Check for updates

Received: 12 April 2026 | Accepted: 22 September 2026

DOI: 10.1111/2041-210x.70430

Methods in Ecology and Evolution

RESEARCH ARTICLE

An integrated model of territory occupancy and mark-recapture data for estimating spatial variation in survival

Jaume A. Badia-Boher[1] | Michael Schaub[1] | Mátyás Prommer[2,3] | Marc Kéry[1]

[1]Population Biology Research Unit, Swiss Ornithological Institute, Sempach, Switzerland

[2]Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, USA

[3]MME-BirdLife Hungary, Budapest, Hungary

Correspondence
Jaume A. Badia-Boher
Email: jaume.badia@vogelwarte.ch

Funding information
Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 310030_207603

Handling Editor: Lei Zhao

Abstract

1. Spatial variation in survival is central to understanding population dynamics and guiding conservation. However, assessing it is hard, since capture-mark-recapture (CMR) data required for such inference must be collected over large spatial extents, which is seldom possible. By contrast, territory occupancy (TO) data are typically spatially rich and widely available for territorial species, but they do not directly inform individual survival.
2. We developed an integrated model combining CMR and TO data. The model links site-level occupancy dynamics, governed by site persistence and colonization probabilities, to survival of the territory owner, allowing both data sources to jointly inform spatiotemporal variation in survival. An estimable scaling parameter (κ) accommodates potential violation of a deterministic occupancy-survival link arising from breeding dispersal or alternative colonization dynamics. We evaluated our model using simulation across different survival scenarios (constant, spatial, spatiotemporal), life histories and CMR detection probabilities, and assessed estimator robustness when the deterministic occupancy-survival link is violated. We applied the model to long-term peregrine falcon (*Falco peregrinus*) data in Hungary, evaluating the effects on survival of the presence of a predator (eagle owl) and the proportion of agricultural land.
3. Survival estimated with the integrated model showed negligible bias and good coverage across all simulation scenarios, while substantially improving precision relative to CMR-only analyses. Precision gains were largest for spatial regression coefficients (up to 80%) and temporal standard deviation parameters (up to 88%); gains increased with greater model complexity and lower detection probability. When the deterministic occupancy-survival link was violated, κ adequately absorbed the discrepancy and prevented bias in survival. In the case study, integration substantially improved the precision of spatiotemporal survival estimates and revealed a negative association with eagle owl presence and a positive one with the proportion of agricultural land.
4. Our new integrated model improves estimation of spatial and temporal variation in survival by leveraging shared information across data sources, extending

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2026 The Author(s). *Methods in Ecology and Evolution* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

spatially explicit demographic inference to systems where CMR data alone are insufficient, and thereby allowing spatial survival inference in a broader range of applications.

KEYWORDS
capture-mark-recapture, dynamic occupancy model, integrated model, occupancy data, peregrine falcon, spatial demography, survival estimation, territorial species

1 | INTRODUCTION

Estimation of survival probability is a central objective in population ecology. Assessing variation of survival over time and space is essential for a sound understanding of population dynamics and for making informed management decisions (Koons et al., 2016; Morrison et al., 2022). The most common mode of survival estimation relies on capture-mark-recapture (CMR) studies, which consist of tagging and repeatedly re-encountering individuals over their lifetimes (Seber & Schofield, 2019). While the resulting data provide a solid basis for inference about survival, collecting them is costly (Lahoz-Monfort et al., 2014). As a result, CMR data are frequently limited in sample size and in their spatial and/or temporal scale (Lahoz-Monfort et al., 2014; Lees et al., 2021).

These constraints are especially limiting when the interest extends beyond average survival to focus on heterogeneity in space. Spatial variation in survival reflects important ecological processes, such as habitat-specific survival and source-sink dynamics, or indicates areas of elevated mortality (Furrer & Pasinelli, 2016; Hernández-Matías et al., 2013). Identifying such patterns is central to conservation planning, especially for prioritizing areas for management (Falcucci et al., 2009). However, models that assess variation of demographic parameters over space require substantially more data than their non-spatial counterparts. In CMR models, this requires large numbers of marked individuals monitored over time and across large spatial extents—a target only few studies have achieved so far (Milleret et al., 2025; Péron et al., 2011; Saracco et al., 2012; Schirmer et al., 2023). Consequently, models that estimate survival variation across space remain very rare, and empirical evidence on spatial survival variation is still very limited for most species, despite its recognized ecological and conservation relevance (but see Saracco et al., 2010; Péron et al., 2011; Milleret et al., 2023).

In contrast to CMR data, biodiversity monitoring programmes that do not involve individual tagging may produce large datasets on presence/absence or population counts over large spatial domains. A typical example is site occupancy data, which record whether discrete spatial units, or 'sites', are occupied by some species during repeated survey occasions (MacKenzie et al., 2002). A special case is territory occupancy (TO) data, in which sites correspond to discrete breeding territories held by at most one individual or pair, such as nests, burrows, nestboxes, cliffs or cavities used by territorial species. While generic site-occupancy data do not inform population size at a site, in TO data the occupancy status of a site (occupied or empty) is directly related to local breeder abundance at that site (one or zero breeding individual or pair), so that changes in territory occupancy patterns reflect changes in breeder population size (Kéry & Royle, 2021). Compared to CMR data, TO data do not need individual recognition of animals, are far easier and less expensive to collect, enabling broader spatial coverage and longer time series. Moreover, TO data are naturally spatially disaggregated, making them convenient for studying spatial heterogeneity (MacKenzie et al., 2018).

Dynamic occupancy models provide a powerful analytical framework for analysing TO data at discrete time steps (MacKenzie et al., 2003; Royle & Kéry, 2007). These models have been widely applied to study changing species distributions and range dynamics, responses to environmental covariates, and they naturally accommodate spatial structure and site-level heterogeneity (MacKenzie et al., 2018). The dynamic occupancy model explicitly links the latent occupancy state of a site at a given time point to its state at the previous time point through a first-order Markov process. This temporal dependence is governed by persistence, that is, the probability that an occupied site remains occupied, and colonization, which is the probability that an unoccupied site becomes occupied.

A key feature of the persistence parameter is that it is ultimately determined by individual-level demographic processes—a link initially recognized by Roth and Amrhein (2010). When site occupancy corresponds to the presence of a single individual or breeding pair, site persistence arises through one of two mutually exclusive mechanisms: (i) survival and site fidelity of the current territory holder/s, or (ii) loss of the holder/s through mortality or dispersal, followed by replacement through a new occupant. However, because individuals are not uniquely identified in TO data, survival cannot be distinguished from the other processes that drive occupancy dynamics without strong assumptions or additional information (Hernández-Matías et al., 2011; Oppel et al., 2016; Roth & Amrhein, 2010).

Interestingly, the strengths and limitations of CMR and TO data are complementary. CMR data provide direct information about survival but are often limited in spatial extent. TO data are often spatially richer but can inform survival only indirectly. It is therefore desirable to combine CMR and TO data in a single model to leverage the strengths of both and mitigate the weaknesses in each.

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Here, we develop an integrated model that combines CMR and TO data (Kéry & Royle, 2021). Extending the work of Roth and Amrhein (2010), we describe the site-level occupancy process as a function of individual-level survival probabilities, allowing us to leverage information from both data sources to improve estimates of survival and its spatiotemporal variation. We first present three proofs of concept of the new model: for survival that is constant, spatially varying and spatiotemporally varying. Using simulation, we assess the performance of all three models by comparing their estimates to data-generating values and to estimates of CMR-only models, to assess the precision gains resulting from the integration of the TO data. We further evaluate model estimates for different life histories and for low versus high recapture probabilities to test model performance when CMR data are scarce. To assess the robustness of the integrated model to assumption violations, we also examine situations in which occupancy patterns are influenced by additional processes other than individual survival, for example, breeding dispersal or alternative colonization dynamics. Finally, we apply the integrated model to long-term monitoring data of a territorial raptor, the peregrine falcon *Falco peregrinus*, to explore the spatial effects of ecological predictors on survival. We expect our model to be particularly powerful for the study of spatial population dynamics, enabling the assessment of spatial variation in survival and testing for factors that drive this variation.

2 | METHODS

We developed an integrated model that combines CMR and TO data within a joint likelihood, thereby linking individual-level survival and site-level occupancy dynamics. The model is formulated hierarchically, with separate individual survival and site occupancy processes that are linked through a shared breeder survival component.

