Peer Community In
Ecology

A new and efficient approach to estimate, from protocol and opportunistic data, the size and trends of populations: the case of the Pyrenean brown bear

Nicolas BECH based on peer reviews by Tim Coulson, and Romain Pigeault

Cécile Vanpé, Blaise Piédallu, Pierre-Yves Quenette, Jérôme Sentilles, Guillaume Queney, Santiago Palazón, Ivan Afonso Jordana, Ramón Jato, Miguel Mari Elósegui Irurtia, Jordi Solà de la Torre, Olivier Gimenez (2022) Estimating abundance of a recovering transboundary brown bear population with capture-recapture models. Missing preprint_server, ver. 4, peer-reviewed and recommended by Peer Community in Ecology.
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In this study, the authors report a new method for estimating the abundance of the Pyrenean brown bear population. Precisely, the methodology involved aims to apply Pollock's closed robust design (PCRD) capture-recapture models to estimate population abundance and trends over time. Overall, the results encourage the use of PCRD to study populations' demographic rates, while minimizing biases due to inter-individual heterogeneity in detection probabilities.

Estimating the size and trends of animal population over time is essential for informing conservation status and management decision-making (Nichols & Williams 2006). This is particularly the case when the population is small, geographically scattered, and threatened. Although several methods can be used to estimate population abundance, they may be difficult to implement when individuals are rare, elusive, solitary, largely nocturnal, highly mobile, and/or occupy large home ranges in remote and/or rugged habitats. Moreover, in such standard methods,

- the population is assumed to be closed both geographically (no immigration nor emigration) and demographically (no births nor deaths) and

- all individuals are assumed to have identical detection probabilities regardless of their individual attributes (e.g., age, body mass, social status) and habitat features (home-range location and composition) (Otis et al. 1978).

However, these conditions are rarely met in real populations, such as wild mammals (e.g., Bellemain et al. 2005; Solbert et al. 2006), and therefore the risk of underestimating population size can rapidly increase because the assumption of perfect detection of all individuals in the population is violated.

Focusing on the critically endangered Pyrenean brown bear that was close to extinction in the mid-1990s, the study by Vanpe et al. (2022), uses protocol and opportunistic data to describe a statistical modeling exercise to construct mark-recapture histories from 2008 to 2020. Among the data, the authors collected non-invasive samples such as a mixture of hair and scat samples used for genetic identification, as well as photographic trap data of recognized individuals. These data are then analyzed in RMark to provide detection and survival estimates. The final model (i.e. PCRD capture-recapture) is then used to provide Bayesian population estimates. Results show a five-fold increase in population size between 2008 and 2020, from 13 to 66 individuals. Thus, this study represents the first published annual abundance and temporal trend estimates of the Pyrenean brown bear population since 2008.

Then, although the results emphasize that the PCRD estimates were broadly close to the MRS counts and had reasonably narrow associated 95% Credibility Intervals, they also highlight that the sampling effort is different according to individuals. Indeed, as expected, the detection of an individual depends on

- the intraspecific home range size variation that results in individuals that move the most being most likely to be detected and
- the mortality rate which is higher on cubs than on adults and subadults (due to infanticide by males, predation, death of the mother, or abandonment).

Overall, the PCRD capture-recapture modelling approach, involved in this study, provides robust estimates of abundance and demographic rates of the Pyrenean brown bear population (with associated uncertainty) while minimizing and considering bias due to inter-individual heterogeneity in detection probabilities.

The authors conclude that mark-recapture provides useful population estimates and urge wildlife ecologists and managers to use robust approaches, such as the RDPC capture-recapture model, when studying large mammal populations. This information is essential to inform management decisions and assess the conservation status of populations.

References:

Bellemain, E.V.A., Swenson, J.E., Tallmon, D., Brunberg, S. and Taberlet, P. (2005). Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. Cons. Biol. 19(1), 150-161. https://doi.org/10.1111/j.1523-1739.2005.00549.x

Nichols, J.D. and Williams, B.K. (2006). Monitoring for conservation. Trends Ecol. Evol. 21(12), 668-673. https://doi.org/10.1016/j.tree.2006.08.007

Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. Wildlife Monographs (62), 3-135.

