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PROCEEDINGS B

Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape

L. Mark Elbroch, Jake M. Ferguson, Howard Quigley, Derek Craighead, Daniel J. Thompson and Heiko U. Wittmer

Article citation details
Proc. R. Soc. B **287**: 20202202.
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Review timeline
Original submission: 10 June 2020
1st revised submission: 5 September 2020
2nd revised submission: 15 October 2020
Final acceptance: 16 October 2020

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

Review History

RSPB-2020-1356.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?
Good

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

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?
Yes

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?
No

Do you have any ethical concerns with this paper?
No

Comments to the Author
Review RSPB-2020-1356

This is an exciting manuscript examining some long-standing questions within the predator-prey literature using a powerful dataset. It has the potential to provide new insights into predator-prey ecology. Field data used are robust and collected over 16 years, and previous research provides the authors with context for their findings.

Below are a few major and minor questions/recommendations:

-- It is enlightening and helpful to management to include that you found annual human hunting = 20 wolves (lines 26-27).
-- Would you please include what percentage of land was National Park vs USFS vs private/agricultural (lines 138-141)? Including these percentages would help readers understand how much human impact was present in the study area. This will also allow for easier comparisons with the landscapes of other studies.
-- What years did this study take place (line 107)? What about your previous research, would you please include the years (lines 73-76)? This would be helpful for reference.
-- Would you please include what years were elk hunted during the liberal quota (lines 133-124), and what percentage of the study area allowed hunting of elk? What percentage of the study area allowed puma hunting (lines 181-183)?
-- When referencing WAIC (line 278), I recommend calling this method the Watanabe-Akaike information criterion (rather than the widely applicable information criterion) to acknowledge the developing authors.
-- If possible, would you please provide a map of the study area. Even better if it includes polygons indicating where wolves vs cougars vs elk were collared.
-- What is the primary summer and winter prey for wolves and cougars in this study area? How might differences in prey affect your findings?

Integrated Population Models (IPMs)
-- It would be helpful to outline how your data does or does not meet the assumptions of an IPM, e.g. meeting assumptions of mark-recapture or mark-recovery models, statistically independent datasets, etc. and how any assumption violations might influence your results (e.g. Riecke et al 2019).
-- I recommend adding a variance-covariance matrix for Table 1, as a supplement, to allow the

reader to better understand the high correlation described between the wolf effect and the off-refuge Elk effects (lines 357-358)? It would be elucidating to see the correlation pairs across all variables.
-- Related to the previous comment about wolf-elk correlation, I recommend that the authors either add a model that that includes both elk populations (Elk + off-refuge Elk) together in the same model, or address why they are split and never combined. It is possible that the effects of elk on the system are diminished by dividing the population in this way. It would also be helpful to see a prey-only model, a wolf-only model, and a model that includes both prey and wolves, or an explanation of why this was not tested. Otherwise, it is unclear if top-down effects were actually found or if wolves are indirectly tracking elk numbers, and thus reinforcing your earlier study's findings of bottom-up effects. Clarifying this difference is critical to the main findings of the paper.
-- It would be helpful to see the posterior distributions that were used to draw conclusions as a supplement.

In general, your findings on the effects of human hunting on pumas were powerful. The effect of wolves is still unclear and would benefit from the explanations or changes recommended above. Very interesting - looking forward to reading more!

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions 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?
Marginal

Is the length of the paper justified?
Yes

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

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
General comments:
The study investigates the relative influence of bottom-up and top-down forces on puma demography. The analysis is based on 16 years of monitoring 147 pumas, including information on the death of 115 individuals. A key conclusion is that the puma population was more strongly driven by top-down forces coming from wolves than by bottom-up forces associated with elk density. Attempting to disentangle the relative strength of top-down and bottom-up effects on large carnivores is certainly a valuable objective. While I like many aspects of this research, a number of points could be addressed.

I am not convinced that the study provides strong evidence that cougar demography is driven by top-down forces. Classic definition of top-down regulation would involve a species occupying a given trophic level regulating a species at the next lower level. The paper should clearly explain why the relationships outlined in the paper should be considered as top-down regulation. Why not simply competition? We can read: "These species compete with pumas for prey, usurp their kills (i.e. kleptoparasitism)…" Should this be considered as top-down effects? I understand that pumas are be subordinate to wolves, but why shouldn't they be considered as simple competitors siting on the same trophic level? There is little evidence that wolves killed pumas during the course of the study (the paper only reports of hunting-related deaths). What if the presence of wolves forces pumas to rely less on elk and more on other species? I would not consider competition by interference or exploitation as top-down forces. We know that 13% of all deaths came from legal hunting. What if most other deaths were from starvation? Would this underscore strong bottom-up forces? Is there any information on what the other 87% died from?

Specific comments

Line 185. Should bottom-up forces be assessed based on more than elk? A previous study (Elbroch et al. 2013. PLoS ONE 8, e83375) seems to indicate that pumas alter their diet during the course of the year, and that other prey species can make up most of the diet, especially for females. It seems rather risky to conclude that top-down forces are dominant without knowing the causes of puma mortalities and the density of alternative prey.

Line 192. "We defined kittens as 0-6 months, subadults as 7-18 months, and adults as > 18 months of age." Given that subadults can be hunted between 12-18 months, should there be two subadult categories (7-12 and 12-18)?

Line 212. More information should be provided on the relative importance of the different causes of death.

Line 264. I am wondering why a survival model that considers time to death was not used (Hosmer et al. 2008. Applied survival analysis: regression modeling of time to event data. Wiley…)? I assume that not all pumas were tracked during the same time period.

P. 12. Have the regression models been checked for multicollinearity?

Line 315. Still, the difference in WAIC is only of 3.52. What if other prey than elk were also accounted for in the model (e.g., deer or moose or overall prey biomass)?

Line 361. Please add a reference at the end of the sentence.

Figure legends – Fig. 3. The caption should indicate that these are not observed changes, but they are projections.

Table 1. I wonder if Table 1 should be in an Appendix.

Decision letter (RSPB-2020-1356.R0)

22-Jul-2020

Dear Dr Elbroch:

I am writing to inform you that your manuscript RSPB-2020-1356 entitled "Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.
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To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

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

Associate Editor
Board Member: 1
Comments to Author:
Both reviewers see merit in the paper but both are unconvinced by the results that are presented and in particular by the statistical analyses that were carried out to arrive at them. Cleary the

study needs more work before we can courier it any further and even then it should be seen by a specialist statistical reviewer (recommended by both referees).