TO data are collected across a set of breeding territories monitored over several years, and each breeding territory is assumed to hold at most one breeding individual or pair. Such data are typically collected by visiting a set of known or potential breeding sites (hereafter also referred to as 'sites') during repeated breeding seasons and ascertaining the presence of an actively breeding individual or pair (e.g. via nest checks, territorial or courtship behaviour, or direct observation of a breeding attempt; Kéry & Royle, 2021; Kéry et al., 2022; Roth & Amrhein, 2010; Prommer, Bagyura, et al., 2026). The resulting TO dataset describes whether each site was occupied or not by a breeding individual or pair in each breeding season.

CMR data originate from individuals marked and observed breeding from at least some of the sites contained in the TO dataset (Schaub & Kéry, 2022). Both data types must refer to the same discrete time steps, so that the interval over which individual survival is defined in the CMR submodel coincides with the interval over which occupancy transitions are modelled. This is satisfied when both data types are sampled at the same time of the year, which in practice is often during the breeding season.

2.1 | Modelling site-level occupancy dynamics

Let $\boldsymbol{z}$ denote the TO data matrix that describes for site s whether it is occupied ($z_{s,t} = 1$) or empty ($z_{s,t} = 0$) at occasion t. The state process in the first occasion ($t = 1$) at site s, $z_{s,1}$, is modelled as a draw from a Bernoulli distribution with probability ψ (Equation 1).

$$z_{s,1} \sim \text{Bernoulli}(\psi) \quad (1)$$

From $t = 2$ onwards, we model the occupancy state $z_{s,t}$ as a function of its state at time $t-1$ through a first-order Markov process. This temporal dependence is governed by two parameters: persistence (ϕ), that is, the probability that a site occupied at occasion $t-1$ remains occupied at time t, and colonization (γ), which is the probability that an unoccupied site at occasion *t-1* becomes occupied at occasion t (Equation 2). For convenience, we express persistence and colonization as time-varying (ϕ_t, γ_t), but they could also be expressed as constant over time.

$$z_{s,t} \sim \text{Bernoulli}\left(z_{s,t-1} \cdot \phi_t + \left(1 - z_{s,t-1}\right) \cdot \gamma_t\right) \quad (2)$$

Since $z_{s,t-1}$ is binary, only one of these two probabilities applies to a given site at a given time step, so the resulting occupancy probability is bounded within [0,1]. Note that, for simplicity, we assumed perfect detection in the occupancy model, but imperfect detection could be accommodated in the usual way if detection/nondetection data from repeated within-season visits or time-to-detection data are available (Royle & Kéry, 2007).

To link the occupancy model with the individual-level survival process that underlies occupancy dynamics, we express persistence (ϕ) as a function of individual survival of the territory holder (S_B) as well as colonization probability (γ). When a site is occupied at $t-1$, it remains occupied at t when either (i) the current breeder survives, or (ii) it dies, and is replaced by another individual within the same interval (i.e. a 'rescue effect', Roth & Amrhein, 2010). These are mutually exclusive events, and hence the probability of persistence at time t (ϕ_t) is the sum of both (Equation 3):

$$\phi_t = S_B + \left(1 - S_B\right) \cdot \gamma_t \quad (3)$$

2.2 | Biological assumptions of the model

The above model represents the demographic relationship expected between site persistence, colonization and breeder survival. Importantly, it relies on four biological assumptions about territory occupancy dynamics and the breeding system. First, each site can host at most one breeding female (or breeding pair in monogamous species), such that sites represent discrete breeding territories. Second, once recruited, females exhibit complete site fidelity to their breeding site, implying that breeding dispersal does not occur in the basic formulation of the model. Consequently, site turnover can arise only through mortality of the breeding female or site colonization by a new female breeder, but not by breeding dispersal. Third, the replacement of just-vacated or 'rescued' sites occurs at the same rate as the colonization of sites that have been empty for one time

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

step or longer (Equations 2 and 3). This assumption is needed because rescue events are typically unobserved and must therefore be inferred from overall colonization dynamics (Roth & Amrhein, 2010). Fourth, at most one turnover (death plus replacement) may occur per site and time interval. We next address situations where these assumptions are violated.

2.3 | Potential mismatch between persistence and its demographic decomposition

In practice, we expect that two of the above assumptions may often be violated. First, breeding dispersal could generate additional site turnover unrelated to mortality. This would lead to a reduction of site persistence while breeder survival remains the same (Roth & Amrhein, 2010).

Second, alternative colonization dynamics can produce the opposite discrepancy. If recently vacated sites are more likely to be filled, turnover events may remain undetected at the site level, inflating observed persistence relative to survival. This may be caused by conspecific attraction, whereby the presence of a remaining breeder of the former pair or conspecific cues increases the probability that a site is rapidly recolonized (Tapia & Zuberogoitia, 2018). This phenomenon is observed in several raptors (Hernández-Matías et al., 2011; Oppel et al., 2016).

Importantly, if site-level dynamics are influenced by these or other mechanisms and they are not represented in the persistence formulation (Equation 3), the strict deterministic link between persistence and breeder survival may induce bias, as the model attempts to reconcile mismatched occupancy patterns by adjusting survival estimates. This motivates the inclusion in our model of a scaling parameter to allow persistence to deviate from its deterministic demographic decomposition.

2.4 | Relaxing the persistence-survival relationship by introducing scaling parameter κ

We introduce a scaling parameter, κ, that adds flexibility to the link between persistence and its demographic decomposition:

$$z_{s,t} \sim \text{Bernoulli}\left(z_{s,t-1} \cdot \left(S_B + \left(1 - S_B\right) \cdot \gamma_t\right) \cdot \kappa + \left(1 - z_{s,t-1}\right) \cdot \gamma_t\right) \tag{4}$$

When the relationship between persistence and individual survival in Equation (3) holds exactly, κ will be equal to 1. Values of $\kappa > 1$ indicate that persistence is greater than predicted from its demographic decomposition, whereas values of $\kappa < 1$ indicate it is lower. Importantly, κ does not distinguish among the biological mechanisms that may alter the persistence-demography relationship, nor is it intended to estimate their strength directly. Rather, it prevents bias in survival when site-level persistence comprises the effects of such additional processes. Note that, to ensure that persistence remains within the (0,1) range, κ and the persistence decomposition (Equation 3) are introduced in their corresponding link scales (see Equation S1).

2.5 | CMR submodel to estimate individual survival

We analysed mark-recapture data using the Cormack–Jolly–Seber (CJS) model (Schaub & Kéry, 2022). For an implementation with a multistate CMR model, see the Case Study.

In the CJS model, $\boldsymbol{y}$ denotes the encounter history matrix that summarizes CMR data for each individual and year. The element $y_{i,t}$ of $\boldsymbol{y}$ takes value 1 if individual i is observed alive at time t, and 0 otherwise. Upon first capture, survival probability $S_{i,t}$ governs the probability of an individual surviving from occasion t to $t+1$, and detection probability $p_{i,t}$ governs the probability of observation of an individual when it is alive.

In all CMR models, we stratified survival and detection probabilities by age class, with the number of age classes depending on the life cycle of the modelled species (see 'Simulations'). We assumed that all individuals start breeding at a fixed age which varies by life cycle. For simplicity, we modelled survival of all pre-breeder age classes as constant. In all cases, breeder survival S_B was the only survival parameter in the CMR submodel that was linked to occupancy dynamics.

To improve computational efficiency, we implemented the CJS and multistate models using a marginalized state-space likelihood that integrates over latent states while preserving individual identification (Schaub & Badia-Boher, 2025).

2.6 | Extending the model to estimate variable survival across space

The model was so far described with spatially homogeneous breeder survival. We next introduce a spatially explicit model by allowing breeder survival to vary between sites. The key to integrating TO and CMR data at the spatial level is to assign each individual in the CMR dataset to a specific breeding territory. Let δ be a categorical variable such that $\delta_i = 1 \ldots M$ denotes the identity of the breeding site of individual i, where M is the total number of territories in the TO dataset. This ensures a one-to-one mapping between individuals and spatial units across the two submodels (Figure 1). Consequently, any site-level covariate in the occupancy model will be linked to the corresponding individual-level survival estimated in the CMR model. For individuals observed breeding at least once, δ_i is known, whereas for individuals that are never observed breeding, δ_i is missing and is therefore treated as a latent variable that is randomly drawn from the set of all sites in the TO dataset using a discrete uniform distribution.