Solberg, K.H., Bellemain, E., Drageset, O.M., Taberlet, P. and Swenson, J.E. (2006). An evaluation of field and non-invasive genetic methods to estimate brown bear (Ursus arctos) population size. Biol. Conserv. 128(2), 158-168. https://doi.org/10.1016/j.biocon.2005.09.025

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bear population with capture-recapture models. bioRxiv, 2021.12.08.471719, ver. 4 recommended and peer-reviewed by PCI Ecology. https://doi.org/10.1101/2021.12.08.471719

Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.1101/2021.12.08.471719
Version of the preprint: 2

Authors' reply, 17 October 2022

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Decision by Nicolas BECH, posted 12 September 2022

Dear authors,
Thank you very well for responding to all the reviewers' comments. The manuscript has been significantly improved and requires only minor suggestions for changes. These suggestions are listed by the reviewers below.

If you decide to revise the work, please submit a list of changes when you submit the revised manuscript.

Yours sincerely.

Nicolas BECH

Reviewed by Tim Coulson, 26 August 2022

I think the authors have done a good addressing my concerns. I have provided a marked-up version of their paper, with some editorial suggestions. There is also a paragraphy about Bayesian methods in the introduction that is rather out of place. Perhaps remove it? It could be moved to the disucssion, where it would be more appropriate, and used to justify the choices made when analysing the data.

This is a good paper that will doubltless be well-cited. I look forward to seeing it published. Perhaps even in Peer Community Journal!

TIm Coulson

Download the review

Reviewed by Romain Pigeault, 09 September 2022

Dear Cécile Vanpé and collaborators,

Thank you for addressing all the comments in such detail. The manuscript now contains additional information very helpful to fully understand your study. I only have a few, minor suggestions for changes.

1) Many sentences are very long and sometimes difficult to understand. I suggest to rewrite some of them in order to facilitate the reading. (e.g., Page 7, Lines 3-6 ; Page 3, Lines 19-23 ; Page 8, lines 8-13 ; Page 9, Lines 13-17)

2) Page 3 lines 18-19 : I am not convinced that it is necessary to indicate these values in the abstract.

3) Page 3, lines 25-26 : I suggest removing the second part of this sentence (isn't a lower survival rate de facto related to a higher mortality rate ?)

4) Page 4, line 3, please remove one "and".

5) Page 17, line 19. In the current form we don't quite understand what effects are being tested. Maybe this sentence should be reworded.

6) Page 24, line 18. I suggest removing the word ”and” at the beginning of the sentence.

Romain

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2021.12.08.471719
Version of the preprint: 1

Authors' reply, 03 August 2022

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Decision by Nicolas BECH, posted 21 March 2022, validated 14 November 2022

This preprint merits a revision

Dear authors of the article «Estimating abundance of a recovering transboundary brown bear population with capture recapture models »

This paper proposes a monitoring of the critically endangered Pyrenean brown bear population using the Pollock's closed robust design (PCRD), a capture recapture method. This study represents the first estimate of the abundance of the Pyrenean brown bear population and its trends since its reinforcement in 1996.

Based on the comments from 3 referees and from my own lecture, I believe that this paper fits well within the topic of PCI Ecology and represents a major contribution to global population studies and in particular to brown bear ones. Althought this article may be acceptable for publication, it requires some clarifications, precisions and a proofreading by a native English speaker before publication. We suggest that authors consider the following suggestion as well as minor coments bellow.

Reviewed by ?, 08 February 2022

Vanpé et al. 2021. Estimating abundance of a recovering transboundary brown bear population with capture-recapture models
Preprint review PCI Ecology
7 February 2021

This paper reports on a new method for estimating abundance of the Pyrenean brown bear population. Given the increase in abundance and distribution in the population, new methods are warranted. I have some concerns about some of the conclusions and the lack of transparency in the methods and results making it difficult to be confident in the conclusions that are reported. There are a lot of details provided for some of the methods but then wholly lacking for others

Additionally, I think there are lot of more recent citations that should be included. Many of the citations are dated (very few are current except a couple with some of the same co-authors) and the citations are sparse throughout. The authors need to spend some time becoming familiar with the current literature and incorporating it into this manuscript. There are many conclusions that are drawn that are inaccurate or could be compared to other, current literature but that does not occur. There is also a lot of important information that is not reported (see specifics and suggestions throughout my comments). It feels more like a report than a manuscript and I would not be comfortable citing this manuscript given the inaccuracies and lack of ability to draw conclusions given the incomplete reporting.

