RESEARCH ARTICLE

Ghostbusting—Reducing bias due to identification errors in spatial capture-recapture histories

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Abstract

1. Identifying individuals is key to estimating population sizes by spatial capture–recapture, but identification errors are sometimes made. The most common identification error is the failure to recognise a previously detected individual, thus creating a 'ghost' Johansson. This results in positively biased abundance estimates.

2. Ghosts typically manifest as single detection individuals ('singletons') in the capture history. To deal with ghosts, we develop a spatial capture–recapture method conditioned on at least K detections. The standard spatial capture–recapture (SCR) model is the special case of $K = 1$. Ghosts can mostly be excluded by fitting a model with $K = 2$ (SCR-2).

3. We investigated the effect of 'singleton' ghosts on the estimation of the model parameters by simulation. The SCR method increasingly overestimated abundance with increasing percentage of ghosts, with positive bias even when only 10% of the detected individuals were ghosts, and bias between 43% and 71% when 30% were ghosts. Estimates from the SCR-2 method showed lower bias in the presence of ghosts, at the cost of a loss of precision. The mean squared error of the estimated abundance from the SCR-2 method was lower in all scenarios with ghosts under high encounter rates and for scenarios with 30% or more ghosts with low encounter rates. We also applied our method to capture histories from camera trap surveys of snow leopards (*Panthera uncia*) at two sites from Mongolia and find that the SCR method produced higher abundance estimates at both sites.

4. Capture histories are susceptible to errors when generated from passive detectors such as camera traps and genetic samples. The SCR-2 method can remove bias from ghost capture histories, at the cost of some loss in precision. We recommend using the SCR-2 method in cases when there may be more than 10% ghosts or surveys with a large number of single detection capture histories, except perhaps when the sample size is very low.

1 | INTRODUCTION

Estimating abundance and tracking changes in population sizes are imperative to inform conservation efforts for wildlife species. Spatial capture–recapture (SCR) methods (Borchers & Efford, 2008; Efford, 2004; Royle & Young, 2008) are widely used to estimate the abundance and distribution of species that can be individually identified. These methods rely on correctly identifying re-detections of animals and may give biased estimates if errors are made in animal identification. Here, we focus on non-invasive surveys in which animals are not marked by surveyors but are uniquely identified from some innate features such as body markings in photographs in the case of a camera trap survey, or genetic fingerprinting from scat samples in the case of a scat survey.

Identification errors in camera trap surveys can occur due to poor observation conditions, poor quality photographs of individuals or variation in markings over time (Stevick et al., 2001). The level of experience of the people who perform the identification may also be a factor. For example, Gibbon et al. (2015) found that observers experienced in working with mountain bongos (*Tragelaphus eurycerus isaaci*) made identification errors in around one-sixth of cases, while inexperienced observers made errors in about one-fifth of cases when asked to determine whether pairs of photographs were of the same individual.

Like camera trapping, genotyping methods are known to be prone to errors. This led to the development of $M_{t,\alpha}$ models for non-spatial capture–recapture (CR) surveys (Lukacs & Burnham, 2005). In this model, identification errors lead to artificially introduced individuals that Yoshizaki (2007) termed 'ghosts'. The $M_{t,\alpha}$ model estimates an additional parameter α, the probability that a single detection was identified correctly, to account for ghosts. Lukacs and Burnham (2005), however, do not model in their likelihood the probability that the misidentified single detection is another individual's recapture. This shortcoming was addressed by Link et al. (2010) and extended by Bonner et al. (2016) using a Bayesian approach. A more efficient maximum likelihood estimator for the $M_{t,\alpha}$ model was subsequently proposed by Vale et al. (2014) which allowed for more thorough investigation of the statistical properties of the model. However, it has been difficult to apply these models to real data, and the resulting population size estimates

suffer from poor precision unless there are high capture probabilities or many capture occasions (Vale et al., 2014). Wright et al. (2009) proposed that the identification error rate may be estimated directly by genotyping all samples at least twice, but this is not always cost-effective, so manual error correction prior to modelling may be preferable (Fewster, 2017). Yoshizaki (2007) proposed and developed a model dropping all single captures and conditioning on at least two captures in the CR likelihood. Conn et al. (2011) generalised this method to account for transient animals in a survey.

