Improved state-space models for inference about spatial and temporal variation in abundance from count data: Response to revision comments

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Reviewer 1 (Comments to Author):

General Comments

In this paper, the authors propose to extend the Dail and Madsen (2011) model to include classical models of population growth. They also propose extensions to deal with zero-inflated data, immigration and variation in observation errors.

This work is novel and important because it proposes to estimate population growth characteristics by accounting for imperfect detection of individuals. Otherwise, actually, population growth models are embedded in state-based models that assume normally distributed errors, as a consequence probability of detection cannot be estimated. Besides, in some models of population growth, the errors of observations are not taken into account. The authors check for the reliability of their model to recover their parameters by using a simulation study. The simulation study covers a large range of different population dynamics as well as additional cases where the simulated data deviates from the assumption of the model used for the analysis. In addition, to the simulation study, the models are applied to real data.

Thank you for your positive comments!

In a general way, effort should be put on tightening the text and better focus on the main goal of the paper, that is about including models of population growth in a framework that account for imperfect detection of individuals. The choice of the model of population growth might be subjective and/or motivated by the knowledge of the life history of the species under study. Even thought, some studies, proposed some procedures based on model selection to discriminate among the different models of population growth. Hence, the Ms would benefit of a better description of the underlying ecological assumptions of the different models of population growth. For example, the exponential model describes population growth in an unlimited environment, where r is the maximum per capita of increase, etc . In Ricker model, the density-dependence becomes stronger at higher densities, due to the exponential function relating to carrying capacity. The Gompertz model is similar to the Ricker model except that there is a constant linear decrease in the instantaneous growth rate (r) as the natural logarithm of population increase, etc..

[We have described the classical population growth models in more detail (lines).]

Specific Comments

I am unclear about the title of the manuscript because it does not reflect the real aim of the paper, which is well stated by the authors, lines 417-418: "one of the primary aims of our paper was to demonstrate how classical population growth models can be embedded in the DM model".

I find that basing the introduction upon the notion of state-based model is rather confusing

regarding the real goal of the paper (see above). The Dail and Madsen model and state-space models are defined in two different "statistical worlds". On the one hand, the constant Dail and Madsen model (2011) has a Markov property so the variables can only take on a finite set of discrete values for a finite period of observation. The distinguish feature of Markov chains is that the conditional probability of x_t given the entire past depends only on the immediately preceding variable x_{t-1}. In addition, the errors of observation are well identified because they are related to imperfect detection of individuals and expressed with a discrete probability distribution. On the other hand, the state-space model framework provides a structure for extending time-series models to handle both observation and process errors. The term "state-space" model refers to models where the process model has an autoregressive property and where the errors have a Gaussian distribution. Autoregressive model are defined for continuous variable, and so the errors are normally distributed. A space-state model, being given its properties, can be estimated by using a Kalman filter. The Kalman filter is an updating procedure whereby the prior estimate of the state is corrected by how well the next observation can be predicted. Even if the Dail and Madsen model also provides a structure to account for time dependence as well as for "process errors" through the birth and death process and for imperfect detection, the Dail and Madsen model and state-space models are defined in two different "statistical worlds". Hence, the analytical results of the Dail and Madsen model and a state-space model would be different. That is why, in my point view, it is unclear and misleading to relate the Dail and Madsen model to a state-space model.

[Richard, can you address these three paragraphs?]

Lines 118 - 174: the description of the model could be shortened (or moved in part in the

appendices) because it has been described now in further publications.

[Richard, any thoughts on this? I can see the reviewer's point - there are a lot of DM papers out now. And this is almost 3 pages. But I like what we've got here, and if we cut or move it we'd have to be careful, because we refer to this section a good deal in our extensions. How we shorten it may depend on how we respond to the DM model as state-space model critique. Please take a stab at this if you have time and ideas on how to shorten or move.]

Line 165: *"propagule rain"* is not an appropriate term here; this term is used in Mainland/Island model to describe something like a continuous source of migrants which can colonise an empty site. A large stable mainland population provides migrants, which is not the case in Dail and Madsen model. Consistency with the original terminology defined in Dail and Madsen (2011) should be kept as much as possible.

We have made the suggested change.

Line 165: *"autoregressive"* model should be kept in quote as it is p. 580 of Dail and Madsen (2011).