Breeder survival can now be modelled as a function of site-level covariates:

$$\text{logit}\left(S_{B_s}\right) = \alpha + \beta \cdot x_s, \tag{5}$$

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Site occupancy data

site	y1	y2	y3	y4	y5
1	1	1	0	1	1
2	0	0	0	1	0
3	1	1	1	1	1
4	0	0	0	0	0
5	0	0	1	1	1
6	0	0	1	0	0
7	0	0	0	1	1
8	0	1	1	1	1
9	0	0	0	0	1

Capture–recapture data

individual	δ_i	y1	y2	y3	y4	y5
1	1	1	1	0	0	0
2	3	0	1	1	1	0
3	3	0	0	0	1	1
4	7	0	0	0	1	1
5	8	1	1	1	1	1

FIGURE 1 Example structure of the territory occupancy (left) and capture-mark-recapture (right) datasets used in the integrated analysis. For illustration, we use a hypothetical 'short-lived' species for which all individuals become breeders at age 1. Each individual i in the capture-mark-recapture dataset is associated with a breeding site δ_i, linking individual encounter histories to the corresponding site in the occupancy dataset. Bold blue entries illustrate observations contributing shared information across the two data sources. Column names starting with 'y-' indicate years.

where x_s is the value of a covariate at site s, α is the intercept and β is the coefficient quantifying how survival changes with x.

To propagate the information on spatial variation in breeder survival to the individual-level CMR likelihood, we assign each individual in the CMR dataset the survival probability associated with its breeding site δ_i. Specifically, for each individual i, individual-level breeder survival S'_{B_i} is:

$$S'_{B_i} = S_{B_{\delta_i}} \tag{6}$$

For instance, if individual $i = 1$ is recorded as a breeder at site $s = 10$, it is assigned the breeder survival probability S_B of site 10.

$$S'_{B_1} = S_{B_{\delta_1}} \rightarrow S'_{B_1} = S_{B_{10}} \tag{7}$$

This mapping ensures that the same site-specific breeder survival parameter applies both for the individual survival process in the CMR submodel and the site persistence process in the dynamic occupancy submodel.

Site persistence is expressed as a function of breeder survival and colonization probabilities as described previously, but now incorporating a site dimension s.

$$\phi_{s,t} = S_{B_s} + \left(1 - S_{B_s}\right) \cdot \gamma_t, \tag{8}$$

The state process of the joint likelihood is modified accordingly, while the remaining components stay the same:

$$z_{s,t} \sim \text{Bernoulli}\left(z_{s,t-1} \cdot \left(S_{B_s} + \left(1 - S_{B_s}\right) \cdot \gamma_t\right) \cdot \kappa + \left(1 - z_{s,t-1}\right) \cdot \gamma_t\right) \tag{9}$$

Modelling temporal variation alongside spatial variation is a natural extension. For instance, we may add independent and identically distributed year random effects for breeder survival, which allows survival to vary among years.

$$\begin{aligned} \text{logit}\left(S_{B_{s,t}}\right) &= \alpha + \beta \cdot x_s + \epsilon_t \\ \epsilon_t &\sim \text{Normal}(0, \sigma) \end{aligned} \tag{10}$$

2.7 | Evaluation of model performance using simulations

We conducted two multi-layered simulation studies. The first evaluated the integrated model's performance across a range of modelling and biological scenarios. The second assessed the role of the scaling parameter κ in ensuring unbiased survival inference when the assumed deterministic demographic link between breeder survival and site persistence is violated.

2.8 | Simulation study 1: Bias, coverage and precision gains of the integrated model under different survival scenarios

Simulations varied along three dimensions: (i) survival from simple to more complex (constant, spatial only, spatiotemporal), (ii) life history (short- vs long-lived species) and (iii) detection probability in the CMR data (low vs. high). For each scenario, we also compared inferences from the integrated and CMR-only models to assess precision gains. We simulated 500 datasets per scenario, totalling 6000 simulated datasets (500 datasets × 3 survival structures × 2 life cycles × 2 recapture effort scenarios) and 12,000 fitted models (an integrated and a CMR model for each dataset).

2.9 | Description of simulations

We simulated data under an individual-based, space-structured population model with a fixed number of breeding sites, each of which could hold at most one breeding female and with discrete annual time steps. We modelled site persistence directly from breeder survival and colonization according to the demographic decomposition in Equation (3). Under these simulation conditions, no mismatch occurs, and hence κ is equal to 1 by definition. For each year, we sequentially simulated survival/mortality, aging, assignment to a breeding site of each individual reaching the age of first breeding, and productivity (for further details see Appendix S1).

2.10 | Comparison with CMR-only models

To evaluate gains in accuracy and precision obtained through data integration, we fitted CJS models to each simulated CMR dataset: For (i) the model with constant survival, we fitted a nonspatial CJS, for (ii) the spatial model and (iii) for the spatiotemporal model, we

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

compared the results to CJS models estimating spatially varying survival and spatiotemporally varying survival, respectively (see Appendix S1).

We assessed the quality of the estimates from both models by computing relative bias (accuracy), mean length of the 95% posterior credible intervals (precision) and coverage of 95% credible intervals.

2.11 | Simulation study 2: The role of the scaling parameter κ in ensuring unbiased survival estimates

Here, we assessed whether the inclusion of the scaling parameter κ results in unbiased estimates of survival when key assumptions of the basic integrated model are violated. We included two processes in the data generation that break the assumed relationship between breeder survival and site persistence: breeding dispersal and altered rescue dynamics. As stated above, breeding dispersal induces values of $\kappa < 1$ and alternative colonization dynamics induces $\kappa > 1$.

We generated three sets of 500 simulated datasets: (i) with breeding dispersal, (ii) with altered rescue dynamics and (iii) with both processes together. We then fitted two models to the resulting simulated datasets: (a) the integrated model including the scaling parameter κ, and (b) an equivalent model without κ. Comparing survival estimates between the two model formulations illustrates the role of κ in ensuring unbiased estimates of survival and illustrates potential biases in breeder survival in its absence. See Appendix S1 for further details.

2.12 | Statistical inference and model fitting

We fitted all models using Bayesian MCMC in package Nimble (de Valpine et al., 2017) run from R version 4.5.2 (R Core Team, 2024). In each analysis, we ran four chains of 20,000 iterations with the first 10,000 discarded as burn-in and the remainder thinned by 1 in 20. Convergence was confirmed visually using traceplots and by values of the Brooks–Gelman–Rubin statistic Rhat <1.06 (Brooks & Gelman, 1998).

We specified vague priors for most parameters. Parameters defined on the probability scale (intercepts of survival and detection, and first-year occupancy probability) were assigned Beta(1,1) priors. Regression coefficients were assigned Gaussian priors with mean 0 and standard deviation 4. For random-effects standard deviations, we used weakly informative half-Cauchy priors with scale parameter 1 (Gelman, 2006), which provide mild regularization while allowing for substantial temporal variation in survival probabilities. Kappa was modelled with a log-link and assigned a uniform prior from 0 to 5.

Data and code to reproduce the simulations and the case study analyses (see below), with their corresponding results, can be found in Badia-Boher, Schaub, Prommer, and Kéry (2026).

2.13 | Case study: Spatial patterns in the survival of Hungarian peregrine falcons

We applied the integrated model to long-term monitoring data from an expanding peregrine falcon population in Hungary over 27 years (1997–2023; Prommer, Bagyura, et al., 2026; Prommer, Badia-Boher, et al., 2026). Data included (i) a TO dataset of 146 breeding territories; and (ii) a CMR dataset with resighting and dead-recovery data for 893 birds ringed as fledglings, of which 104 were ever resighted, 61 were resighted as breeders, and 23 were recovered dead (details in Appendix S1). Data collection was done with all necessary permits granted by environmental authorities of the Hungarian government (licence IDs: OKTF-KP/56-25/2015, PE-KTFO/1867-9/2018, PE-KTFO/1867-10/2018, PE-KTFO/1867-11/2018, PE-KTFO-507-16-2019, PE-KTFO-1466-3-2023, PE-KTFO-1951-17-2024 and PE-KTFO-1005-23-2025, see documents in Magyar Madártani és Természetvédelmi Egyesület, 2026).

We fitted the integrated model to the combined CMR and TO data and, for comparison, we also fitted a CMR-only model. CMR data (including recoveries) in both models were analysed using multistate capture-mark-recapture-recovery models implemented via a marginalized state-space likelihood (Burnham, 1993; Schaub & Badia-Boher, 2025). We assumed individuals started breeding at the age of 2 years (Prommer, Badia-Boher, et al., 2026), and modelled breeder survival as varying spatially according to two site-level covariates, one discrete and the other continuous, and also included an unstructured random effect of the year. Full model specifications are shown in Appendix S1.