Identification errors from photographs can be more complex than simply creating ghosts. Different types of misidentification errors can have different impacts on the structure of a capture history (the record of detections for each individual), and hence on abundance estimates. As outlined in Johansson et al. (2020), *splitting errors* occur when a photographic capture of an individual is not matched to the correct individual, and is not matched to any other individual, splitting the capture history of the correct individual in two and creating a 'ghost'. A *combination error* occurs when all captures of an individual are falsely matched to a different individual, removing an entire capture history and reducing the (recorded) number of individuals detected. A *shifting error* is when a splitting error, reducing the capture history of one individual, is combined with a combination error from another individual; the capture event moves between individuals without changing the number of individuals detected. An *exclusion error* occurs when photographs are discarded despite containing sufficient information to make an identification, reducing the number of captures in their capture history. Splitting errors will lead to positively biased abundance estimates, combination errors will lead to negative bias. Johansson et al. (2020) found abundance estimates using closed population capture–recapture methods to be largely unaffected by shifting errors, but may be biased due to exclusion errors if these do not also cause a reduction in the number of animals within capture histories, or if there is heterogeneity in the probability of exclusions among individuals.

If marking patterns do not change considerably over the survey period and vary sufficiently between individuals, falsely identifying captures of two different individuals as being from the same individual (as in combination errors and some shifting errors) should be rare (Morrison et al., 2011). Van Horn et al. (2014) found that

observers who continued to make errors after training were twice as likely to falsely identify two photos of the same bear as two different Andean bears (*Tremarctos ornatus*) than falsely match two different individuals. Stevick et al. (2001) found that observers did not falsely match different individuals, they only produced false-negative errors in which a photograph and a biopsy were falsely identified as being of two different humpback whales (*Megaptera novaeangliae*), mainly due to poor photographic quality. Johansson et al. (2020) found that the impact of splitting errors far outweighed the impact of combination errors in snow leopard (*Panthera uncia*) CR surveys, resulting in systematically positively biased abundance estimates—by one-third on average. They further noted that splitting errors, typically resulting in singleton ghosts, were the most common of the misidentification errors.

Spatial capture–recapture methods have been developed to deal with situations in which no identities are known (Chandler & Royle, 2013), in which only a fraction of the population is marked and these animals are identifiable without errors (Sollmann et al., 2013; Whittington et al., 2018), and in which single flanks of individuals are observed without errors, but the two flanks of the same individual cannot be confidently matched (Augustine et al., 2018). Jiménez et al. (2021) implemented a random thinning model to account for exclusion errors—detections that are discarded as a result of not being able to identify them either as an existing or as a new individual. There is currently no method that can effectively account for ghosts in SCR.

Here, we extend the method proposed by Yoshizaki (2007) for non-spatial CR, to deal with ghosts in SCR. We do this by developing a maximum likelihood estimator for capture histories that involve at least K detections of individuals. We fit the SCR model conditioned on at least two captures (SCR-2) to exclude ghosts, the rationale being that ghosts are predominantly singletons and so can be excluded by using $K = 2$.

We first investigate the properties of the SCR-2 method by simulation. We investigate the bias, standard error and mean squared error of SCR and SCR-2 parameter estimates caused by ghost capture histories, and use the simulation results to identify when using the SCR-2 method would be advisable. We also implement the SCR-2 method on two camera trap surveys of snow leopards (*Panthera uncia*) and compare estimates from the SCR and SCR-2 models.

2 | MATERIALS AND METHODS

2.1 | Model formulation

Consider a passive detector survey, such as hair snares (binary detectors) or camera traps (count detectors) across multiple occasions over a survey period. We assume the individuals $i = 1, 2, \ldots, N$ move around their activity centres, and we model the spatial distribution of these activity centres as a realisation of a Poisson point process over the survey region $X \in \mathbb{R}^2$. Let $s \in X$ denotes the location of any activity centre and s_i denotes the activity centre of individual i. The intensity of the point process that generates activity centres is

$D(z_s, \phi)$, or $D(s; \phi)$ for brevity, where z_s is a vector of covariate values at s and ϕ is the parameter vector of the point process.