The primary author has a good handle on the English language but the manuscript would benefit immensely from proofreading and contribution by a native English speaker. Most journals prefer active voice when writing so instead of “sites were visited to collect samples”, “we visited sites to collect samples”. I recommend changing this throughout the manuscript for easier reading.

I also would recommend getting a paper in as “finished” as form as possible prior to submitting for peer-review, otherwise it is an immense amount of work for a reviewer. This took me more than 6 hours to review. It seemed like this was a pretty rough draft of a manuscript that is supposed to be ready for publication. PCI Ecology is specifically “not designed to be a free peer reviewing service for authors aiming to improve their articles before submission to a journal” but in this submission, that is what it seemed like. In the results and discussion, I spent less time making suggestions about how to reword sentences given the lengthy nature of the review already.

Because each page is numbered beginning with 1, it was a bit difficult to make comments since I had to check the page number before listing the line number. Continuous page numbering would be much easier to work with and is standard when submitting a manuscript.

I have specific comments in the following pages.

Abstract Lines 18–20: This is not novel (i.e., that PCRD can provide reliable estimates) but it is written that this is something new that you found in this study. I would rephrase to say something to make it clear that this method worked for your species/study. Something like we used PRCD to reliably estimate abundance of Pyrenean brown bears, etc.

Main document:
Page 3
Line 7: I would change “almost impossible” to difficult

Line 7–8: Often relies on? How about something more like camera trapping or noninvasive/molecular techniques have been increasing or are commonly used methods now. And then you can cite some more recent studies that have used these techniques as examples.

Line 13: “so-called minimum detected size”. Is there a citation for this? I don’t know this as a “popular” monitoring method at least not by this name so I would include a citation here.

Line 15–16: I would argue that this is changing. Costs are coming down for genetic analysis, analytical (statistical) techniques are improving so that fewer samples can be collected thus reducing cost, time, and logistics. The cited paper is 9 years old at this point and a lot has changed since then.

Line 19: I would include more citations here aside from just Solberg et al. There are many relevant citations.

Line 22: remove the word exhaustively. It is unnecessary.

Lines 22–25 and onto page 4: Noninvasive DNA sampling does not “imply” these things you mention. You could, for example, know exactly the date a scat or hair sample was deposited (i.e., you saw the animal defecate or you had cleared the area of scat the day before and there was new scat when you resampled). Also you talk about CR surveys and then change to CR models. Maybe stick to models (i.e. change in line 21)? I also suggest splitting up these lines and adding some citations. Could change to something like: Whereas CR models were originally limited to live-trapping studies, they have been adapted for use with non-invasive DNA sampling (insert citation here). Then go on to mention these issues and cite them: individual identification errors due to genotyping errors, uncertainty in the date of individual detection, and possibility of collecting multiple samples of the same individual across space within a single sampling occasion (Lukacs 2005; Lukacs & Burnham 2005). Although now as I get down to page 4, it seems that these lines and lines 8–10 on pg 4 should be combined. These 2 paragraphs should be restructured because they say much of the same thing

Page 4:
Line 5: change "supposed" to assumed. You could also shorten by removing everything after detection probabilities.

Lines 3–8: I would split these sentences differently as the first one is long and then the sentence starting with "But..." seems out of place: In standard closed-population CR models, the population is assumed to be closed to changes in abundance both geographically (no immigration nor emigration) and demographically (no births nor deaths). Additionally, all individuals are assumed to have identical detection probabilities whatever their individual attributes (e.g., age, body mass, social status) and habitat features (home-range location and composition) (Otis et al. 1978), although these conditions are rarely fulfilled met in real populations of wild mammals (insert appropriate citation here).

Line 9 and 13: remove probability and probabilities—i.e., change to detection heterogeneity or heterogeneity in detection

Line 11: what about citing Pollock here?

Line 12: replace "study" with "estimate" since I think that is what you really mean here.

