Received: 21 March 2024 | Accepted: 14 May 2024

DOI: 10.1111/2041-210X.14359

Methods in Ecology and Evolution
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Guidelines for estimating occupancy from autocorrelated camera trap detections

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Funding information
National Science Foundation, Grant/Award Number: 2206783, 2206784 and 2211768

Handling Editor: Robin Boyd

Abstract

1. Site occupancy models (SOMs) are a common tool for studying the spatial ecology of wildlife. When observational data are collected using passive monitoring field methods, including camera traps or autonomous recorders, detections of animals may be temporally autocorrelated, leading to biased estimates and incorrectly quantified uncertainty. We presently lack clear guidance for understanding and mitigating the consequences of temporal autocorrelation when estimating occupancy models with camera trap data.
2. We use simulations to explore when and how autocorrelation gives rise to biased or overconfident estimates of occupancy. We explore the impact of sampling design and biological conditions on model performance in the presence of autocorrelation, investigate the usefulness of several techniques for identifying and mitigating bias and compare performance of the SOM to a model that explicitly estimates autocorrelation. We also conduct a case study using detections of 22 North American mammals.
3. We show that a join count goodness-of-fit test previously proposed for identifying clustered detections is effective for detecting autocorrelation across a range of conditions. We find that strong bias occurs in the estimated occupancy intercept when survey durations are short and detection rates are low. We provide a reference table for assessing the degree of bias to be expected under all conditions. We further find that discretizing data with larger windows decreases the magnitude of bias introduced by autocorrelation. In our case study, we find that detections of most species are autocorrelated and demonstrate how larger detection windows might mitigate the resulting bias.
4. Our findings suggest that autocorrelation is likely widespread in camera trap data and that many previous studies of occupancy based on camera trap data may have systematically underestimated occupancy probabilities. Moving forward, we recommend that ecologists estimating occupancy from camera trap data use the join count goodness-of-fit test to determine whether autocorrelation is present in their data. If it is, SOMs should use large detection windows to mitigate

bias and more accurately quantify uncertainty in occupancy model parameters. Ecologists should not use gaps between detection periods, which are ineffective at mitigating temporal structure in data and discard useful data.

KEYWORDS
autocorrelation, bias, camera trap, occupancy

1 | INTRODUCTION

The hierarchical site occupancy model (SOM) is one of the most common tools that ecologists use to analyse ecological field data (MacKenzie et al., 2002). The SOM is used to estimate the probability that a species is present at each of a number of sites when detection is imperfect, that is, surveys can fail to detect the species even if it truly occupies the surveyed area. Today, the SOM is often estimated using data collected by passive monitoring, such as with acoustic recorders or camera traps (Furnas, 2020; Kays et al., 2020). These sampling methods produce detections of animals in continuous time. The continuous survey period can be 'discretized' into a series of detection–nondetection data for use in the SOM framework.

Estimating the SOM with data collected under continuous-time passive monitoring protocols such as camera traps poses an apparent problem. The SOM was originally developed to describe traditional discrete field surveys, in which a target species is observed or not on each of several surveys at clearly defined sites. Data collected under passive monitoring protocols do not satisfy the model's assumptions as originally stated. Most prominent among these assumptions is the 'closure' assumption, which states that the occupancy state of the surveyed area is constant (closed) across replicate observations. For data collected by camera traps, which may survey tens of square metres for several weeks, the target species is rarely present in the survey area for the duration of the study. Ecologists resolve this mismatch via an 'asymptotic' interpretation of the occupancy process where a site surveyed by a camera is defined as 'occupied' throughout the survey period if an individual of the species occupies the survey area for any amount of time (Efford & Dawson, 2012; Latif et al., 2016). The parameters of the SOM are then estimated as usual. Under the asymptotic interpretation, inference still depends on meeting other assumptions of the SOM. To extend ecological inference beyond the small areas surveyed by each camera, these assumptions include that the placement of cameras on the landscape is representative of the study area. This requires that sites follow, for example, that they are selected using random or stratified random placement or are placed on a systematic grid (Burton et al., 2015).

When the SOM is estimated using data collected under a continuous survey protocol, there is a risk that assumption violations occur in addition to those which are resolved via the asymptotic interpretation of occupancy. In particular, when discretizing continuous-time data, ecologists risk inducing nonindependence between replicate surveys. Nonindependence could arise if there are unmodeled, temporally structured variables that drive detection, such as weather. Another likely source of nonindependence is animal behaviour: Individuals may remain at or near a site for days, with the same individual triggering a camera multiple times before moving on (Neilson et al., 2018). The reverse may also occur—a slow moving animal that uses the surveyed area might happen to remain in another part of its home range for the duration of the survey period, leading to autocorrelated nondetections. We refer to any such temporally structured nonindependence between consecutive surveys as 'temporal autocorrelation'.

Temporally autocorrelated detection events violate the assumptions of the SOM regardless of their cause or the interpretation framework. Autocorrelated detections result in pseudoreplication, whereby non-independent events are treated as independent. Failure to consider nonindependence in modelling can lead to overconfident estimates of model parameters (Hurlbert, 1984). In an occupancy model, pseudoreplicated detections can cause bias since the occupancy model's estimate of imperfect detection is directly informed by the number of supposedly independent detection events at occupied sites (see 'Generating autocorrelated detections').

Ecologists have investigated several aspects of the autocorrelation problem in camera trap studies, but little practical guidance exists. In a simulation study, Neilson et al. (2018) showed that animal movement resulted in biased occupancy estimates. However, most treatments of the effect of animal movement on occupancy estimation focus on implications for the occupancy–abundance relationship (Bollen et al., 2023; Linden et al., 2017; Parsons et al., 2017; Stauffer et al., 2021). Some SOM extensions and alternatives have been proposed to deal with temporal structure in replicate surveys (Guillera-Arroita et al., 2011; Hines et al., 2010). These models may reduce bias and improve inference in most cases; however, since the SOM continues to dominate occupancy modelling, it is worthwhile to develop clear guidance for ecologists to mitigate the impact of autocorrelation on the performance of the SOM applied to camera trap data. To this end, Wright et al. developed a goodness-of-fit test that may be able to identify nonindependence between replicate surveys (Wright et al., 2016), though the usefulness of this test across sampling conditions has not been tested. In terms of mitigating bias due to autocorrelation, some authors have discussed choosing a detection window—the temporal bin used to discretize data—in such a way as to enforce independence between detection events at a site, but to our knowledge, no studies exist producing evidence-based recommendations for the detection window.

In this study, we investigate the impact of autocorrelated camera trap detections and provide concrete, practical guidance for estimating occupancy. We first discuss autocorrelation in the context of a data-generating model by building intuition about how non-independent detections affect the estimation of detection and occupancy processes in the SOM. We then conduct a simulation study to investigate the conditions under which autocorrelation impacts model performance. We investigate the impact of varying the detection window used to discretize continuous-time data, an issue relevant to any analysis of observational data produced by continuous-time monitoring, including camera traps or passive acoustic surveys, which has nonetheless received little attention in the literature. We then illustrate the impact of modelling choices using a case study of camera trap data from across the United States. We present a set of practical recommendations for assessing whether autocorrelation causes biologically relevant bias in estimates of animal occupancy and inference on species' habitat associations.

2 | METHODS

2.1 | Generating autocorrelated detections

Here, we present a data-generating model for producing detection–nondetection data in a hierarchical occupancy framework with autocorrelated detections. See Table 1 for a glossary of important terms.