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
Review RSPB-2020-1356

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Referee: 2

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General comments:
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I am not convinced that the study provides strong evidence that cougar demography is driven by top-down forces. Classic definition of top-down regulation would involve a species occupying a given trophic level regulating a species at the next lower level. The paper should clearly explain why the relationships outlined in the paper should be considered as top-down regulation. Why not simply competition? We can read: "These species compete with pumas for prey, usurp their kills (i.e. kleptoparasitism)…" Should this be considered as top-down effects? I understand that pumas are be subordinate to wolves, but why shouldn't they be considered as simple competitors siting on the same trophic level? There is little evidence that wolves killed pumas during the course of the study (the paper only reports of hunting-related deaths). What if the presence of wolves forces pumas to rely less on elk and more on other species? I would not consider competition by interference or exploitation as top-down forces. We know that 13% of all deaths came from legal hunting. What if most other deaths were from starvation? Would this underscore strong bottom-up forces? Is there any information on what the other 87% died from?

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P. 12. Have the regression models been checked for multicollinearity?

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Line 361. Please add a reference at the end of the sentence.

Figure legends – Fig. 3. The caption should indicate that these are not observed changes, but they are projections.

Table 1. I wonder if Table 1 should be in an Appendix.

Author's Response to Decision Letter for (RSPB-2020-1356.R0)

See Appendix A.

RSPB-2020-2202.R0

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?
Excellent

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?
Yes

Comments to the Author
The revised version provides valuable information to evaluate the robustness of the study's conclusions. I can now accept the idea that wolves have a dominant influence on the demography of pumas. Still, I believe the 'conclusion' should indicate some of the uncertainties associated with the dataset and the analysis. I can see a few points of uncertainty. First, while only elk were considered in the current study, summer diet includes other species, especially mule deer. The lack of information on overall prey biomass is a weakness, especially in the context that many pumas died from starvation. Second, a larger number of adult deaths have been linked to starvation than to predation. When considering all age classes, 22 deaths have been linked to starvation and 26 to predation. Given that cause of death could not be assigned for 28 pumas, there is a reasonable risk that bottom-up forces have been underestimated. This is certainly relevant given that the second top-ranking model excludes wolf, but includes elk (delta WAIC = 3.52). I thus believe that the discussion should recognize such points of uncertainty and briefly discuss their implication. That being said, I believe that the paper draws reasonable conclusions.

Minor points
Table 2. The title should include more information (e.g., what is the model testing; density is for which species?)

Fig. 4. Could confidence intervals be included in the figure?

Figure S2. I do not find the scale completely clear because the negative signs touce the scale. Maybe a + sign could be added for the positive values?
Also, the study provides tests of collinearity. I suggested to assess 'multicollinearity' in the multivariate models using, for example, Variance Inflation Factor (VIF). This seems even more relevant now that some correlations are rather high.

Review form: Reviewer 3

Recommendation
Accept with minor revision (please list in comments)

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

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

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

Is the length of the paper justified?
Yes

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

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

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

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
I've attached a .pdf with my comments. (See Appendix B)

Decision letter (RSPB-2020-2202.R0)

01-Oct-2020

Dear Dr Elbroch

I am pleased to inform you that your manuscript RSPB-2020-2202 entitled "Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape" 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 (https://royalsociety.org/journals/authors/author-guidelines/#data).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
• 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
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
Two reviewers have seen the last version of this MS, one of which who was asked specifically to look at the statistical tools employed in the analysis. Both are quite favourable but both also make a number of suggestions that, in my view, would, when dealt with at least, significantly enhance the potential impact of the publication. In particular, it might be useful to discuss the potential bias caused by the starvation / predation issue identified by one of the reviewers. The statistical reviewer recommends (among other things) to standardise the way significance is calculated. I don't know how easy it is to adopt this, but it is certainly worthy of consideration.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
The revised version provides valuable information to evaluate the robustness of the study's conclusions. I can now accept the idea that wolves have a dominant influence on the demography of pumas. Still, I believe the 'conclusion' should indicate some of the uncertainties associated with the dataset and the analysis. I can see a few points of uncertainty. First, while only elk were considered in the current study, summer diet includes other species, especially mule deer. The lack of information on overall prey biomass is a weakness, especially in the context that many pumas died from starvation. Second, a larger number of adult deaths have been linked to starvation than to predation. When considering all age classes, 22 deaths have been linked to starvation and 26 to predation. Given that cause of death could not be assigned for 28 pumas, there is a reasonable risk that bottom-up forces have been underestimated. This is certainly relevant given that the second top-ranking model excludes wolf, but includes elk (delta WAIC = 3.52). I thus believe that the discussion should recognize such points of uncertainty and briefly discuss their implication. That being said, I believe that the paper draws reasonable conclusions.

Minor points
Table 2. The title should include more information (e.g., what is the model testing; density is for which species?)

Fig. 4. Could confidence intervals be included in the figure?

Figure S2. I do not find the scale completely clear because the negative signs touce the scale. Maybe a + sign could be added for the positive values?
Also, the study provides tests of collinearity. I suggested to assess 'multicollinearity' in the multivariate models using, for example, Variance Inflation Factor (VIF). This seems even more relevant now that some correlations are rather high.

Referee: 3

Comments to the Author(s).
I've attached a .pdf with my comments.

Author's Response to Decision Letter for (RSPB-2020-2202.R0)

See Appendix C.

Decision letter (RSPB-2020-2202.R1)

16-Oct-2020

Dear Dr Elbroch

I am pleased to inform you that your manuscript entitled "Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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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

16 August, 2020

RSPB-2020-1356 – Resubmission of Revised Manuscript

Dear Dr. Locke Rowe, *Proceedings B*,

Thank you for the opportunity to revise and resubmit our manuscript,“ Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape” (RSPB-2020-1356), to *Proceedings B*. The reviewers provided excellent feedback and here we resubmit a stronger manuscript for further consideration as a Research Article for possible inclusion in *Proceedings B*. Please find our responses to their criticisms below, in dark red.

Thank you for the link to submit our data and code to the Dryad Depository as well. We have successfully archived these materials, and finalized a single supplementary materials file for review and to support the manuscript.

(From our original submission) *Why its relevant with broad appeal?*

1. Top-down effects exhibited by apex predators are modulated by human impacts on communities, and therefore have been predominantly documented in protected areas. Here, we use a distinctive approach to show top-down effects of wolves in a multi-use landscape, which are now prevalent across modern ecosystems.
2. Documenting competition among apex predators is difficult, and even when evidence is found, it doesn't necessarily equate to fitness effects for the subordinate species being affected. Here, we show for the first time, that wolves impact the abundance of pumas (*Puma concolor*), providing novel insights into the possible historic distributions and interactions between these two apex species in North America.
3. Current methods with novel approach: We capitalized upon 16 years of puma population monitoring from across the time period during which wolves reclaimed historic range. We utilized an integrated population model to disentangle the concurrent contributions of a reintroduced apex predator (the gray wolf), human hunting, and prey abundances on vital rates and abundance of a subordinate apex predator (the puma). We also separated out human hunting from other top-down effects to gain insights into the system.
4. We were able to quantitatively determine that the average annual impact of human hunting on puma abundance was approximately equivalent to the effects of 20 wolves.

