Re: Estimating species occupancy across multiple sampling seasons with temporal autologistic occupancy models via the autoOcc R package.  Fidino, Mason.  
  
Thank you for submitting your manuscript to Journal of Animal Ecology.  
  
I have now received reviewers' reports and the Associate Editor's comments on your manuscript and looked at it myself. As you can see, both reviewers and our AE found the manuscript to be well-written, clear, and to provide valuable guidance on using the autoocc R package, supported by practical simulations and application examples that enhance accessibility for users. However, several aspects require major attention. At the moment, the framing lacks clarity regarding the model’s position within the broader literature, particularly by using the term “temporal autologistic” instead of the more standard “first-order Markov” or acknowledging its equivalence to a constrained form of the MacKenzie et al. (2003) dynamic occupancy model. The authors should better articulate this connection, clarify assumptions about model structure (e.g., covariate effects on colonization vs. extinction), and improve the manuscript’s practical utility by including comparative schematics, clearer terminology, and additional context on limitations and flexibility of the approach.  
  
  
Associate Editor  
Associate Editor Comments for Authors:  
This manuscript has been reviewed by two experts who had differing assessments. Reviewer 1 had a largely positive assessment of this manuscript, whereas reviewer 2 questioned the novelty and technical framing of the model. Both reviewers made important points that would need to be satisfactorily addressed prior to publication.  
  
REFEREES'COMMENTS TO AUTHORS  
  
(nb. If there is no comment from a Reviewer listed below, this probably means that they have uploaded a separate 'file for author' to the ScholarOne Manuscripts Site. You can see these comments in your Author's Centre by clicking ‘manuscripts with decisions’ and then using the 'files attached' link at the bottom of the decision letter)  
  
Reviewer: 1  
  
CONFIDENTIAL COMMENTS TO AUTHORS  
This is a Research Methods Guide for running autologistic occupancy models with the R package ‘autoocc’. I found the manuscript to be very clear, well written, with an interesting choice of two different application examples as well as a useful simulation. I am strongly in support of the publication of this manuscript and only provide minimal line comments.

**Thanks for the kind words.**   
  
Line comments:  
  
38. I know that McKann et al. 2012 is already published, but this requirement (120 sites) doesn’t make sense, as the power of a dynamic occupancy model also depends on the number of seasons, the number of visits per season, the average probability of detectability, etc. If you have many seasons (e.g., 40) and moderate detectability and no temporal trend in colonization, you certainly need many fewer than 120 sites for adequate power.

**The reviewer has a valid point here, and stating some set sample size that would ‘work’ for all dynamic occupancy models likely does not make the most sense given that the number of sites is only one part of the sample size. We have moved the McKann reference and dropped the 120 site acknowledgement. This specific part of the first paragraph now reads:**

**“Dynamic occupancy models are unfortunately also data hungry (Briscoe et al. 2021, Mckann et al. 2012), which can limit how useful they are to study rare species or apply them in regions where data are limited. Consequently, there is a need for an accessible tool that effectively quantifies species distributions through time, especially with reduced sample sizes.”**

52. I don’t believe that it \*is\* guaranteed that temporal dependence is “absorbed by site-level random effect”? The random effect will treat all annual draws of occurrence as random and uncorrelated, essentially a non-Markovian process. Where does obvious Markovian temporal dependence go? It could be partly absorbed by the random effect, it could just remain in error, or it could (unfortunately) be mistakenly applied to other fit parameters. Imagine if you put in a seasonally-varying covariate, that covariate might become over-fit or biased due to remnant temporal dependence in the data. My view is that the mistaken assumption of stacked models that there is no temporal dependence is partly why no one should use them.