Line 16–18: Simplify: In recent years, the implementation of Bayesian PCRD models has been made simpler by the development of user-specified models (insert citations here) (not sure this is the correct wording but something like this).

Lines 19–21: Again, I would simplify this because it is very wordy: In the mid-1990s after decades of persecution, the brown bear (Ursus arctos) population in the Pyrenees Mountains at the border of France, Spain and Andorra (a study area figure would be good to reference here) had only five individuals remaining (Taberlet et al. 1997).

Line 24: Provide a reference where the Cantabrian population is (as in a country) because not everyone is familiar with this.

Line 26: if you are going to use the word "high" here, I would state what the rate is. High is a subjective word so perhaps provide the rate along with each citation.
Lines 26– 3 (on the next page): Simplify............ Thus implementing reliable methods to accurately estimate population abundance trend over time is crucial to monitor the conservation status of this population threatened with extinction and implement successful management plans. I also recommend changing one of the "implement" to develop or something else for smoother reading.

Page 5:
Line 4–5: Make it clear that this is what currently happens. So, currently, monitoring of the Pyrenean….
And again, I would simplify: Currently, monitoring of the Pyrenean brown bear population relies on either opportunistic collection of bear data or samples (e.g., scat or hair) by the public with no specific sampling design or a systematic sampling approach (Sentilles et al. 2021a; Sentilles, Vanpé & Quenette 2021).

Line 8: Change to: Similar to many large carnivore populations…..

Lines 8–12: I think you can remove some words here such as "highly", "divided in", "specific" and it will still say the same thing, just simpler. Also, you don't specifically mention ANdorrra here but I assume you are referencing it. I would include Andorra here since you mention it in the next sentence but it sounds like somewhere different in that sentence.

Lines 16–19: Simplify: The aim of this study was to use cross-border non-invasive sampling data and collected from 2008 to 2020 in France, Spain and Andorra and PCRD and for which individual identification was possible through genetic analyses or visual evidence to provide the first published estimates of annual abundance of the Pyrenean brown bear population. You mentioned what the data is above so I don't think you need to specify it again here.

End of page 5 and onto page 6: I would remove the entire section on brown bear biology. I am not sure why this is included but it is not relevant to the current manuscript.

Page 6:
Line 17: are you saying the area ranges over 10,000 sq km in 2020? Or the population? This isn't clear. Also, active voice would be preferred, i.e., We carried out our study….or our study area was….

Line 18: Same here—active voice and simplify: We used four different non-invasive methods……..

Line 20: Simplify.. Systematic by trails (ST) corresponded to walking 8 to 10 km transects (from long),

Lines 23–25: I am not sure exactly what this means because of the French-English translation so this needs to be clarified. I can't figure out what this is describing: Trails were set in function of available bear habitats and passage areas detected using VHF and GPS collars or bear presence signs. I think you are talking about how the transects (i.e., trails?) were delineated and decided upon but it needs clarification.

Line 25: accompanied occasionally by a scat detection dog? Like in certain years or months or locations? This needs more details here even if it is in the cited work so the reader can know the basics of the methods.

Page 7:
This entire section describing the 4 methods needs appropriate citations—a lot of people have used these methods and I am guessing you based your sampling on some of these studies.
Line 1: What do you mean "immediate surroundings"? Was there some kind of delineation of how far off the trail you could go to look? Or how far off the trail you could see and collect sign or was this random?
Line 2–3: "scattered along each itinerary". Do you mean they were along the trail on each transect?

Line 4: what is smola?

Line 6: when you say “similar to the camera method”, I would note that this is described below since you haven’t described it yet.

Line 10: Why this height?

Lines 13–15: Where do these grid cell sizes come from? And what are the known female range areas and where do they come from? More examples of where citations are needed.
Oh, okay, now I got to the next lines and see where it came from. So I would put Lines 15–18 before lines 13-15. But you still need a citation of where the Pyrenees bears home range size comes from.

Lines 18–20: how did you predict the best bear habitat? “bear expert opinion” included what? Was this systematically determined in some kind of expert elicitation? Is it cited somewhere?

Line 22: remove the words “automatic-triggered” since this is clarified with “movement detection” on lines 254 and 25 and “essentially”, as it is unnecessary

Line 25: how were these areas with frequent animal passages determined? And I assume by animal you mean bear? So areas of high use by bears? But clarify how you determined these areas.

