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ARTICLE

Methods, Tools, and Technologies

Balancing detection probability and survey effort in multistate occupancy models: A camera trap simulation analysis

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Abstract

Camera trapping has become crucial in wildlife research, enabling detailed observations of elusive and nocturnal species with limited human interference. The use of occupancy modeling to analyze camera trap data is rapidly increasing, aiding in the assessment of species distribution, multispecies dynamics, and the presence of different states of a species (e.g., reproducing or non-reproducing), while considering imperfect detection. Multistate occupancy models, which capture these different states, are particularly effective tools. However, the design of camera trap studies—typically involving large grids with a limited number of cameras and animal observations—often results in sparse data and low detection probabilities, impacting model performance (e.g., convergence) and inference reliability (e.g., accuracy and precision) in basic occupancy models. The effect of these factors on more complex models (e.g., multistate occupancy models) remains largely unexplored. Here, we conducted a series of simulations with varying detection probabilities, numbers of sites, and survey periods for both single- and multistate occupancy models, to evaluate the impact of these factors on model performance and reliability. Our results revealed that multistate models require higher detection probabilities compared to the single-state models. Additionally, minimum needed detection probabilities decreased as the number of surveys increased for all models. Furthermore, the number of sites required was substantially higher for multistate models compared to single-state models. We conclude that when detection probabilities are low, occupancy models encounter difficulties in fitting and produce unreliable results. Strategies such as deploying clustered cameras, targeted camera placement (e.g., at frequent wildlife paths) or using bait to increase detection rates could be used to address these issues but may introduce other biases. The gained model performance from higher detection probabilities might outweigh these biases. Moreover, different data aggregation strategies in combination with increasing the length of the study can increase detection probabilities, addressing reliability issues; however, this is not always feasible due to time constraints (e.g., season-based research questions). This study highlights key thresholds and considerations for improving the use of multi-state occupancy models using camera trap data, aiding in the design of more effective wildlife research studies.

KEYWORDS
Bayesian, camera trap, hierarchical modeling, imperfect detection, jags, wildlife research

INTRODUCTION

Camera trapping has become a common technology in wildlife research, enabling detailed observations of species in their natural habitats without the need for direct human interaction (Delisle et al., 2021; Fisher, 2023). This technology has proven particularly valuable in the study of elusive and nocturnal species, where traditional observation methods fall short or are too cost-prohibitive (Wearn & Glover-Kapfer, 2019). Camera trap data are often used to estimate species abundances, distributions, and to analyze habitat selection. However, key challenges arise when using these data, primarily due to imperfect detection. Imperfect detection occurs when not all animals present at a location are captured by the camera traps. This issue typically arises from low survey efforts, where a limited number of camera traps with short deployment durations, narrow view angles, and restricted detection distances sample only small parts of the spatial landscape (Burton et al., 2015; McIntyre et al., 2020; O'Connor et al., 2017). Not properly accounting for imperfect detection could lead to biased inference and thus faulty conclusions (Burton et al., 2015).

Occupancy modeling has gained popularity as a solution, as it explicitly accounts for imperfect detection, thereby allowing for more accurate estimates of species abundance and distribution (Burton et al., 2015; Rovero & Zimmerman, 2016). However, parameterization of occupancy models using camera trap data could be hindered by the data sparsity that results from the combined influence of imperfect detection and low survey effort. In these studies, camera traps are distributed across larger grid cells (hereafter "sites"), each containing one or more sampling locations (Burton et al., 2015). Grid cell sizes are often arbitrarily chosen because they do not correspond well to the actual field of view of the camera, which is often much smaller than the grid cell (as discussed in Efford & Dawson, 2012; Steenweg et al., 2018). This leads to sparse datasets with infrequent repeated detections at occupied sites and across survey periods (Survey period is defined as the discrete time interval [e.g., hours, days, or weeks] across the total survey duration/length, during which detection/non-detection data are collected). Additionally, for species with larger home ranges, this results in high occupancy estimates and low detection probabilities (the likelihood of detecting a species during a survey period, conditional upon the site being used) because occupancy is interpreted as the "use" of a site, and these species use multiple sites, albeit rarely (MacKenzie et al., 2017; Mackenzie & Royle, 2005; Steenweg et al., 2018). Consequently, the resulting low detection probabilities in combination with a limited number of sites affect the accuracy of occupancy estimates of species (Kéry & Royle, 2020; Pautrel et al., 2024; Steenweg et al., 2019). Namely, data sparsity could lead to biased and unstable parameter estimates and put constraints on the number of parameters that can reliably be estimated (Guillera-Arroita et al., 2010; Royle & Dorazio, 2008). Low detection probabilities are a well-documented challenge in occupancy modeling; detection probabilities below 0.2 often lead to significant biases and convergence issues, even in the simplest single-state models (Delisle et al., 2023; Guillera-Arroita et al., 2010; Kéry & Royle, 2015; Mckann et al., 2013; Pautrel et al., 2024; Steenweg et al., 2019). These issues highlight the importance of understanding how study design (e.g., survey length, size of a site, number of cameras, and number of sites) and model complexity (e.g., number of identifiable parameters) influence the statistical power of occupancy modeling, the reliability of parameterization and thus the robustness of the ecological inferences that can be drawn from such studies.

Expanding basic occupancy models (i.e., single-season two-state [presence–absence] models sensu MacKenzie et al., 2017) to more complex specifications, such as multistate, multispecies, or community models (e.g., Fidino et al., 2019; Nichols et al., 2007; Rota et al., 2016) introduces additional layers of complexity. These models capture more nuanced ecological patterns than basic occupancy models by accounting for various occupancy states (e.g., unoccupied, non-reproducing, reproducing; Nichols et al., 2007) or analyzing spatiotemporal patterns (e.g., unoccupied, occupied by day, occupied by night, or occupied in both; Rivera et al., 2022). However, the increased complexity of these models can elevate the existing issues associated with occupancy models. Multistate models require the estimation of additional parameters for each state, such as those accounting for potential misclassification in the detection process between different states (Nichols et al., 2007). Additionally, estimating habitat relationships through covariates, a practice almost always employed when using occupancy models, can become complicated in multistate models. Covariates help explain the variations in detection and occupancy across sites and can also be used to predict occupancy in unsampled locations. However, in multistate models, where different occupancy states are often conditional upon one another, the inclusion of covariates can complicate parameter estimations. For basic occupancy models, Kays et al. (2020) suggested that with 60 sites, most covariate relationships could reliably be estimated. However, for multistate models, similar information is lacking. This added complexity of multistate models, both for the detection process and covariate relationships, may make estimating detection probabilities and habitat associations more challenging.