**We have revised this paragraph to add the nuance the reviewer brings up here, which helps make this point much stronger. Thank you for the suggestion. This part here now reads:**

**“This model does not account for temporal dependence in occupancy between seasons and instead assumes that site-level occurrence per season is random and uncorrelated. Any temporal dependence in the data—which is likely present—would therefore be absorbed by some combination of the random effect term, the residual variance of the model, or regression coefficients associated with covariates that vary through time, if included. As there is no way to know where the temporal dependence is absorbed, using a “stacked” design could bias covariate effect estimates and hinder model interpretation.”**

90. Would it be possible to add in a schematic table that shows a single multi-season sampling scheme with the different models (dynamic, stacked, autologistic) and what parameters they inform?

**We think that the revised modeling section that begins with a dynamic occupancy model more clearly shows the relationship between the dynamic occupancy model and the autologistic occupancy model. We have not explained the stacked occupancy model any further as it is not a model we would suggest people use. As such, we have decided not to create a schematic table here.**  
  
133. Andy Royle and others, I think, have referred to this phenomenon (Theta having no effect when z[t-1]=0) as the autologistic model providing persistence correlation but not colonization correlation. In other words, a high theta can keep occupancy at {1, 1, 1, 1, …}, but it has no effect on a no-occupancy site such as {0, 0, 0, 0, …}. Mathematically, it’s why the autologistic parameterization has been referred to as a ‘half-dynamic’ model, I believe.

**You have hit the nail on the head. The second reviewer provided an incredibly helpful description of the relationship between the dynamic model and the autologistic model, and we hope that by more fully describing the model and it’s history, people will be able to understand more fully what the autologistic model does and what theta is used for.**

210. Worth parenthetically mentioning that missing surveys would be just ‘NA’s?

**Great suggestion. This sentence has been changed to:**

**As with the dynamic occupancy model outlined in MacKenzie et al. (2003), the autologistic occupancy model can accommodate covariates via the logit link and handle missing surveys by including NA values in the detection history where data were not collected**  
  