Page 8
Lines 1–2: as you did in the previous section, state that each station was visited to collect samples and maintain cameras, or whatever it was you did there.

Lines 2-3: You could simplify this by saying you followed the same layout as above instead of repeating the 4 x4 km, etc. again.

Lines 4-7: I don’t understand this. You need to describe this more. I understand if there was a radio collar or ear tag or a really distinguishing physical feature you didn’t do genetic analysis so you just counted this as a “capture”? This would definitely affect the problem of heterogeneity since these individuals could potentially be more easily identified if, for example, you had a confirmed “capture” by the camera but if you had used the DNA and it failed, you would not have a detection. So any individuals that were not visually identifiable and then if the DNA didn’t amplify they would be detected less often and with lower probability of detection. If you do not address this later on, it is something that needs to be addressed. How many “captures” or instances did this include?

Lines 8–9: What is the bear potential range? How was this determined?

Line 10: What are “eating clues”? And scratches? How were these determined to be from brown bears?

Lines 10–11: “gathered by mountain users”. How were these reported and to whom? And what kind of data was collected in these reports? Were people trained in collection of data and samples. Did you provide sample collection materials to them? And how were these screened for verification of the data? And then how was this data used in the analysis?

Lines 16–18: I am assuming these are the areas you are referring to above when you mention autonomous regions and you should specify that above. Also, not all readers know where Catalonia and Aragon and Navarra are so specify this.

Lines 18–20: you say you focused on noninvasive data but what about the data from individuals that you identified on camera?

Line 21: You paid particular attention to the date for the opportunistic monitoring? Or for all monitoring?

Page 9:

Line 1: What do you mean “validated”? How did you validate it—and what was required for validation? I also thik you should include more details about your collection methods here. I am guessing you followed a standard protocol? And had citizens (mountain users) collecting samples in a systematic way too? Provide citations for these methods too.

Lines 6–7: This seems out of place here. Maybe up on page 6 would be a better location? Either starting on line 17 or 19 would be my suggestion.

Line 8: This acronym (LECA-CNRS) needs defining.

Line 11: what/where is “our laboratory”? Is that different from LECA-CNRS? And I would suggest that if you are going to specify how they were analyzed from 2008–2012 (i.e., multi-tube PCR) vs 2013–2016 (i.e., Illumina), you also say how they were analyzed in “our laboratory”. Otherwise, you could simplify and say you analyzed the samples with multiple methods and provide the details for all methods in the supplementary materials.

Lines 12–13: What do you mean 4 repeats? You need to describe these methods. And what kind of genotyping errors are you referring to? How did you calculate genotyping error? You mention further information on genotyping error rate can be found in these references but are these the methods you followed?

The entire section Population abundance estimation using capture-recapture models needs citations and better description. For example there are many more studies using PCRD than Kendall et al. And how specifically did you account for imperfect detection and temporary emigration?

Page 10: Lines 16-18: Another example of where citations should be used (along with, again, all throughout this section). What do you mean you were exploring effects on survival etc? Effects of what? And you need more description of what is meant by “detection structures”.

Okay I see now what you mean you were exploring. I would combine/restructure the first two sentences here to state that you built the 24 models to explore the effects on survival, etc. A table would be really useful here to explain the models and the different “structures”. It is difficult to follow in the text.

And now I found the table—you should mention Table 1 here and again in the results.

Line 24–25: You can delete that allows calling....and just state that you used RMark in R and cite both.

Same lines, I don’t know what this means: “Because we run into boundary estimates issues....” like upper and lower bounds of abundance? Or physical boundaries across countries? I am guessing you mean with the estimates but why did you use both RMark and Bayesian? Why did you not just use Bayesian if you had these problems? You need to explain why you used both—or at least why you decided to report on both.

Page 11

Results: I would suggest following the same flow as you did in the methods. So maybe state how many samples were collected and then point to Table S1. If there were only 2,524 genetic samples and 10,019 validated samples (still don’t know what that means), what was the breakdown of the other samples? This should be in a table somewhere too—a complete breakdown of the samples that were collected by year and type. You also could include by year the number of individuals identified each year. And the range of times individuals were detected—maybe the median and min/max.