In most basic occupancy models, the detection probability parameter is estimated based on individual survey periods. Simulation studies for basic occupancy models have shown that detection probabilities above 0.2 are required for reliable model estimation (i.e., consistency of accurate results across multiple analyses; Kéry & Royle, 2015). However, detection probabilities based solely on individual survey periods are not the only factor influencing model reliability. Guillera-Arroita et al. (2010) revealed that increasing the overall survey length, while keeping survey period constant, can still result in reliable basic models with detection probabilities below 0.2. This is reflected by the cumulative detection probability ($p*$), which reflects the likelihood for detecting a species at least once over the entire survey length. Consequently, this means that the required survey length is directly related to the chance of detecting an individual during a survey period. For basic occupancy models, $p*$ should be >0.9 for maximum reduction in bias (Guillera-Arroita et al., 2010; Mckann et al., 2013). In basic models, $p*$ is calculated by $1-(1-p)^J$, where p represents the detection probability, and J represents the number of survey periods. However, in multistate models, the calculation of $p*$ becomes less straightforward, as detection probabilities are subdivided into a complex conditional matrix reflecting the various states of occupancy (MacKenzie et al., 2017; Nichols et al., 2007). The current knowledge of model functioning given detection probability thresholds, number of sites, and required survey length is based on various parameterizations of basic occupancy models, but for more complex model specifications (e.g., multistate or multispecies models), this is yet to be explored (but see recent efforts of Cowans et al., 2024 exploring similar issues for co-occurrence occupancy models). Given that these more advanced models are increasingly applied in wildlife research (Rozylowicz et al., 2024), and given increased model complexity can hamper model performance and affect the accuracy and precision of resulting inferences, addressing this knowledge gap is important for assuring the performance and reliability of these methods in real-world ecological studies.

Given the complexity introduced by multistate models, we hypothesize that, everything else being equal, (1) multistate occupancy models require higher detection probabilities than basic occupancy models to produce reliable estimates; (2) the number of sites needed to accurately estimate habitat relationships is substantially higher for multistate models due to the additional parameters and conditional dependencies; and (3) increasing the number of survey periods reduces the required minimum detection probabilities for both basic and multistate models. To address these hypotheses, we conducted a series of simulations with varying detection probabilities, numbers of sites, and survey periods. These simulations were analyzed using both multistate and basic occupancy models, with and without a covariate, to evaluate the impact of these factors on model accuracy and reliability. Accuracy was assessed as the bias in parameter estimates relative to the known values from the simulated "true" system, while reliability was measured by the consistency of these estimates both across replicates and across detection probability scenarios. By comparing the performance of multistate and basic models under different scenarios, we aim to provide a clearer understanding of the required data that are necessary for applying these models in wildlife research. This study serves as a reference for designing future studies using camera traps to model occupancy for multiple states while highlighting key considerations for obtaining reliable ecological inferences.

METHODS

Multi state occupancy modeling framework

Model structure

For this simulation study, we used both a hierarchical basic occupancy model as described by MacKenzie et al. (2002) and a multistate model that was structured as a hierarchical, multistate occupancy model with four states, akin to the model described by Nichols et al. (2007) and implemented in BUGS by adjusting code from a three-state model by Kéry and Royle (2020, Volume 2; Chapter 6). For this simulation study, we used the Eurasian moose (*Alces alces*) as an example species that can produce twins to focus on multiple states, particularly multiple reproductive states. However, this model can be applied to various study systems, including other wildlife species, such as birds with different nesting stages or amphibians with multiple developmental stages (Kéry & Royle, 2020; MacKenzie et al., 2017). The multi-state model we use for this simulation is a single-season multistate model with four states. The multistate model is detailed below (Figure 1), while the basic model is implemented directly from Kéry and Royle (2020, Volume 1; Chapter 10). All models used for simulation, along with the code and implementation details, can be found in a repository for further reference (Osinga et al., 2025).

The multistate model considers a total of four states, with one state representing unoccupied sites and the other three representing occupied sites with varying reproductive outcomes. The probability of site occupancy

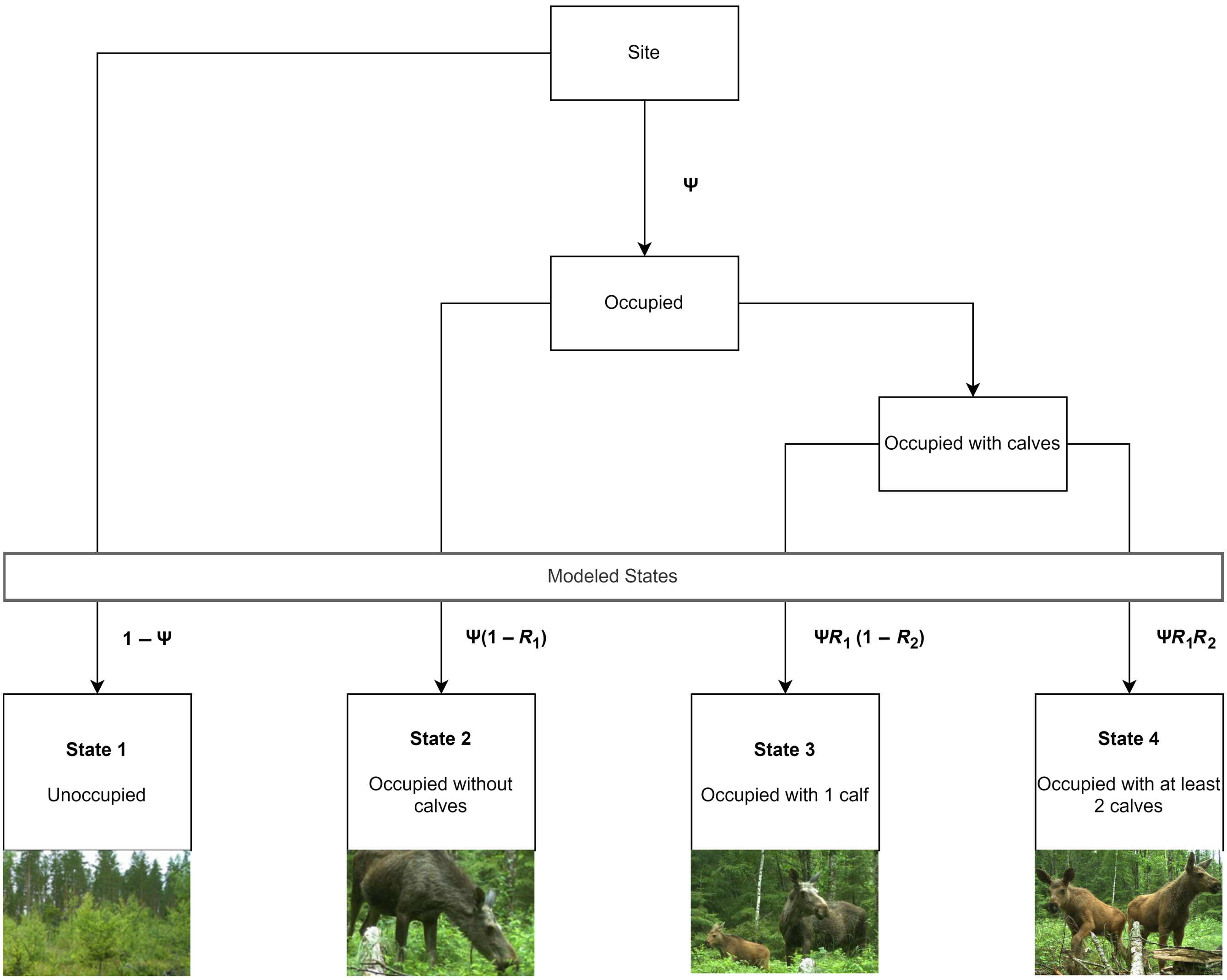

FIGURE 1 The structure of the multistate occupancy model used in this study, indicating dependencies and probability parameters. Ψ indicates the probability of site occupancy, whereas $1 - \Psi$ indicates the probability of a site not being occupied. The formulas (at state 2–4) indicate the probability of each of the states (see text and Equation 1 for elaboration). Image credit: Tim Hofmeester.