Suppose J traps are placed across the survey region on T occasions. Let $x_j \in X$ denotes the location of the jth trap. Let ω_{ijt} be the number of times individual i was detected at trap j on occasion t. For binary detectors, $\omega_{ijt} = 1$, if individual i was detected at trap j on occasion t and zero otherwise. For detectors that record counts $\omega_{ijt} \in \mathbb{N}$. Let $\omega_{ij} = (\omega_{ij1}, \ldots, \omega_{ijT})$ be the vector of the ith individual's capture history at trap j, $\omega_{ij.} = \sum_{t=1}^{T} \omega_{ijt}$ be the number of times individual i was detected at trap j across all T occasions, $\omega_i = (\omega_{i1}, \ldots, \omega_{iJ})$ be the vector of the ith individual's capture history at each of the J traps across all occasions and $\omega_{i.} = \sum_{j=1}^{J} \omega_{ij.}$ be the total number of times individual i was detected. Let $n^{(K)}$ be the number of individuals detected at least K times in the survey (so that $n^{(1)}$ is the total number of individuals detected). $\Omega^{(K)} = (\omega_i; i = 1, \ldots, n^{(K)})$ denotes the set of capture histories for the $n^{(K)}$ individuals with $\omega_{i.} \geq K$, that is, the capture histories with at least K detections.

The conditional probabilities of the capture histories given the activity centres $\omega_{ijt} \mid s_i$ are assumed to be independent. Based on the type of observations generated by the detector, any suitable distribution can be used to model them. For binary detector surveys, we define the probability of detecting an individual i with an activity centre at s_i at trap j located at x_j on occasion t to be $p_{jt}(s_i; \theta)$, and this is typically modelled as $\omega_{ijt} \mid s_i \sim \text{Bernoulli}(p_{jt}(s_i; \theta))$. For detectors that record counts, we define the expected number of encounters at trap j located at x_j for an individual i with an activity centre at s_i to be $\lambda_{jt}(s_i; \theta)$. This is most commonly modelled as, $\omega_{ijt} \mid s_i \sim \text{Poisson}(\lambda_{jt}(s_i; \theta))$. Other distributions such as the negative binomial may also be used to model count data. Here, θ is the vector of observation process parameters; for readability, we omit the θ term below.

The observation process for binary data modelled by a Bernoulli distribution can be reformulated in terms of the expected encounter rate of a Poisson distributed for a given T (Efford et al., 2013) varying. For a single occasion,

$$p_{jt}(s_i) = 1 - e^{-\lambda_{jt}(s_i)}. \tag{1}$$

If the detection probability or the expected encounter rates do not depend on occasion, then the capture histories can be further collapsed across occasions and $\omega_{ij.} \mid s_i \sim \text{Binomial}(T, p_j(s_i))$ and $\omega_{ij.} \mid s_i \sim \text{Poisson}(\lambda_j(s_i))$, where $p_j(s_i) = p_{jt}(s_i)$ and $\lambda_j(s_i) = \sum_{t=1}^{T} \lambda_{jt}(s_i) = T\lambda_{jt}(s_i)$. From Equation 1, we also have $p_j(s_i) = 1 - e^{-\lambda_j(s_i)/T}$.

The expected number of encounters $\lambda_j(s_i)$ can be modelled by various functions based on how we expect the animal to move around its activity centre s_i. Most commonly, $\lambda_j(s_i)$ is modelled as a function of d_{ij}, the distance between individual i's activity centre s_i and trap j, and the encounter parameters $(\lambda_0, \sigma) \in \theta$, where λ_0 is the encounter rate at the individual's activity centre and σ is the range parameter. The detection probability can be modelled with parameters $(g_0, \sigma) \in \theta$, where g_0 is the detection probability at the individual's activity centre. In what follows, we work in terms of the expected encounter rate.