Reviewer: 2  
  
CONFIDENTIAL COMMENTS TO AUTHORS  
While I think there are things to like in this paper, it suffers from some serious flaws in terms of framing and understanding its place in the broader literature, which I detail below:  
The use of the term "temporal autologistic" models is, in my opinion, confusing. I know these authors are not the first ones to use this term, but the perpetuate this term. The term autologistic has been used for a much longer time to refer to situations in which the probability that a patch is occupied is a function of whether neighborhood patches are occupied. Augustin (1996) is the first use of the term in the ecological literature that I am aware of and they referred to modelling of static patterns. Wikle (2003) and Hooten et al. (2007) applied autologistic modelling in a dynamic context, while Bled et al. (2011), and Yackulic et al. (2012) applied it specifically in a dynamic occupancy context using the status of neighbors in time t to model the likelihood of colonization and extinction in time t+1. More recently, the use of the term “temporal autologistic” has been used to describe situations that the broader statistical literature and the narrower occupancy literature often refers to simply as a 1st order Markov model (i.e., a model in which the probability of being in a given state at time t+1 depends on the state at time t)– there is, in my opinion, no need to introduce the temporal autologistic term when a 1st order Markov model is a more generally understood term. Failure to recognize the broader term, in my opinion, has led folks who use the term to not understand that there model is really a special case of the general dynamic occupancy model introduced by MacKenzie et al. (2003) – which is the bigger issue.  
In the Mackenzie et al. (2003) model, colonization (γ\_(i,t)) and extinction (ε\_(i,t)) at site i, in interval t, are modelled separately:  
logit(γ\_(i,t))=α\_0+βX\_(i,t)  
logit(ε\_(i,t))=δ\_0+ηY\_(i,t)  
Where α\_0 and δ\_0 represent intercepts, β and η represent vectors of estimated slopes, and X and Y are arrays of covariates (with dimensions given by the number of sites, the number of intervals, and the number of covariates, where X\_(i,t) yields a row vector of the covariates values for site i, in interval t). Using latent variable notation as was used in the paper , the probability of occupancy in time t+1 is given by:  
ψ\_(i,t+1)=〖(1-ε\_(i,t) )\*z〗\_(i,t-1)+〖γ\_(i,t)\*(1-z〗\_(i,t-1))  
It is fairly common, particularly in Bayesian applications of dynamic occupancy models to model persistence (r\_(i,t)) instead of extinction, where persistence is defined as (1-ε\_(i,t)) or alternatively as logit(r\_(i,t) )=〖-δ〗\_0-ηY\_(i,t) if we maintain equation a above. Switching to persistence is useful here because it illustrates how the “temporal autologistic” model is merely a special case of the Mackenzie et al. (2003) model. Using persistence, occupancy is defined as:  
ψ\_(i,t+1)=〖r\_(i,t)\*z〗\_(i,t-1)+〖γ\_(i,t)\*(1-z〗\_(i,t-1))  
Now, if we define a term, θ, as  θ=〖-δ〗\_0-α\_0, slightly change our notation of β and X and make two assumptions we can reach the model presented in this paper on equation 2. Specifically, we must assume assume β=-η and use the same set of covariates (i.e., set X=Y). Then in terms of notation, we add α\_0 to the vector  β and add a matrix of 1’s to the array X and voila we have the temporal autologistic model.  
Summarizing the math from 2, the model presented here is simply a special form of the Mackenzie model in which the slope of covariate effects of extinction are assumed to be the exact inverse of the slopes of covariate effects on colonization (or alternatively where the slopes are assumed to be same on colonization and persistence) and where instead of estimating independent intercepts, we estimate the colonization and intercept and the difference that yields the extinction intercept – this is the exact same as switching between a means and difference parameterization in standard regression. The means vs. difference parameterization may be useful in some contexts (depending on the object of inference) but yields the same AIC in a model and both have been used in the broader dynamic occupancy literature. The assumptions of inverse (or equal in the case of persistence) slopes has also been used in the literature, can be easily implemented in programs like unmarked, MARK or Presence, and may make sense in some situations, however it includes a specific assumption (that covariates don’t affect colonization and extinction/persistence in different ways). The simulations don’t address this assumption.

**I thank the reviewer for the comment they provided above, which not only had a wealth of history about the use of the word autologistic, but also explicitly detailed how a dynamic occupancy model can be modified to represent an autologistic occupancy model. I have made some extensive revisions to the manuscript to place this model within it’s history in the development of occupancy models, and note that the model is in fact a first-order Markov process. I still use the phrase autologistic for few reasons though. First, as the reviewer states, this phrase is already being widely used in the literature. Renaming the model would risk some confusion, especially with more recent literature that use this term for this model. Second, as the reviewer states, autologistic occupancy models can be spatio-temporal and as such the models share the same sort of structural idea. If we assume that the spatial effect is highly localized (i.e., species present at a site in the previous timestep may affect occupancy in the current timestep) and it varies through time, then the model simplifies to a first-order Markov process, which is what we have here. Thus, there is still a conceptual link between the historical use of the term autologistic and how it is applied in this context. I have taken effort to explain this in the revised introduction, which now includes a new paragraph that reads:**

**“****Autologistic occupancy models are another approach to account for spatial or temporal dependence in species distributions. Developed for spatial statistics by Besag (1974), autologistic models entered the ecological literature under that name over 20 years later (Augustin et al. 1996). In their classical form, autologistic models were used to quantify whether the occupancy probability at a site depended on the occupancy status of neighboring sites. Wikle et al. (1998) later extended the model to include spatiotemporal dependence so that site occupancy could be influenced by the occupancy status of neighboring sites in the previous timestep. Spatiotemporal autologistic models have been used in a variety of ecological contexts (e.g., Hooten and Wikle, 2007) and have also been extended to dynamic occupancy models (Bled et al. 2011a, Bled et al. 2011b, Yackulic et al. 2012, Kase et al. 2025). More recently, however, autologistic occupancy models are only temporal such that the occupancy probability at a site can vary if it was also occupied in the previous timestep (e.g., Tingley et al. 2016, Fidino et al. 2024). This temporal formulation is therefore equivalent to a first-order Markov process and is not explicitly autologistic because it lacks a spatial component. Nevertheless, I will retain the term ‘autologistic’ here for the temporal form to maintain consistency in the literature. γ”**