(Ψ) is the foundational layer, upon which the reproductive states are conditional. These states are represented as $\Omega_s[m]$, where m indexes the specific state. The R coefficients determine the relationship between the states (Equation 1).

$$\Psi_s = \Pr(\text{Occupied}) = \Omega_s[2] + \Omega_s[3] + \Omega_s[4]. \tag{1}$$

$$\Omega_s[m] : \text{Probability of each state (m) per site.}$$

$$\Omega_s[1] = \Pr(\text{Not occupied}) = 1 - \Psi_s.$$

$$\Omega_s[2] = \Pr(\text{Occupied without calves}) = \Psi_s\left(1 - R_s^1\right).$$

$$\Omega_s[3] = \Pr(\text{Occupied with 1 calf}) = \Psi_s R_s^1\left(1 - R_s^2\right).$$

$$\Omega_s[4] = \Pr(\text{ Occupied with} > 1 \text{ calf}) = \Psi_s R_s^1 R_s^2.$$

In this simulation study, we modeled the occurrence of a species (in this case moose) across a network of camera traps sampled over a specified timeframe to understand the distribution of multiple states and detection patterns. Specifically, we conducted a series of surveys across distinct sites to collect categorical data (i.e., the state; Equation 1). For each site s, ranging from 1 to S sites, we carried out J surveys, where j spans from 1 to J and stored the observations in an S by J matrix $\mathbf{Y}$. The latent true state Z_s, was modeled at each site during each survey using a categorical distribution, with the probabilities of each state defined by $\boldsymbol{\Omega_s}$ (Equations 2 and 3).

$$\Omega_s = \left[(1 - \Psi_s), \Psi_s\left(1 - R_s^1\right),\ \Psi_s R_s^1\left(1 - R_s^2\right), \Psi_s R_s^1 R_s^2\right]. \tag{2}$$

$$Z_s \sim \text{Categorical}(\boldsymbol{\Omega}_s). \tag{3}$$

As part of our simulation, we also included a covariate in our models. Specifically, we modeled the influence of an environmental and site-specific covariate on state occupancy ($\boldsymbol{\Omega_s}$) using hierarchical multinomial logit functions (Equations 4–6). In the models with a covariate, the relationships were represented by the following equations:

$$\text{logit}(\Psi_s) = \beta_{\Psi,0} + \beta_{\Psi,1} \times X_{1,s} + \ldots + \beta_{\Psi,r} \times X_{r,s} \tag{4}$$

$$\text{logit}(R1_s) = \beta_{R_1,0} + \beta_{R_1,1} \times X_{1,s} + \ldots + \beta_{R_1,r} \times X_{r,s} \tag{5}$$

$$\text{logit}(R2_s) = \beta_{R_2,0} + \beta_{R_2,1} \times X_{1,s} + \ldots + \beta_{R_2,r} \times X_{r,s} \tag{6}$$

where $X_{r,s}$ represents the covariate matrix and r indicates the specific covariate for each site s. $\beta_{r,s}$ represent the slopes of the relationship with these covariates, $\beta_{0,r}$ is the intercept for each model providing a baseline of state occupancy.

To account for missing detections and misclassifications, the model incorporates detection probability (Θ), which reflects the likelihoods of detecting an observed state given the true latent state. The detection probabilities were kept constant across sites and surveys for simplicity. The detection matrix (Equation 7) presents the probability of detection based on the latent state $z_{[s]}$, where each row represents an observed state (j), and each column corresponds to a modeled latent state (z); both ordered from state 1 to state 4. The values within the matrix indicate the probability of detecting an observed state given the modeled latent state.

$$\Theta = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1 - p^{1,1} & p^{1,1} & 0 & 0 \\ 1 - \left(p^{2,1} + p^{2,2}\right) & p^{2,1} & p^{2,2} & 0 \\ 1 - \left(p^{3,1} + p^{3,2} + p^{3,3}\right) & p^{3,1} & p^{3,2} & p^{3,3} \end{bmatrix}. \tag{7}$$

Here, $p^{z,j}$ represents the probability of detection of an observed state j given the latent true state z.

$$\boldsymbol{y}_{s,j} \sim \text{Categorical}\left(\Theta, z_{[s]}\right). \tag{8}$$

The latent state $z_{[s]}$ and the accompanying detection probabilities (Θ) are then combined to model the observation state through Equation (8).

The full commented model codes can be found in our repository (Osinga et al., 2025).

Simulation and power analysis

Simulation design

In this simulation study, we varied the number of sites and survey periods for both basic and multistate occupancy models to test what minimum detection probabilities were required to derive estimates of occupancy close to the true state, as well as estimate accurate covariate relationships. The simulations were conducted both with and without a covariate, depending on the scenario. For the models where we varied the number of sites, we included covariate models and models with no covariates, while for the models where we varied the number of surveys, we focused only on models without covariates.

We simulated data for five different numbers of sites between 60 and 1000 (Table 1), to assess how the number

TABLE 1 Summarizing model scenarios run; combination of these scenarios resulted in a total of 380 distinct model parameterizations.

Model type	No. sites	No. surveys	Covariate	Detection probability	No. model scenarios
Basic	60, 120, 240, 500, 1000	7, 14, 35	Yes	0.001, 0.005, 0.01, 0.05, 0.1, 0.2, 0.3, 0.5, 0.7, 0.9	150
Basic	60	35, 70, 140, 280	No	0.001, 0.005, 0.01, 0.05, 0.1, 0.2, 0.3, 0.5, 0.7, 0.9	40
Multistate	60, 120, 240, 500, 1000	7, 14, 35	Yes	0.001, 0.005, 0.01, 0.05, 0.1, 0.2, 0.3, 0.5, 0.7, 0.9	150
Multistate	60	35, 70, 140, 280	No	0.001, 0.005, 0.01, 0.05, 0.1, 0.2, 0.3, 0.5, 0.7, 0.9	40

of sites impacts model performance, especially in the context of multistate models, which we hypothesize require more data to detect covariate relationships accurately. The number of survey periods varied across six levels, between 7 and 280 surveys (Table 1), to evaluate how an increasing number of surveys influences detection probability and occupancy estimates. We followed recommendations from Kays et al. (2020) for our minimum values for both the number of sites and the number of surveys (where we assumed the grouping of multiple days into single surveys often used in camera trapping studies), as these should ensure reliable covariate relationships and accurate occupancy estimates for the basic model.