Line 16: you should report the estimates ± SE or some confidence interval, not just say "the estimates were around. The estimates are nearly identical and if you report 2 decimal places, they are identical. I don't think the difference in SE in survival of subadults between 0.028 and 0.029 is important! It would make it simpler and correctly reported.

I didn't realize in Table 2 (until I looked at it several times) that 1 column is for model 1 and 1 for model 2. You should label the columns so that is clear.

In your methods, you also don't mention that you are estimating anything except population abundance, but you also were estimating survival. Clarify this in the methods.

Table 2 refers to "class 1 of mixture" but this is never described anywhere else. I assume this is referring to the heterogeneity but the wording needs to be clear as to what you are estimating here.

Page 12:

The entire discussion lacks relevant citations. Typically in the discussion you would discuss your results and compare them to other studies. This is rarely done. And when it is, it is compared to very old studies—there are so many current published studies using this same analysis that would be good for comparison.

Line 2: You reference fig 2 and include MRS in Fig 2 but it has not yet been mentioned. If you are going to include this in your results, it needs to be discussed in the methods. Given you also say you are monitoring the trend, you should mention it in the results. Something like it was a generally increasing trend through time.

Lines 5-10: you can substantially shorten this since you have already said all of this earlier in the manuscript. You could even remove it and jus start with "To assess the effectiveness of the translocation and………"

Pages 12-13: Minimum retained size. This is the first mention of this and seemingly comes out of the blue. You need to include it earlier.

Page 13:

Line 4: this isn't clear—"individuals still alive" are more detectable than what? Dead individuals—of course they are so I am not understanding what you mean here.

Lines 11–12: I don't see how Table S1 clarifies this. The number of samples is not largely different from other years. This provides support perhaps for why you should include the number of samples collected in each year and the number analyzed. And then if there is a big difference (as you say there is in 2017and 2018), you could then mention why that is the case.

Lines 21–23: This is not an accurate conclusion. Random temporary emigration does not impact abundance or survival estimates, only detection probability (see Schwarz and Stobo 1997. Estimating Temporary Migration Using the Robust Design). What about the detection heterogeneity in contributing to this bias? It makes sense if you have, for example, trap happy individuals coming to your baited sites (you never report any of this kind of information which would be useful), or you are detecting your tagged individuals more frequently (which would be unsurprising since you are more likely to have genotyping failure than not detect a radio collar), then your estimates will be negatively biased.

You do address this a bit in the next paragraph but not in the sense of the abundance estimate.

Page 14:

Line 9–10: You talk about 4 individuals with long detection histories, how about reporting in the results the range of length of time of monitoring.

Line 11: what do you mean “big males”? As in adult males? Big is subjective word and should not be used. I also suggest removing reference to specific “named” individuals, i.e., Pyros, Balou, etc. They are not referenced anywhere else and there is no context for “who” these bears are. I also think it is not appropriate for professional scientific publication to include named animals.

Lines 18–20. I agree. SCR would be a much better idea in this analysis—particularly as the population size and distribution grow.

Lines 21–4 on next page: This could be simplified. For cubs, you don’t need to list all of these reasons again (you already did that earlier) but can say that cubs have lower survival. You also should clarify that this is cub survival at older than a few months. You mention these mortality risks aren’t limited to the early months, but you aren’t measuring those first months either since you don’t know actual cub survival (i.e., some die before you even detect them and you don’t know about them).

All of this discussion to detection heterogeneity is 100% relevant to the abundance estimate, so I suggest including it there. What about ease of access for heterogeneity? Particularly for the public collecting data. Locations that are more easily accessible will likely have more people out looking for sign. Some kind of accounting for effort would be reasonable to include in the models.

Page 15:
Lines 10–18: All of this has been said previously (this is the 4th mention of the fivefold increase and the second time in the discussion) so I suggest some rewording. If these are your major conclusions, perhaps they should not also be in the introduction.

Line 17: genetic aleas? Typo? Not sure what this word means.

Line 21: I would suggest sticking to either consanguinity or inbreeding. I assume you are using them interchangeably here but this is the first mention of inbreeding.