First, consider the SOM as applied to camera trap data. At each of N sites, a camera is deployed, generating continuous-time detections over a period of T days. We typically discretize this continuous-time data into J replicate detections of some length. For example, if sampling for 20 days, we might choose to use 1-day detection events such that $T = J = 20$, or we might choose 5-day detection windows, in which case $J = 4$. We refer to these J survey periods as 'occasions', and the duration of an occasion is the 'detection window'. The SOM is defined by the following set of equations:

$$y_{i,j} \overset{\text{iid}}{\sim} \text{Bernoulli}(z_i p_{i,j})$$

$$z_i \overset{\text{iid}}{\sim} \text{Bernoulli}(\psi_i)$$

$$\text{logit}(p_{i,j}) = \text{logit}(p_0) + \beta_2 x_{2,i}$$

$$\text{logit}(\psi_i) = \text{logit}(\psi_0) + \beta_1 x_{1,i}$$

where y_{ij} is 0 if the species was *not* detected during the jth occasion at site i and 1 if it was; ψ_i is the probability that site i is occupied; and p_{ij} is the probability of detecting the species during the jth occasion at site i, if site i is occupied. In the following simulation, occupancy and detection are each linearly determined by a site-level covariates x_1 and x_2. The parameters ψ_0 and p_0 are the occupancy and detection probabilities when $x_{1,i} = 0$ and $x_{2,i} = 0$, respectively (mean occupancy and detection if $\mathbf{x}_1$ and $\mathbf{x}_2$ are scaled), while the parameters β_1 and β_2 are the effects of the covariates on occupancy and detection, respectively.

To induce autocorrelation, we adapt a model given by Hines et al. developed to describe autocorrelation in transect sampling (Hines et al., 2010). The Hines et al. occupancy model (hereafter 'the clustered model') adds a temporally autocorrelated site use process to the occupancy–detection hierarchy (Figure 1). The clustered model is defined by the following equations:

$$y_{i,j} \mid w_{i,j} \overset{\text{iid}}{\sim} \text{Bernoulli}(w_{i,j}\pi_{i,j}) \text{ for } j = 1 \ldots J$$

$$w_{i,1} \mid z_i \overset{\text{iid}}{\sim} \text{Bernoulli}(z_i\bar{\theta})$$

$$w_{i,j} \mid z_i, w_{i,j-1} \overset{\text{iid}}{\sim} \text{Bernoulli}(z_i(\theta(1 - w_{i,j-1}) + \theta' w_{i,j-1})) \text{ for } j = 2 \ldots J$$

$$z_i \overset{\text{iid}}{\sim} \text{Bernoulli}(\psi_i)$$

$$\text{logit}(\pi_{i,j}) = \text{logit}(\pi_0) + \gamma_1 x_{2,i}$$

$$\text{logit}(\psi_i) = \text{logit}(\psi_0) + \beta_2 x_{1,i}$$

$$\bar{\theta} = \frac{\theta}{\theta + (1 - \theta')}$$

The clustered model's occupancy process is identical to that of the SOM. The true site-level occupancy state, z_i, is a Bernoulli random variable with occupancy probability ψ_i. We can parameterize ψ_i as logit-linked to a linear model via a probability-scale occupancy intercept, ψ_0, and β_1, the logit-scale effect of site covariate x_1. Then, conditional on occupancy, we define a temporally autocorrelated site use process. The site use latent state, $w_{i,j}$, has a value of 1 if the species used the area surveyed by the camera during the jth sampling occasion at site i, and 0 if it did not. The probability of site use is determined by two parameters, θ and θ', which correspond to the probabilities that the species uses the site in one occasion given that it did not or did use the site during the previous occasion. The probability of site use during the first occasion, $j = 1$, is the asymptotic mean of site use, $\bar{\theta}$. Finally, detections arise as Bernoulli random variables conditional on site use. The probability of detecting the species on the jth occasion at site i, given that the site is in use, is $\pi_{i,j}$. In this model, we parameterize $\pi_{i,j}$ as a logit-linear model with probability scale intercept π_0 and parameter β_2 representing the effect of the site-level covariate x_2 on detection.

The relative values of the parameters θ and θ' determine the degree of autocorrelation in the site use process. We define the strength of autocorrelation as $\frac{\theta'}{\theta}$. When $\frac{\theta'}{\theta} = 1$, no autocorrelation occurs, while when $\frac{\theta'}{\theta} > 1$, detections are autocorrelated (Figure 1). Under the clustered model, we refer to the quantity $\pi_0\bar{\theta}$ as the 'detection rate', as it gives the expected number of detections per unit time at occupied sites when all covariates are 0. The SOM's equivalent to this parameter is p_0. To make comparisons between autocorrelation levels with a constant model, we hold the detection rate fixed while adjusting the autocorrelation strength.

TABLE 1 Glossary of key terms used in this paper.

Term	Definition
Deployment	A continuous sampling period at a single camera
Sampling occasion	A temporal subdivision of a deployment used as a replicate detection in a discrete occupancy-type model. A sampling occasion is associated with either a detection or nondetection datum
Detection window	The amount of time used to delineate sampling occasions within each camera (e.g. 1 day, 7 days)
Detection gap	A period of inactivity between sampling occasions (e.g. 0 days, 1 day). For example, a 23-day deployment could be subdivided into sampling occasions with 7-day windows and 1-day gaps between them
Occupancy state	The binary condition representing whether the area surveyed by a camera was used by the target species during the deployment (0 = not occupied, 1 = occupied)
Occupancy probability	The model parameter having values [0, 1] giving the Bernoulli probability that a camera's occupancy state was 1
Site use	The process describing whether individual animals of the target species exist in a deployment's sampled area on a particular occasion. Under the asymptotic interpretation of the SOM, site use is confounded with detection and is implicitly assumed to be independent across sampling occasions. In the clustered model, site use is modelled explicitly as a temporally structured process
Detection probability	A model parameter with model-specific meanings. In the SOM, detection probability is the probability of observing the species, during a single sampling occasion, at an occupied camera
Detection rate	In this paper, we use 'detection rate' to unify detection probability concepts across models by describing the rate at which detections occur in the realized data. The mean detection rate at occupied sites is p_0 in the occupancy model and $\pi_0\overline{\theta}$ in the clustered model (see section 'Generating autocorrelated detections')
Autocorrelation	A phenomenon whereby detections that are close to one another (e.g., in time) 0 are more similar than expected under an assumption of independence. In this study, we focus on autocorrelation—that is, nonindependence—between consecutive sampling occasions within a deployment
Cumulative detection probability (CDP)	The probability that a camera whose sampled area is truly occupied will detect the species in at least one survey occasion across the entire deployment
Realized CDP	In simulated data with known occupancy states, the realized CDP of a given data set is calculated as the number of deployments with ≥1 detection divided by the number of truly occupied deployments
Estimated CDP	The estimated CDP can be calculated from the parameter estimates associated with a fitted model at the deployment level, or summarized across sites (e.g. median), based on the estimated detection probabilities at each sampling occasion (Equation 13)

We can illustrate introducing autocorrelation with the following example (Figure 2). First, we simulate a data set under the clustered model with 80 cameras each deployed for 21 days with mean occupancy $\psi_0 = 0.6$, mean detection probability $\pi_0 = 0.4$, and site use probability $\theta = \theta' = \overline{\theta} = 0.4$. In this case, $\frac{\theta'}{\theta} = 1$, so no autocorrelation occurs. Second, we simulate a data set using the same underlying occupancy process but introduce autocorrelation. We hold the mean detection rate $\pi_0\overline{\theta}$ fixed at 0.16 while setting the autocorrelation strength to $\frac{\theta'}{\theta} = 10$, yielding parameters $\pi_0 = 0.4$, $\theta \approx 0.087$ and $\theta' \approx 0.87$. Graphically, the autocorrelated data contain many consecutive detections, compared to the data generated without autocorrelation, which are more mixed (Figure 2a). Additionally, while the number of detections per site with at least one detection is the same between the two data sets (Figure 2b), the total number of sites with detections is lower in the autocorrelated case (Figure 2c). By reducing θ while holding $\pi_0\overline{\theta}$ fixed, the probability of an animal beginning to use the survey area is reduced. When the true value of $\frac{\theta'}{\theta} = 1$, and no autocorrelation occurs, the clustered occupancy model produces data equivalent to that generated by an SOM with $p_{i,j} = \overline{\theta}\pi_{i,j}$, and we expect the SOM to accurately estimate ψ_0 and β_1. When data are generated with autocorrelation, then estimating the SOM is equivalent to estimating the clustered occupancy model under the erroneous assumption that $\frac{\theta'}{\theta} = 1$.