For the covariate model, we simulated occupancy states across a landscape gradient, using the covariate to predict occupancy probabilities for each state. The landscape covariate was uniformly distributed and scaled between −2 and +2, applied using a linear model on the logit scale with fixed regression coefficients. For the basic model without covariates, we set the baseline occupancy (Ψ) at 0.6. In the multistate models without covariates, occupancy probabilities were determined by fixed parameters for Ψ (0.6), R_s^1 (0.5), and R_s^2 (0.2; see Equation 1). Each simulation retained the same sequence of 'true states' across different detection probability settings to ensure consistency.

We modeled 10 different detection probabilities ranging from 0.001 to 0.9 ($p^{1,1}$, $p^{2,2}$, $p^{3,3}$; Table 1) for all models. In the multistate models the misclassification probabilities were held constant at 0.05 ($p^{2,1}$, $p^{3,1}$, $p^{3,2}$). For each detection probability scenario, we generated at least 100 datasets for the simulations without a covariate, and 260 datasets for the simulations with one covariate, each sampled from the occupancy matrix $\mathbf{\Omega}_{s,\text{state}}$ (Equation 1) and the detection matrix $\Theta_{p[i]}$ (Equations 7 and 8).

Statistical modeling

The simulation data were analyzed using JAGS (Just Another Gibbs Sampler; ver. 4.3.2; Plummer, 2003) in R (ver. 4.4.1; R Core Team, 2024) utilizing the jagsUI package (ver. 1.6.2, Kellner, 2024). We applied Bayesian occupancy models in JAGS to estimate the multiple states of occupancy, accounting for both direct detections and misclassification errors. For covariate models, we examined the relationship between a landscape covariate and the occupancy state(s). For basic occupancy models, we estimated posterior distributions of the parameters over 25,000 iterations, with the first 12,500 discarded as burn-in. Since multistate models are hard to fit, we ran 50,000 iterations discarding the first 32,500 iterations as burn-in. Each model was run across three chains, and a thinning rate of five was applied to avoid autocorrelation. Convergence of the occupancy models was assessed using the Gelman–Rubin statistic ($\widehat{R}$). Models were considered to converge if $\widehat{R} \geq 1.1$ for all parameters. Model specifications, including priors for the fixed effects (i.e., intercept and slope for the landscape covariate) and the detection probabilities, are fully detailed in the model script available in the repository (Osinga et al., 2025).

Model performance was assessed using three metrics: (1) the detection probability at which the model reached stability, (2) the bias at that point, and (3) the SD at that point. Stability was defined, for each parameter across all replications, as the point at which both the bias and the SD of the posterior summary changed by no more than 10% or 0.05 between successive detection probability scenarios, relative to their respective values at a detection probability of 0.9. For example, if the final model ($p = 0.9$) had a bias and SD of 1, stability was considered reached when two consecutive model scenarios produced bias and SD values between 0.9 and 1.1. The absolute threshold (0.05) was included to prevent declaring instability based on very small values, where even minor numerical differences could exceed the 10% criterion.

RESULTS

Simulation results

The effect of survey length

As expected, increasing the number of surveys decreases the required detection probabilities for reliable inference (Figure 2). Basic and multistate models behaved similarly with increasing detection probabilities and number of survey periods. Most parameters for both models reached

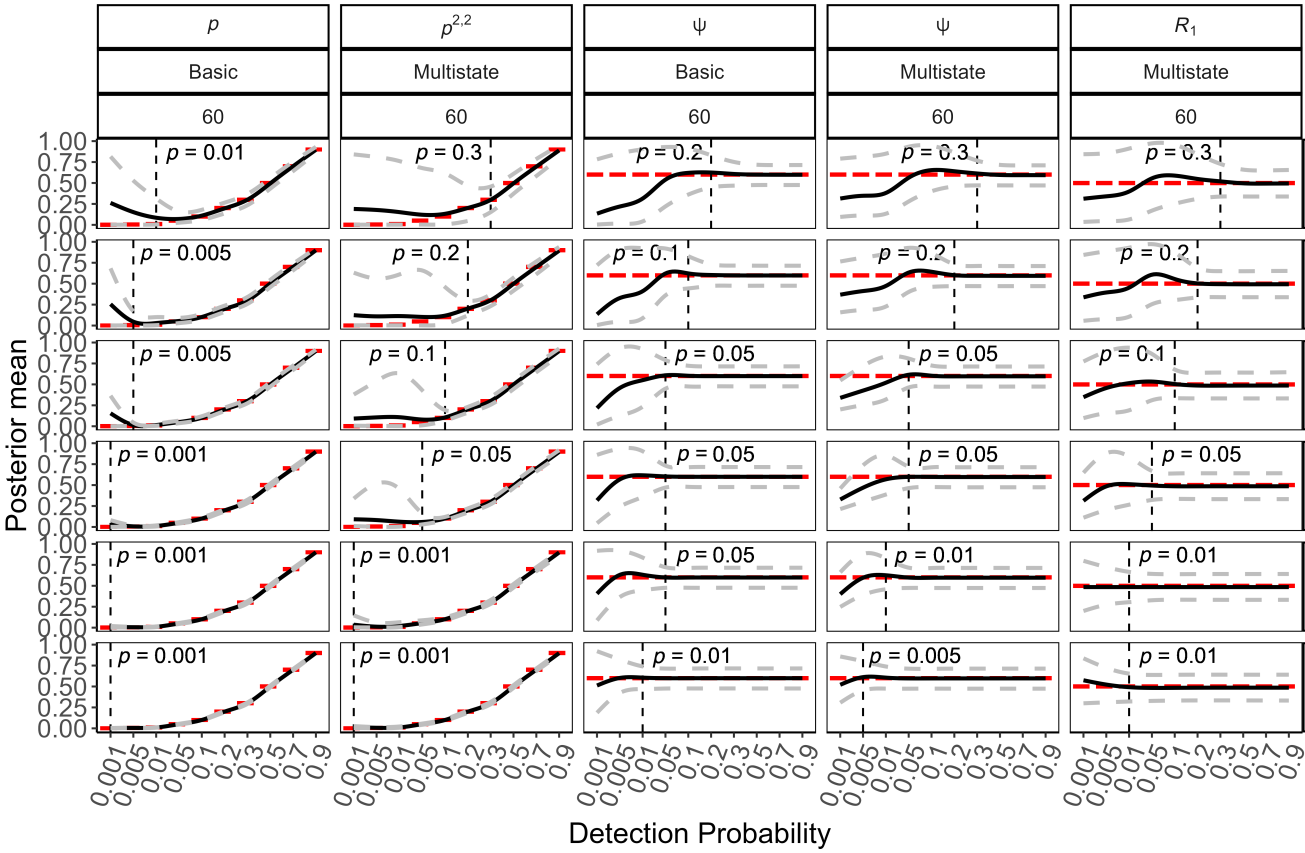

FIGURE 2 The average posterior estimates for the means and 95% credible intervals across 260 simulations from both the multistate and basic models (without covariates) are shown for a selection of fitted parameter (*y*-axis). These simulations were conducted across six different numbers of survey periods (7, 14, 35, 70, 140, and 280; rows) with 60 sites. The *x*-axis represents 10 different simulation scenarios with varying detection probabilities. The gray dashed lines indicate the average upper and lower credible intervals, while the solid black lines show the average mean posterior estimates. Horizontal red lines represent the true parameter values used in the simulations. The vertical lines indicate where the model converged to a stable average estimate. See the model description in *Methods* for an explanation of the different parameters.

