more sample size from the ancillary camera-trap data. Already the effect of top down on mesopredator in terms of probability detection through occupancy model has been tested in other studies such as Staying safe from top predators: patterns of co-occurrence and inter-predator interactions in South Africa.

*Author's Response:* We have made further efforts to highlight the novelty of this work, namely that, to our knowledge, we are the first study to describe large-scale geographical variation in the characteristics of mesocarnivore communities at multiple biological organization levels (species richness and occupancy rates, proxy for local abundance) as a function of lion presence.

We do agree that inter-predator associations involving large and mesocarnivore species (themselves largely overlooked in past research efforts; Brooke et al. 2014 *PLoS ONE*) have been subject of (limited) previous studies, e.g., Rich et al. (2017), Kamler et al. (2020), and the paper mentioned, Ramesh et al. (2017). However, we note that there has been very little focus on specific associations between smaller carnivores and the apex predator, the lion. For example, in Ramesh et al. (2017), the association between lion and mesocarnivores is not assessed directly, but rather in the way lion presence may modulate other interspecific carnivore interactions, which were investigated in terms of probability of detection, a common, if imperfect, proxy for fine scale behavioural responses. Moreover, studies specifically focused on lion-mesocarnivore associations have typically adopted pairwise single species approaches (e.g., Allen et al. 2018 *Mammalian Biology*), which focus on a single path embedded within a complex and diverse interaction network, a characteristic of species-rich African mesocarnivore assemblages

Thus, we believe that our work does make an important contribution, particularly for current conservation management paradigms in southern Africa, where lions are promoted as a proxy of protected areas' ecological health and management capacity (Lindsey et al. 2018 *PNAS*) and often derive management priorities in small, fenced ecotourism-oriented reserves, frequently under claims of conservation surrogacy that lack empirical support. We provide empirical testing of these ideas.

16) However, this paper has been relatively well written from introduction - discussion by authors. They have used appropriate methods to analyse the large camera trapping data. The provided information has conservation implication for biodiversity management.

*Author's Response:* Thank you.

17) My major concern is that the effect of other co-occurring large predators such as leopard cannot be ruled out on its influence on mesopredators since leopard is widely distributed across all the study areas. Their abundance/occupancy could play a major role in determining the occupancy/detection probability of mesopredators. Hence, I would strongly suggest that abundance/occupancy of leopard should be taken into the modelling process to ascertain whether lion solely is having the effect or with the combination of leopard abundance on mesopredators. Spotted hyena may also exert competition with mesopredators like jackals. Maybe you could also include the effect of spotted hyena and leopard along with lion.

*Author's Response:* Thank you for this valuable comment. Indeed, the concurrent potential effect of other sympatric large carnivore species - leopard, spotted and brown hyena, cheetah, and wild dog - is something we considered to be important and which we mentioned in the discussion (see lines 288-290). In order to better clarify this, we have now expanded correspondent text passages to more clearly convey the need for separate studies that elucidate the predicted net suppressive effects of large carnivores over smaller carnivore species, besides that of the apex predator, and how these may propagate across guild levels (e.g., cascading or supper additive manners) as potentially mediated by lion presence (as highlighted in Ramesh et al. (2017), – an important reference we have now included, thank you). Please see lines 290-292 in the manuscript.

After careful consideration in the initial stages of the project, we decided to maintain the manuscript focus on the apex predator and its association with management capacity. In the next two points we present the conceptual and logistical arguments which substantiated our decision to not formally integrate other large carnivore species in our analysis:

1. While decisions to reintroduce lions can be described by a binary state with direct linkage to local management idiosyncrasies, other large carnivores such as leopards and hyenas are free-ranging predators in South Africa, occurring in almost all of our target reserves. This fundamental contrast implies navigating into a broader narrative of large predator effects, with less clear links to management priorities and umbrella species conservation concepts, and more nuanced interpretations of how top-down effects may scale with population density and structure. Such approach would require detailed large carnivore population data, rather than broad presence-absence information (as we have done for lions), that we do not possess or could readily estimate - as per original data sharing agreement, challenges of individual identification and density estimation, and