2.2 | Detection windows and gaps in the literature

To estimate discrete-time models such as the SOM or the clustered model with data collected in continuous time, one chooses a fixed time interval over which to discretize observations into a series of detection–nondetection data. For example, if a camera is deployed for 10 days, a common choice is to divide the sampling into 10 24-h occasions. We refer to this as a choice to use a 1-day 'detection window' (Table 1). Choosing a particular detection window is necessary whenever camera trap data are used to fit a discrete-time SOM or SOM extension, but the optimal detection window is unclear.

When autocorrelation occurs in camera trap data, the choice of detection window may influence the degree of bias in estimates of occupancy parameters. In an extreme example, if the detection window is 1 month, it is unlikely that autocorrelated processes like animal movement will link detections between 1-month long sampling occasion and the next, but if the detection window is 1 s, an individual animal making its way through the surveyed area will regularly be detected during multiple sampling occasions. In the latter case, the amount of independent information regarding animal detectability is inflated.

Similarly, authors might choose to impose a detection gap, a period of downtime in between each sampling occasion during which any

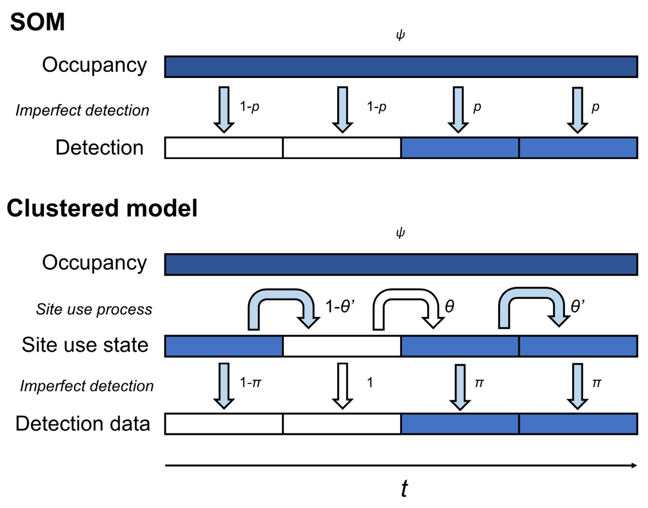

FIGURE 1 Unifying the perspectives of the clustered occupancy model and the SOM. At one camera, both models assume that occupancy is constant throughout the study duration. Under the asymptotic interpretation of occupancy, the camera is occupied if it is used by the species at any point during the study period. The clustered model explicitly separates a site use process from an autocorrelated detection process. In the SOM, site use and detection are confounded, and it is assumed that no autocorrelation occurs in site use, that is, $\theta = \theta'$.

detections are discarded (e.g. Ferreguetti et al., 2015). For instance, one could divide a 23-day deployment into three sampling occasions with a 7-day window, imposing a 1-day gap between each occasion during which any detections are discarded. Gaps create separation between consecutive samples and seem to reduce the degree of dependence between consecutive surveys. However, using gaps reduces the content of information available for modelling, which could be undesirable, particularly for species that are rarely detected.

In practice, detection windows vary. In a review of camera trap methods, Burton et al. (2015) found that occupancy modellers working with camera trap data used detection windows varying in duration from 1 to 15 days, with a median duration of 5 days (Burton et al., 2015). To provide updated context for the recommendations in this study, we conducted a brief review of the use of detection windows and detection. We randomly selected 100 papers published in the last 10 years associated with the search terms 'occupancy' and 'camera trap'. We noted the detection windows and detection gaps used in each paper. For full details, see the Supplemental Materials.

2.3 | Simulation study

2.3.1 | Simulation 1: Impact of autocorrelation on the SOM

In the first phase of the simulation, we evaluated how the performance of the SOM changed when autocorrelation was induced in the detection process.

Strong autocorrelation may bias occupancy estimation only under certain sampling conditions or in certain systems. To investigate this, we varied levels of four parameters of the data-generating model (mean abundance ψ_0, mean detection rate $\pi_0\overline{\theta}$, detection breakdown $\overline{\theta}/\pi_0$ and autocorrelation strength $\frac{\theta'}{\theta}$) and two effort parameters (number of cameras and duration of sampling at each camera). We list these parameters, their interpretations and the levels we considered in Table 2. At each combination of these variables, we simulated 1000 data sets using a 1-day detection window and a 0-day detection gap, then estimated the SOM.

We evaluated the performance of the occupancy model under each simulation condition in terms of inference and prediction. To characterize variation in inference, we calculated the median absolute error in the estimates of the occupancy parameters (ψ_0 and β_1), the median standard error of the estimates of these parameters, and the rates at which 95% confidence intervals of parameters contained the true value, each across 1000 replicate simulations. To track predictive performance, we calculated the root mean squared error (RMSE) of each fit model according to the formula

$$\text{RMSE} = \sqrt{\frac{1}{N}\sum_{i}^{1\ldots N}\left(\hat{\psi}_i - \psi_i\right)^2}$$

where ψ_i is the true simulated occupancy probability at camera i, $\hat{\psi}_i$ is the estimated occupancy probability at camera i and N is the total number of cameras (Zulian et al., 2021).

For each fitted model, we also calculated the true cumulative detection probability (CDP) and the model estimated CDP. True CDP was calculated as the number of sites with detections divided by the number of truly occupied sites. At one camera, estimated CDP is calculated as

$$\widehat{\text{CDP}}_i = 1 - \left(1 - \hat{p}_i\right)^J$$

For each model, we calculate the median $\widehat{\text{CDP}}$ across all sites.

2.3.2 | Simulation 2: Goodness-of-fit checking

Ecologists commonly use goodness-of-fit checks to identify discrepancies between assumed and realized data distributions (MacKenzie & Bailey, 2004). A candidate goodness-of-fit test for identifying autocorrelation in data is the join count test given by Wright et al. (hereafter 'join count test') which compares the observed count of consecutive detections to a bootstrapped expectation (Wright et al., 2016). To evaluate the performance of this test, we simulated an additional 1000 data sets under each combination of system and sampling parameters in Simulation 1. We estimated the SOM with each data set, then conducted the join count test on each fitted model. We tracked the rate at which the join count test produced evidence of bad model fit (p-value < 0.05) under each simulation condition.