model stability at detection probabilities between 0.2 and 0.5 with 7 surveys, decreasing to between 0.01 and 0.001 with 280 surveys. Notably, multistate occupancy models required higher detection probabilities to obtain reliable results compared to basic models, particularly for multistate parameters (e.g., R^2 and $p^{3,3}$; Figure 2). These trends were consistent across most fitted parameters (Appendix S1: Section S1). Once basic models without covariates reached stability, they exhibited minimal bias (bias <0.003) and low SD (<0.06). For multistate models, these were higher for both metrics (bias <0.04, SD < 0.1; Appendix S2: Table S1).

Multistate models were generally more unstable in their detection estimates compared to basic models, particularly at lower detection probabilities, but especially detection parameters associated with occupancy state 4 ($p^{3,1}$, $p^{3,2}$, $p^{3,3}$). These were unstable even at the highest detection probability (0.9) for several simulations (Appendix S1: Figure S2).

Model convergence in terms of MCMC diagnostics was generally robust, with fewer than 5% of models failing to converge, even at the detection probabilities as low as 0.001 in models without covariates (Appendix S1: Figures S1 and S2). This indicates that the MCMC chains generally mixed well and reached stationarity, even at low detection probabilities. Importantly, this suggests that the biases observed at low detection probabilities were not due to a lack of iterations within the MCMC algorithm but instead arose from high uncertainty in the estimates (large variation between simulations; see Appendix S1) and potential parameter non-identifiability under simulation scenarios with low detection probabilities.

The effect of the number of sites

The simulation of the covariate models produced similar results to the simulation without covariates regarding detection and occupancy estimates. Both basic and multistate models reached stability at a detection probability of 0.2 (Figure 3). Once the basic models stabilized, they showed minimal bias in occupancy estimates for 60 sites (bias <0.01, SD < 0.8), which decreased further when the number of sites increased to 1000 sites (bias <0.002, SD < 0.2), thus aligning closely with the values of the simulated "true" system (Appendix S2: Table S2). Credible intervals for basic models were narrow for all parameters when model stability was reached, indicating a high degree of confidence in the parameter estimates (Appendix S2: Table S2).

However, when multistate models stabilized at a detection probability of 0.2, notable bias remained in the regression coefficients, with a positive bias of 3.2 for β_{R_2} at 60 sites (SD = 3.24), which decreased to 0.13 for 1000 sites (SD < 0.5; Figure 3; Appendix S2: Table S2). This highlights that increasing the number of sites reduces the bias and SD of these parameters. While all multistate models that reached stability correctly identified the direction of the covariate effect, the magnitude of the effect sizes had significant bias and uncertainty. Importantly, once stabilized, the true values did fall within the 95% credible intervals, indicating that despite the overestimation in the posterior means, the uncertainty was appropriately captured.

Model convergence in terms of MCMC diagnostics was substantially worse for covariate models. Basic models performed well with detection probabilities of >0.05. However, multistate covariate models with detection probabilities <0.1 had over 50% convergence failure (Appendix S1: Section S2). Multistate covariate models with detection probabilities >0.1 were generally robust with fewer than 5% of the models failing to converge (Appendix S1: Section S2). Increasing the number of iterations from 50.000 to 70.000 resulted in little improvement in convergence and no reduction in bias; it only resulted in several very uncertain simulations to reach MCMC convergence.

Combined effect of sites and surveys

Increasing the number of sites to 500 or 1000 slightly reduced the minimum detection probability required for