pitfalls of occurrence indices as implicit proxies for density of more vagile large carnivores. Population density estimates in our study areas are only available for leopards (data in Rogan et al. 2019 *Ecosphere*, complemented by Panthera's internal reports), meaning that we could only attempt a very incomplete view of broader large carnivore top-down effects on mesocarnivore communities. Perhaps more importantly, we believe that specificities of apex predator's ecological effects and lion-oriented management (e.g., lines 54-60), particularly under disputed claims of conservation surrogacy in small South African reserves, warrant the focused approach we have pursued here. Lion populations epitomise megafauna-centric decisions on southern African reserve management (either conservation or tourism driven) – see Lindsey et al. (2018) *PNAS*. As such, this study tapped directly into that decision framework. A broad overview of large carnivore effects, in all its complexity, would not only be hard to implement analytically, as it would dilute this topical narrative. While such an overview would be of value in-of-itself, it is beyond the scope of what we try to achieve in this manuscript.

2. Importantly, for the specific case of the leopard and the main concern raised by referee 2 (“...to ascertain whether lion solely is having the effect or with the combination of leopard abundance on mesopredators.”), we actually did test whether estimates of reserve-scale average leopard density differed significantly between reserves where lions are present vs. absent (data sources detailed above). Despite accentuated across-reserve variation, differences in leopard densities (individuals/100km<sup>2</sup>) when lions were absent (mean = 6.1, sd = 3.5) compared to when they are present (mean = 7.1, sd = 3.0) were not statistically significant,  $t(31) = 0.33$ ,  $p = 0.74$ . This was important to ascertain that the observed patterns are not highly confounded, or an artefact, of possible density-dependent leopard effects over mesocarnivores covarying with lion presence.

18) Another concern is by looking at Fig 2. It doesn't seem that there is a major difference in the mesopredator richness between both scenarios so one cannot make a statement on positive correlation between lion presence and richness and generalise this relationship to the entire discussion. Such generalised discussions should be avoided throughout the manuscript.

*Author's Response:* We appreciate the word of caution. Indeed, a clear difference in mesocarnivore species richness is not easily identifiable by visually inspecting Fig. 2A. Notwithstanding, we report on a observed positive association between mesocarnivore richness and lion presence derived from formal testing of an effect of LION (lion presence/absence covariate) on  $\Omega_r$  (reserve-specific species richness) in our Bayesian modelling framework ( $\beta_{\Omega, \text{LION}} = 0.48$ , BCI: -0.19 – 1.19, i.e., 0.93 probability of a lion effect

greater than zero), while taking into account inherent environmental and anthropogenic variation among reserves potentially influencing geographical variation in mesocarnivore richness (reserve size, surrounding human population density and structural habitat diversity). Our Bayesian approach allows us to make direct probability statements about specific effects rather than rely on significance cut-offs.

Importantly, however, we do highlight throughout the manuscript that despite a statistical effect lion presence was associated with only slightly more mesocarnivore-rich communities (lines 32-33, 250-251, 268-269). This interpretation stands at the core of the idea presented at the end of the discussion's paragraph on species richness patterns: *"The positive association between increased mesocarnivore richness and lion presence corroborates claims for broader biodiversity benefits of maintaining lions [7]. However, in absolute terms, lion presence translated into, on average, just one additional species in the mesocarnivore community. While such small difference may be intrinsically valuable and ecologically relevant for relatively species poor taxa, depending on species identity and functional redundancy [54], this pattern suggests that direct and indirect effects of lion presence are more likely to manifest at the population level rather than modulate extreme extinction events."* (lines 267-273). In accordance, for the rest of the discussion we focused on the apparent dichotomy between the lack of a negative emergent response in species richness in the presence of lions and the negative signal observed for occupancy rates (lines 301-314).

#### Minor comments

18) L24-26: Delete this part of the sentence "a striking knowledge gap ..... over Africa's diverse mesocarnivore communities". The impact of lions on mesopredator community is a known pattern. Please modify the statement

*Author's Response:* We opted to maintain this statement as we believe such information is both lacking and relevant from a theoretical and applied perspective. Please see our response to comment 15.

19) Line 33: "Distributional contractions of xxxxxx ....within lion reserves??" Is it mesocarnivore community? Its not clear in the beginning of the statement

*Author's Response:* Changed to "Distributional contractions of mesocarnivore species within lion reserves,...".

20) Considering above comments, line 242-243 should be reworded.