We hope you find our work concise and intriguing, and worthy of inclusion in *Proceedings B.* Thank you for your time and we look forward to your feedback.

Kind regards,

Mark Elbroch, Jake Ferguson, Howard Quigley, Derek Craighead, Daniel Thompson, and

Heiko Wittmer

Correspondence: Mark Elbroch, melbroch@panthera.org

Referee: 1

** Please note that line numbers refer to our clean document without track changes. Thank you.

Comments to the Author(s)
Review RSPB-2020-1356

This is an exciting manuscript examining some long-standing questions within the predator-prey literature using a powerful dataset. It has the potential to provide new insights into predator-prey ecology. Field data used are robust and collected over 16 years, and previous research provides the authors with context for their findings.

Below are a few major and minor questions/recommendations:

-- It is enlightening and helpful to management to include that you found annual human hunting = 20 wolves (lines 26-27).

Thank you.

-- Would you please include what percentage of land was National Park vs USFS vs private/agricultural (lines 138-141)? Including these percentages would help readers understand how much human impact was present in the study area. This will also allow for easier comparisons with the landscapes of other studies.

Certainly, thank you for your attention to detail. We've added the size of protected areas including the Park in our core study area in Lines 110, 112, 114 (percentage).

-- What years did this study take place (line 107)? What about your previous research, would you please include the years (lines 73-76)? This would be helpful for reference.

Again, thank you. We have added this information in Lines 106.

-- Would you please include what years were elk hunted during the liberal quota (lines 133-124), and what percentage of the study area allowed hunting of elk? What percentage of the study area allowed puma hunting (lines 181-183)?

Liberal hunting occurred every year of the study. We have modified the text in lines 133 to clarify this fact: "Our study occurred during the time period in which managers implemented

liberal hunting". Elk hunting occurred across the entire study area (it's the only National Park with a legal hunt, being highly controversial).

-- When referencing WAIC (line 278), I recommend calling this method the Watanabe-Akaike information criterion (rather than the widely applicable information criterion) to acknowledge the developing authors.

Thank you, we have added this text (line 290)

-- If possible, would you please provide a map of the study area. Even better if it includes polygons indicating where wolves vs cougars vs elk were collared.

We have added a new figure 1 of the study area—elk are present across the study area, as are wolves now that they are established…so adding information on their distribution would require either selecting a specific point in time, or overlaying the entire image with some marker representing elk and wolves (since they are everywhere). Instead we have delineated our core study area within the larger landscape. (we moved the old figure 1 to the supplementary materials)

-- What is the primary summer and winter prey for wolves and cougars in this study area? How might differences in prey affect your findings?

Wolves are elk specialists throughout the year (Metz et al. 2012). Pumas are elk specialists in winter, but expand their diet to include deer in summer (Elbroch et al. 2013). However, they still most strongly select for elk calves in summer (Elbroch et al. 2017). The study area lacks defensible deer estimates, as state agency personnel do not have any protocols for counting deer and only do so when lacking other work to do…thus we cannot say how incorporating deer estimates into larger prey estimates would change things. In past analyses we have used deer numbers from an area in which our study area sits to determine proportional abundance (versus elk, for example, at equal spatial scales), but not actual numbers given the uncertainty of their distributions in our study area. Nevertheless, based on what we know of prey selection of wolves, elk represent the greatest source of competition between the two species, in terms of food.

Elbroch, L. M., P. Lendrum, J. Newby, H. Quigley, D. Craighead. 2013. Seasonal foraging ecology of non-migratory cougars in a system with migrating prey. *PLoS ONE* 8(12): e83375.

Elbroch, L. M., J. Feltner, H. Quigley. 2017. Human-carnivore competition for antlered ungulates: Do pumas select for bulls and bucks? *Wildlife Research* 44(7) 523-533.

Metz, M.C., Smith, D.W., Vucetich, J.A., Stahler, D.R. & Peterson, R.O. (2012) Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. The Journal of Animal Ecology, 81, 553–563.

Integrated Population Models (IPMs)

-- It would be helpful to outline how your data does or does not meet the assumptions of an IPM, e.g. meeting assumptions of mark-recapture or mark-recovery models, statistically independent datasets, etc. and how any assumption violations might influence your results (e.g. Riecke et al 2019).

Thank you, we have added a paragraph found in lines 240-247, with several supporting citations. Briefly, our models do a good job of meeting the assumptions of the IPM. One potential issue is of transient individuals in the study area that may enter briefly, or seasonally, such that we cannot tag them. This would lead to biased estimates of interspecific competition. Given that pumas are a land-tenure species, however, transients are much more likely to be negatively affected by competition than territory holders, reducing any bias associated with this issue—we've added this information in lines 245-247.

-- I recommend adding a variance-covariance matrix for Table 1, as a supplement, to allow the reader to better understand the high correlation described between the wolf effect and the off-refuge Elk effects (lines 357-358)? It would be elucidating to see the correlation pairs across all variables.

Thank you we have added a new Figure S2 in the supplementary materials that has covariate correlation values. We have also added text to draw the reader to this figure in lines 256-257, 274, 378.

-- Related to the previous comment about wolf-elk correlation, I recommend that the authors either add a model that that includes both elk populations (Elk + off-refuge Elk) together in the same model, or address why they are split and never combined. It is possible that the effects of elk on the system are diminished by dividing the population in this way. It would also be helpful to see a prey-only model, a wolf-only model, and a model that includes both prey and wolves, or an explanation of why this was not tested. Otherwise, it is unclear if top-down effects were actually found or if wolves are indirectly tracking elk numbers, and thus reinforcing your earlier study's findings of bottom-up effects. Clarifying this difference is critical to the main findings of the paper.

Elk

Thank you. We did in fact combine on- and off-refuge elk in our "Elk model" to determine whether just off-refuge or total elk abundances better explained variation in our data.

Wolves + Prey

Following your suggestion, we have tested a model with the effects of wolves, off-range elk and density dependence (DD) together, but ultimately decided not to include it in the manuscript for the following reasons: 1) off-range elk and wolves exhibited high correlation (R^2= 0.71), well beyond the typical cut-off of 0.6 included as a threshold level of correlation in deciding whether two covariates should be included in the same model (see supplementary Fig. S2). 2) This model added a further 4 parameters (total number of parameters = 23), which,

given our sample size of pumas, likely exceeds the number of parameters recommended for our sample size, potentially influencing model performance. 3) The model did not rank higher than the more parsimonious model Wolf + DD (ΔWAIC 1.11). 4) When we compared the standardized parameter estimates from both models (Wolf + DD vs. Wolf + off-Refuge Elk + DD), wolves had higher effects on fecundity, adult survival and kitten survival, while off-range elk only had a larger effect on subadult survival. However, this estimate for subadults also had a large amount of uncertainty and overlapped 0, potentially obviating its interpretation as having an impact at all ($\beta_{S,E} = 0.44, \sigma_{S,E} = 0.61$). The comparison of the two models thus emphasized the importance of our initial results—that of an effect of wolves.