As a first, discrete site-level covariate, we used a binary indicator of the presence of Eurasian eagle owl (*Bubo bubo*) breeding territories within a 2 km radius of peregrine breeding sites (see Appendix S1 for further details). Eagle-owl predation and competition are suspected to be a main contributor to current declines of some peregrine falcon populations across Europe (e.g. Kéry et al., 2022, 2025), including regional productivity declines in the Hungarian study population (Prommer, Badia-Boher, et al., 2026; Prommer, Bagyura, et al., 2026). Furthermore, there are increasing reports of predation of young and adult peregrine falcons by eagle owls (own unpublished data). Nevertheless, to date, no studies have provided direct estimates of eagle owl effects on peregrine survival.

As a second, continuous site-level covariate, we included the annual proportion of agricultural land within each peregrine falcon territory (i.e. within a 4 km buffer around the nest; Prommer, Bagyura, et al., 2026). Open agricultural areas may enhance survival by favouring the peregrine's mid-air hunting mode and increasing availability of key prey like pigeons, relative to forested habitats (Ratcliffe, 1993). However, they may also decrease survival due to higher densities of power lines and pylons, increasing electrocution and collision risks.

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

3 | RESULTS

3.1 | Simulation study 1: Bias, coverage and precision gains of the integrated model under different survival structures

The integrated model accurately recovered data-generating values across survival structures, life histories and detection probabilities (Figure 2; Tables S1–S3). Coverage of estimates of survival parameters (mean survival in constant scenarios, survival intercepts in spatial models and survival hypermeans in spatiotemporal models) was at the nominal level around 95%. Relative bias for these parameters was low to negligible (<2%). The largest, but still mild, bias (<5%) occurred in the spatiotemporal model fitted to short-lived species under low detection.

Estimates of spatial regression coefficients (β) showed negligible bias across all spatial and spatiotemporal scenarios, and coverage was slightly below the nominal level (89%–95%; Tables S2 and S3). In the spatiotemporal scenario, temporal standard deviation estimates showed small positive bias (3–13%), but this was also present in CMR-only models, and coverage was near nominal across scenarios (94%–97%; Table S3). Year-specific survival estimates in spatiotemporal models showed negligible bias across most scenarios (<1.2%), with slightly larger bias (3.8%) under low detection for short-lived species (Table S3).

In this first simulation study, κ was 1 by definition, since we modelled no disagreement between persistence and its demographic decomposition. Using this value as a reference, estimates of κ achieved coverage over 95% across scenarios, and bias was low under high detection (0%–4%) and modest under low detection (1%–7%). Estimates of colonization probability γ also achieved coverage over 95% and negligible bias (Tables S1–S3).

We quantified precision gains as the proportional reduction in credible interval length of integrated models, relative to that from CMR-only models (Figure 3, Table S4). In models with constant survival, gains were modest (0%–4%), particularly under high detection. In spatial models, however, gains became more pronounced, reaching, under high and low detection scenarios

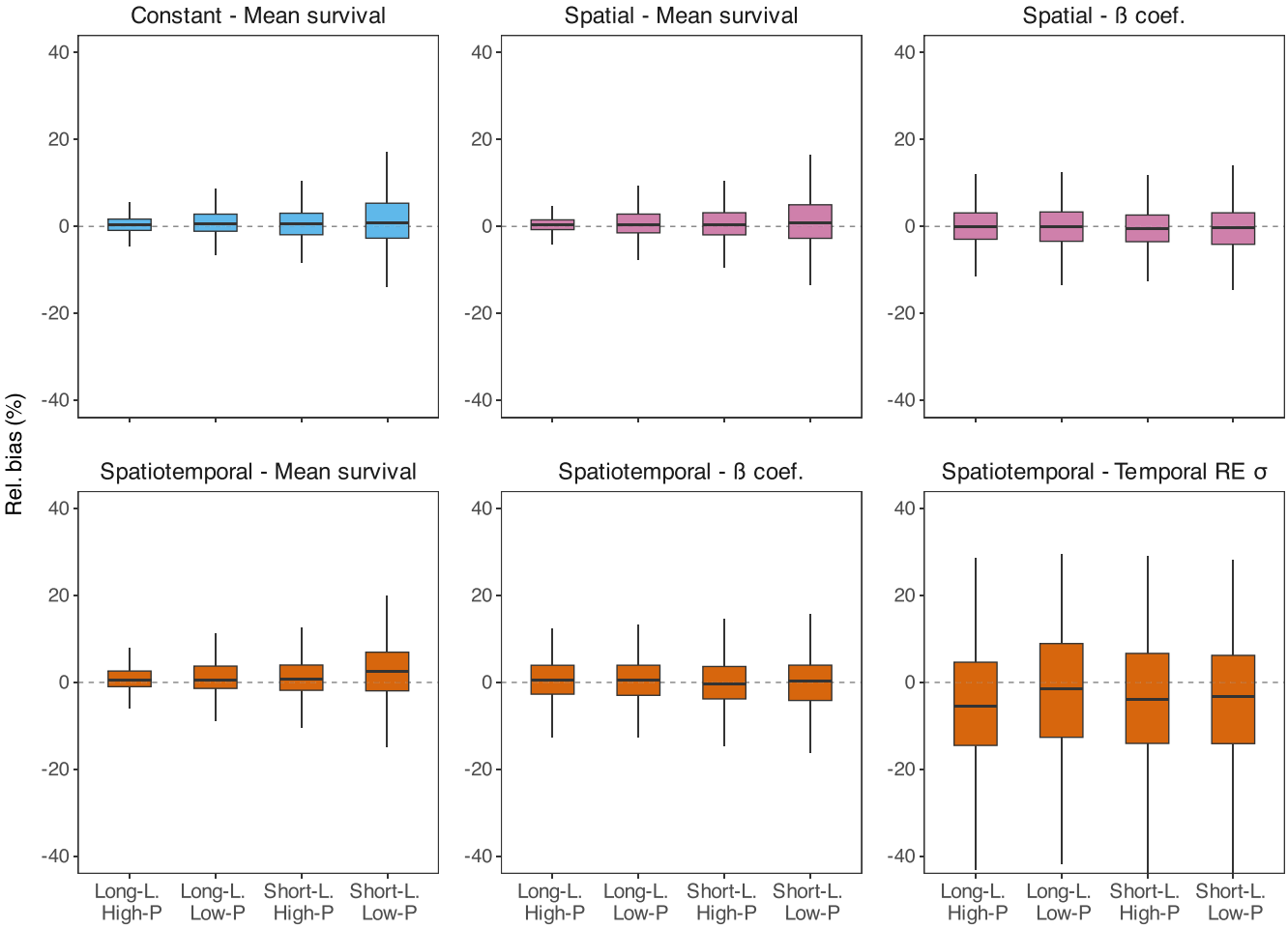


FIGURE 2 Relative bias (%) of survival parameters across simulated survival scenarios (constant, spatial, spatiotemporal), life histories ('Long-L' and 'Short-L' for long-lived and short-lived species) and capture-mark-recapture detection efforts ('Low-P' and 'High-P' for low and high detection efforts). Colours indicate survival scenarios. Boxplots summarize results across simulations per scenario and depict median bias (central line), interquartile range (IQR, box) and whiskers extending to the most extreme observations within 1.5×IQR; outliers are not shown.