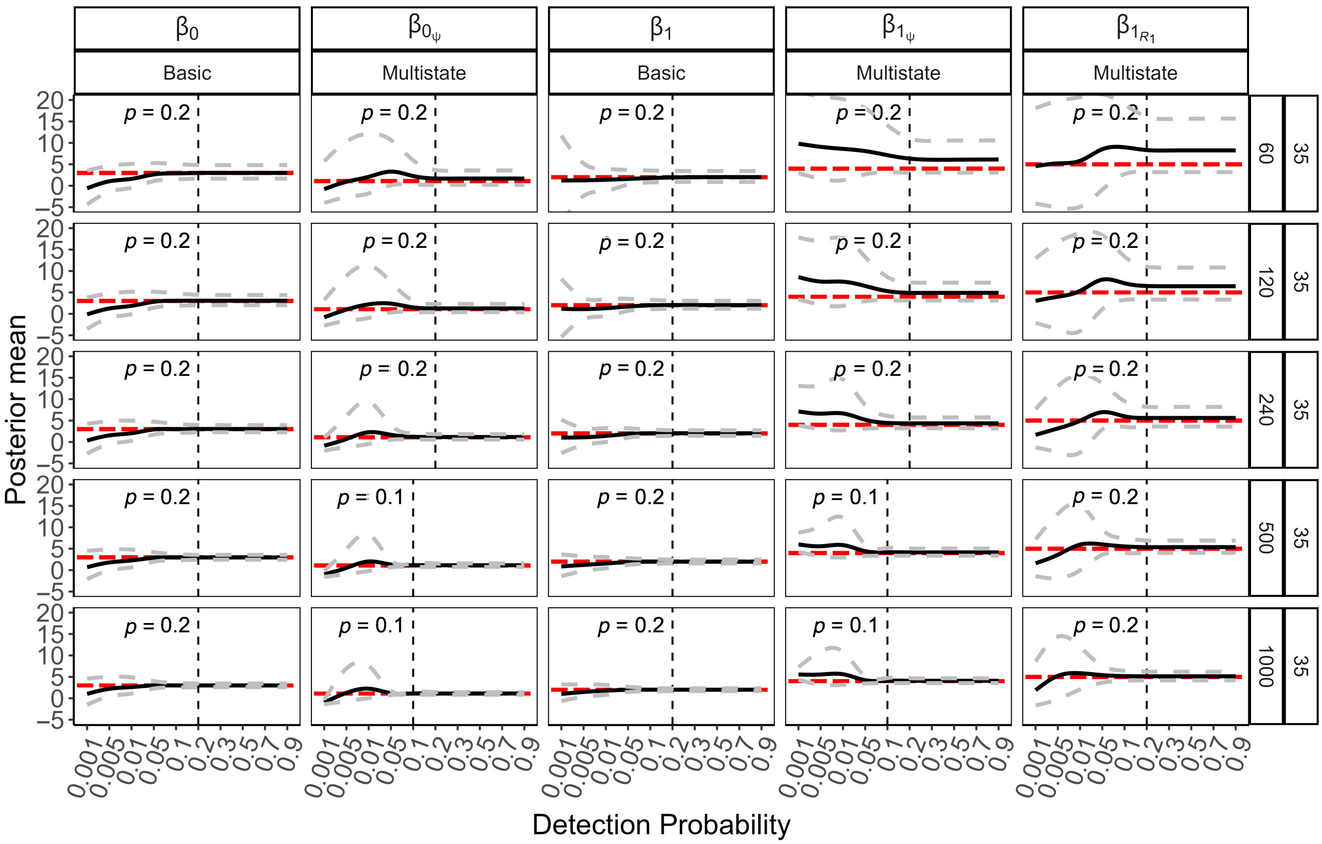

FIGURE 3 The average posterior estimates for the mean and 95% credible intervals across 260 simulations from the multistate and basic covariate models for 60, 120, 240, 500, and 1000 sites (rows) with 35 surveys shown for a selection of fitted parameter (y-axis) across 10 different simulation scenarios with varying detection probabilities (x-axis). The gray dashed lines represent the average upper and lower credible intervals, while the solid black line represents a smooth function through the mean posterior estimates. The horizontal red line indicates the true parameter values used in the simulations. The vertical dashed lines indicate when the model converged to a stable average estimate. See the model description in *Methods* for an explanation of the different parameters.

parameter stability (Figure 3), likely due to improved model fit. In some cases, models with 35 survey periods showed parameter stabilization at detection probabilities as low as 0.1 (Figure 4), rather than the previously observed threshold of 0.2 (Figure 3). However, this effect was not consistent across all parameters. Importantly, reducing the number of survey periods continued to necessitate higher detection probabilities, often exceeding 0.5, to achieve reliable parameter estimates.

DISCUSSION

Multistate occupancy models are increasingly used in ecological studies using camera traps to study, for example, patterns in reproductive status and spatiotemporal patterns in species occurrence. However, simulation studies identifying the sampling effort needed to achieve reliable estimation in these complex models are currently lacking. We therefore simulated a variety of scenarios to examine the combined impact of detection probabilities, ranging from low to high, and varying numbers of survey periods and sites on the fitting of basic and multistate occupancy models. These simulations aimed to establish the minimum detection probability, number of sites, and surveys required to ensure reliable model performance. Our findings suggest that detection probabilities must exceed 0.2 for multistate occupancy models to perform well when using around 35 survey periods. Increasing the number of survey periods decreased the required detection probability; with 280 survey periods, a detection probability of 0.05 was required for obtaining reliable results. As hypothesized, when holding the number of sites constant, more complex multistate models require a higher detection probability compared to the simpler, basic models (Figure 2). Additionally, our second

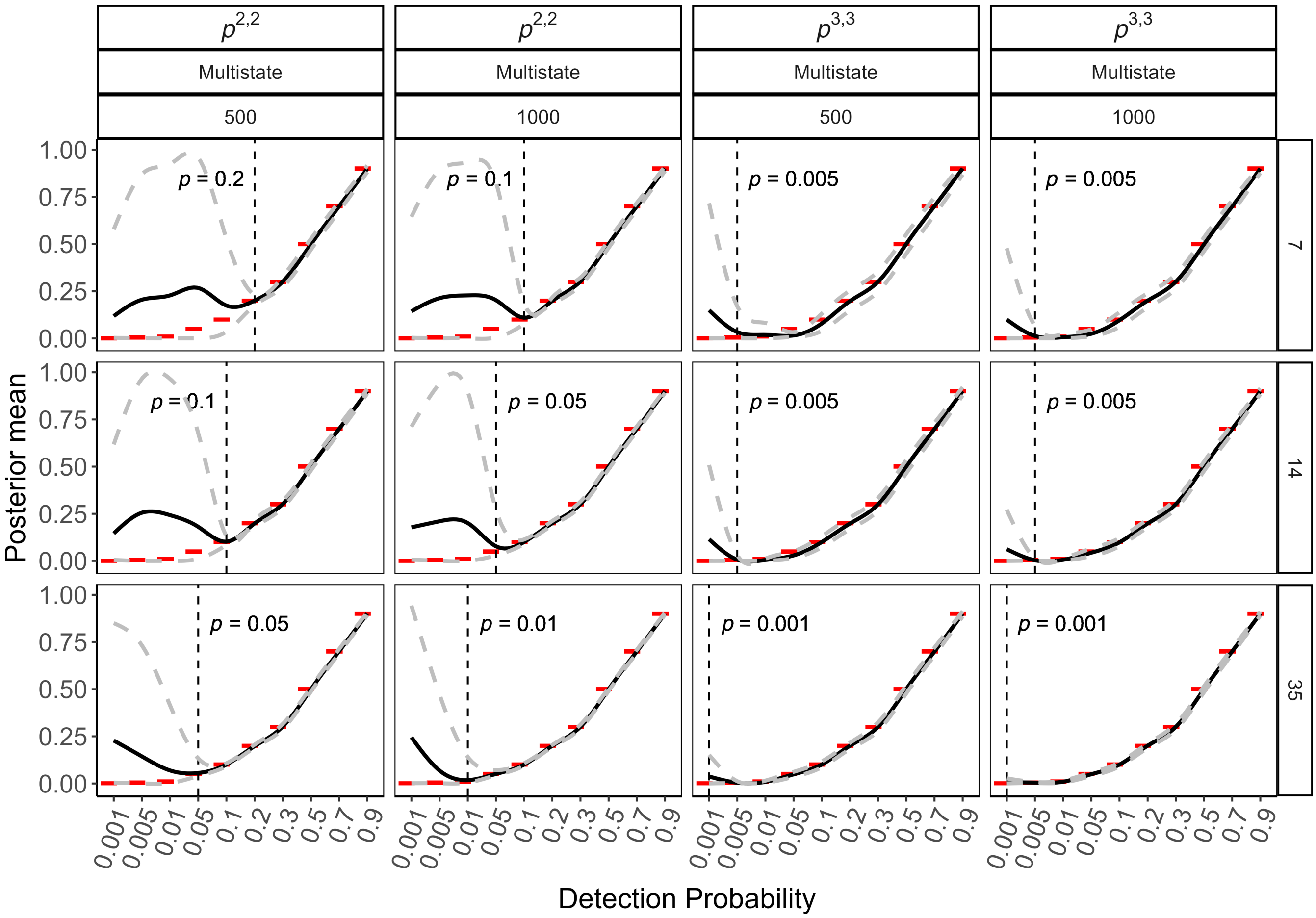

FIGURE 4 The average posterior estimates for the mean and 95% credible intervals across 260 simulations from the multistate and basic covariate models for 500 and 1000 sites (columns) with 7, 14, 35 survey periods (rows) shown for a selection of fitted parameter (y-axis) across 10 different simulation scenarios with varying detection probabilities (x-axis). The gray dashed lines represent the average upper and lower credible intervals, while the solid black line represents a smooth function through the mean posterior estimates. The horizontal red line indicates the true parameter values used in the simulations. The vertical dashed lines indicate when the model converged to a stable average estimate. See the model description in *Methods* for an explanation of the different parameters.