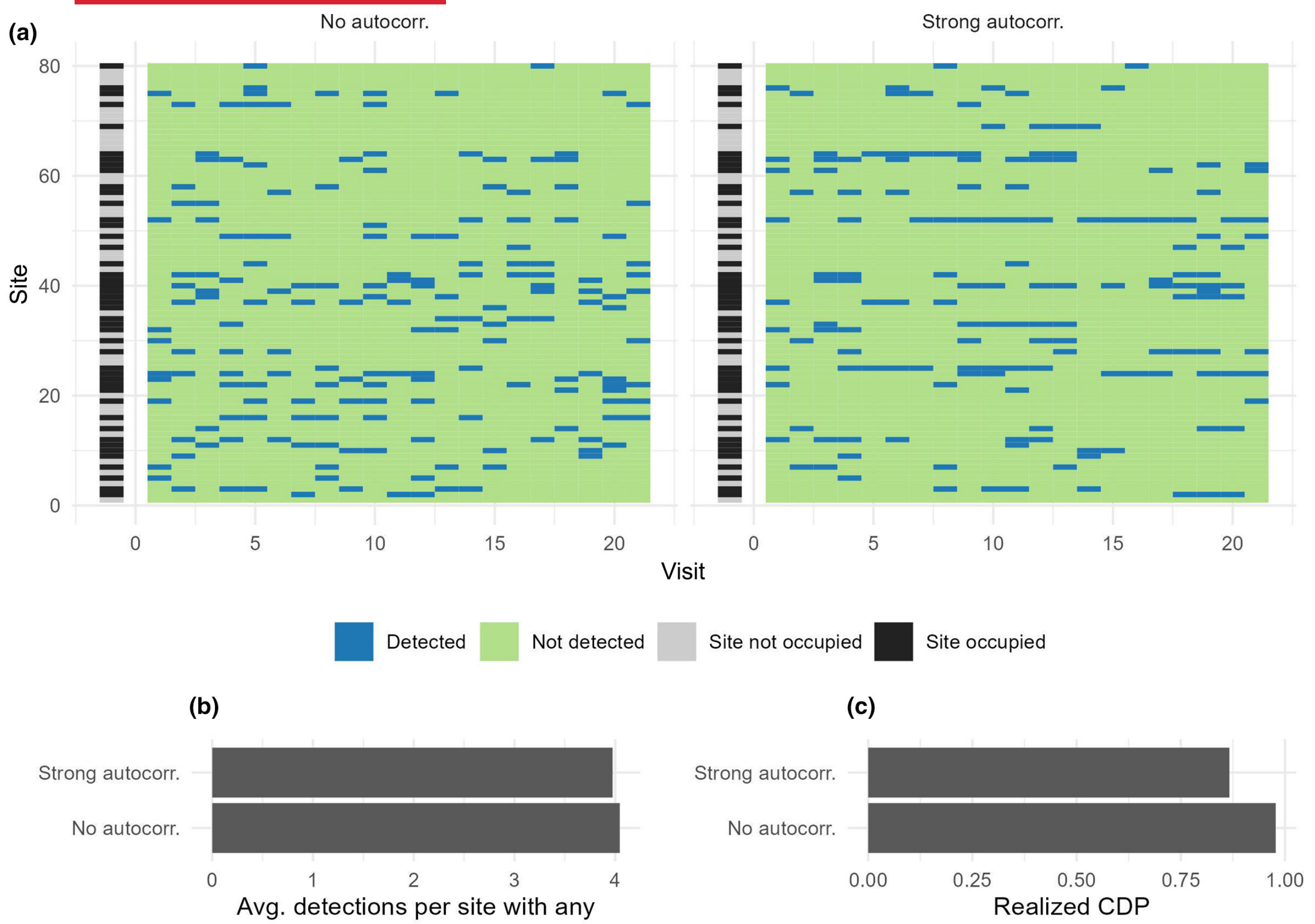

FIGURE 2 Comparing data generated with no autocorrelation to data generated with strong autocorrelation. (a) Two simulated detection histories. Both comprise 21 replicate detections at each of 80 identical sites. The data generated with strong autocorrelation (right panel) contain visually striking strings of repeat detections, while detections in the data set generated with no autocorrelation appear randomly dispersed. (b) The two data sets are roughly equal in the average number of detections per site with at least one detection. (c) However, the fraction of truly occupied sites with at least one detection—the realized cumulative detection probability (CDP)—is lower in the autocorrelated data set. When estimating the occupancy model, this will lead to an overestimation of the cumulative detection probability and a subsequent underestimation of occupancy.

2.3.3 | Simulation 3: Choosing a detection window and detection gap

In a subsequent exercise, we simulated detection histories using various detection windows and detection gaps. To represent the data manipulation process from which windows and gaps arise, data were first simulated under the clustered model with 1-day windows and 0-day gaps, then aggregated. During the aggregation process, incomplete sampling occasions were discarded: for example, simulating data under a 21-day sampling scenario with a detection window of 5 and a detection gap of 1 yielded three 5-day periods each buffered by 1 day, with 4 days of discarded data at the end of sampling.

We fixed state parameters at $\psi_0 = 0.4$, $\pi_0\overline{\theta} = 0.3$ and $\overline{\theta} / \pi_0 = 1$ and the number of sites at 80, one case from Simulation 1 where the 1–0 SOM produced biased estimates. We allowed the total amount of effort at each site to take values of 21 days, 35 days or 70 days. We varied detection windows from 1 day to 20 days and detection gaps from 0 to 3 days. We did not consider combinations of design parameters where the length of one window and gap exceeded half the total sampling duration. At each combination of these three parameters, we simulated 1000 data sets, estimated the SOM and evaluated model performance following Simulation 1.

2.3.4 | Simulation 4: Estimating the clustered occupancy model

In some cases, estimating a model that explicitly accounts for autocorrelation may be the best strategy. However, such models have more complex hierarchical structure, so they may produce estimates with increased uncertainty and worse or comparable predictive power than simpler models (Pautrel et al., 2024). To assess the costs and benefits of using a more complex model, we investigate how the clustered model used to generate the data performs

TABLE 2 Sampling and occupancy system parameters considered in Simulation 1.

Simulation parameter	Type	Interpretation	Simulated levels
Number of sites	Sampling	How many cameras were deployed?	40, 80, 120
Sampling effort	Sampling	For how many days was each camera deployed?	21, 35, 70
Occupancy probability (ψ_0)	System	Average probability that a site is occupied	0.3, 0.4, 0.5, 0.6
Mean detection rate ($\pi_0\overline{\theta}$)	System	Average probability of detection at an occupied site. Number of overall detections increases as this value increases	0.15, 0.2, 0.25, 0.3
Detection breakdown ($\overline{\theta}$ / π_0)	System	Relative importance of site use vs. imperfect detection in driving nondetections at occupied sites. Site use increases in importance as this value decreases	1/3, 1
Autocorrelation strength ($\frac{\theta'}{\theta}$)	System	Strength of autocorrelation in site use. If this value is > 1, the species is more likely to use the site during time t if they used the site during time t-1. In all figures, 'strong autocorrelation' refers to $\frac{\theta'}{\theta} = 10$ and 'no autocorrelation' refers to $\frac{\theta'}{\theta} = 1$	1, 5, 10
Effect of occupancy covariate (β_1)	System	The logit-scale effect of a simulated site-level occupancy covariate	0.5
Effect of detection covariate (β_2)	System	The logit-scale effect of a simulated site-level detection covariate	−0.5

in comparison to the SOM in a simulation and case study. At each combination of system and effort variables (Table 2), we simulated an additional 1000 data sets. We fit each to both the SOM and the clustered occupancy model. We tracked the performance, in terms of inference and prediction, of both models as in Simulation 1.

In all four simulations, we estimated the SOM via maximum likelihood estimation with the package 'unmarked' (Fiske & Chandler, 2011). We estimated the clustered model using custom code in R with the compiled hidden Markov model distribution provided in the R package nimbleEcology (Goldstein et al., 2020). Parallel processing was executed using the R package 'parabar' v1.1.0 (Constantin, 2023). All analysis was conducted in R version 4.3.1 with visualizations produced using the R package 'ggplot2' (Wickham, 2016). We provide all code used to conduct simulations in an accompanying repository (Goldstein et al., 2024).

2.4 | Case study: Snapshot USA

To develop practical recommendations for dealing with autocorrelation in real camera trap data, we conducted a case study using camera trap observations of North American mammals. We retrieved camera sequences and deployment metadata from Snapshot USA's 2020 season (Kays et al., 2022). Snapshot USA cameras were distributed across the continent in arrays of 5–65 cameras. Within each array, cameras were placed a minimum distance of 200 m apart. Sites were selected so as to be random with respect to animal movement: Cameras were not baited and were not intentionally aimed at attractants like game trails or water sources (Kays et al., 2022). For modelling, we identified all species observed on at least 100 camera days. For each species, we removed all camera deployments outside the species range (IUCN [International Union for Conservation of Nature], 2023). At each deployment, we then divided the sampling duration into 24-h occasions beginning at noon of the first day. We constructed a detection history at each site indicating whether the species was detected during each occasion.