*Author's Response:* Thank you for alerting us for this unwarranted claim. As mentioned in our response to comment 15, we concur that previous studies have, directly or indirectly, provided insights into the potential role of the African lion as structuring agents of mesocarnivores communities. Therefore, we have removed “the first” from “We provide the first empirical support...” in line 243.

21) Line 124: Suggest delete “spanning a region of approximately 220,000 km<sup>2</sup>”.

*Author's Response:* Deleted, as suggested.

22) Line 129-131: Provide citation for the climatic gradient

*Author's Response:* We included the correspondent citation: “Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. 2006 World Map of the Köppen-Geiger climate classification updated. Meteorol. Zeitschrift 15, 259–263. (doi:10.1127/0941-2948/2006/0130)”. We also adapted nomenclature of climate types to fully match the classification scheme used in the source paper: “Climate typically varies along a North-South gradient from arid in the north to warm temperate climates at the more southern sites [36].” (lines 129-131).

## Appendix B

Proceedings of the Royal Society B: Biological Sciences

Editor-in-Chief

Lisbon, 15<sup>th</sup> of February 2021

Re: Mesocarnivore community structuring in the presence of Africa' apex carnivore (Manuscript ID RSPB-2020-2379.R1)

Dear Dr Maurine Neiman

Thank you for the opportunity to address the remaining comments raised and the invitation to resubmit our manuscript. We are very grateful to you, the associate editor and the reviewer for the time and effort invested in our manuscript which we feel has improved the manuscript by sharpening the message and better highlighting the relevance of our contribution. Below we provide a point-by-point response to the additional point raised by reviewer 2. We hope you agree that the manuscript has again benefitted from the peer review process and we eagerly await your judgment of the revised manuscript.

Yours sincerely,

Gonçalo Curveira-Santos, on behalf of all authors

### **Associate Editor's Comments to Author:**

1) We appreciate that effort was made to address the import of leopards in the study region, but the reviewer raises legitimate concerns that analyses involving leopards can and should go further.

*Author's Response:* Thank you for your assessment of our work and the additional comments made by the reviewer. As per reviewer 2 main suggestion, we conducted a new set of analysis formally including the effects of local leopard densities on mesocarnivore occupancy in our multi-region community occupancy model. We frame the inclusion of this covariate under the important role of leopards on intraguild dynamics, particularly this species role as the local apex predator in the absence of lions, and known influence over mesocarnivore species (lines 114-115, 180-182), as highlighted by reviewer 2. We describe a mix of negative and positive responses (4 species each) of mesocarnivore occupancy to leopard density but failed to identify a clear community-level effect (lines 237-239, Fig. 3B). Finally, we discuss these new

results in light of hypothesized leopard-induced suppression patterns and how these might be masked by common benefits of more effective protection in lion reserves or by ecological theory on non-linear scaling of top-down effects with predator density (lines 355-359). This adds to previous changes to the manuscript reinforcing the need for detailed studies that further elucidate the predicted net suppressive effects of large carnivores (lines 294-296). We hope that the formal inclusion of leopards and associated discussion sufficiently alleviates the concern raised.

Encouragingly, the results, including the reported association between lion presence and geographical variation in mesocarnivore richness and occupancy, were unchanged after including leopards.

### **Reviewer(s)' Comments to Author:**

#### **Referee: 2**

2) I am not satisfied completely with author's response in response to point no. 15. as their data also used as simple lion presence from ancillary camera-trap data but not tested directly. Please also remember that either detection probability/occupancy are abundance measures only. Richness and multispecies occupancy have been also already explained across reserves including reserve with lion (see: Native habitat and protected area size matters: Preserving mammalian assemblages in the Maputaland Conservation Unit of South Africa). It can be only an extension of existing one with larger geographical focus. So, the authors should be cautious with their "first ever study" statement and again suggest make changes throughout the manuscript.

*Author's Response:* While we had already removed any potentially misplaced claims of novelty or 'firsts', we have gone through the entire manuscript again and ensured no such claims remain, focusing instead on how our work tests and contributes to standing theory.