We have made this change.

Line 135: typography error in *"The third process describes the relationships between"* should be *"The third process describes the relationships between."*

We have fixed the typographic error (surplus "the") here.

Line 190: More explanations on the Gompertz model should be added here, especially on the link between the Ricker model and the Gompertz model. The original reference of the

Gompertz logistic growth equation should be added here.

[We have described the Gompertz model in more detail (lines).]

Line 199: I am unclear about the meaning of *"internal and external (immigration) contributions to population growth."* Then, the authors proposed to account for immigration but they do not mention anything about emigration. In the Dail and Madsen model, the survival rate is a reduced demographic parameter that accounts for both death and emigration. Some words, in the discussion, about how emigration is (or not) handled in this novel extension would be welcome.

We have edited the text for clarity (lines). We have added discussion about emigration (lines).

Line 225: I am unclear about *"semelparous organisms with one generation per sampling interval (year)."* Semelparous refers to organisms that died after reproduction, (i.e. they can have solely one single reproduction event in their life because they die after this reproduction event). So, semelparous organisms cannot have "one generation per sampling interval" but only one generation.

Lines 225 - 229 This paragraph needs to be clarified semelparous organisms cannot have more than one generation per year because they can have only one single reproduction event in their life (see above).

We were referring to generations of the population or species, not the individual. We have edited this paragraph for clarity.

Lines 281 - 296: The paragraph about the simulation of the data needs to be clarified to

understand better how the data are simulated. Some references to the different equations of the model should help to clarify this section. For the simulation study, the time series which are simulated are rather long (40 years) and also the length of the time series of the application are about 40 years. If the time series were shorter, how the estimation of the parameters would be affected.

We have added clarification and equation references to this paragraph. We expect that the models would not perform as well with far fewer years of data, and have commented on this in the discussion (lines).

Discussion: The text of the discussion needs to be reduced and tightened. The authors should better focus on discussing the results of this study and relate them to other studies on models of population growth.

[Richard, I commented out the two paragraphs on IPMs. What do you think?]

The figure A1 and A2 describe results of the simulation based on the Ricker and Gompertz models, and both are much more "realistic" than the model of exponential growth when applied to population ecology. So, the Fig. A1 and A2 represent core results of the manuscript and should be rather presented in the main text than in appendices.

[Between this comment and the one by the other reviewer, sounds like we should put all three of these figures in the main text. If we still have to keep it to 30 pages, that requires a page and a half of additional cutting, which is a lot. This reviewer suggests cutting text from DM model description and discussion. I have worked on those (see above), but maybe we should also consider emailing Evan Cooch about the length limit.]

Reviewer 2 (Comments to Author):

General Comments

The authors build on hierarchical state-space models that describe population dynamics proposed by Dail and Madsen (2011). The paper is clear, well-written, and provides important advances and tests of the original DM formulation and extensions. The authors cover a lot of ground, but to me, the principal novel contribution of the paper is the embedding of classical population-growth and density-dependence functions into the population dynamics model, rather than relying on the original DM formulation that models population change as a function of demographic (survival and recruitment) parameters. The authors also propose a sort of hybrid set of models that combine a functional form for population growth with a parameter representing immigration from outside of the indexed spatial location. The paper also introduces negative binomial and zero-inflated versions of the state model as well as models that include demographic or environmental stochasticity. An important extension that the authors propose that would greatly enhance the practical utility of these models in ecological applications is the modeling of dynamics parameters as functions of site-time specific environmental covariates or random effects. The authors state that code will be provided for implementing models with maximum likelihood and Bayesian McMC methods using freely available software packages, which should facilitate the use of these models in the future. Overall, the paper advances the state of the art of this class of models in many directions, and the authors do a good job in highlighting both the potential and limitations of the various model flavors.

Thank you for your positive comments!