To construct ecologically realistic occupancy submodels, we retrieved values of four covariates at each deployment. We retrieved estimates of maximum annual temperature at a 2.5 arc-minute resolution from the MERRAclim climate data set (Vega et al., 2017), percent forest cover at a 1-km resolution (Jung et al., 2020) and estimated canopy height in 2019 at 30 m resolution (Potapov et al., 2021). For these three variables, each camera was associated with the covariate value of the raster cell in which it occurred. We also computed the distance to the nearest road at each camera (Meijer et al., 2018).

For each species, we estimated three SOMs using detection windows of 1 day and 10 days. For comparison, we also fit the clustered occupancy model to each single-species data set using 1-day intervals. We scaled and centred all four covariates separately for each species. In all three models, we included percent forest cover and maximum temperature as covariates on occupancy and canopy height and log-scale distance to road as covariates on detection. These simple occupancy models were designed to be sufficiently realistic while remaining generalizable across species with different ranges and life histories. We found maximum likelihood estimates of model parameters and calculated estimated CDP. To assess evidence of autocorrelation, we applied the join count test to each species' 1-day window model, adjusting p-values for multiple testing by controlling the false discovery rate (Benjamini & Hochberg, 1995).

3 | RESULTS

3.1 | Detection windows and gaps in the literature

Of 100 papers using camera trap data to estimate occupancy that were randomly selected from a Web of Science query, 66 papers qualified for analysis and 62 clearly reported the choice of detection window used (Figure S1). The most common choice of detection window was 1 day (18 papers), followed by 5 days (15 papers) and 7 days (7 papers). The longest window we observed was 60 days, and no study in our sample used a detection window of less than 1 day. Notably, only two of 66 papers indicated using detection gaps. Larger detection windows were typically presented as increasing the per-occasion detection rates to improve model convergence, rather than as a means of addressing autocorrelation. The median sampling duration was 35 days, though surveys ranged from only 5 days to more than 3 years at each site.

3.2 | Simulation study

3.2.1 | Simulation 1 results: Impact of autocorrelation on the SOM

Across 864 simulation conditions, SOMs fit to data simulated without autocorrelation showed no systematic bias under any conditions. We provide results across all conditions in Supplemental Table S1 and are visualized in Figures S2–S9. When autocorrelation was introduced, systematic bias occurred when estimating the occupancy intercept under certain conditions (Figure 3a). The most important determinant of bias in the presence of autocorrelation was sampling duration. In the worst case, logit-scale systematic bias in the intercept was −0.4 (a 16% underestimation). When the sampling period was extended from 21 days to 35 days, logit-scale bias was reduced to −0.26 (an 11% underestimation). When the sampling period was 70 days, the worst-case bias in occupancy was a logit-scale bias of −0.1 (a 4% underestimation). Autocorrelation also led to bias in estimating the effect of a covariate on occupancy (Figure 3b), which like the occupancy intercept was biased downward when autocorrelation was strong and sampling duration was low. A low-magnitude (<0.05) positive bias persists in cases of long survey times, which is observed across autocorrelation simulation conditions (Figure S6). This positive bias, which is masked by autocorrelation-driven negative bias at low survey durations, decreases towards 0 as the number of sites increases (Figure S7).

Models fit to data with autocorrelation also showed worse predictive performance. RMSE in predictions of occupancy at out-of-sample sites increased under conditions matching those that produced biased occupancy estimates (Figure 3c). In the worst simulation scenarios, RMSE increased by 106%, from 0.066 to 0.136, when autocorrelation was introduced.

Across all simulation conditions, error in estimating cumulative detection probability (CDP) corresponded to bias in estimating the occupancy intercept (Figure 4). This relationship was strongly linear (R^2 = 0.945). This suggests that the effect of autocorrelation on bias is mediated through its effect on estimated CDP.

3.2.2 | Simulation 2 results: Goodness-of-fit checking

Across all conditions, the join count test goodness-of-fit test yielded evidence of autocorrelation in 0.3% of simulations where no autocorrelation was present, and 93% of simulations where autocorrelation was present. The power of the join count test to detect autocorrelation depended on sample size and occupancy rate (Figure 5): The test detected autocorrelation 76% of the time in moderately autocorrelated data sets simulated at 40 cameras with mean occupancy of 0.3, and 100% of the time in data sets simulated at 120 cameras with mean occupancy of 0.6.

3.2.3 | Simulation 3 results: Choosing a detection window and detection gap

Choice of detection window had a substantial impact on model performance (Figure 6). When bias occurred in the baseline (1-day window, 0-day gap) model, increasing the detection window decreased bias in the occupancy estimate. For example, in the 21-day sampling scenario, the use of a 10-day window decreased the magnitude of bias by more than half compared to a 1-day window, and in the 35-day scenario, the use of the maximum possible 17-day window reduced bias by more than 90% (Figure 6a,b). Larger detection windows were associated with larger uncertainties (Figure 6c), but those uncertainties better reflected the true coverage of the 95% confidence intervals (Figure 6d). In cases where the baseline model was unbiased, changing the detection window had little effect on model performance.

Detection gaps were not helpful in mitigating the impacts of autocorrelation. Introducing detection gaps did not meaningfully change bias in the model (Figure 6a,b). Instead, detection gaps were

FIGURE 3 Effect of autocorrelation on estimating occupancy parameters. (a and b) Each tile shows the change in median absolute error of an occupancy submodel parameter estimate across 1000 replicate simulations when strong autocorrelation is introduced ($\frac{\theta'}{\theta}=10$) at one simulation condition. All results reflect a model with 1-day detection windows and no detection gaps. (a) Absolute median error in estimating the occupancy intercept in a strong autocorrelation condition compared to estimating data with no autocorrelation. Bias increases as the detection rate decreases, mean occupancy probability increases and sampling time decreases. (b) Absolute median error in estimating the effect of a site covariate on occupancy. Bias follows a similar pattern to the intercept, but the magnitude of bias is much less, and noise becomes relevant (note that panel B reports error on the logit scale of the covariate effect, while panel a reports error on the probability scale). (c) Change in predictive error (RMSE) between strong autocorrelation and no autocorrelation simulation conditions. Predictive error increases when occupancy increases, detection rate decreases and sampling time decreases, a pattern matching that of induced bias in panels (a and b).