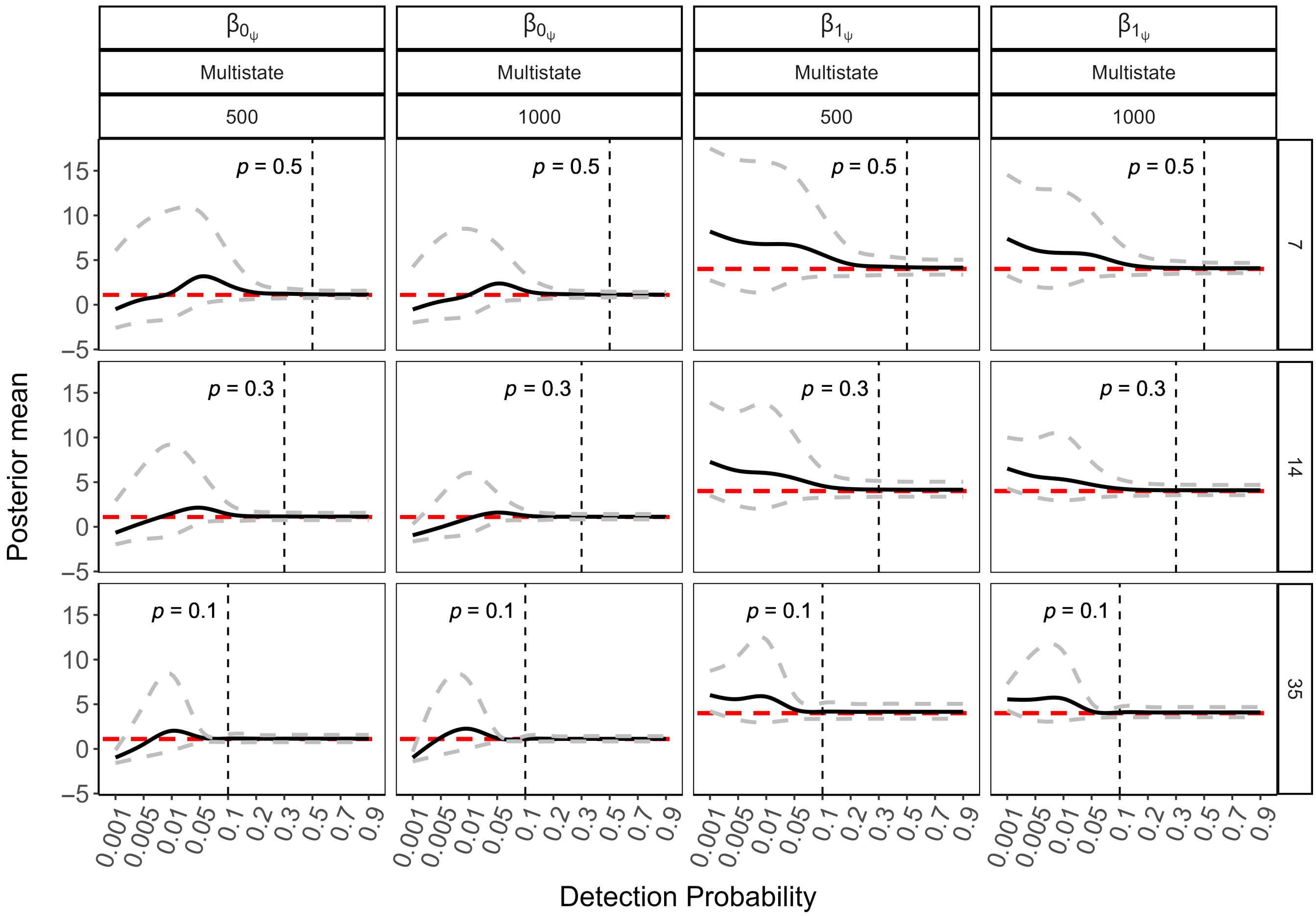

FIGURE 4 (Continued)

hypothesis was supported: multistate occupancy models need significantly more sites compared to basic models to accurately estimate covariate relationships (Figure 3). Furthermore, the compensating effect of the increased number of surveys resulted in a lower minimum detection probability needed in multistate models, similarly to what we hypothesized. This effect was less explicit in basic models, as for detection parameters these models already functioned at lower detection probabilities (Figure 2). Furthermore, all models with detection probabilities <0.05 did not give reliable results even with 280 survey periods. Given that achieving a high number of sites and a high number of survey periods or high detection probabilities can be challenging in camera trap studies, we suggest that all mentioned aspects should be carefully considered during the design of multistate occupancy studies.

It is important to note that the required detection probability can be influenced by the occupancy probability (Guillera-Arroita et al., 2010; Mackenzie & Royle, 2005), which was held constant at around 0.6 in this study, a value commonly observed for many species detected by camera traps (e.g., Hofmeester et al., 2021; Rich et al., 2016; Steenweg et al., 2019; Wevers et al., 2021). Contrary to what one might expect, when occupancy increases in basic models, a higher detection probability is required to get confident estimates (Mackenzie & Royle, 2005; Steenweg et al., 2019). We ran some initial simulations testing the effect of occupancy on multistate model functioning and noticed that, contrary to what is known about basic occupancy models, lower occupancy values ($\Psi = 0.1 - 0.3$) substantially reduced model precision, especially for multistate parameters (e.g., R^1 and R^2); results not shown, but see repository (Osinga et al., 2025). This might be the result of data scarcity as detections are spread across multiple states, making the number of sites the factor limiting performance rather than detection. Furthermore, we expect that fitting covariate relationships for models with low occupancy will be even more challenging for areas with low occupancy without many sampling sites (>1000). We encourage further studies on the relationship between occupancy probabilities, detection probabilities and model performance for rare species, especially for multistate covariate models. Additionally, we strongly recommend researchers planning multistate occupancy studies to conduct pilot studies and perform simulations based on these pilot data. This approach can provide tailored information to their specific case, thereby determining the necessary number of sites and the required study period to ensure that their questions can be effectively addressed using these complex models.

In occupancy studies that are not bound by time, low detection probabilities might not substantially limit the analysis. Namely, our results demonstrate that by increasing the survey duration and consequently the number of survey periods, you can partly compensate for lower detection probabilities. This is in accordance with previous studies on basic occupancy models and capture–recapture models, which show that when the cumulative probability of detecting a species at least once during the study period (p^*) exceeds 0.8 or 0.9, occupancy estimates remain reliable even when detection probabilities are low (Guillera-Arroita et al., 2010; Smith et al., 2009; Steenweg, 2016; Steenweg et al., 2019). However, achieving a cumulative detection probability of >0.8 can be challenging for elusive species or species with low abundance, especially in studies with time constraints (e.g., due to season-bound research questions). Furthermore, while basic occupancy models only need to account for detection probability (MacKenzie et al., 2002), multistate models must address the detection probability of each state and address the potential misclassification of states (MacKenzie et al., 2017; Nichols et al., 2007). Consequently, we found that the more complex multistate models require larger datasets to achieve reliable estimates and that with covariate models this is aggravated (Appendix S1: Section S2). This need for extensive data presents a challenge when dealing with rare or elusive species. Consequently, while multistate models offer potential advantages for ecological studies, their successful application requires careful consideration of data availability, as well as specific challenges of detecting and correctly classifying different states within wildlife populations.