The expected number of encounters across all J traps of an individual with an activity centre at $\boldsymbol{s}_i$ is $\lambda_.(\boldsymbol{s}_i) = \sum_{j=1}^{J} \lambda_j(\boldsymbol{s}_i)$. Via the additive property of the Poisson distribution $\omega_{i.} \mid \boldsymbol{s}_i \sim \text{Poisson}(\lambda_.(\boldsymbol{s}_i))$. The probability of detecting animal i with an activity centre at $\boldsymbol{s}_i$ at least K times is:

$$p_.^{(K)}(\boldsymbol{s}_i; \boldsymbol{\theta}) = 1 - \sum_{k=0}^{K-1} p(\omega_{i.} = k \mid \boldsymbol{s}_i). \qquad (2)$$

Based on our assumption that the number of detections follows a Poisson distribution, $p_.^{(K)}(\boldsymbol{s}_i; \boldsymbol{\theta}) = 1 - \sum_{k=0}^{K-1} \frac{\lambda_.(\boldsymbol{s}_i)^k \exp[-\lambda_.(\boldsymbol{s}_i)]}{k!}$. This allows us to compute the probability of the capture history of an individual conditioned on at least K encounters.

Under our assumptions, the number of individuals detected at least K times, $n^{(K)}$, is a Poisson random variable with parameter:

$$\Lambda^{(K)} = \int_X D(\boldsymbol{s}; \boldsymbol{\phi}) p_.^{(K)}(\boldsymbol{s}; \boldsymbol{\theta}) d\boldsymbol{s}. \qquad (3)$$

Adapting the likelihood function of Borchers and Efford (2008) to deal only with animals that were detected at least K times, we have the likelihood function:

$$L(\boldsymbol{\theta}, \boldsymbol{\phi} \mid \Omega^{(K)}, n^{(K)}) = \frac{e^{-\Lambda^{(K)}}}{n^{(K)}!} \prod_{i=1}^{n^{(K)}} \int_X \prod_{j=1}^{J} p(\omega_{ij} \mid \boldsymbol{s}; \boldsymbol{\theta}) D(\boldsymbol{s}; \boldsymbol{\phi}) d\boldsymbol{s}. \qquad (4)$$

The likelihood function of Borchers and Efford (2008) is recovered by setting $K = 1$. From the maximum likelihood estimate of the density, the expected abundance, $E[N]$ can be derived by

$$E[N] = \int_X D(\boldsymbol{s}; \hat{\boldsymbol{\phi}}) d\boldsymbol{s}. \qquad (5)$$

In common with other SCR inference methods, we discretise $\boldsymbol{X}$ into a mesh. Likelihood maximisation was performed using the R programming language (R Core Team, 2022). Standard SCR models were fit using the `secr` package (Efford, 2022). We also develop a hypothesis test that can be used to diagnose the presence of 'ghosts' within capture histories (Supporting Information S2).

2.2 | Simulations

The performance of the methods was assessed using a simulation study. In particular, we investigated the impact of ghosts in the capture histories on the bias of the parameter estimates for both models. Reducing sample size by dropping single detections in the SCR-2 method is bound to increase the variance of the estimated parameters. To understand the trade-off between bias and variance between the two models, we checked the mean squared errors of the parameter estimates to identify when using the SCR-2 method would be advisable over using standard SCR.

We simulated 100 survey regions as a 64×64 square grid with each grid cell having an area of 4307m^2. The surveys consisted of 25 traps deployed in a grid layout with a spacing of 450m. Each of the grid cells in a landscape was assigned a spatial covariate value drawn

from a standard normal distribution and the entire grid was smoothed to introduce spatial correlation. To reduce any site-specific effects, each of the 100 landscapes was simulated with different realisations of the spatial covariate. One realisation of a landscape with the trap layout is shown in Figure 1.

Populations within each survey were simulated as an inhomogeneous Poisson point process, modelled with a log-linear relationship to the simulated spatial covariate: $D(\boldsymbol{s}) = \exp(\beta_0 + \beta_1 z_{\boldsymbol{s}})$; where $z_{\boldsymbol{s}}$ is the value of the spatial covariate at point $\boldsymbol{s}$ and β_0, β_1 are the intercept and slope of the log-linear model. A high abundance ($\beta_0 = 0.06$) and a low abundance ($\beta_0 = 0.03$) scenario were simulated for each of the landscapes. The slope was fixed at $\beta_1 = 0.1$ in both cases. This generated a total of 200 populations. Sets of capture histories were simulated from these populations, assuming a Poisson detection process, using a half normal encounter rate, $\lambda_j(\boldsymbol{s}_i) = \lambda_0 e^{-d_{ij}^2 / 2\sigma^2}$. $\lambda_0 = 1$ and $\lambda_0 = 2$ were used to generate capture histories with low and high encounter rates, respectively. σ was fixed at 300. This resulted in 400 sets of capture histories.