As we stated above, we did not include this model in the manuscript, but we certainly could. If the reviewers feel strongly that we should include it in the manuscript, we are happy to add it during a further revision of the manuscript.

-- It would be helpful to see the posterior distributions that were used to draw conclusions as a supplement.

Thank you we have added a new figure 3 with posterior estimates from our top model.

In general, your findings on the effects of human hunting on pumas were powerful. The effect of wolves is still unclear and would benefit from the explanations or changes recommended above. Very interesting - looking forward to reading more!

Thank you for all your feedback, which have no doubt strengthen the manuscript and made our final conclusions more defensible. We would argue that wolves have a more variable, but sometimes greater impact than human hunting on puma abundance, as illustrated in Figure 4. With the additional notes we described following your advice to explore a model with wolves + prey, we believe in our results that much more.

Referee: 2

Comments to the Author(s)
General comments:
The study investigates the relative influence of bottom-up and top-down forces on puma demography. The analysis is based on 16 years of monitoring 147 pumas, including information on the death of 115 individuals. A key conclusion is that the puma population was more strongly driven by top-down forces coming from wolves than by bottom-up forces associated with elk density. Attempting to disentangle the relative strength of top-down and bottom-up effects on large carnivores is certainly a valuable objective. While I like many aspects of this research, a number of points could be addressed.

I am not convinced that the study provides strong evidence that cougar demography is driven by top-down forces. Classic definition of top-down regulation would involve a species occupying a given trophic level regulating a species at the next lower level. The paper should clearly explain why the relationships outlined in the paper should be considered as top-down

regulation. Why not simply competition? We can read: “These species compete with pumas for prey, usurp their kills (i.e. kleptoparasitism)…” Should this be considered as top-down effects? I understand that pumas are be subordinate to wolves, but why shouldn’t they be considered as simple competitors siting on the same trophic level?

Thank you for your feedback. We acknowledge that most “top-down” research, including those that originally described the phenomenon, describe impacts across trophic levels. Nevertheless, the terminology is also applied to describe within trophic level interactions among dominant and subordinate competitors (e.g. Levi and Wilmers 2012). Therefore, we have changed terminology to avoid confusion in some places, and maintained “top-down” in others. Further we added text to define top-down, and acknowledge its multiple uses early in the introduction, to prepare the reader (Lines 47-49), and the above mentioned reference as well.

There is little evidence that wolves killed pumas during the course of the study (the paper only reports of hunting-related deaths). What if the presence of wolves forces pumas to rely less on elk and more on other species? I would not consider competition by interference or exploitation as top-down forces.

Thank you and we apologize for the confusion, as we were relying upon references to save space and minimize redundancy with our previous publications. Wolves killed 10 pumas during our study (9 of which were reported in Elbroch et al. 2018). Cause-specific mortality was a focus of our Elbroch et al. 2018 paper, and so we thought to minimize overlap. Nevertheless, based upon your feedback, we have added a new table 1 with cause-specific mortality information so as not to require readers to refer to another paper to find that information (Table 1) (we moved the old table 1 to supplementary materials as you suggested below).

Wolves were the leading cause of death for kittens < 6 months of age but we found little evidence that this death rate varied with wolf density

We know that 13% of all deaths came from legal hunting. What if most other deaths were from starvation? Would this underscore strong bottom-up forces? Is there any information on what the other 87% died from?

Please see above comment, and new Table 1.

Specific comments

Line 185. Should bottom-up forces be assessed based on more than elk? A previous study (Elbroch et al. 2013. PLoS ONE 8, e83375) seems to indicate that pumas alter their diet during the course of the year, and that other prey species can make up most of the diet, especially for females. It seems rather risky to conclude that top-down forces are dominant without knowing the causes of puma mortalities and the density of alternative prey.

Pumas are elk specialists in winter, but expand their diet to include deer in summer (Elbroch et al. 2013). However, they still most strongly select for elk calves in summer (Elbroch et al. 2017). The study area lacks defensible deer estimates, as state agency personnel do not have

any protocols for counting deer and only do so when lacking other work to do…thus we cannot say how incorporating deer estimates into larger prey estimates would change our results. In past analyses we have used deer numbers from a larger area in which our study area sits to determine proportional abundance (versus elk, for example, at equal spatial scales), but not actual numbers given the uncertainty of their distributions in our study area. Nevertheless, based on what we know of prey selection, elk are by far the dominant prey for local pumas and thus best reflect bottom-up forces (and competition with wolves).

Elbroch, L. M., P. Lendrum, J. Newby, H. Quigley, D. Craighead. 2013. Seasonal foraging ecology of non-migratory cougars in a system with migrating prey. *PLoS ONE* 8(12): e83375.

Elbroch, L. M., J. Feltner, H. Quigley. 2017. Human-carnivore competition for antlered ungulates: Do pumas select for bulls and bucks? *Wildlife Research* 44(7) 523-533.

Line 192. "We defined kittens as 0-6 months, subadults as 7-18 months, and adults as > 18 months of age." Given that subadults can be hunted between 12-18 months, should there be two subadult categories (7-12 and 12-18)?

Yes, we did include this variation in our initial models, but we can see that we were not clear. The survival term in equation (2) did include the effects of hunting for individuals that have remained in this group for the past 6 months (i.e., the entry in row 2, column 2 of the transition matrix: $\phi_{S,hunt} \cdot (\mathbf{1} - \boldsymbol{p}_{\boldsymbol{harvest}}) \cdot (1 - \pi)$). We have made changes to make explicit the two stages of this age class (lines 228, 235). Thank you.

Line 212. More information should be provided on the relative importance of the different causes of death.

Thank you and we apologize for the confusion, as we were relying upon references to save space and minimize redundancy with our previous publications. Wolves killed 10 pumas during our study (9 of which were reported in Elbroch et al. 2018). Wolves were the leadsing cause of death for kittens. Cause-specific mortality was a focus of our Elbroch et al. 2018 paper, and so we though to minimize overlap. Nevertheless, based upon your feedback, we have added a table with cause-specific mortality information so as not to require readers to refer to another paper to find that information (Table 1).