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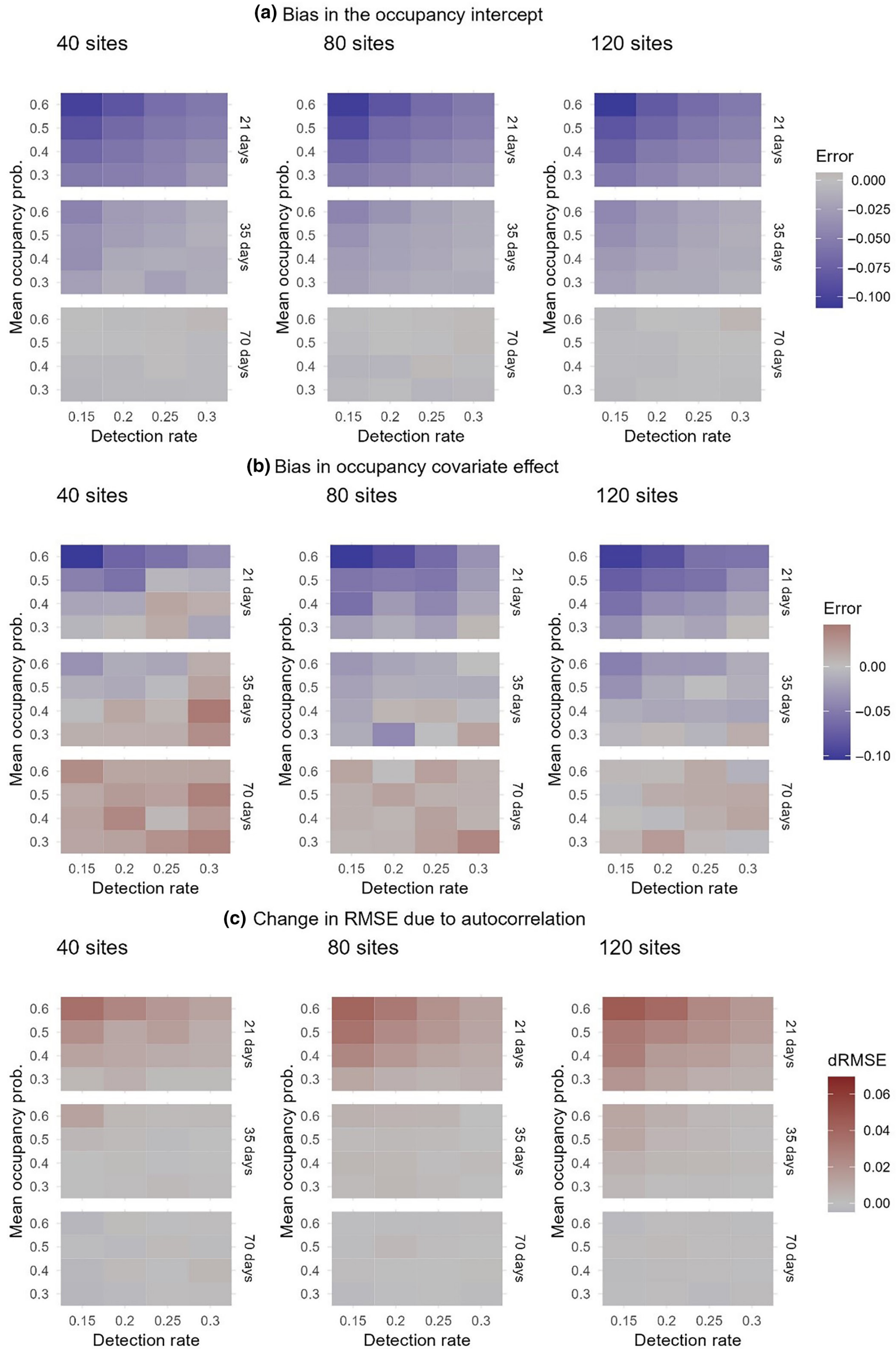

associated with greater uncertainty in model estimates in low-information scenarios (Figure 6c) as information was discarded.

3.2.4 | Simulation 4 results: Estimating the clustered occupancy model

We estimated the clustered occupancy model used to generate the autocorrelated data to 1000 data sets under each sampling condition. The clustered occupancy model produced effectively unbiased estimates of mean occupancy under all conditions, except when autocorrelation was very strong and sampling durations were short, in which case the clustered model overestimated occupancy (Figure S2). However, under this condition, the clustered model still outperformed the SOM by RMSE (Figure S3).

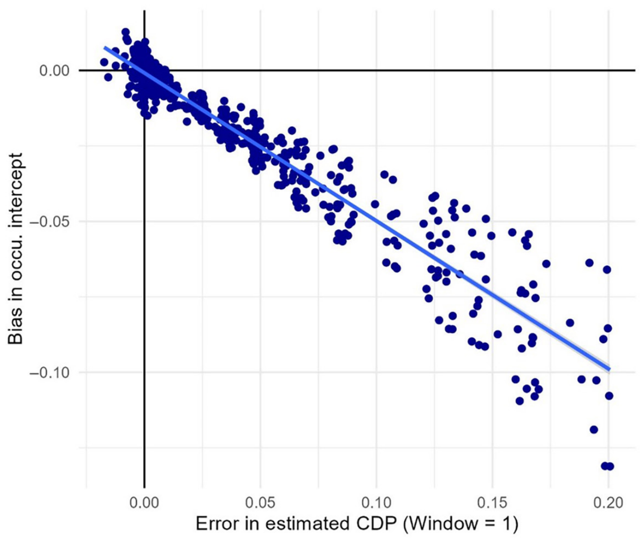

FIGURE 4 Across 864 simulation conditions (blue points), mean error in estimated cumulative detection probability (CDP) was strongly correlated with mean logit-scale bias in the estimated occupancy intercept. The blue line shows the best-fit line for a linear relationship between estimated CDP and the bias in estimating the occupancy intercept.

3.3 | Case study: Snapshot USA

We identified 23 species with sufficient Snapshot USA data for analysis. One species, the desert cottontail (*Sylvilagus audubonii*), was excluded due to insufficient variation in the covariates of interest across its range, leaving 22 modelled species. A full list of species with data summary statistics is available in Table S2.

We applied the join count test to the fitted SOM using 1-day windows for each species. Adjusted p-values for 20 of 22 species were less than 0.05, indicating evidence of autocorrelated detections for those 20 species (Figure 7). Across species, 10-day detection windows yielded consistently higher estimates of occupancy probabilities compared to 1-day windows (Figure 7b). The clustered model also produced consistently higher occupancy estimates. However, we observed no change in point estimates of the effect of forest and temperature on occupancy when changing the detection window (Figure 7b). The 10-day SOM and the clustered model were associated with comparable low-magnitude increases in parameter uncertainty compared to the 1-day SOM (Figure 3c).

4 | DISCUSSION

In this study, we investigated the consequences of having unmodeled temporal structure in detections produced by continuous-time camera trap sampling when estimating occupancy. In simulations, temporal autocorrelation in detections biased occupancy estimates downward. Autocorrelation inflates detection probabilities, leading to overestimation of CDP. Consequently, the probability of occupancy at sites with no detections is underestimated and bias occurs. Bias was strongest in the occupancy intercept, with relative effects of covariates being subject to less bias, and bias was strongest when

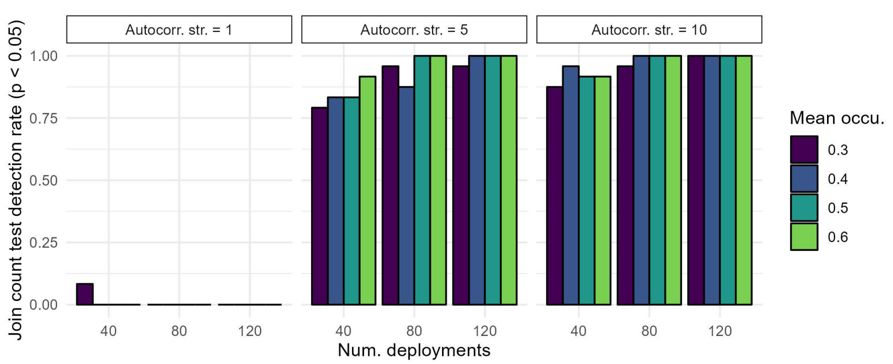

FIGURE 5 Performance of the join count test for identifying autocorrelation in simulated data. The join count test had a very low false-positive rate, almost never indicating that autocorrelation was present when it was not. When autocorrelation was present (2nd and 3rd panels), the join count test indicated as such 76%–100% of the time, with better performance as the number of deployments and mean occupancy rate increased. Results are summarized across all simulation conditions using a 1-day detection window and no detection gap; full results are shown in Figure S10.