Ghosts were then introduced to each set of the simulated capture histories by randomly splitting detections of individuals encountered more than once and creating new single detection ghost capture histories. More than one detection of any individual could become a ghost as long as there remained at least one detection in the original individual's capture history. The number of ghosts introduced was proportional to the total number of individuals detected in each simulation. For each simulated set of capture histories, three new sets of capture histories were created with 10%, 20% and 30% of the total number of individuals truly detected introduced as ghosts.

This resulted in a total of 1600 sets of capture histories. The SCR and the SCR-2 models were fit to each data set. Both models were fit assuming an inhomogenous point process, modelled to the simulated spatial covariate. We investigated relative bias, the standard error and the mean squared error (MSE) (Bias^2+Variance) of the estimated parameters λ_0, σ and $E[N]$ for both models. To investigate computation costs, we measure the time taken, under our
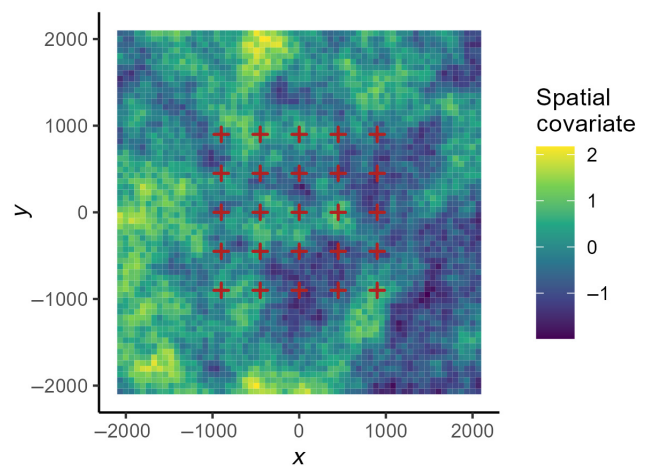

FIGURE 1 One realisation of the simulated survey landscape. The colour in each grid cell represents the value of the spatial covariate at that cell. Traps are shown by the red crosses.

naive implementation, to evaluate the likelihood once for 100 different simulated sets of capture histories using both models. We also run simulations under identical scenarios for binary detections (Supporting Information S1).

2.3 | Case study: Snow leopards in Mongolia

The population assessment of the world's snow leopards (PAWS) is a multinational survey programme that aims to produce a robust estimate of the distribution and abundance of the world's snow leopards. Mongolia has been one of the leaders in conducting surveys for this programme. Bayandonoi et al. (2021) obtained estimates of the distribution of snow leopards across the country using occupancy methods (MacKenzie et al., 2017) to bolster abundance estimates from existing camera trap surveys. These occupancy estimates were used to design further surveys that spanned the estimated distribution range of snow leopards in Mongolia. For this case study, we verify data from two of these sites: Munkhkhairkhan and Tost. Tost has been a long-term monitoring site for snow leopards, with annual camera trap surveys being conducted for over a decade. Snow leopard individuals in Tost have been followed across years, with several cats that have been captured and collared. We expect fewer misidentification errors in the Tost capture histories compared to Munkhkhairkhan which was surveyed for the first time.

Munkhkhairkhan was surveyed between May and September 2017 where 102 traps were deployed over an area of 9841 km^2. The Tost survey for PAWS was conducted between September 2019 and January 2020. Forty traps were set up over an area of 1902 km^2 in Tost. Survey regions and trap layouts are shown in Figure 2.

We estimated abundance and related parameters in both sites using standard SCR methods (including singletons) and the SCR-2 model (removing the singletons). Density was modelled as a log-linear function of the estimated occupancy probability that was obtained from Bayandonoi et al. (2021). The half normal encounter rate was used to model the counts of detections at the traps conditional on the activity centres.