One strategy for increasing detection probability is to adjust the segmentation strategy of camera trap data. For instance, reducing the number of survey periods (by aggregating camera trap data into larger intervals, e.g., weekly) can boost detection probabilities and potentially enhance model performance. However, finding the right balance between the number of surveys and detection probability is a delicate task. We found no published literature that tried to optimize this balance; however, Pautrel et al. (2024) and Guillera-Arroita et al. (2010) show that when detection probability increases (e.g., by aggregating your camera trap data into fewer survey periods) a shorter study duration can achieve reliable models for basic occupancy models. This is in line with our results: when detection probabilities are low, models often fail to fit, even with a high number of surveys. Increasing detection probabilities makes these models fit with a relatively low number of surveys. However, aggregating data results in data loss, decreasing precision in final occupancy estimates. Therefore, the correct segmentation strategy should be carefully chosen based on the data, balancing between achieving higher detection probabilities and minimizing the loss of information that comes with data aggregation.

A potential solution for study areas or species with low detection probabilities is to extend the duration of the study, thereby allowing for larger aggregation of camera trap data to enhance detection probabilities. However, this approach should be undertaken with caution, as longer study durations increase the risk of violating the closure assumption in occupancy models. The closure assumption posits that the occupancy status of a site remains constant throughout the study period. To address this, one could adjust the interpretation of the occupancy parameter. Specifically, occupancy can be redefined as "the probability of site use by any number of individuals at any point during the study period," rather than an instantaneous snapshot (see Efford & Dawson, 2012; Steenweg et al., 2018 for further discussion on this topic). This reinterpretation aligns the occupancy parameter with the dynamic nature of longer study periods, thereby maintaining model validity despite potential violations of the closure assumption. Nonetheless, we are cautious about recommending >200 daily detection periods for most camera trap studies without explicitly modeling seasonal changes (e.g., through dynamic occupancy models) as the prolonged duration likely exceeds the timeframe within which the drivers of occupancy ("probability of use") remains stable for most species.

While increasing the study period and segmentation strategies can enhance detection probabilities, practical strategies like using bait (e.g., salt licks, peanut butter, or sardines; Sebastián-González et al., 2020), or positioning cameras in favorable spots like along animal trails (Burton et al., 2015) are also widely employed to increase detection probability. However, these approaches can introduce biases that may compromise model assumptions, unlike segmentation, which primarily affects uncertainty in detection estimates (Hofmeester et al., 2019; MacKenzie et al., 2017). Deploying multiple cameras per site is another strategy to increase detection probability without necessarily violating model assumptions (Evans et al., 2019; Hofmeester et al., 2021), but this approach is often impractical due to the limited availability of cameras in many study designs (Hofmeester et al., 2021). While using bait or strategically placing cameras is effective in increasing detection rates, they often compromise the model's assumption of random sampling (Braczkowski et al., 2016; Wearn et al., 2013). Despite these drawbacks, such strategies may be required to collect adequate data for functional models, especially when studying elusive species or in areas with low population densities. The extent to which these biases affect the validity of the model is not entirely clear. However, when a grid-based study design is used and the bait only attracts animals from within the designated grid cell, the resulting data can still support robust models. These models are effective for addressing questions on a larger scale, such as landscape and geographical habitat selection (Gilbert et al., 2021; Hofmeester et al., 2021). It is important to balance the need for higher detection probabilities while adhering to the model assumptions. When possible, increasing the number of survey periods, survey duration, or employing multiple cameras per site is preferred to avoid bias, but other strategies may be justified if they substantially improve data quantity and model functionality. Thus, these methods could provide valuable opportunities to enhance the understanding of wildlife ecology and inform conservation efforts.

In addition to the balance between detection probabilities and survey segmentation, the number of sites plays a crucial role in study design, particularly when incorporating covariates. Previous research suggested that 60 sites is sufficient to establish covariate relationships using basic occupancy models (Kays et al., 2020). However, our findings show that this is not the case for multistate models; none of the models based on 60 or 120 sites in this study accurately estimated the beta coefficients. Our simulation using 240 sites shows great improvement in beta estimates, but estimates, even at high detection probabilities, are still not always without bias (Figure 3). This is consistent with findings by Kéry and Royle (2020), who were unable to fit the simplest form of a multispecies model with a subsample of 140 sites from an original dataset of 1400 sites, despite finding clear relationships with the full dataset. Additionally, successful modeling efforts involving multistate, species, or community occupancy models incorporating covariates typically involve between 100 and 2000 sites (e.g. Fidino et al., 2019; Hepler & Erhardt, 2021; Pautrel et al., 2024; Rota et al., 2016; Wohner et al., 2023). Further, even multistate models without covariates show high uncertainty in occupancy predictions (Appendix S1: Figure S1). The added complexity of multistate and multispecies models, which involve estimating additional parameters, likely explains the increased data demand compared to simpler occupancy models.

Our study emphasizes the importance of achieving adequate sampling effort for reliable multistate occupancy modeling. We recommend that researchers planning to apply multistate occupancy models to camera trap data conduct a pilot study and an accompanied simulation study to ensure that detection probabilities exceed the required thresholds for the number of survey periods one can run. Researchers should also carefully consider data segmentation strategies to balance detection probabilities with the need for enough survey periods. Methods such as deploying multiple cameras per site, targeted placement, or baiting can enhance detection probabilities and improve model performance, but they may introduce biases that compromise model assumptions. Furthermore, our results indicate that multistate models require significantly more sites than basic occupancy models to accurately estimate covariate relationships. Overall, these recommendations and findings are crucial for designing robust wildlife research studies that can reliably incorporate covariates and produce meaningful ecological inferences.

AUTHOR CONTRIBUTIONS

Thomas Osinga, Henrik J. de Knegt, Magali Frauendorf, and Tim R. Hofmeester contributed to this work as follows: Conceptualization was led by Thomas Osinga with equal support from Henrik J. de Knegt and Tim R. Hofmeester. Formal analysis and investigation were carried out by Thomas Osinga. Funding acquisition was led by Tim R. Hofmeester with support from Henrik J. de Knegt. Methodology was developed by Thomas Osinga alongside Henrik J. de Knegt Tim R. Hofmeester, and Magali Frauendorf. Project administration and resources were overseen by Thomas Osinga, with additional support from Henrik J. de Knegt and Tim R. Hofmeester. Supervision was provided equally by Henrik J. de Knegt and Tim R. Hofmeester, with Magali Frauendorf in a supporting role. Visualization was led by Thomas Osinga with support from Henrik J. de Knegt and Tim R. Hofmeester. Writing—original draft and writing—review and editing were led by Thomas Osinga, with support from Henrik J. de Knegt, Tim R. Hofmeester, and Magali Frauendorf.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw results and model code (Osinga et al., 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.13992729.

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