Peer Community In Ecology

Useful clarity on the value of considering temporal variability in detection probability

Benjamin Bolker *based on peer reviews by* ***Dana Karelus*** *and* ***Ben Augustine***

Rahel Sollmann (2023) Mt or not Mt: Temporal variation in detection probability in spatial capture-recapture and occupancy models. bioRxiv, ver. 2, peer-reviewed and recommended by Peer Community in Ecology.
https://doi.org/10.1101/2023.08.08.552394

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As so often quoted, "all models are wrong; more specifically, we always neglect potentially important factors in our models of ecological systems. We may neglect these factors because no-one has built a computational framework to include them; because including them would be computationally infeasible; or because we don't have enough data. When considering whether to include a particular process or form of heterogeneity, the gold standard is to fit models both with and without the component, and then see whether we needed the component in the first place – that is, whether including that component leads to an important difference in our conclusions. However, this approach is both tedious and endless, because there are an infinite number of components that we could consider adding to any given model.

Therefore, thoughtful exercises that evaluate the importance of particular complications under a realistic range of simulations and a representative set of case studies are extremely valuable for the field. While they cannot provide ironclad guarantees, they give researchers a general sense of when they can (probably) safely ignore some factors in their analyses. This paper by Sollmann (2024) shows that for a very wide range of scenarios, temporal and spatiotemporal variability in the probability of detection have little effect on the conclusions of spatial capture-recapture and occupancy models. The author is thoughtful about when such variability *may* be important, e.g. when variation in detection and density is correlated and thus confounded, or when variation is driven by animals' behavioural responses to being captured.

Reference

Sollmann R (2024). Mt or not Mt: Temporal variation in detection probability in spatial capture-recapture and occupancy models. bioRxiv, 2023.08.08.552394, ver. 2 peer-reviewed and recommended by Peer Community in Ecology. https://doi.org/10.1101/2023.08.08.552394

Reviews

Evaluation round #2

Reviewed by Dana Karelus, 09 December 2023

The author has addressed all of my comments well and I have no further comments. Thank you for a well-written and useful paper!

Reviewed by Ben Augustine, 04 December 2023

To be honest, I wasn't thinking about sources to cite when mentioning the relevance of ignoring time effects to the efficiency of fitting Mb. I've traced my knowledge of this back to a comment by Dan Linden in the SCR Google Group associated with Andy Royle and the workshops he has hosted over the years in conjunction with others. This comment was from 2017 and Dan can't provide a citation either (I followed up with him). I think this is a good point to make in this paper and it could really help people out, but I'm not sure how best to handle the citation. One idea is to contact Dan and then provide a personal communication citation. Or perhaps it's more trouble that it is worth.

Regardless, I look forward to seeing the paper in print.

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2023.08.08.552394
Version of the preprint: 1

Authors' reply, 06 November 2023

Benjamin Bolker

* I saw a couple of typos (l. 201 ”chosen”, l. 273 ”Scenario 1”

Response: I have re-read everything and attempted to weed out all typos.

* on l. 341, you refer to ”ecological inference”. While that's likely to be understood properly by everyone who actually reads this paper, it has a different meaning in econometrics (i.e., inference based on observational data rather than experimentally randomized outcomes) - you might want to change this to ”inference for ecological parameters” or something like that.

Response: Thank you, I deleted 'ecological' (line 361).

* in Figure 1, if I understood it correctly, what's actually on the y-axis (and hence should be the y-axis label) is relative _error_, not relative bias; relative bias would be represented by the position of the median in the

boxplots (i.e., bias is the median of the relative error across simulations, whereas this figure shows the full distribution of the errors)

Response: This is correct; I changed the terminology to 'error' in the captions of both Figures 1 and 2 and also fixed the y axis labels in both figures.

* you make a point of the computational difficulty of SCR (especially with the current widely used methods implemented in BUGS), and the problems that will cause with the rapid expansion/scaling of the size of data sets that people want to apply SCR to. Are there methods under development/on the horizon (based e.g. on Stan or NIMBLE) that will allow computation to scale better as well? If so, it might be worth mentioning.

Response: Yes, there have been considerable improvements in efficiency in Nimble that make it possible to fit models one could not fit (or at least not in a reasonable timeframe) in JAGS. I have added some text to that effect in the Discussion (lines 450ff). SCR models have also been implemented in Stan (https://discourse.mc-stan.org/t/spatial-capture-recapture-in-stan/14721), but I am not aware of any studies investigating the gains in efficiency, or of developments that specifically target SCR models, the way recent Nimble developments have. I therefore did not add a reference to Stan to the Discussion.