Page 16:
Line 6–7: I would suggest that you do not account enough for detection heterogeneity in this study—and you even say that several times. So I am surprised this is your final paragraph and conclusion. I am also surprised that you recommend using the PCRD method (as opposed to SCR) as one of your main conclusions—particularly since you say SCR would be a good method to use in an above paragraph.

Supplementary materials:
Line 65: Did you have a freshness scale? And how did you use the freshness information—like did you subsample by freshness? Or not use samples determined to be not fresh?

Line 76–77: Another introduction of heterogeneity. These cubs in captivity are 100% detectable—unlike other bears. Why include these and not the relocation data from radiocollared bears? It is the same thing so justifying its use for cubs but not for radiocollared individuals does not make sense.

Table S1: Was the number of samples analyzed different than the number collected?

Table S2: This table isn't really necessary. It doesn't add anything and isn't necessary information for this manuscript and you could simply report the PIDsibs in the text.

Table S3 is never referenced in the text so I am not sure why it is included.

Download the review

Reviewed by **Romain Pigeault**, 09 March 2022

Dear Recommender,

The manuscript entitled "**Estimating abundance of a recovering transboundary brown bear population with capture-recapture models**" submitted by Cécile Vanpé et al to PCI Ecology aimed to applied Pollock's robust design capture recapture models to estimate the abundance of the Pyrenean brown bear population and its trends over time. The subject of this article falls perfectly within the scope of PCI Ecology and is timely and very interesting. I really enjoyed reading this manuscript which is well written as well as very well structured. I do, however, have some comments and suggestions that I hope will help the authors bring some clarity to the manuscript. Indeed, the dataset as well as the analyses run by the authors are quite complex and some clarification seems to me necessary.

Main comments:

A) Abundance estimates in this study are in the majority of cases lower than "naïve" (MDS) and corrected counts (MRS, 10/13), which is not what we expect since the Bayesian Pollock's robust design capture-recapture approach should correct for detection imperfections and individual heterogeneity. Authors report that the differences observed between PCRD and MDS/MRS are explained by the fact that the PCRD framework includes temporary emigration, that samples that are difficult to date have been eliminated and that mortality is not managed in the same way in the different analyses, but how to explain the accentuation of the differences at the end of the study period (2017/2018 and 2019)? To what extent does the lack of funding to conduct genetic analysis in 2017 and 2018 impact the results?

B) In view of the significant differences observed between PCRD and MDS/MRS, it would be appropriate to mention in the conclusion that at present MSR remains the most accurate method to estimate bear abundance. But given that the bear population in the Pyrenees is constantly increasing, the development of new monitoring methods is timely because it gives the possibility to compare the results obtained with the modeling approach with the more robust results obtained with the "naive" counts.

C) Some information concerning the non-invasive methods used to monitor the brown bear population is missing:

- Would it be possible to add on Figure 1 the location of the camera traps and the baited hair traps?
- Is the data collection effort uniformly distributed throughout the bear area range (e.g., walking transects, camera traps)? It seems at first sight that the data collection effort is more important in France, could this lead to an underestimation of the size of the bear population?
- The data collection effort has fluctuated a lot over the years. The number of camera traps has increased almost tenfold, and the SBHT has only been conducted over four years. In addition, there were years when not all samples could be analyzed due to lack of funding. Should such large variations in data collection effort not be accounted for in the analyses? For example, it is possible to compartmentalize the analysis into several sub-blocks and then test whether a model containing this compartmentalization obtains a better AICc.
- Why the division of the study area, the installation of camera traps and baited hair traps (grid cell size, SBHT, SCT) are based only on the female range area and not on the male range area?

D) Analyses:

The analyses proposed in this study seems to me relevant and the github associated with this article is very useful to understand what was done. However, I have some questions/suggestions:

- It would have been interesting to add an additive time effect to study the yearly variation in survival rate.

- Wouldn't it be relevant to study the effect of the sex of the bears on all the parameters tested (survival rate, emigration, detection)? Moreover, there is no information in the manuscript about the sex ratio in the bear population. Is it stable over time? Is the important increase in the number of individuals from 2018 not explained by a sex-ratio biased towards adult females?
- I am not familiar with PCRD models, but I'm wondering if there are goodness-of-fit tests for PCRD?
- Regarding the estimation of annual population abundance, authors used a Bayesian approach but there is no information in the main text. There is no information on the type of prior used, nor on how authors diagnose the fit of the bayesian model. It would be relevant to describe the analysis a little bit more (e.g., n.iter, n.burnin, thinned).