3 | RESULTS

3.1 | Simulations

Summaries of the populations and capture histories simulated are shown in Table 1. Ten percent of the population introduced as ghosts resulted in an average of 1.86 (SD = 0.49) ghosts, for the low abundance, low encounter scenario; 2.34 (SD = 0.57) ghosts, for the low abundance, high encounter scenario; 3.91 (SD = 0.77) ghosts, for the high abundance, low encounter scenario and 4.86 (SD = 0.89) ghosts, for the high abundance, high encounter scenario. This resulted in an average increase of around five single detection capture histories under the high abundance scenarios and two single detection capture histories under the low abundance scenarios irrespective of the encounter rates. Lower encounter rates result in capture histories with fewer recaptures, which are more prone to being turned to single detection capture histories by misidentification errors.
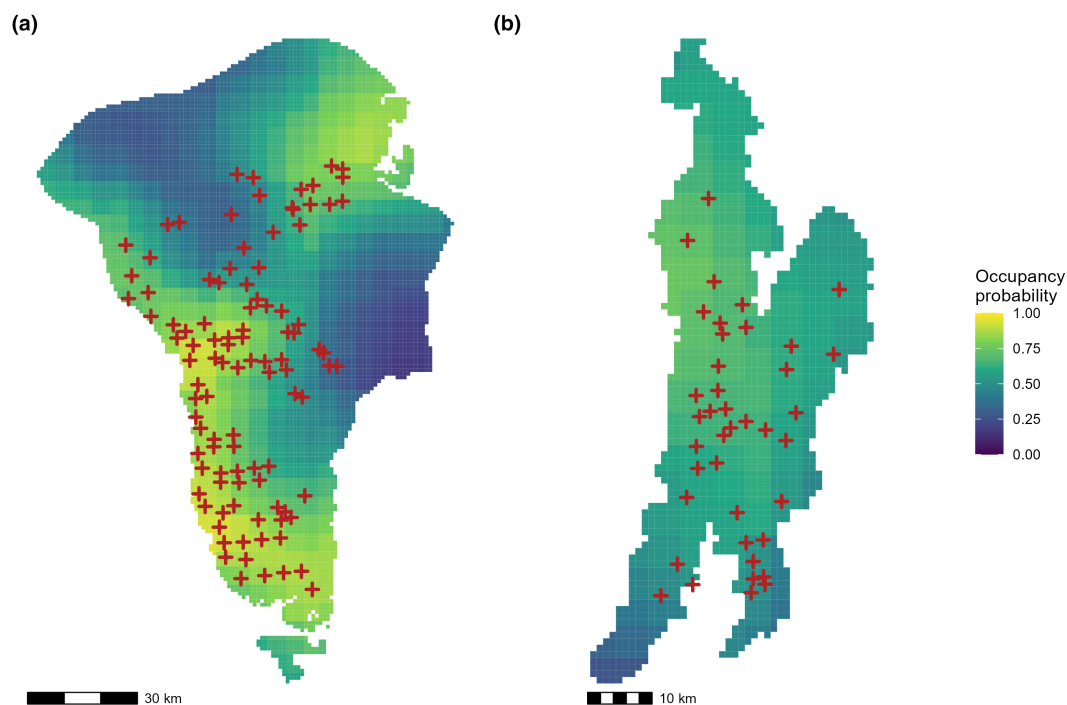

FIGURE 2 Survey regions of (a) Munkhkhairkhan and (b) Tost. Background colours show the occupancy probabilities estimated by Bayandonoi et al. (2021), used to model densities. Configurations of traps across the two survey sites are represented by red crosses. The survey regions are not to scale.

TABLE 1 Summaries of the simulated populations and sets of capture histories under the various scenarios. β_1 and σ were both fixed under all scenarios at 0.1 and 300, respectively.