* note one reviewer's comment about a missing file in the Zenodo code - additionally, it would be convenient to tell readers more specifically how to get the 'scrbook' package with the data (i.e., going to https://sites.google.com/site/spatialcapturerecapture/scrbook-r-package or running 'remotes::install_github("jaroyle/scrbook/Rpackage/scrbook")' in R). If you have permission/licensing is OK, it may even be worth making a copy of the data that you are using, in order to make the repository more self-contained/future-proof.

Response: I apologize – I added the missing file to the repository and am including a link and doi for the new release of the repository. Following one of the reviewers' comments, I replaced the bear case study with a new one (see response below for details). I have updated the repository and scripts accordingly.

* it might be worth adding an explicit license to your Zenodo materials (Creative Commons or some open-source code license such as GPL) to make it easier for others to re-use your material.

Response: Unless I am misunderstanding the information on the Zenodo repository, it already has a Creative Commons license.

In addition, please note that in looking for a reference on different ways of handling effort in SCR models, I came across a 2013 paper by Efford et al. that performed a very limited test of ignoring temporally varying effort (and thus, detection probability) in SCR models. They found that it did not matter for density estimates, but only explored a single scenario and did not link this to temporal variation in detection more broadly. I added the findings of this paper to the Introduction (l 92ff) and Discussion (l 380f).

Reviewer 1

In this paper, the author investigates the effect of ignoring temporal variation in detection across sampling occasions in single-season occupancy models and closed spatial capture-recapture models. They tested this with both simulated data and real-world data and found that in most cases, for these models, temporal variation in detection can be safely ignored. While some studies/data sets following a single-season/closed study design may be simple enough that testing temporal variation in detection is easy and does not add significant computing time, there are other cases where the added time may be prohibitive. Additionally, this could be useful for sparse datasets that may not converge with the additional complexity of including temporal variation (and can therefore chose to test potentially more important/impactful covariates instead without as much worry).

I think this paper would benefit many people, even if they chose to include a temporal covariate on detection, because it provides readers with a better overall understanding of how the models behave and can alleviate concerns when the temporal covariate on detection cannot easily/readily be included in the models. The paper was very well written, the title is good, the figures are clear, the statistical methods are appropriate, and the scenarios tested are consistent with the questions, the conclusions are supported by the results, and

interpretations of the analysis are appropriate, etc. I only have a few questions and comments that I think will help improve the paper for readers (especially students who might be new to the topics) and I believe to help ensure the results of this paper are not accidentally misconstrued.

Response: Thank you for your very positive feedback and your constructive suggestions below.

1. Generally, in the abstract and maybe the introduction (and a few things here apply to the discussion as well): I think it would be beneficial to include just a little more emphasis on the cases tested here/when this can be applied and also some more detail regarding when someone might not want to skip testing for temporal variation. (I very much appreciated the last paragraph of the discussion where the author discusses all of this!)

Response: I added a sentence to the Abstract highlighting cases when we cannot or may not want to ignore temporal variation in detection (l 42ff); and qualifying that in occupancy models, extreme temporal variation may lead to biased parameters if not modeled (l36ff).

A) What about the impact of lure/bait causing detection to decrease over time? I imagine the scenarios you tested with the simulated data may vary widely enough to account for it, but I think it would be beneficial to point out this case [in addition to the others you mention] as it is so commonly used and has [assumed to have been] the cause of a decline in detection throughout sampling occasions.

Response: I added that application of lure/bait to all detectors at the beginning of a study could also lead to a situation that is reflected in scenario 1 (l 134ff).

B) Line 127 and again in lines 459-464: I think what you're getting at is the case where detectors across the study site cannot be set out at the same time (usually when the study covers a very large area, e.g., might be moving camera traps from one place to another every few weeks)? However, I'm not 100% sure and I think these two areas of the paper could be improved to make it more clear what you mean. Maybe give an example like the camera scenario I mentioned so readers don't get so confused?

If I am incorrect and you mean something different, then in addition to providing more clarity on those aspects, please also address this case I mentioned (large study area and having to move detectors/transects around the landscape because they cannot all be done at the same time, but treating it as a single-season because there are not repeat surveys at locations).