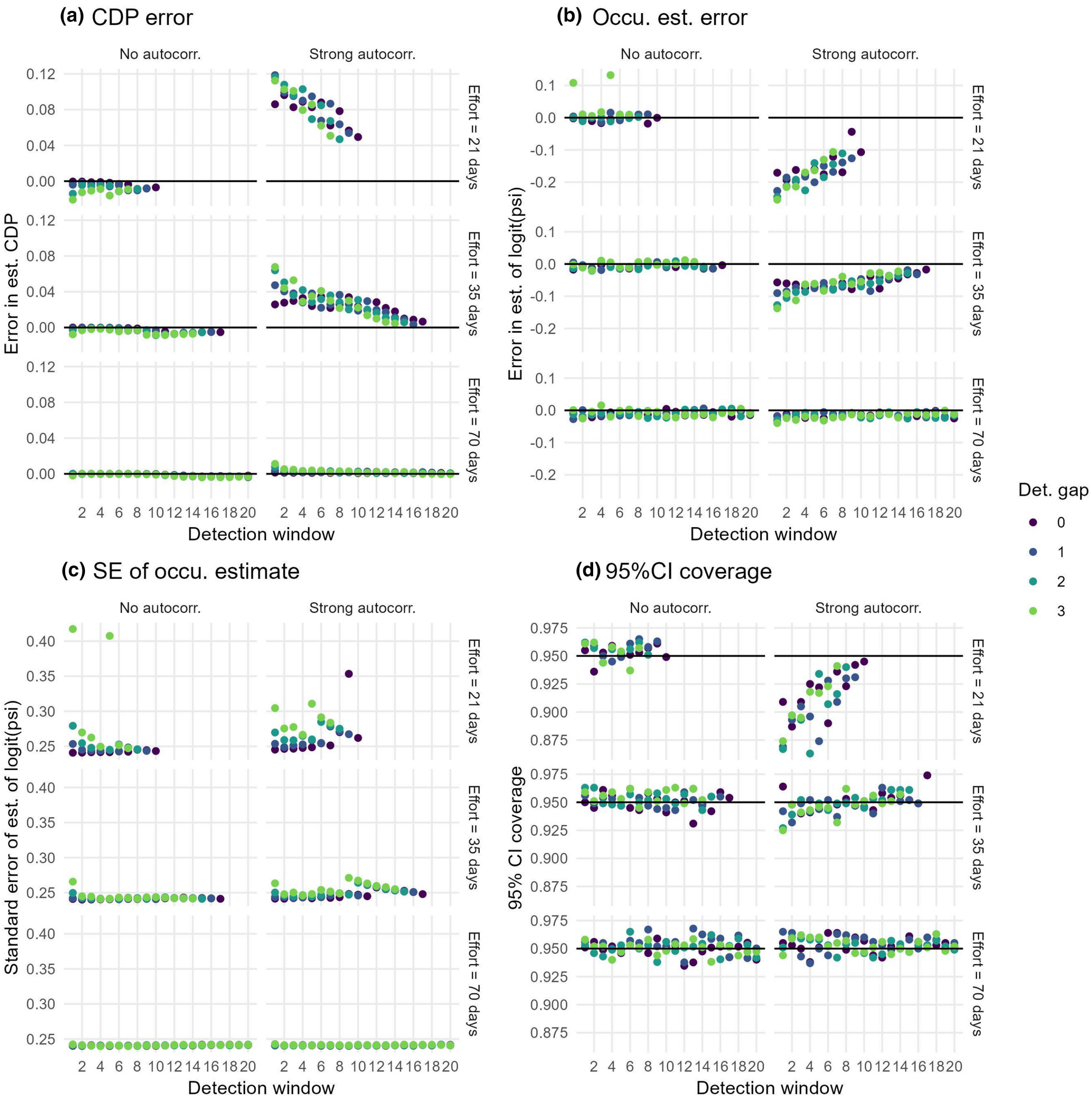

FIGURE 6 Consequences of varying the detection window and detection gap. All results come from data simulated under the parameters $\psi_0 = 0.4$, $p_0\overline{\theta} = 0.3$ and $\overline{\theta} / \pi_0 = 1$ at 80 sites. Note that errors in occupancy estimates are reported on the logit scale in this figure. (a) Increasing the detection window reduced error in estimated CDP and (b) error in the estimate of mean occupancy probability, while detection gaps had no meaningful effect on either. (c) Increasing the window increased standard error in the estimate of mean occupancy when autocorrelation occurred. Detection gaps also increased standard error. (d) In the most problematic simulation condition (low sampling and strong autocorrelation) the coverage of the 95% confidence interval was below 90%.

camera deployments were short. When true CDPs were close to 1 due to long sampling durations, bias was very small even when autocorrelation was strong.

To investigate autocorrelation in an empirical data set, we conducted a case study modelling the occupancy of 22 mammals based on detections from a camera trapping network across North America. We found evidence of 1-day temporal autocorrelation in these data in 20 of 22 species studied, suggesting that autocorrelated detections are present in camera trap data across a variety of taxa and life-history traits. Results were consistent with the simulation, where bias occurred in the occupancy intercept but not in the estimates of relative effects of covariates on occupancy. Bias in 1-day models was mostly mitigated by the use of longer (10-day) detection windows. Furthermore, 10-day models produced larger

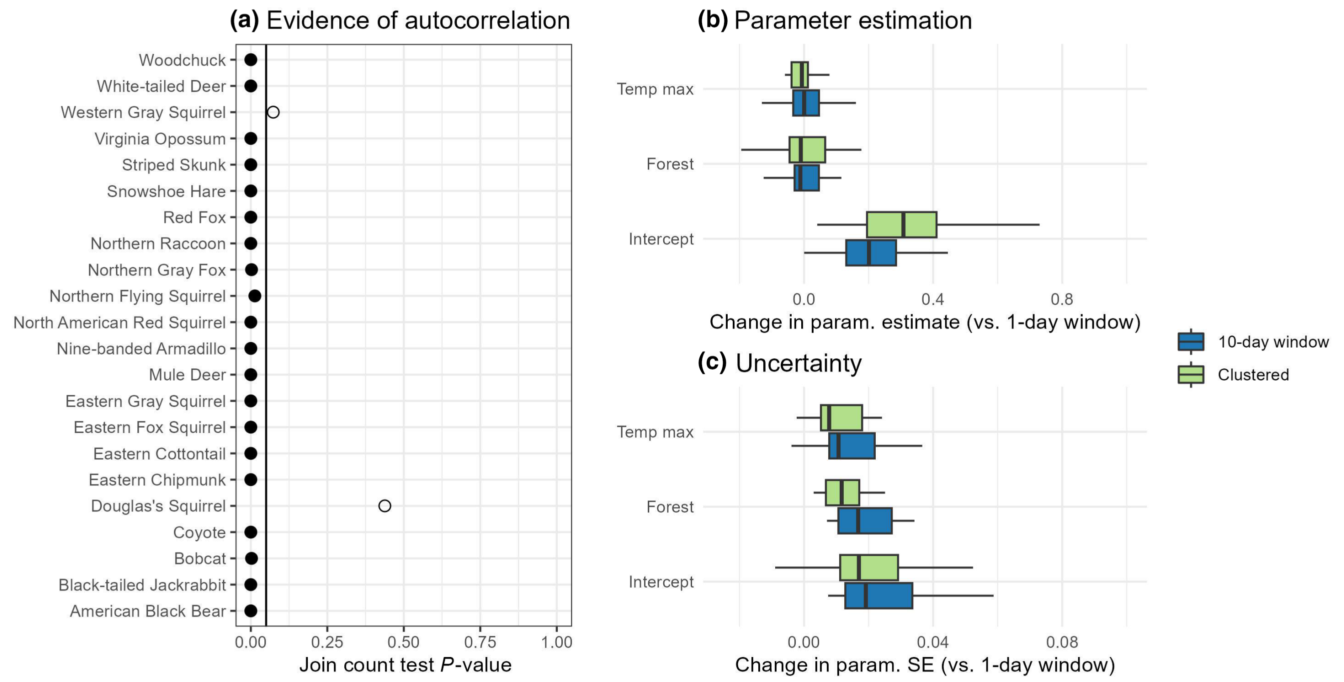

FIGURE 7 Results from a case study estimating occupancy with camera trap data from Snapshot USA. (a) Goodness-of-fit tests yielded evidence of autocorrelation in detections of 20/22 species. (b) Estimates of the occupancy intercept yielded by 10-day window site occupancy models (SOMs) and by the clustered model were higher than those produced by a 1-day window SOM. Point estimates of the effects of temperature and forest cover did not change. (c) Ten-day window SOMs and clustered models had higher uncertainty in model estimates, consistent with simulation results, where estimates based on larger detection windows were wider and more accurate.

estimates of uncertainty, comparable to those obtained from the clustered model. This suggests that, even when point estimates were unbiased, occupancy parameter estimates derived from SOMs with 1-day windows were overconfident.