			Mean (SD) values across simulations			
Density intercept (β_0)	Encounter rate (λ_0)	Proportion of ghosts introduced	Population size	Total detections	Individuals detected	Single detections
High (0.06)	High (2)	0%	107.3 (11.4)	177.2 (33.9)	48.4 (7.9)	11.8 (3.5)
		10%	107.3 (11.4)	177.2 (33.9)	53.2 (8.8)	17.2 (4.2)
		20%	107.3 (11.4)	177.2 (33.9)	58 (9.5)	22.4 (4.7)
		30%	107.3 (11.4)	177.2 (33.9)	62.9 (10.2)	27.8 (5.6)
	Low (1)	0%	107.3 (11.4)	87.1 (17.2)	39.3 (7.1)	15.8 (4.5)
		10%	107.3 (11.4)	87.1 (17.2)	43.2 (7.8)	20.9 (5.2)
		20%	107.3 (11.4)	87.1 (17.2)	47.1 (8.5)	25.8 (6)
		30%	107.3 (11.4)	87.1 (17.2)	50.8 (9.2)	31.1 (7)
Low (0.03)	High (2)	0%	53.5 (6.7)	81.4 (20.9)	23.5 (5)	6.1 (2.5)
		10%	53.5 (6.7)	81.4 (20.9)	25.8 (5.5)	8.6 (2.8)
		20%	53.5 (6.7)	81.4 (20.9)	28.1 (6)	11.3 (3.3)
		30%	53.5 (6.7)	81.4 (20.9)	30.5 (6.5)	14 (3.8)
	Low (1)	0%	53.5 (6.7)	41.8 (11.9)	18.3 (4.4)	7 (2.9)
		10%	53.5 (6.7)	41.8 (11.9)	20.2 (4.8)	9.4 (3.3)
		20%	53.5 (6.7)	41.8 (11.9)	22 (5.3)	11.7 (3.8)
		30%	53.5 (6.7)	41.8 (11.9)	23.6 (5.8)	14 (4.4)

Relative bias (RB) for no-ghost scenarios was generally smaller for estimated parameters compared to scenarios with ghosts for both methods (Figure 3). The SCR model, however, consistently overestimated abundance when ghosts were introduced and the RB of abundance increased with the proportion of detected individuals introduced as ghosts. The RB was always higher for the estimated abundance and λ_0, in scenarios with lower detection rates when ghosts were introduced. The variance of the parameters for all estimates from the SCR-2 model was higher than those from the SCR model due to lower sample sizes and MSE was therefore higher for all parameter estimates for the SCR-2 models when no ghosts were introduced. Considering only expected abundance: For high encounter rate scenarios, SCR-2 had comparable MSE to SCR at 10% of the detected individuals introduced as ghosts, the MSE for SCR-2 is notably lower for higher proportions of ghosts introduced; for low encounter rate scenarios, SCR-2 had higher MSE to SCR at 10% of the detected individuals introduced as ghosts, performed comparably to SCR at 20% of detected individuals introduced as ghosts. The MSE of the estimates of the expected abundance from the SCR-2 models outperformed SCR models at 30% of the detected individuals being introduced as ghosts under all scenarios.

Estimates of σ showed minimal bias for both models even when ghost capture histories were introduced. Furthermore, there was little loss in precision for σ estimates using the SCR-2 model as the MSE was similar to that of SCR models under all simulation scenarios. The SCR model underestimated λ_0 when ghosts were introduced and bias increased with the proportion of individuals detected as ghosts. Even in the SCR-2 model, the increasing trend in bias of λ_0 with increasing number of ghosts is observable. Fewer recaptured individuals imply lower encounter rates. In the SCR model, ghosts misinform the model

by falsely suggesting lower encounter rates. Ghosts are recaptured falsely made into singletons; in the SCR-2 model, dropping all singletons translates to dropping all true single-capture individuals and some misidentified recaptures. Dropping misidentified recaptures is analogous to an exclusion error, which results in lower encounter rates. While they may increase the uncertainty of estimates due to fewer detections, random exclusions do not bias the abundance estimate.

Under our implementation of the models, evaluating the likelihood once for 100 different simulated sets of capture histories took 45.21 s for the SCR model and 34.99 s for the SCR-2 model. While the SCR-2 model requires the additional computation of the conditional probability of detecting an animal once given an activity centre, the computation time was expected to be lower due to fewer individuals in the data.

3.2 | Case study: Snow leopards in Mongolia

Across the 102 traps in Munkhkhairkhan, 54 detections of snow leopards were made. Of these detections, 19 unique individuals were identified, of which eight were detected just once. In Tost, 177 detections of 22 uniquely identified individuals were made at the 40 traps. Three of the 22 were singletons. Estimates from both models are given in Table 2.