Line 264. I am wondering why a survival model that considers time to death was not used (Hosmer et al. 2008. Applied survival analysis: regression modeling of time to event data. Wiley…)? I assume that not all pumas were tracked during the same time period.

We agree this would be a reasonable approach but we felt that the capture-recapture analysis was more congruent with a stage-based model since it directly models the discrete hazard function. Using standard time-to-event models we would presumably need to integrate those quantities over the appropriate time periods to discretize them to be on the same timescale as the matrix model.

P. 12. Have the regression models been checked for multicollinearity?

Thank you we have added a new Figure S2 in the supplementary materials that has covariate correlation values. We have also added text to draw the reader to this figure in lines 256-257, 274, 378.

Line 315. Still, the difference in WAIC is only of 3.52. What if other prey than elk were also accounted for in the model (e.g., deer or moose or overall prey biomass)?

We cannot predict what would change if we added other prey abundance, as we lack such data. As discussed above, however, based on what we know of puma prey selection, elk are by far the dominant prey for local pumas and thus best reflect bottom-up forces.

Line 361. Please add a reference at the end of the sentence.

We apologize for the confusion, we moved the reference from mid-sentence to the end of the sentence.

Figure legends – Fig. 3. The caption should indicate that these are not observed changes, but they are projections.

Thank you, we have made the change.

Table 1. I wonder if Table 1 should be in an Appendix

Following your suggestion, we have moved this table to the supplementary materials, where it is now Table S1.

Appendix B

RSPB-2020-2202

Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape

Elbroch LM, Ferguson JM, Quigley H, Craighead D, Thompson DJ, & Wittmer HU

The authors use long-term demographic data to examine the interactions between humans, predators and their prey, with a focus on puma population dynamics. The authors clearly spent substantial time carefully considering the analytical approach they employed. I believe they explained their approach clearly and thoughtfully, with a few minor caveats. More broadly, I found their ecological arguments compelling, and believe this manuscript has the potential to have a substantial positive impact on ecosystem management.

I was invited to review the manuscript as a specialist statistical referee, thus I've focused my comments on the methods and the analytical techniques the authors used. Line comments marked * are simply suggested editorial changes I noticed while reading the paper. Given that I was asked to specifically review the statistical aspects of the manuscript, I encourage the authors to ignore the suggested editorial comments if they're not suitable to the author or editor.

Comments

Lines 8* ZIP is 83011

Lines 47-49* (Interference) Competition? It seems there is already a perfectly suitable phrase for this. I understand this is a complex issue, and I'm sure the authors have put more thought into it than I have, but I was confused by the use of top-down effects throughout the manuscript. The authors explain these processes well, but I was confused by the re-definition of one scientific term rather than just using a separate more suitable term.

Line 51* Remove 'In part,'? This reads as if it might have been reorganized and not completely put back together.

Line 62* top-down should be hyphenated throughout.

Line 64* who is 'we?'

Line 80-82* It might be more appropriate to cite Abadi *et al.* (2010) here with Arnold *et al.* (2018). It might also be helpful to 'soften' the language somewhat. Perhaps 'Integrated population models provide the opportunity to include multiple types of data, and allow researchers to simultaneously examine abundance and the demographic drivers underlying changes in abundance (Abadi *et al.*, 2010; Arnold *et al.*, 2018).'

Line 94-95 & 390-391 Accounting for the effects of hunting is never adequately described from my perspective. The authors mention in the discussion that their results support the 'additive' effects of hunting, yet they never seem to test or consider other forms of hunting mortality, simply $S(1 - p_{\text{harvest}})$. I don't disagree that anthropogenic harvest is additive for

long-lived organisms, but given that the authors did not consider other forms of harvest mortality (e.g., harvest compensation, partial harvest compensation, depensatory harvest, etc.), I don't think they can make this statement unless they're willing to substantially revise their analyses (i.e., test additional hypotheses).

Lines 119-121* This sentence seems unnecessary, and the entire section might be compressed and shortened if space is an issue.

Lines 143 What does 'sufficient' mean? The authors monitored about four adult pumas per year throughout the study. This is a fairly small sample size.

Lines 186-189 Are there any baseline data for the annual total harvest of pumas from the authors' study area? This was in a WDFG brochure on mountain lion hunting, I'm unsure how long this policy has been in place.
(g) Reporting and Registering Kills. Hunters harvesting mountain lions shall retain the pelt and skull from each mountain lion harvested for registration purposes. Even if the skull is damaged, it shall accompany the pelt. Visible external evidence of sex shall remain naturally atached to the pelt.
(i) Within three (3) days (seventy-two (72) hours) after harvesting a mountain lion, the licensee shall present the pelt and skull to a district game warden, district wildlife biologist or Department personnel at a Department Regional Office during business hours for registration. The entire pelt and skull shall be presented in an unfrozen condition in order to allow collection of two (2) premolar teeth to be utilized to determine the age of the mountain lion and to allow examination of the pelt to determine the sex of the mountain lion and lactation status of females. At the time of registration, the licensee shall furnish the Department with their license, the date of kill, the location of the site of kill to include hunt area, section, township and range or UTM coordinates
What proportion of these harvested individuals had been previously collared? I apologize if these were included in the supplementary material and I was unaware, but these data might help the authors substantiate their points that they've marked a majority of the individuals in the area and their population estimates are accurate, etc. They could also serve as a separate index of abundance, albeit with some additional assumptions. If the vast majority of pumas that are being shot in this area are collared then I don't really have any criticisms of the analyses. If it's an extremely small proportion then I'd be concerned. Obviously the authors would know better than me, and may have excluded or not included these data for excellent reasons. Perhaps their is heterogeneity in the reporting rates of collared vs. non-collared individuals?

As an aside, Michael Schaub has developed IPMs using age-at-harvest and telemetry data. It'll be out in his new book on IPMs in 2021.

Lines 181-182 It seems that their is substantial multicollinearity between hunting and other ecological drivers that might influence puma survival. The authors explain this well here.

Lines 202-207 The inclusion of the π parameter seems like a very nice solution to a challenging problem.

Line 239* perhaps 'dependence' rather than 'nonindependence'

Lines 241-242 Heterogeneity can simply refer to latent variation in survival probability among individuals (e.g., some individuals have higher inherent 'quality' than others). I would remove the second part of this sentence. I'm not criticizing the analysis, I just don't think it's necessary to make this statement, and it might not be completely accurate.

Line 249 Was uncertainty incorporated for the annual elk counts in any way? I would assume they suffer from similar issues as other large scale surveys of large numbers of animals.

Lines 257-278 This section could use some additional clarification. I don't believe the authors made any mistakes in their analytical approach, but some of the descriptions and mathematical equations are inconsistent. A simple supplementary table with one column listing the models, and two additional columns listing the effects on survival and fecundity considered in each model respectively might replace multiple paragraphs. Alternatively, the authors might simply write out each model in the supplementary material following Lines 281 and 286? This would be fairly easy to do, and would end any confusion.