3) Again, see the comments with the reference to point no. 17. Since you have not found any significant variation reserve-scale average leopard density and insignificant variation in species richness among sites with lion or without lion, and known fact that reserve-scale average leopard density will not have any differences. It should be tested at site level like how lion abundance indices/presence used in the modelling process using the information recorded from the same

camera trap sites which doesn't require any extra research projects. Another point If you haven't used lion presence already at camera site level then suggested to use at individual camera site level.

*Author's Response:* We are not completely clear on what is being asked here. Given that data are seldom available/analysed over such large spatial scales we focused our inference on geographic variation, at the reserve-scale, in higher order ecological organization levels (species richness and occupancy rates, proxy for local abundances). From an applied management and conservation standpoint, we believe this focus is appropriate, and interesting, given that more often than not, the management unit for decision making is the reserve, at least in this region and from our collective experience. The lion presence-absence data and leopard density data are reserve-scale summaries that do not lend themselves to modelling within-reserve spatial variation in response to predators. Our approach does include lion and leopard as a camera-level covariate, but one that is shared across all cameras in a reserve. We agree that fine-scale patterns (i.e., apex predator effects at the camera level) and associated behavioural responses within reserves would be interesting (lines 296-297) but it is beyond the scope of our approach and the mesocarnivore-only camera-trapping data we have access to. We note, however, that we have now included the leopard density data (see our response to the comment below).

4) I don't see anywhere reserve-scale average leopard density in your manuscript. It is suggested to give it in the supplementary. Leopard play a major role as an apex predator in the absence of lion in several landscapes/countries in particular their abundance/occupancy play a major role in determining the occupancy/detection probability of mesopredators. The carnivore biologists easily assume that why abundance/occupancy of leopard not taken into the modelling process from the same camera trap. If your data sharing agreement doesn't allow to abundance/occupancy, you can use at least site level leopard presence need to be used in the modelling process. Otherwise, I find this study is incomplete with the reference to the objective of the manuscript.

*Author's Response:* We thank the reviewer for highlighting the fact that, in the absence of lions, leopards play an important role as the local apex predator which we agree justifies a specific view of leopard influence even if a broad overview of large carnivore effects is beyond the scope of what we try to achieve in this manuscript. Therefore, we have now formally included the effects of local leopard density in the multi region



community occupancy model (see response above to the Associate editor). Specifically, we used reserve-level leopard density estimates (LEOP) from spatial capture–recapture models applied to leopard data from the same camera-trap surveys (Panthera, South African National Leopard Monitoring Project 2020) (lines 192-194).

5) With reference to point no. 18., I think it is not advisable to conclude anything solid from insignificant positive relationship. Just addition of one species may not make much sense to me. It can be the artifact of microclimatic, micro habitat condition and other local parameters which you couldn't use in the modelling process.

*Author's Response:* Our use of Bayesian methods meant that we can make probabilistic statements about effect sizes rather than be restricted to frequentist notions of significance. We have explicitly reported the probability of a non-zero lion effect and it is the collective opinion of the authors that a 0.93 probability for a positive effect (line 217-218) is worth reporting and discussing (even if not the nominal  $p=0.05$  that would be used in a frequentist interpretation). It is also worth mentioning that the statistical effect arises after considering the concurrent effect of alternative descriptors (reserve size, surrounding human population density, and structural habitat diversity) even if there is only a slight difference in the emergent pattern. Nevertheless, we stress that the focus of our interpretation stands in the dichotomy between the lack of a negative emergent response in species richness in the presence of lions and the negative signal observed for occupancy rates (lines 272-277). Such pattern suggests that important subtleties could be missed if we approach the often-proposed conservation surrogacy of lions considering only species richness estimates (as is often done under umbrella conservation concepts) (lines 364-373). Specifically, the duality we identified suggests that direct and indirect effects of lion presence are more likely to manifest at the population level rather than modulate extreme local extinction events defining species richness.

6) Reference to point no. actually 19 (minor comments), There are too many literatures available and the presented information is not novel. Better to delete the statement.

*Author's Response:* We have tempered this statement by removing the “striking” adjective. Our reference to a knowledge gap is in respect to well-described size-biases in carnivore research towards the largest species (Brooke et al. 2014 *PLoS One*) and

the considerable less attention that has been given to intraguild dynamics between lions and smaller mesocarnivores (<20kg as defined here) compared to the many studies focused on lions and subordinate large carnivores (hyaenas, leopard, cheetah and wild dog).