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

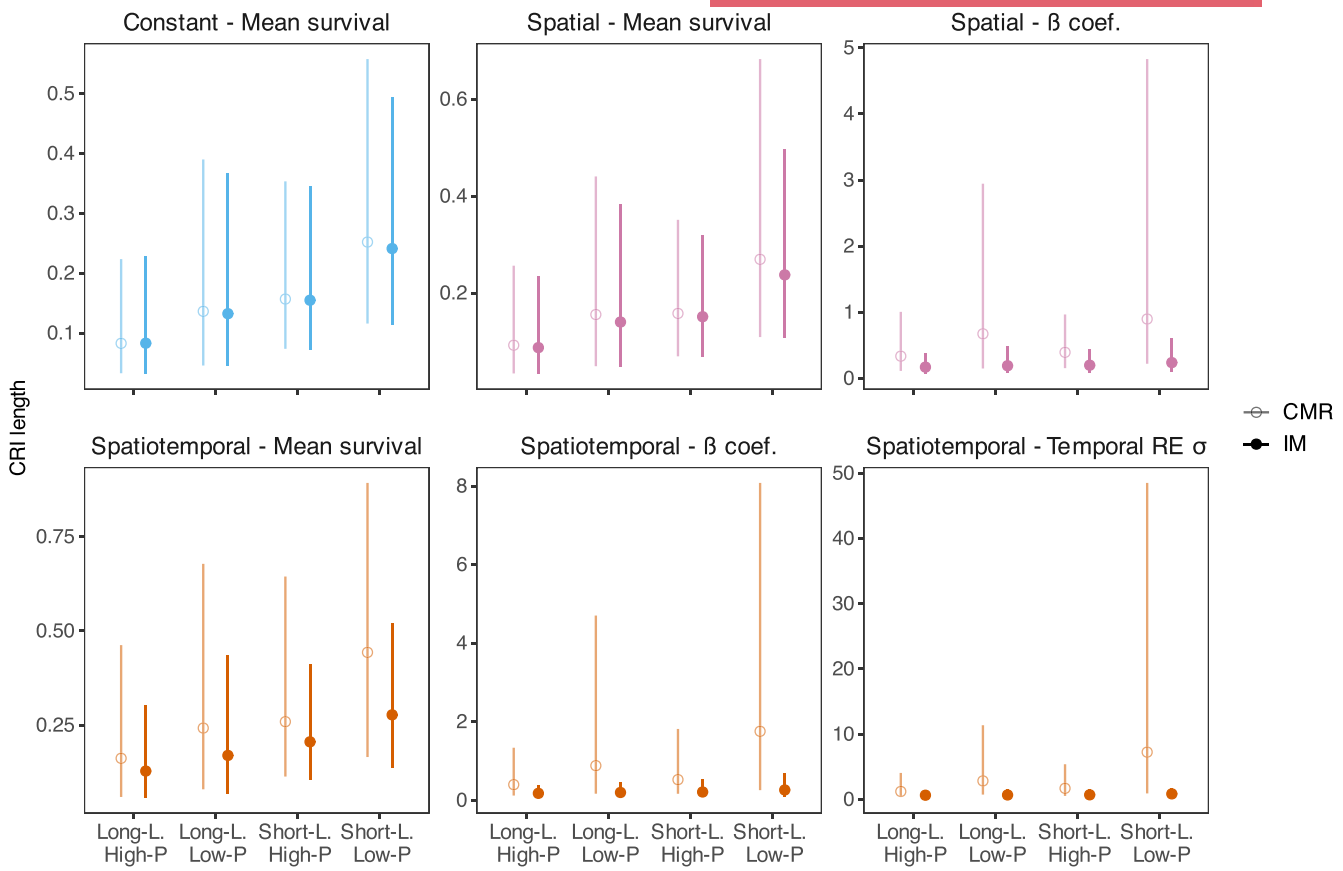


FIGURE 3 Mean credible interval (CRI) length, that is, precision, for survival parameters across simulated survival scenarios (constant, spatial, spatiotemporal), life histories ('Long-L' for long-lived species and 'Short-L' for short-lived species), and capture-mark-recapture detection efforts ('Low-P' and 'High-P' for low and high detection efforts). For each simulation scenario, the results of capture-mark-recapture-only and integrated models are compared. Points show mean CRI lengths, and vertical lines denote 2.5th and 97.5th percentiles of CRI lengths.

respectively, 5%–12% for the survival intercept and 49%–73% for the spatial regression coefficient. The largest gains occurred in spatiotemporal models: precision increased by 21% and 38% for high and low detection scenarios respectively for the survival hypermean, 55% and 80% for the spatial regression coefficient, 47% and 88% for the temporal standard deviation parameter, and 31% and 46% for yearly survival estimates. Across most parameters, precision gains were slightly greater for short-lived species, especially when detection was low.

3.2 | Simulation study 2: The role of the scaling parameter κ in ensuring unbiased survival estimates

Under all three mismatch scenarios (breeding dispersal, altered rescue dynamics and both processes combined), models excluding κ produced survival estimates whose bias increased approximately linearly with the magnitude of the violation (Figure 4). Including κ substantially reduced this bias across all scenarios (Figure 4). Estimates of κ declined progressively with increasing dispersal probability and increased progressively with the strength of the rescue effect, consistent with our expectations (Figure S1).

3.3 | Case study: Spatial patterns in the survival of Hungarian peregrine falcons

The integrated model estimated mean breeder survival at 0.772 (95% CRI: 0.69, 0.85), very similar to the CMR-only estimate (0.779, 95% CRI: 0.65, 0.92), but 39% more precise (Figure S2). Annual survival estimates in the integrated model mostly ranged between 0.6 and 0.85. Relative to the CMR-only model, precision of annual estimates increased by ca. 50% in early years (1997–2008), when CMR samples were smallest, and by ca. 30% in later years when sample sizes were larger (Figure 5a).

There was a tendency for peregrine territories overlapping with eagle owl territories to have lower survival (−0.07, 95% CRI: −0.22, 0.07), with an 82% probability of a negative effect (Figure 5b). Similarly, we found a moderate positive association between the proportion of agricultural land within territories and survival ($\beta = 0.07$, 95% CRI: −0.05, 0.19), with 86% probability of a positive effect (Figure 5c). Precision of the coefficients of the two spatial covariates in survival increased by 42% and 71%, respectively, in the integrated model relative to the CMR-only model (Figure 5c, Figure S3). Overall, mean territory-specific survival probabilities ranged between 0.68 and 0.8 and reached lowest values in territories with

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

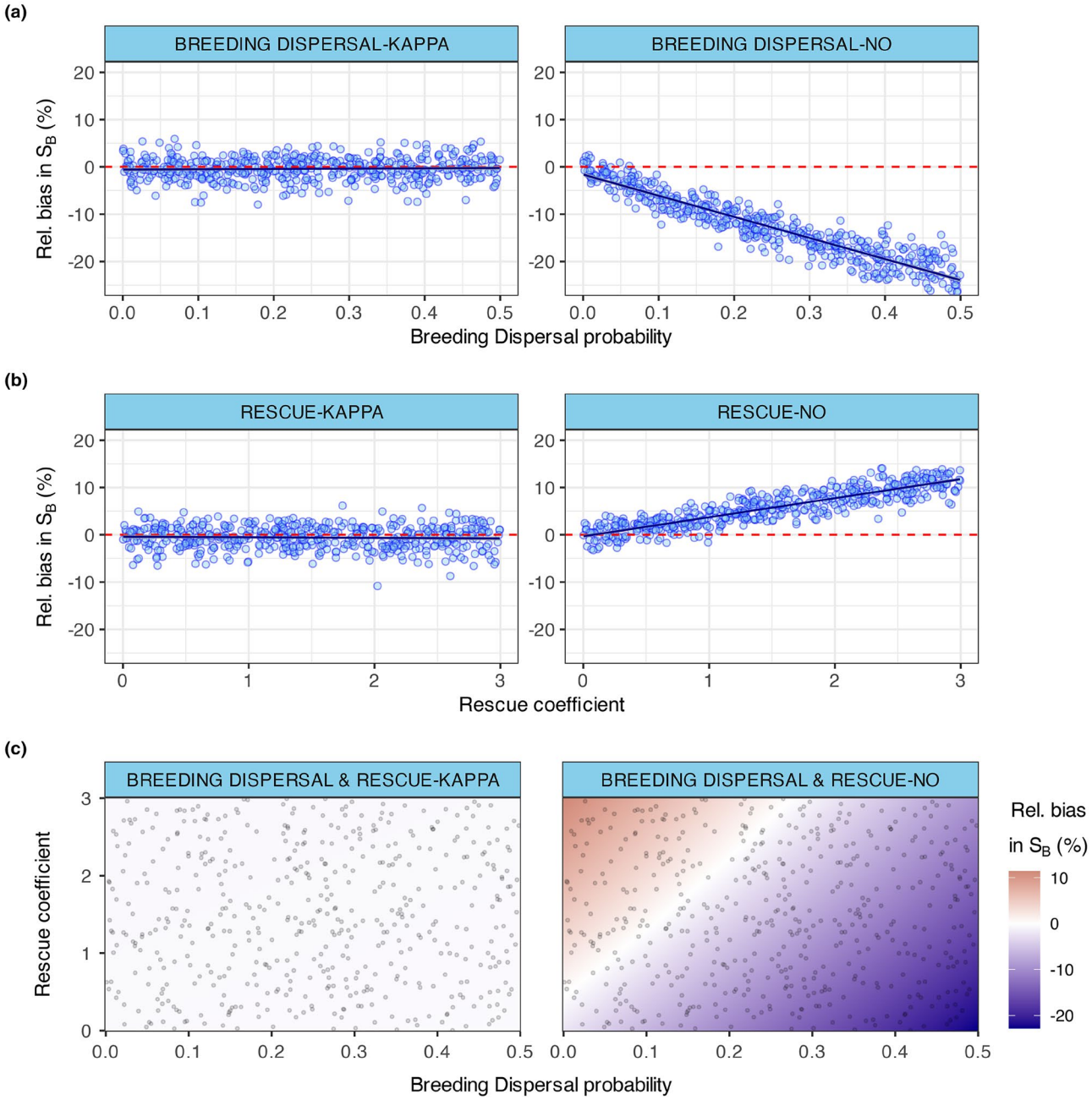


FIGURE 4 Relative bias (%) in breeder survival estimates S_B under increasing mismatch between persistence and its demographic decomposition: (a) Relative bias as a function of breeding dispersal probability; (b) Relative bias as a function of rescue effect strength; (c) Combined effects of breeding dispersal and rescue dynamics on the relative bias. The coloured surface in (c) shows a smoothed relative bias surface estimated using a generalized additive model, with points indicating simulation-specific S_B estimates. Facets indicate models including κ ('KAPPA') and excluding κ ('NO').

eagle owl presence combined with low proportions of agricultural land (Figure 5d). The scaling parameter κ was estimated as substantially greater than 1 (3.42, 95% CRI: 2.27, 4.96; Figure S4).