Line 258 It could be more appropriate to simply refer to this as the 'null' model. 'Density-independent' somewhat implies that other biotic or abiotic effects were accounted for in the model.

Line 257-278 Did the authors perform any power analyses or goodness-of-fit testing?

Line 257-278 Did the authors consider or test any abiotic covariates such as snowpack?

Line 257-278 The authors strongly push back against a previous reviewer's suggestion to incorporate deer populations as a covariate as well. We appreciated their reasoning. However, it might be helpful to indicate somewhere in the manuscript if deer populations are correlated with elk populations (at a minimum)?

Line 293 We determined convergence of the MCMC *chains* by a ...

Line 294* $\hat{R}$

Line 298* We simulated potential puma populations 25 years into the future

Line 326 Please use stronger language here. Many quantitative ecologists believe in interpreting the proportion of the posterior distribution on the same side of zero as the mean as the probability of an effect. For instance, this beta estimate ($\beta = -2$, 95% BCI -4 – 0) would have 97.5% of its posterior distribution indicating a negative effect, where classical approaches would indicate it is 'non-signficant' because the upper credible limit is 0. The author's might use the f-value from JAGS and directly report these as probabilities of effects, in this case 'there was a 97.5% probability of a negative effect of covariate x. Also note that Arnold (2010) demonstrates that AIC approaches, such as those used in this manuscript, use 85% confidence intervals. Thus the authors should present 85% CIs if they prefer to continue to use credible intervals rather than proportions of distributions. I appreciate the author's being conservative, but again suggest stronger language highlighting their points.

Lines 348-351 Are there credible intervals around these estimate? Please include the actual estimates. These talking points can be (and are!) made strongly in the discussion.

Figure S1 Excellent figure.

Table S1 Inconsistent commas for numbers of elk (Elk on NER column has no commas). Insanely nitpicky, apologies!

Table S2 I greatly appreciated the inclusion of this table. It could be helpful to specifically state which symbols correspond to which distributions in the table legend. I followed along fairly well, but this could be confusing for some readers. If space is limiting I understand. It might also be helpful to present σ or σ^2 for demographic parameters on the probability scale. The precision of demographic paramaters estimated on logit link is challening to interpret. For instance, the size of the precision estimate can also relative to the position of the estimate on the curve of the logit link. In other words, values that range from 0.9-1 on the probability scale will have much smaller precisions than values that range from 0.45-0.55. These values are not comparable across age-classes.

Conclusion

I enjoyed reading this manuscript, and feel that it has the potential to serve as a valuable contribution to our understanding of puma population dynamics, and more broadly to the field of ecology. I thought the authors made many salient points. I believe the manuscript may be improved following the addition of some diction clarifying the statistical approaches used by the authors, and a few minor revisions to the presentation of the results that I believe would serve to strengthen the authors conclusions. I'm appreciative of the opportunity to constructively improve the manuscript.

Sincerely,
Thomas Riecke

References

Abadi, F., Gimenez, O., Arlettaz, R. & Schaub, M. (2010) An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology*, **91**, 7–14.

Arnold, T.W. (2010) Uninformative parameters and model selection using akaike's information criterion. *The Journal of Wildlife Management*, **74**, 1175–1178.

Arnold, T.W., Clark, R.G., Koons, D.N. & Schaub, M. (2018) Integrated population models facilitate ecological understanding and improved management decisions. *The Journal of Wildlife Management*, **82**, 266–274.

Appendix C

14 October, 2020

Manuscript ID RSPB-2020-2202– Resubmission of Accepted Manuscript with minor revision

Dear Dr. Locke Rowe, *Proceedings B*,

Thank you for the opportunity to share our work with your broader audience via *Proceedings B*. We are thrilled. Please find below our responses to reviewers in brick red, and then following these, our minor revision—the entire manuscript with track changes with line numbers so we could reference changes to ease your review.

Thank you again.

Kind regards,

Mark Elbroch, Jake Ferguson, Howard Quigley, Derek Craighead, Daniel Thompson, and Heiko Wittmer
Correspondence: Mark Elbroch, melbroch@panthera.org

Associate Editor
Comments to Author:
Two reviewers have seen the last version of this MS, one of which who was asked specifically to look at the statistical tools employed in the analysis. Both are quite favourable but both also make a number of suggestions that, in my view, would, when dealt with at least, significantly enhance the potential impact of the publication. In particular, it might be useful to discuss the potential bias caused by the starvation / predation issue identified by one of the reviewers. The statistical reviewer recommends (among other things) to standardise the way significance is calculated. I don't know how easy it is to adopt this, but it is certainly worthy of consideration.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
The revised version provides valuable information to evaluate the robustness of the study's conclusions. I can now accept the idea that wolves have a dominant influence on the demography of pumas. Still, I believe the 'conclusion' should indicate some of the uncertainties associated with the dataset and the analysis. I can see a few points of uncertainty. First, while only elk were considered in the current study, summer diet includes other species, especially mule deer. The lack of information on overall prey biomass is a weakness, especially in the context that many pumas died from starvation. Second, a larger number of adult deaths have been linked to starvation than to predation. When considering all age classes, 22 deaths have been linked to

starvation and 26 to predation. Given that cause of death could not be assigned for 28 pumas, there is a reasonable risk that bottom-up forces have been underestimated. This is certainly relevant given that the second top-ranking model excludes wolf, but includes elk (delta WAIC = 3.52). I thus believe that the discussion should recognize such points of uncertainty and briefly discuss their implication. That being said, I believe that the paper draws reasonable conclusions.

Thank you. We have added some text about interpreting the starvation data, and the complexity of disentangling wolf from elk effects—which highlights the uncertainties raised by this reviewer. The new text (lines 713-720) reads: "Further evidence for this complexity is found in interpreting the potential cause of puma starvation, which nearly equaled mortality attributed to predation (Table 1). Puma starvation may have increased over the study due to the declining elk herd (i.e. bottom-up effects), decreased accessibility to elk, as mediated by exploitive and interference competition with wolves (top-down effects), or both [21]."

Minor points
Table 2. The title should include more information (e.g., what is the model testing; density is for which species?)

Thank you, we've added additional details to Table 2.

Fig. 4. Could confidence intervals be included in the figure?

We have added intervals to the discussion of this figure on lines 677-680 to capture the uncertainty in these projections, but refrained from adding the intervals to the figure to aid in its interpretation (to keep it simpler).

Figure S2. I do not find the scale completely clear because the negative signs touch the scale. Maybe a + sign could be added for the positive values?