Specific comments

Model Extensions: Immigration models The immigration models are an interesting idea, combining classical growth and density-dependence functions or the mechanistic geometric growth functions with an additional parameter that represents immigration. As the authors note, an important limitation of several proposed models without the immigration parameter (including Dail and Madsen's geometric growth model) is that they do not accommodate recovery following extinction, so the introduction of the immigration parameter would seem a critical component in those models in cases where local extinction is likely. I must admit, however, that I don't completely understand how the parameters of these models are informed. For example, in the exponential, Ricker, and Gompertz models, the r parameter includes a mixture of local apparent survival (i.e., site fidelity + true survival) + local recruitment (through birth processes) dynamics, while the iota parameter supposedly reflects immigration from outside the site. How is there information to separate recruitment components of r from immigration components of iota? Similarly, how are both gamma and iota identifiable in the geometric growth model? I suppose that somehow because the iota parameter does not depend on the any of the other population parameters, it can be estimated separately. But this is not entirely clear to me. Maybe a sentence or 2 could clarify this a bit?

We believe the reviewer has hit upon it - the population contribution from immigration does not depend on current abundance, whereas the contributions from r in the density-dependent models and from γ in the geometric-recruitment model do (in different ways). With sufficient temporal and spatial replication, these parameters are separately estimable. We have added text to that effect (lines).

Line 347-348: As re: memory requirements, why not do multiple single-chain runs (to yield multiple chains)?

We now have multiple chains for this model as well, and the convergence is good with very similar results.

Results: Why present the graphical display of simulation results for the exponential models in the main text (Fig 1), but relegate all of the tables and graphical summaries for other models to Appendix A? I would prefer to see all of the summary tables (first choice) or all of the figures (but not both) in the main text.

[Between this comment and the one by the other reviewer, sounds like we should put all three of these figures in the main text.]

Fig. 1: for initial abundance on x-axis, replace little lambda with big lambda to match text.

[Richard, can you do this, and also increase the resolution of this figure? I don't have the simulation results from the exponential model. Alternatively, you could send me the results and I can replot it (I think I have your plotting code). It looks like you used a file called process.RData to store the results.]

Fig. 2 legend, in parentheses could replace "mean and" with +/-, given that it is already stated that the panel shows the mean.

We have made the suggested change.

Line 358: replace 'inaccurate' with 'imprecise'.

These terms have multiple meanings and are defined differently in different places. We like the definition of Williams et al. (2002): "Accuracy combines both bias and precision in an assessment of estimator performance." On the same page (45) those authors describe mean squared error (MSE) as a measure of estimator accuracy. Therefore root mean squared error (RMSE) and relative RMSE are best described as measures of accuracy as well. In another case (line ?) we used the word "imprecise" when the RMSE was high, but only after we established that bias was low. In this case, since bias is high, we feel it is more correct to describe the estimates as "inaccurate."

Lines 424-429: Could difficulty in estimating vital rates derives from having survival and recruitment parameters taking similar values? For example many small songbirds have apparent survival rates of ∼ .5; for a stable population, recruitment would be similar, which in lieu of direct information on vital rates, might make the 2 parameters difficult to separate. In the American Robin example in Dail and Madsen (2011), survival and recruitment were estimated at reasonable values of .7 and .5 (although precision was still fairly low). Could low detection probability have something to do with this problem? From the p estimates in Fig. B1, detection probabilities were < .2 (which seems low to me given that ovenbirds are loud and sing a lot, although I suppose it has to do with large sample radius). In the simulations in the Dail-Madsen paper, lowest coverage for gamma and omega was found at lowest p values (p = .25). I realize I'm stretching a bit here, but it was a little unsatisfying to me that the vital rates parameters could not be estimated, and the reason for why this was so wasn't too clear. The authors suggest individual heterogeneity might be an issue and suggest incorporating prior information or data via integrated population models to improve vital rate estimation. However, I wonder if some additional conjecture might be added here?

[Unsatisfying to us too! I can work on this. Richard, I seem to remember that you had done some simulations on why p estimates are so low from BBS data (and it was exactly because of large radius). Did you publish those results somewhere we can cite? If not, maybe we should not address that point here. The additional speculations the reviewer provides seem possible, although in our robustness testing we tried DM simulations with $\omega = \gamma = 0.5$ and $p = 0.25$, and though the DM estimator didn't do perfect, they weren't nearly as bad as the real data. Maybe they would have been with a lower simulated p, but it seems more likely to me that the real data somehow came from a different process than the DM model assumes.]

References

Dail, D. and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67:577–87.

Williams, B. K., J. D. Nichols, and M. J. Conroy, 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, New York, New York.