4 | DISCUSSION

We developed a new integrated model that combines TO and CMR data by expressing persistence probability in the former as a function of individual-level survival. The model yielded substantially improved inferences on survival and its spatiotemporal variation, while preserving statistical accuracy. Across all simulated survival scenarios, life histories and CMR detection scenarios, the integrated model maintained adequate coverage and low to negligible bias, while consistently increasing precision relative to CMR-only analyses. Precision gains increased with greater complexity of the survival model and lower detection probability. Parameters that are typically harder to estimate in a CMR-only

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

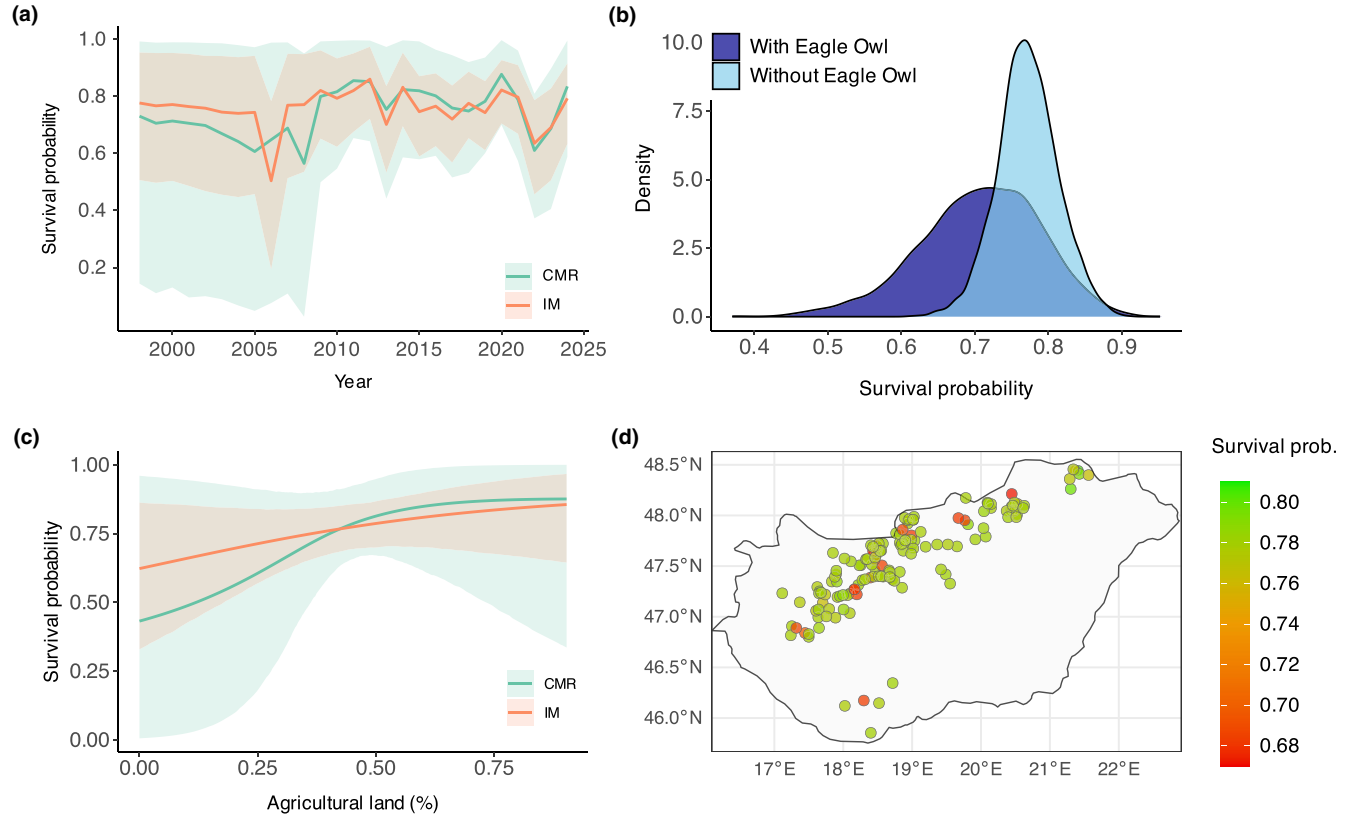


FIGURE 5 Results of the case study with Hungarian peregrines. (a) Annual breeder survival probabilities estimated by the integrated and the capture-mark-recapture-only model. Lines represent posterior means and shaded areas 95% credible intervals. (b) Posterior distributions of mean breeder survival probability under presence versus absence of eagle owl territories. (c) Estimated relationship between breeder survival probability and the proportion of agricultural land surrounding territories in integrated and capture-mark-recapture-only models. (d) Mean breeder survival probabilities across breeding territories in Hungary; coordinates are displayed as geographical longitude (X) and latitude (Y) in decimal degrees (WGS84).

framework—spatial regression coefficients and temporal standard deviations—benefited most from the integration of the TO data, with precision gains of up to 80%. These results demonstrate that our model performs well across a broad range of scenarios and is particularly effective for estimating spatial variation in survival, one of the most 'elusive' parameters in the study of animal demography.

Compared to existing approaches that estimate spatial variation in survival, our new model differs in the following manners. CMR-only models (Milleret et al., 2023; Péron et al., 2011; Saracco et al., 2010) can estimate survival variation across space and can accommodate spatial covariates, but the information to estimate survival in these settings is entirely derived from data of marked individuals, which may include genetic samples or natural markings. When recaptures are sparse or sample sizes small, estimates of spatial effects may become uncertain or inestimable. This restricts the application of these methods to large datasets of marked individuals with a very wide distribution (e.g. Milleret et al., 2025; Saracco et al., 2010, 2012). Our approach relaxes this constraint by using additional information from TO data on unmarked individuals, which are naturally spatially disaggregated and typically more abundant. This substantially extends the capacity to estimate spatial patterns in survival to systems where marking data might be sparse, but TO data are available.

Our new model is an integrated model but differs from Integrated Population Models (IPMs; Schaub & Kéry, 2022) in both spatial resolution and focus. Currently, most IPMs assume spatially constant survival (Schaub & Kéry, 2022) and the development of spatially explicit IPMs capable of estimating spatial variation in survival is still in its infancy (Ketwaroo et al., 2026; Zhao, 2020). Interestingly, population counts used in IPMs often originate from TO data that are naturally spatially disaggregated but are collapsed into population-wide totals at analysis (e.g. Badia-Boher, Schaub, Mollet, et al., 2026; Martin et al., 2026). Our model retains the original spatial structure in the counts by directly using TO data, and hence, as opposed to typical IPMs, we utilize all the spatial information these data naturally contain. Another difference is that our model remains focused on survival rather than on estimating full population dynamics as IPMs do (Schaub & Kéry, 2022). However, our model could be a foundation for the development of a spatially explicit IPM based on TO, CMR and productivity data.

Our model requires that occupancy information refers to the presence or absence of a single breeder or breeding pair at each site. If instead occupancy denotes the presence of more than two

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

breeders or may include nonbreeding individuals, the assumed link between site persistence and individual survival will no longer hold. This restricts application to territorial systems with discrete, identifiable breeding sites, yet such systems span a broad range of taxa that are often intensively monitored (Maher & Lott, 2000), such as cliff-nesting raptors, cavity-nesting or nestbox birds, and territorial burrowing mammals and reptiles. Some territorial passerines may also be suitable, provided territories remain spatially stable across years—this usually holds in species that rely on fixed resources such as particular habitat patches or food sources (Efford & Dawson, 2012; Roth & Amrhein, 2010). Consistent with this taxonomic breadth, our simulations across short- and long-lived species suggest that the model performs well across life histories, supporting its general applicability even with low detection probabilities and small sample sizes.