Minor comments

- Page 4, line 13: Add some additional information about the PCRD models.
- Suggestion: I am wondering if the paragraph on page 12 (lines 18-25) and page 13 (lines 1-17) would not be more appropriate in the introduction. This paragraph is very important and sets the framework for the study. It alone justifies the importance of developing a new estimation method.
- Page 6, line 8: What is the average home range of males and females?
- Page 8, line 15: What does "during the same period" mean? 2008 to 2020 or from May to November?
- Page 9, line 14: Why several sex markers were used?
- Page 10, line 19: Could you please define "finite mixtures"
- Page 11, line 17: Do you have any information on individuals with a low detection probability? Is there an effect of sex? of age?
- Page 13, line 2-4: I don't understand this argument. Why is the increased likelihood of detection of specific types of individuals a bias in the estimation of the MRS?
- Page 13, lines 10-11: Don't the funding restrictions also directly impact the PCRD models?
- Page 15, lines 14-18: Is it possible to used PCRD models to make some predictions about abundance evolution in the coming years?
- Page 29, is it possible to do paternity analysis with your genetic data?
- Page 30, what is the proportion of samples not used because of a dating problem?

Reviewed by Tim Coulson, 08 March 2022

The preprint "Estimating abundance of a recovering transboundary brown bear population with capture recapture models" by Vaupe et al. describes a statistical modelling exercise of European brown bear sightings, scats, and hair samples from the Pyrenees. More specifically a mix of hair samples and scats used for genetic identification, and camera trap data of recognised individuals, from a mixture of structured and opportunistic encounters with signs of bear activity, are used to construct mark-recapture histories from 2008 to 2020. These are then analysed in R Mark to provide detection and survival estimates. The final model is then used to provide Bayesian estimates of population estimates. The authors conclude that mark-recapture provide useful estimates of a population of a large and elusive carnivore.

The statistical modelling is appropriately conducted, the results make good biological sense, and I only have a few significant suggestions, plus several language and grammar edits included on the marked-up pdf.

Significant suggestions

1. In the abstract, and towards the end of the discussion, the authors conclude that the Pollock method they used provides accurate estimates of bear abundance. I suspect that this is true, but because the truth is not known, it is not possible to state this so strongly. Please tone down these statements to say that even

in cases where sampling effort is large compared to population size, mark-recapture methods can provide estimates of survival and population size, having corrected for imperfect detection, that diverge from the minimum number known to be alive.

2. I would like a bit more information on the analysis of individual photos to identify bears. Was this done visually by bear experts, or was pattern recognition software used? This section is a bit light on detail.

3. A frequentist framework is used for the mark-recapture analysis to estimate survival rates, and a Bayesian approach for population size estimates due to boundary issues encountered when estimating population size in a frequentist manner. I was left wondering: why not conduct all the analysis in a Bayesian framework? I am not requiring this to be done but would like some justification added as to the choice of an initial frequentist approach.

4. At the beginning of the discussion there is some text I have flagged that should be moved into the methods and results. It is about calculation of the MRS estimates. It is not discussion but provides methodological approaches and new results. It could be removed completely given the following point.

5. I found the MRS estimates to be rather unnecessary. They depart from the MDS and PCRD estimates, suggesting the 'correction' used to calculate them from the MDS estimates is adding bias rather than insight. The authors set up a straw man by calculating a new index that differs from the MDS and PCRD estimates that in fact align quite well. Why invent a new index, the MRS index that is only introduced in the discussion as an apparent after thought, and then compare it to established method, discover it is wanting, but then it use to criticise the MRS and the MDS methods. It is all rather unnecessary. The MDS estimates are actually pretty good. Perhaps this lessens the conclusions of the paper with regards to the PCRD and MDS approach, but I would argue you should use the best statistical tools available - i.e. PCRD – unless they significantly complicate analyses. I would recommend removing the MRS estimates, or if they are to be kept, much more strongly justifying their calculation and inclusion.

I hope these comments are useful.
Tim Coulson, February 2022
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