Based on this work, we recommend that anyone seeking to estimate occupancy with camera trap or other continuous-time data consider the following recommendations.

1. Always check fitted SOMs for evidence of autocorrelation by applying the join count test (Wright et al., 2016). A p-value of less than 0.05 indicates strong evidence that autocorrelation is present, though it does not necessarily mean that occupancy estimates are biased. To aid in the uptake of this test, we provide an R function for applying it to an 'unmarked' fitted occupancy model object (see Supplemental Materials).
2. Use simulations to assess the degree of bias in occupancy estimates expected under different degrees of autocorrelation. For a given study, the most useful simulations will use the true number of sites and sampling days per site with reasonable values of occupancy and detection. We also provide a reference table that readers can use to cross-reference their data characteristics (Table S1).
3. If autocorrelation is present when using a 1-day window, and simulations indicate that meaningful bias might occur, reprocess your detection histories to maximize the length of the detection window. As a guideline, we propose windows of up to half the median deployment duration. If sampling is very long and variable across sites, a shorter window could be used to avoid losing information at sites with shorter deployments, such as half the duration of the 25th quantile of sampling durations.

These recommendations are applicable to any occupancy model fit to camera trap data with within-site temporal structure, including most SOM extensions (e.g. dynamic or community occupancy models). Most such extensions disentangle occupancy from detection based on the assumption that replicate detections at closed sites are independent. Consequently, autocorrelation within closed sites will lead to inflated CDP and estimates of occupancy that are biased downward. The use of the join count test to check for autocorrelation may be useful in such cases. Follow-up studies exploring the consequences of autocorrelated detections on inference from SOM extensions would be useful to provide additional guidance.

In many cases, such as in cases with large numbers of sites and low cumulative detection probabilities, estimating the clustered model directly may be a more straightforward strategy than reformatting data for use with the SOM. However, the clustered model is more complex and may produce more uncertain estimates with lower power to detect differences under typical sampling designs. Ultimately, the focus of this study was to evaluate the performance of the SOM, and further investigation into the performance of the clustered model is necessary.

The strategies we recommend are less effective in low-information contexts, so autocorrelation should be considered at the study design stage of research in addition to the analysis stage. If sampling is insufficient and few detections are generated, goodness-of-fit checks will have low power to detect autocorrelation and autocorrelation will result in greater relative bias. More complicated models that explicitly account for non-independent detections also perform worse in low-information contexts. Ideally, ecologists should sample for as long as is feasible under species-specific closure assumptions to maximize the true cumulative detection probability at each site. When longer deployments are infeasible, either due to pragmatic considerations or because of population closure assumptions, ecologists should consider using clustered or continuous time models, which may require sampling at more sites for useful inference and which may introduce additional computational obstacles (Guillera-Arroita et al., 2011; Hines et al., 2010; Pautrel et al., 2024). Furthermore, the recommendations we produce are not intended for studies where the primary goal is inference on the detection process. The detection window determines the scale at which detection effects may be interpreted. When conducting inference on detection, adjusting the size of the detection window may not be an appropriate solution. Ecologists aiming to conduct inference on the detection process from data containing autocorrelated detections should prioritize fitting models that give a better representation of the process of interest, that is, a model that explicitly estimates autocorrelation or one with a detection submodel in continuous time (Guillera-Arroita et al., 2011; Hines et al., 2010). We also note that different representations of temporal structure may fit certain data sets more or less well. Ecologists conducting inference on detection should test their findings for sensitivity to the choice of detection model or use model selection.

Observations of wildlife generated by camera traps and autonomous acoustic recorders are increasingly used to estimate animal occupancy (Furnas, 2020; Kays et al., 2020). Temporal nonindependence can occur in any study where detections are temporally structured; in camera trap data, they may arise due to animal movement, but in other contexts, autocorrelation could be driven by missing temporally structured covariates, time-series effects, or other unknown phenomena. Regardless of the cause, unmodeled nonindependence leads to understated uncertainties and can cause bias (Hurlbert, 1984). Here, we showed that temporal nonindependence in temporally structured data can lead to underestimation of occupancy when data are treated as arising from independent consecutive surveys, as is common in the literature. Practitioners applying old models to new methods should be vigilant for new sources of nonindependence and should seek out practical strategies for mitigating consequent bias.

AUTHOR CONTRIBUTIONS

Benjamin R. Goldstein and Krishna Pacifici initiated the study. Benjamin R. Goldstein processed all data, implemented all analyses, prepared all visualizations and wrote the first draft of the manuscript. All authors contributed to methodological development and review of the manuscript.

ACKNOWLEDGEMENTS

Benjamin R. Goldstein and Krishna Pacifici were supported by NSF grant 2206784. Alex J. Jensen, Roland Kays, Michael V. Cove, William J. McShea and Elizabeth M. Kierepka were supported by NSF grant 2206783. Roland Kays was also supported by NSF grant 2211768.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14359.

DATA AVAILABILITY STATEMENT

Code and data needed to reproduce all analyses are available on Github at https://github.com/dochvam/autocorr_occ_camtraps_reproducible and are archived on Zenodo at https://zenodo.org/doi/10.5281/zenodo.11199279 (Goldstein et al., 2024). This repository includes all R code used to generate simulated data and estimate models, as well as all Snapshot USA observations, covariate data and R code used in the case study.

STATEMENT ON INCLUSION

This study relied primarily on simulated data. As such, there was no data collection involved. In a case study, we used data from the Snapshot USA wildlife monitoring network. The author team includes leads and project coordinator of the Snapshot USA team, who worked closely with a network of regional experts across the United States to produce those data.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. A lookup table giving the estimated bias in the logitscale occupancy intercept, bias in the covariate effect, and RMSE, summarized by simulation conditions.

Table S2. Data summaries for 27 species included in the Snapshot USA case study exercise.

Figure S1. Characterizing the variability in detection windows used across 66 randomly selected camera trap studies of occupancy.

Figure S2. Error in estimating the occupancy intercept by the clustered occupancy model used to generate the data across simulation conditions.

Figure S3. Difference in RMSE between the clustered occupancy model and the 1-0 SOM across simulation conditions.

Figure S4. RMSE of SOM across simulation conditions and window sizes.

Figure S5. Bias in estimating the occupancy intercept across simulation conditions and window sizes.

Figure S6. Bias in estimating a coefficient on occupancy across simulation conditions and detection window sizes.

Figure S7. For a subset of system parameter levels, we extended the simulation to conditions with even greater numbers of sites and visits.

Figure S8. Standard error of the occupancy intercept estimate across simulation conditions and window sizes.
Figure S9. Error in estimating the cumulative detection probability across simulation conditions.
Figure S10. Rate at which the Wright et al. join count goodness-of-fit test indicated autocorrelated detections in data.

How to cite this article: Goldstein, B. R., Jensen, A. J., Kays, R., Cove, M. V., McShea, W. J., Rooney, B., Kierepka, E. M., & Pacifici, K. (2024). Guidelines for estimating occupancy from autocorrelated camera trap detections. *Methods in Ecology and Evolution*, *15*, 1177–1191. https://doi.org/10.1111/2041-210X.14359