Thank you, we have moved the numbers in the figure so the negative signs are visible.

Also, the study provides tests of collinearity. I suggested to assess 'multicollinearity' in the multivariate models using, for example, Variance Inflation Factor (VIF). This seems even more relevant now that some correlations are rather high.

Thank you for your suggestion. We did not include models in the final manuscript that included multiple correlated predictors due to the difficulty in understanding how to interpret those effects. The one exception to this was in our local perceptions model that included the effects of both elk and wolves on adult survival, however since there are only two predictors, we believe pairwise correlations are sufficient to aid in their interpretation.

Referee: 3

Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape

Elbroch LM, Ferguson JM, Quigley H, Craighead D, Thompson DJ, & Wittmer HU

The authors use long-term demographic data to examine the interactions between humans, predators and their prey, with a focus on puma population dynamics. The authors clearly spent substantial time carefully considering the analytical approach they employed. I believe they explained their approach clearly and thoughtfully, with a few minor caveats. More broadly, I found their ecological arguments compelling, and believe this manuscript has the potential to have a substantial positive impact on ecosystem management.

I was invited to review the manuscript as a specialist statistical referee, thus I've focused my comments on the methods and the analytical techniques the authors used. Line comments marked * are simply suggested editorial changes I noticed while reading the paper. Given that I was asked to specifically review the statistical aspects of the manuscript, I encourage the authors to ignore the suggested editorial comments if they're not suitable to the author or editor.

Comments
Lines 8* ZIP is 83011

Thank you, added!

Lines 47-49* (Interference) Competition? It seems there is already a perfectly suitable phrase for this. I understand this is a complex issue, and I'm sure the authors have put more thought into it than I have, but I was confused by the use of top-down effects through- out the manuscript. The authors explain these processes well, but I was confused by the re-definition of one scientific term rather than just using a separate more suitable term.

We prefer to keep the "top-down" narrative as it fits with the larger discussion in the literature about top-down effects outside protected areas. We feel that the introduction highlights "competition" as those top-down effects well enough, but based on this feedback we tweaked the Discussion slightly to emphasize competition again, and remind the reader about what types of top-down effects wolves would have on pumas. For example, in the first sentence of the Discussion we added "(i.e. competition)" after top-down forces (line 686, 684).

Line 51* Remove 'In part,'? This reads as if it might have been reorganized and not com- pletely put back together.

Done, thank you.

Line 62* top-down should be hyphenated throughout.

Done, thank you.

Line 64* who is ‘we?’

Changed to “researchers”, thank you.

Line 80-82* It might be more appropriate to cite Abadi *et al.* (2010) here with Arnold *et al.* (2018). It might also be helpful to ‘soften’ the language somewhat. Perhaps ‘Integrated population models provide the opportunity to include multiple types of data, and allow researchers to simultaneously examine abundance and the demographic drivers underlying changes in abundance (Abadi *et al.*, 2010; Arnold *et al.*, 2018).’

Thank you, we have changed the text as you suggested. (lines 392-393)

Line 94-95 & 390-391 Accounting for the effects of hunting is never adequately described from my perspective. The authors mention in the discussion that their results support the ‘additive’ effects of hunting, yet they never seem to test or consider other forms of hunting mortality, simply $S(1 - p_{harvest})$. I don’t disagree that anthropogenic harvest is additive for long-lived organisms, but given that the authors did not consider other forms of harvest mortality (e.g., harvest compensation, partial harvest compensation, depensatory harvest, etc.), I don’t think they can make this statement unless they’re willing to substantially revise their analyses (i.e., test additional hypotheses).

This is fair criticism but all literature studying the impacts of human hunting on pumas has concluded that the effects are additive. We have reworded this sentence to highlight the literature: “Our results supported previous research emphasizing the additive effects of hunting on puma mortality [12,13].” (Line 730)

Lines 119-121* This sentence seems unnecessary, and the entire section might be com- pressed and shortened if space is an issue.

We did not make this change as this information was specifically requested in our first review. We’re trying our best to be inclusive of all feedback!

Lines 143 What does ‘sufficient’ mean? The authors monitored about four adult pumas per year throughout the study. This is a fairly small sample size.

Thank you, we have changed this to “proportion of the population”…yes our samples were small, but this study area supported one of the lowest densities of pumas in western North America and camera traps of unmarked animals suggested we had caught 85% of residents…

Lines 186-189 Are there any baseline data for the annual total harvest of pumas from the authors’ study area? This was in a WDFG brochure on mountain lion hunting, I’m unsure how long this policy has been in place.
(g) Reporting and Registering Kills. Hunters harvesting mountain lions shall retain the pelt and skull from each mountain lion harvested for registration purposes. Even if the skull is damaged,

it shall accompany the pelt. Visible external evidence of sex shall remain naturally atached to the pelt.

(i) Within three (3) days (seventy-two (72) hours) after harvesting a mountain lion, the licensee shall present the pelt and skull to a district game warden, district wildlife biologist or Department personnel at a Department Regional Office during business hours for registration. The entire pelt and skull shall be presented in an unfrozen condition in order to allow collection of two (2) premolar teeth to be utilized to determine the age of the mountain lion and to allow examination of the pelt to determine the sex of the mountain lion and lactation status of females. At the time of registration, the licensee shall furnish the Department with their license, the date of kill, the location of the site of kill to include hunt area, section, township and range or UTM coordinates

What proportion of these harvested individuals had been previously collared? I apologize if these were included in the supplementary material and I was unaware, but these data might help the authors substantiate their points that they've marked a majority of the individuals in the area and their population estimates are accurate, etc. They could also serve as a separate index of abundance, albeit with some additional assumptions. If the vast majority of pumas that are being shot in this area are collared then I don't really have any criticisms of the analyses. If it's an extremely small proportion then I'd be concerned. Obviously the authors would know better than me, and may have excluded or not included these data for excellent reasons. Perhaps their is heterogeneity in the reporting rates of collared vs. non-collared individuals?

This is interesting to ponder but we do not think it will be a useful metric for what % of the population we captured for these reasons: 1) harvest includes resident and transient (animals without a home range) pumas, and our population estimates were for residents only; 2) our study area only composed approximately 30% of Hunting Unit 2, and therefore pumas harvested in this unit and reported by the state agency were often beyond the study area; 3) hunting was biased away from our core study area because of the presence of wolves that killed trained hunting hounds in 2005. 4) The state agency may be able to provide location data for all harvested animals over the course of the study, but we do not have access to this information at this time.

Over the course of the study, collared cats comprised 20% of the total harvest in Hunting Unit 2, but given the above biases this is difficult to interpret in terms of what it tells us about our effort.

As stated above, we estimated that we captured approximately 85% of the resident population during the second half of the study via camera traps placed in the field that captured images of marked and unmarked animals.