Response: I clarified that varying effort can arise when surveys cannot be fully standardized, for example because they are volunteer-run or because detectors malfunction or are set up and removed in a staggered fashion (l 141ff). The case where detectors such as camera traps are moved around to different locations is a special case of time-varying effort, but I would not suggest using effort as a covariate in these circumstances. Rather, on days when a certain detector location is not sampled at all, detection probability at that detector and that day should be set to 0. That is easily done in unmarked and secr. Because this is different from including effort as a covariate, I did not refer to this scenario in the manuscript. I did, however, add that when sampling locations are sampled at different times due to logistic constraints, then that can lead to differences in sampling conditions and therefore, spatio-temporal variation in detection.

I am not sure what the reviewer is referring to with respect to lines 459-464 (lines 490ff in revised ms). In these lines I clarify that I am only looking at variation in detection within a primary occasion. I don't see the connection to the issue of spatio-temporally varying detection covariates or sampling effort. I'll be happy to address this comment if the reviewer can clarify what is unclear about these lines.

C) Related to line 464 that "in maybe cases where detection is a mere nuisance variable and behavioral responses to capture/detection are unlikely (as is often the case with non-invasive survey methods)…":

C1. Once again, I think pointing out the potential effect of lure/bait might be worthwhile because even though there might not be a behavioral response to being "detected", there is/could be a behavioral change in response to bait/lure becoming less novel and/or less aromatic over time and thus causing a change in detection. I don't mean to pick, I just think it is useful for readers to keep that case in mind and would be useful for you to add that idea to your discussion.

Response: I disagree that the response to lure described by the reviewer is akin to a behavioral response to

detection. Lure wearing off can definitely induce a change in detection probability over time (and that is now stated in l 134ff). But this applies to all individuals in the population, whether they have been captured before or not. Therefore, lure becoming less aromatic/strong over time does not cause the individual variation in detection that is caused by trap response (and that is problematic when ignored). It is conceivable that an individual's detection history also affects its response to lure – maybe trapping is so traumatic that captured individuals avoid lure after first capture, associating the smell with an unpleasant experience. But (a) I have never seen any mention of such capture-dependent response to bait, and (b) that is a very specific topic that only applies to a small subset of survey methods that can be used for SCR and occupancy surveys. Given the breadth of possible survey methods and of factors that may affect detection probability, I did not think it necessary to discuss the specific case of bait/lure here again.

C2. While as you state, usually the parameters of main interest are occupancy/density etc. and I think it is fair to say that detection is often a nuisance (a common statement), I feel that it might also be useful to point out briefly that variation in detection can be useful to explore to help guide future study design and such. For example, in scenarios where a researcher is trying to design a study where there is concern about potential low detection and/or when to sample, reports from past studies that tested for a temporal effect could help (might help a researcher decide what time frame to target for their study, might indicate that they need to think about replacing bait/lure more frequently, etc.). Of course, I do recognize this is slightly outside the point of your paper, but I think results regarding detection are more useful than a lot of people may give credit for, even if the main parameter of interest is unaffected by ignoring potential temporal effects on detection. I think just maybe a quick parenthetical reference to this idea could be useful, especially thinking of those new to these types of studies/analyses and who may be quick to use your paper to ignore temporal variation on detection without putting more thought into it. If you feel I am out of line in this request and chose to ignore, I understand. (side note, all this being said, it's reassuring to know that ignoring temporal variation in detection might not be a problem for density/occupancy estimates, so thank you!)

Response: This is a great suggestion; I added a statement (with reference) about how knowledge about detectability can inform future study design in lines 488ff.

D) Lines 379-380: I think so as to not minimize the point, remove the parenthesis from middle part of the sentence (and then maybe have to rearrange the structure of the sentence as needed) and perhaps (parenthetically if necessary), point the reader to the last paragraph where you explain when it might matter.

Response: Changed statement as suggested (l 400ff).

2. Second larger scale comment/question: Why did you choose the bear dataset as the case study for SCR when the aspect of temporal variation in detection was already explored in the past? I'm guessing this was probably because Royle et al. used a Bayesian analysis in WinBUGS and instead you were using secr? I think this example is useful, but you should make it more clear why you chose to use this example when it seems you would already know the outcome.

Response: I chose this dataset because it is freely accessible and there is ecological reason to believe that detectability of bears would change over time. But in hindsight I agree with the reviewer that it looks odd to choose this dataset given that I already knew ignoring temporal variation in detection would not affect density estimates. I therefore did some more digging through the SCR literature and found an alternative dataset for which parameter estimates with and without time-varying detection in the model structure had not been compared previously. I have switched the case study text in the manuscript (l 237ff) and R code in the repository.