The scaling parameter κ plays an important role in ensuring an adequate demographic link between individual survival and site persistence. Our simulations showed that including κ effectively removes bias in survival probabilities when the assumed persistence decomposition is violated. Such violations are probably common in real data, where unmodelled biological processes that are rarely quantified (breeding dispersal, alternative colonization dynamics) could affect the persistence-survival relationship. We therefore recommend including κ by default when implementing the model. This carries little cost when no violation is present, as shown in Simulation 1, where κ was 1 by construction but nonetheless estimated freely, and the models still achieved negligible bias and large precision gains. Conversely, when a violation does occur, κ prevents bias in survival, as shown in the case study with Hungarian peregrine falcons, where κ was substantially larger than 1. A plausible biological explanation for that result is a strong rescue effect related to conspecific attraction (see Methods), common in territorial raptors (Hernández-Matías et al., 2011; Tapia & Zuberogoitia, 2018). Such dynamics generate $\kappa > 1$, as also demonstrated in our simulations (Figure 4b). But even then, mean annual breeder survival was estimated as practically identical to that of CMR-only models, but more precise, and consistent with published estimates for other peregrine falcon populations (e.g. Badia-Boher, Schaub, Mollet, et al., 2026; Kéry et al., 2025; Smith et al., 2015).

In the case study, consistent with the findings of our simulations, data integration substantially increased the precision for estimates of spatial coefficients, temporal standard deviation and annual survival relative to CMR-only models. The inconclusive (82% posterior probability), but suggestive negative association between eagle owl presence and peregrine falcon survival, is consistent with plenty of field reports of eagle owl predation of adult peregrines and with documented effects on productivity (e.g. Prommer, Bagyura, et al., 2026). Similarly, the 86% posterior probability that a higher proportion of agricultural land within territories is associated with greater breeder survival is consistent with the species' tolerance of human-modified landscapes and potentially reflects enhanced hunting opportunities relative to forested areas (Ratcliffe, 1993). Besides, the integrated model also enables the construction of territory-specific survival maps (Figure 4d), which may serve as practical tools for prioritizing conservation efforts at sites with elevated mortality risk.

Several extensions of our model could be envisioned. If detection/nondetection data from repeated visits within a breeding season are available, an observation model could relax the assumption of perfect detection (MacKenzie et al., 2002). Incorporating productivity data into the integrated model would allow fully spatially disaggregated IPMs that jointly estimate site-level fecundity and survival rates plus complete population dynamics. Additional refinements could focus on modelling processes that are now subsumed in the parameter κ: explicitly modelling breeding dispersal or—in systems where persistence depends on survival of both territory holders—modelling pair survival. Additionally, the covariate-based approach to spatial survival variation implemented here could be replaced or complemented with spatially structured random effects (e.g. CAR or Gaussian process structures; Saracco et al., 2012; Schaub & Kéry, 2022; Ketwaroo et al., 2026). This would allow estimating smooth spatial survival surfaces across the landscape even without measured covariates, which may be particularly valuable when the drivers of spatial variation are unknown. Lastly, future studies could explore how spatial and temporal misalignment between CMR and TO sampling areas affects model performance (Efford & Dawson, 2012).

A natural question is how to proceed when occupancy data available do not correspond to a known, fixed number of individuals, as in generic site-occupancy data. Two untested options seem worth exploring. The most direct could be a dynamic extension of the Royle–Nichols model (Royle & Nichols, 2003), which relates detection probability to local abundance from repeated-visit presence–absence data. In a similar spirit to Zhao (2020), who integrated a spatially explicit dynamic N-mixture model (Dail & Madsen, 2011) with CMR data, the Royle–Nichols model could be extended to link spatiotemporal abundance dynamics to survival. A second option would follow Pacifici et al. (2017), relaxing the direct demographic link assumed in our model, and instead associating survival and occupancy through a shared covariance term or derived covariate.

In conclusion, by linking site-level persistence dynamics to individual-level survival, our model extends spatial and temporal survival inference to systems where marked samples are limited but territory occupancy data are available. This broadens the range of species and populations for which spatial heterogeneity in survival can be reliably estimated, and spatial conservation insights can subsequently be generated. More broadly, we hope the framework will open new avenues for integrated analyses that retain the spatial structure inherent in territory occupancy data.

AUTHOR CONTRIBUTIONS

Jaume A. Badia-Boher, Marc Kéry and Michael Schaub conceived the main ideas of the study. Mátyás Prommer designed and performed fieldwork, arranged the data and helped with discussions about the case study. Jaume A. Badia-Boher performed the statistical analyses with support from Marc Kéry and Michael Schaub and led

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the writing of the manuscript. All authors provided critical feedback during manuscript elaboration.

ACKNOWLEDGEMENTS

We thank members and supporters of the Hungarian Peregrine Falcon Conservation Working Group and the Eurasian Eagle Owl Conservation Group coordinated by Zoltán Petrovics, initiatives led by MME-Birdlife Hungary, for their commitment over more than two decades of monitoring. We are also grateful to other volunteers and institutions that supported data collection. We thank the members of the Population Biology Unit, Swiss Ornithological Institute, for constructive scientific discussions, and two anonymous reviewers for helping to improve the manuscript. This research was funded by the Swiss National Science Foundation grant number 310030_207603.

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.70430.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are available via Zenodo vogelwarte.ch Open Repository and Archive, https://doi.org/10.5281/zenodo.22750198 (Badia-Boher, Schaub, Prommer, & Kéry, 2026).

ORCID

Jaume A. Badia-Boher https://orcid.org/0000-0003-2162-6355
Michael Schaub https://orcid.org/0000-0003-2745-0557

REFERENCES

Badia-Boher, J. A., Schaub, M., Mollet, M., Van Geneijgen, P., Van Der Jeugd, H. P., Caliendo, V., & Kéry, M. (2026). Evaluating the demographic impacts of the highly pathogenic avian influenza panzootic. *Journal of Applied Ecology*, *63*(1), e70234.

Badia-Boher, J. A., Schaub, M., Prommer, M., & Kéry, M. (2026). Data and code from: An integrated model of territory occupancy and mark-recapture data for estimating spatial variation in survival. Zenodo vogelwarte.ch Open Repository and Archive https://doi.org/10.5281/zenodo.22750198

Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434–455.

Burnham, K. P. (1993). A theory for combined analysis of ring recovery and recapture data. In J. D. Lebreton & P. M. North (Eds.), *Marked individuals in the study of bird populations* (pp. 199–213). Birkhäuser Verlag.

Dail, D., & Madsen, L. (2011). Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics*, *67*(2), 577–587.

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Temple Lang, D., & Bodik, R. (2017). Programming with models: Writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics*, *26*, 403–413.

Efford, M. G., & Dawson, D. K. (2012). Occupancy in continuous habitat. *Ecosphere*, *3*(4), 1–15.

Falcucci, A., Ciucci, P., Maiorano, L., Gentile, L., & Boitani, L. (2009). Assessing habitat quality for conservation using an integrated occurrence-mortality model. *Journal of Applied Ecology*, *46*(3), 600–609.

Furrer, R. D., & Pasinelli, G. (2016). Empirical evidence for source–sink populations: A review on occurrence, assessments and implications. *Biological Reviews*, *91*(3), 782–795.

Gelman, A. (2006). Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Analysis*, *1*(3), 515–533.

Hernández-Matías, A., Real, J., Moleón, M., Palma, L., Sánchez-Zapata, J. A., Pradel, R., Carrete, M., Gil-Sánchez, J. M., Beja, P., Balbontín, J., Vincent-Martin, N., Ravayrol, A., Benítez, J. R., Arroyo, B., Fernández, C., Ferreiro, E., & García, J. (2013). From local monitoring to a broad-scale viability assessment: A case study for the Bonelli's Eagle in western Europe. *Ecological Monographs*, *83*(2), 239–261.

Hernández-Matías, A., Real, J., & Pradel, R. (2011). Quick methods for evaluating survival of age-characterizable long-lived territorial birds. *The Journal of Wildlife Management*, *75*(4), 856–866.

Kéry, M., Banderet, G., Müller, C., Pinaud, D., Savioz, J., Schmid, H., Werner, S., & Monneret, R. J. (2022). Spatio-temporal variation in post-recovery dynamics in a large Peregrine Falcon (*Falco peregrinus*) population in the Jura mountains 2000-2020. *Ibis*, *164*, 217–239.

Kéry, M., Monneret, R. J., Badia-Boher, J. A., & Schaub, M. (2025). Demographic causes of the pesticide crash in the peregrine falcon. *Ecoevorxiv*, https://doi.org/10.32942/X2R05B

Kéry, M., & Royle, J. A. (2021). *AHM1—Modeling distribution, abundance and species richness using R and BUGS. Volume 2: Dynamic and Advanced Models*. Academic Press.