As an aside, Michael Schaub has developed IPMs using age-at-harvest and telemetry data. It'll be out in his new book on IPMs in 2021.

Wonderful to know, thank you.

Lines 181-182 It seems that their is substantial multicollinearity between hunting and other ecological drivers that might influence puma survival. The authors explain this well here.

Thank you.

Lines 202-207 The inclusion of the π parameter seems like a very nice solution to a challenging problem.

Thank you.

Line 239* perhaps ‘dependence’ rather than ‘nonindependence’ 2

Done, thank you.

Lines 241-242 Heterogeneity can simply refer to latent variation in survival probability among individuals (e.g., some individuals have higher inherent ‘quality’ than others). I would remove the second part of this sentence. I’m not criticizing the analysis, I just don’t think it’s necessary to make this statement, and it might not be completely accurate.

Thank you, we agree with the reviewer and have removed the clause.

Line 249 Was uncertainty incorporated for the annual elk counts in any way? I would assume they suffer from similar issues as other large scale surveys of large numbers of animals.

No, as the Wyoming Game and Fish Department does not report uncertainty in their annual estimates.

Lines 257-278 This section could use some additional clarification. I don’t believe the authors made any mistakes in their analytical approach, but some of the descriptions and mathematical equations are inconsistent. A simple supplementary table with one column listing the models, and two additional columns listing the effects on survival and fecundity considered in each model respectively might replace multiple paragraphs. Alternatively, the authors might simply write out each model in the supplementary material following Lines 281 and 286? This would be fairly easy to do, and would end any confusion.

Thank you for this suggestion. We have added Table S3 with the vital rate models for each of the demographic candidate models. Please see Supplementary Materials, as we did not include them below with the track changes

Line 258 It could be more appropriate to simply refer to this as the ‘null’ model. ‘Density-independent’ somewhat implies that other biotic or abiotic effects were accounted for in the model.

Updated throughout, thank you.

Line 257-278 Did the authors perform any power analyses or goodness-of-fit testing?

Yes, we conducted several tests to determine goodness-of-fit. We tested the sensitivity of our survival estimates to removing the abundance data from the integrated model and found very

little change in the point estimates of model parameters (less than 5% change). We also tested how well the model predicted abundances when removing the final four years of data (2013-2016). We found that prediction of overall trends in the population density were accurate, though as typical in these models we missed some of the annual fluctuations away from these trends. In both cases the diagnostics were run on the density-dependent model to determine whether the integrated modeling approach was working as expected. We did not report these metrics since the assessments were rather informal and not conducted on the density + wolf model, which we spend most of the time discussing.

Line 257-278 Did the authors consider or test any abiotic covariates such as snowpack?

No.

Line 257-278 The authors strongly push back against a previous reviewer's suggestion to incorporate deer populations as a covariate as well. We appreciated their reasoning. However, it might be helpful to indicate somewhere in the manuscript if deer populations are correlated with elk populations (at a minimum)?

We do not know whether the deer correlate with elk in the study area, because the data on deer are that bad. We tried to incorporate it in some way but after interviewing the people who collected the data, it was clear that sampling was so inconsistent that no comparisons across years were possible. We realize this is less than ideal, but we think it worse to include the deer data as it will come along with all sorts of human biases.

Line 293 We determined convergence of the MCMC *chains* by a ...
Line 294* $\hat{R}$

Fixed, thank you.

Line 298* We simulated potential puma populations 25 years into the future

Done, thank you.

Line 326 Please use stronger language here. Many quantitative ecologists believe in interpreting the proportion of the posterior distribution on the same side of zero as the mean as the probability of an effect. For instance, this beta estimate ($\beta = -2$, 95% BCI -4 – 0) would have 97.5% of its posterior distribution indicating a negative effect, where classical approaches would indicate it is 'non-signficant' because the upper credible limit is 0. The author's might use the f-value from JAGS and directly report these as probabilities of effects, in this case 'there was a 97.5% probability of a negative effect of covariate x. Also note that Arnold (2010) demonstrates that AIC approaches, such as those used in this manuscript, use 85% confidence intervals. Thus the authors should present 85% CIs if they prefer to continue to use credible intervals rather than proportions of distributions. I appreciate the author's being conservative, but again suggest stronger language highlighting their points.

We thank the review for introducing this measure to us. We have added it to the main text (lines 650-657), but still report credible intervals in the supplementary material for those interested in the magnitude and precision of the effects.

Our understanding of Arnolds point is that he proposes using 85% CI's if you are using CIs to select variables. This would make the selection criteria is consistent with the commonly used rule of a delta 2 cutoff used with AIC. Here, we are not trying to perform posthoc model selection, simply report the precision of our estimates so stick with 95% CI's for the reported parameter estimates in Table S2 and for the CI's added in the passage discussing Figure 4.

Lines 348-351 Are there credible intervals around these estimate? Please include the actual estimates. These talking points can be (and are!) made strongly in the discussion.

Added.

Figure S1 Excellent figure.

Thank you.

Table S1 Inconsistent commas for numbers of elk (Elk on NER column has no commas).

Insanely nitpicky, apologies!

Wonderful, thank you!

Table S2 I greatly appreciated the inclusion of this table. It could be helpful to specifically state which symbols correspond to which distributions in the table legend. I followed along fairly well, but this could be confusing for some readers. If space is limiting I understand. It might also be helpful to present σ or σ^2 for demographic parameters on the probability scale. The precision of demographic paramaters estimated on logit link is challening to interpret. For instance, the size of the precision estimate can also relative to the position of the estimate on the curve of the logit link. In other words, values that range from 0.9-1 on the probability scale will have much smaller precisions than values that range from 0.45-0.55. These values are not comparable across age-classes.

Thank you, we have clarified the symbols used in the distributions in the table caption. While we agree reporting the variance on the logit scale is not ideal in terms of interpretation it is not clear to us where to report it on the logistic scale. We could report the variance of the rate evaluated at the mean of the estimated parameters and over the mean of the predictor variables but that also seems difficult to interpret. We have chosen to keep the parameters as is, though if we misunderstood this comment we are willing to readdress it.

Conclusion

I enjoyed reading this manuscript, and feel that it has the potential to serve as a valuable contribution to our understanding of puma population dynamics, and more broadly to the field of ecology. I thought the authors made many salient points. I believe the manuscript may be improved following the addition of some diction clarifying the statistical approaches used by the authors, and a few minor revisions to the presentation of the results that I believe would serve to strengthen the authors conclusions. I'm appreciative of the opportunity to constructively improve the manuscript.

Sincerely, Thomas Riecke

References

Abadi, F., Gimenez, O., Arlettaz, R. & Schaub, M. (2010) An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology*, 91, 7–14.

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