3. Lastly for the paper itself, I wonder if maybe a small table of the scenarios that you tested would be helpful for readers to keep track as they read. Though perhaps it's unnecessary, so this is just a suggestion that you can ignore if you disagree.

Response: Thank you for this suggestion; I added an overview table over the scenarios (new Table 1).

Regarding the code: the two case study codes look good overall and I got the same results as in the

paper when I ran them. But in the two simulation R scripts, you reference the file, source('Occupancy/Helper functions.txt') or source('Helper functions.txt') and that file is not in the zip file with the others nor is there any direction that I see on where to get it. The code gets stuck on the function spcov2. Please fix this!

Response: I sincerely apologize for this oversight. I have added the missing code to the repository; the new link/doi should lead directly to the updated release of the github repository with all code and an updated README file.

Reviewer 2 (Ben Augustine)

This manuscript investigates the impact of ignoring temporal varaibility in detection in spatial capture-recapture (SCR) and occupancy model on parameter estimates of ecological interest. Over the range of scenarios considered, it is shown that temporal variation can be safely ignored, except possibly in some more extreme cases for occupancy models. This investigation should be of wide interest to ecologists for many reasons, but particularly for the reason described in the manuscript–we can fit more complex models to larger data sets if we can remove the temporal dimension from the data structure.

A potential concern is that these results from a limited number of scenarios are extrapolated to scenarios where they may not hold; however, I believe appropriate warnings are made throughout the manuscript. Generally, I have no major comments or concerns–the manuscript looks solid to me. I will, though, point out that I may have somewhat of a conflict of interest since I have been ignoring the temporal dimension in complex SCR models quite often and so these results support my past decisions.

Response: Thank you for your very positive feedback!

One minor comment that could easily go unaddressed with regard to this statement:

"The first is by necessity: Some SCR observation models cannot be reduced to two-dimensional data, for example, the multinomial model in which an animal can only be detected in a single trap in a given occasions (Royle et al., 2014). Also in SCR models we may have to account for a behavioral response to being captured (or otherwise detected). Such a behavioral response effectively creates individual heterogeneity in detection over time, and ignoring such heterogeneity will bias estimates of density (e.g., Royle et al., 2014)"

It is true that the data cannot be reduced to 2 dimensions when using Mb. But you can reduce it to 2 2-D detection histories, one for first capture and another for subsequent capture. If you have a lot of occasions, this can provide a huge efficiency gain. But this is not the main focus of the manuscript, so I don't think it needs to be pointed out.

Response: This is brilliant! If the reviewer had provided a source that had taken this route to make computation faster (or if he's willing to provide that source in the next round of comments), I would be happy to include it as an observation.

Decision by Benjamin Bolker, posted 16 October 2023, validated 16 October 2023

minor revisions suggested

Both reviewers liked the paper, thought it was clear and useful, and had only minor suggestions for improvement; I did too. However, I do think that going through and making these revisions will strengthen the paper, so I am not recommending it yet.

A few comments of my own:

* I saw a couple of typos (l. 201 "chosen", l. 273 "Scenario 1"

* on l. 341, you refer to "ecological inference". While that's likely to be understood properly by everyone who actually reads this paper, it has a different meaning in econometrics (i.e., inference based on observational data rather than experimentally randomized outcomes) - you might want to change this to "inference for ecological parameters" or something like that.

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* it might be worth adding an explicit license to your Zenodo materials (Creative Commons or some open-source code license such as GPL) to make it easier for others to re-use your material.

Reviewed by Dana Karelus, 12 September 2023

In this paper, the author investigates the effect of ignoring temporal variation in detection across sampling occasions in single-season occupancy models and closed spatial capture-recapture models. They tested this with both simulated data and real-world data and found that in most cases, for these models, temporal variation in detection can be safely ignored. While some studies/data sets following a single-season/closed study design may be simple enough that testing temporal variation in detection is easy and does not add significant computing time, there are other cases where the added time may be prohibitive. Additionally, this could be useful for sparse datasets that may not converge with the additional complexity of including temporal variation (and can therefore chose to test potentially more important/impactful covariates instead without as much worry).

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1. Generally, in the abstract and maybe the introduction (and a few things here apply to the discussion as well): I think it would be beneficial to include just a little more emphasis on the cases tested here/when this can be applied and also some more detail regarding when someone might not want to skip testing for temporal variation. (I very much appreciated the last paragraph of the discussion where the author discusses all of this!)

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Overall, again thank you for a very interesting, useful, and well written paper!

Reviewed by **Ben Augustine**, 06 October 2023

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