**Because the manuscript is already quite long, I have opted to show how the autologistic model is a simplication of the dynamic model in a new supporting information. This way people who are interested in this can still view it while those who simply want to see the autologistic formulation can still do so. Again, I thank the reviewer for walking through this in their comment above.**

**Finally, I have decided to not include additional simulations to determine how ‘covariates don’t affect colonization and extinction / persistence in different ways’ for two reasons. First, the simulations I used target small-sample performance conditional on each model being correctly specified. Testing the robustness of the various models to model mis-specification is outside of the aim of these simulations. Second, the autologistic model is intentionally more parsimonious than the dynamic model, as it reduces the number of parameters that need to be estimated from the data. This can be especially helpful when data are limited, which is an issue I would argue many ecologists face when analyzing their data. Certainly, a systematic exploration of the robustness of this suite of models is very valuable future work but is outside the scope of introducing this R package / showing how to fit this class of model. We have added this additional assumption to the paragraph that details the models assumptions in the methods.**

Minor comments:  
Line 104-105 This is not strictly true. While in a first-order Markov process state transitions only depend on the state in the previous time step, the states themselves may be autocorrelated over much larger lags with the memory of the Markov chain depending on the turnover rate (i.e., with high colonization and high extinction rates turnover is higher and memory lower, with low colonization and low extinction rates autocorrelation (memory) is higher and turnover lower).

**This is a great point. Correlations over longer time spans (e.g., t-1 to t+2) are not modeled directly (i.e., are indirect), they are instead mediated through z\_t-1 and decay with increasing lag. We have modified the text to be more specific about what the reviewer brought up, thanks for catching this. This sentence now reads:**

**Third, autologistic occupancy models assume a first-order Markov process such that the occupancy status of a site at time t conditionally depends on the preceding state at t-1. Temporal dependence over longer time spans (e.g., t-3 to t) is therefore indirectly estimated through the first-order Markov process, which lessens with increasing time span.**

Line 150 you can also do it via Bayesian inference (see Yackulic et al., 2020).

**True, and this would be the way you would have to code up the model to fit in stan. However, as the estimation approach matters little in this case (i.e., Bayesian vs frequentist) I don’t think there is much a need to add this nuance (especially as we have already greatly lengthened the manuscript to more fully detail the history of autologistic occupancy models).**

Line 219 This is the unconditional (i.e., not conditioned on the actual observations at a particular site) steady-state approximation (steady-state because it doesn’t account for expected occupancy in prior intervals (either conditional or unconditional) and is not a good estimate of occupancy under many circumstances.

**I would agree that the steady-state approximation is not a good estimate of occupancy under some circumstances (e.g., what if the steady state is never reached). However, when displaying how the occupancy probability of a species changes over an environmental covariate (i.e., making a figure) we would either need to choose to plot it like so (i.e., the steady-state approximation) or with / without the theta term. As theta just moves the model intercept, the overall shape of the relationship does not change all that much (so long as the theta term is not so large), and so I would argue that the steady-state approximation is a great choice for this.**

**As the reviewer brings up, if we had more information about a the occupancy status of a species at specific site, then yes we would want a more specific estimate. However, that would be difficult or likely impossible to do over an entire study area. In fact, if I could just know where my species of interest is located throughout my whole study area I would in fact not need any modeling at all to estimate the species distribution. As such, I still see the need to provide the unconditional estimate. Perhaps in the future I can add an argument to the predict function within this R package so that you can indicate which estimate you want (e.g., conditional vs unconditional).**