Ketwaroo, F. R., Muller, M. H., Saracco, J. F., & Schaub, M. (2026). An integrated population model to incorporate Spatio-temporal heterogeneity in demographic rates. *bioRxiv: the preprint server for biology*. https://doi.org/10.64898/2026.03.03.709263

Koons, D. N., Iles, D. T., Schaub, M., & Caswell, H. (2016). A life-history perspective on the demographic drivers of structured population dynamics in changing environments. *Ecology Letters*, *19*(9), 1023–1031.

Lahoz-Monfort, J. J., Harris, M. P., Morgan, B. J. T., Freeman, S. N., & Wanless, S. (2014). Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. *Journal of Applied Ecology*, *51*(2), 534–543.

Lees, K. J., MacNeil, M. A., Hedges, K. J., & Hussey, N. E. (2021). Estimating demographic parameters for fisheries management using acoustic telemetry. *Reviews in Fish Biology and Fisheries*, *31*(1), 25–51.

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., & Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, *84*(8), 2200–2207.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248–2255.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2018). *Occupancy estimation and modelling. Inferring patterns and dynamics of species occurrence* (2nd ed.). Academic Press.

Magyar Madártani és Természetvédelmi Egyesület. (2026). Ragadozómadár-védelmi Szakosztály. https://mme.hu/csoportok/ragadozomadarvedelmi_szakosztaly.

Maher, C. R., & Lott, D. F. (2000). A review of ecological determinants of territoriality within vertebrate species. *The American Midland Naturalist*, *143*(1), 1–29.

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Martin, E. C., Riecke, T. V., Ravussin, P., Arrigo, D., & Schaub, M. (2026). Identifying the demographic pathways linking environmental covariates to population dynamics in an avian migrant. *Ecological Applications*, *36*(1), e70166.

Milleret, C., Dey, S., Dupont, P., Brøseth, H., Turek, D., De Valpine, P., & Bischof, R. (2023). Estimating spatially variable and density-dependent survival using open-population spatial capture–recapture models. *Ecology*, *104*(2), e3934.

Milleret, C., Dupont, P., Dey, S., Brøseth, H., Kindberg, J., Turek, D., de Valpine, P., Åkesson, M., Wabakken, P., & Zimmermann, B. (2025). Map of death: Spatially explicit mortality of the grey wolf. *Proceedings. Biological sciences*, *292*(2053), 20250948.

Morrison, C. A., Butler, S. J., Clark, J. A., Arizaga, J., Baltà, O., Cepák, J., Nebot, A. L., Piha, M., Thorup, K., Wenninger, T., Robinson, R. A., & Gill, J. A. (2022). Demographic variation in space and time: Implications for conservation targeting. *Royal Society Open Science*, *9*(3), 211671.

Oppel, S., Dobrev, V., Arkumarev, V., Saravia, V., Bounas, A., Kret, E., Skartsi, T., Velevski, M., Stoychev, S., & Nikolov, S. C. (2016). Assessing the effectiveness of intensive conservation actions: Does guarding and feeding increase productivity and survival of Egyptian Vultures in the Balkans? *Biological Conservation*, *198*, 157–164.

Pacifici, K., Reich, B. J., Miller, D. A. W., Gardner, B., Stauffer, G., Singh, S., McKerrow, A., & Collazo, J. A. (2017). Integrating multiple data sources in species distribution modeling: A framework for data fusion. *Ecology*, *98*(3), 840–850.

Péron, G., Ferrand, Y., Gossmann, F., Bastat, C., Guenezan, M., & Gimenez, O. (2011). Nonparametric spatial regression of survival probability: Visualization of population sinks in Eurasian Woodcock. *Ecology*, *92*(8), 1672–1679.

Prommer, M., Badia-Boher, J. A., Kéry, M., Schaub, M., Bagyura, J., & Oli, M. K. (2026). Evaluating population resilience to anticipated stressors using integrated population modelling: A case study of Peregrine Falcons. *EcoEvoRxiv*. https://doi.org/10.32942/X2BH31

Prommer, M., Bagyura, J., Kéry, M., & Oli, M. K. (2026). Repopulation of the former breeding range: Spatio-temporal patterns and drivers of reproduction in the Peregrine Falcon (*Falco peregrinus*) population in Hungary. *Ibis*, *168*(1), 63–78.

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ratcliffe, D. A. (1993). *The peregrine falcon*. T & AD Poyser.

Roth, T., & Amrhein, V. (2010). Estimating individual survival using territory occupancy data on unmarked animals. *Journal of Applied Ecology*, *47*(2), 386–392.

Royle, J. A., & Kéry, M. (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology*, *88*(7), 1813–1823.

Royle, J. A., & Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology*, *84*(3), 777–790.

Saracco, J. F., Royle, J. A., DeSante, D. F., & Gardner, B. (2010). Modeling spatial variation in avian survival and residency probabilities. *Ecology*, *91*(7), 1885–1891.

Saracco, J. F., Royle, J. A., DeSante, D. F., & Gardner, B. (2012). Spatial modeling of survival and residency and application to the monitoring avian productivity and survivorship program. *Journal of Ornithology*, *152*(S2), 469–476.

Schaub, M., & Badia-Boher, J. A. (2025). Comparison of Bayesian models to estimate survival from dead-recovery alone and together with live-encounter data: Challenges and opportunities. *Ecology and Evolution*, *15*(6), e71517.

Schaub, M., & Kéry, M. (2022). *Integrated population models: Theory and ecological applications with R and JAGS*. Academic Press.

Schirmer, S., Korner-Nievergelt, F., Von Rönn, J. A. C., & Liebscher, V. (2023). Estimating survival in continuous space from mark-dead-recovery data—Towards a continuous version of the multinomial dead recovery model. *Journal of Theoretical Biology*, *574*, 111625.

Seber, G. A. F., & Schofield, M. R. (2019). *Capture-recapture: Parameter estimation for open animal populations*. Springer.

Smith, G. D., Murillo-García, O. E., Hostetler, J. A., Mearns, R., Rollie, C., Newton, I., McGrady, M. J., & Oli, M. K. (2015). Demography of population recovery: Survival and fidelity of Peregrine Falcons at various stages of population recovery. *Oecologia*, *178*(2), 391–401.

Tapia, L., & Zuberogoitia, I. (2018). Breeding and nesting biology in raptors. In J. H. Sarasola, J. M. Grande, & J. J. Negro (Eds.), *Birds of prey: Biology and conservation in the XXI century* (pp. 63–94). Springer International Publishing.

Zhao, Q. (2020). On the sampling design of spatially explicit integrated population models. *Methods in Ecology and Evolution*, *11*(10), 1207–1220.

SUPPORTING INFORMATION

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

Figure S1. Posterior means of κ estimates under increasing breeding dispersal probabilities (left) or strength of the rescue effect in the altered colonization dynamics scenario (right).

Figure S2. Posterior means and 95% credible intervals of the hypermean of survival probability of breeders in capture-mark-recapture-only (CMR) and integrated models (IM) for the case study of Hungarian peregrine falcons.

Figure S3. Posterior distributions of mean breeder survival probability under presence versus absence of eagle owl territories for capture-mark-recapture-only (CMR) and integrated models (IM).

Figure S4. Posterior distribution of κ in the peregrine falcon case study, based on the integrated model. The dashed line indicates $\kappa = 1$, the value that would indicate no mismatch between site-level persistence and its deterministic demographic decomposition.

Table S1. Relative bias (%), credible interval ('CRI') length, coverage of different parameters, life histories, and capture-mark-recapture detection scenarios for constant survival models.

Table S2. Relative Bias (%), credible interval ('CRI') length, coverage of different parameters, life histories and capture-mark-recapture detection scenarios for spatial survival models.

Table S3. Relative Bias (%), credible interval ('CRI') length, coverage of different parameters, life histories and capture-mark-recapture detection scenarios for spatiotemporal survival models.

Table S4. Credible interval ('CRI') lengths of main survival parameters under different survival structures, life histories and capture-mark-recapture detection probabilities for integrated models (IM) and capture-mark-recapture-only models (CMR). Column 'Gain in IM' indicates the percentage of credible interval length reduction in integrated models compared to CMR models.

How to cite this article: Badia-Boher, J. A., Schaub, M., Prommer, M., & Kéry, M. (2026). An integrated model of territory occupancy and mark-recapture data for estimating spatial variation in survival. *Methods in Ecology and Evolution*, *17*, 3220–3232. https://doi.org/10.1111/2041-210x.70430

2041210x, 2026, 11, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210x.70430 by Jaume-Adria Badia-Boher - Schweizerische Vogelwarte , Wiley Online Library on [04/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License