$E[N]$, the expected number of individuals, estimated by the SCR-2 method was lower in both sites as compared to SCR. The SCR estimate was around 8% higher in Tost and over 24% higher in Munkhkhairkhan. The higher estimates in abundance is reflected inversely in lower encounter rates (λ_0) estimated by the SCR method.
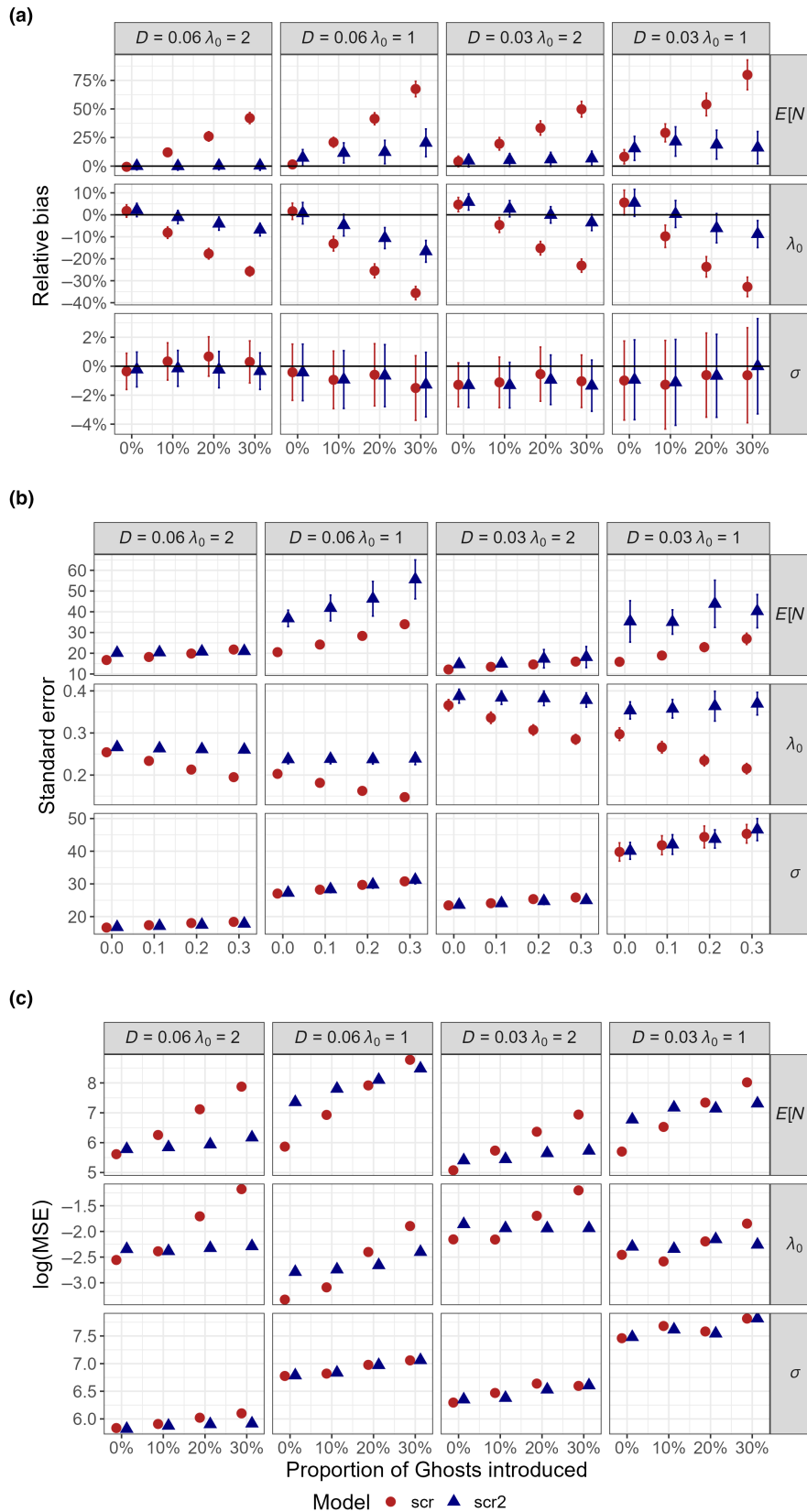
FIGURE 3 Results from the simulation study. Red circles represent the mean of simulation estimates from the SCR model and the blue triangles represent the mean of simulation estimates from the SCR-2 model. 95% error bars for the mean of the simulation estimates are also provided. (a) Relative bias computed as the ratio between the difference of the estimate from the true value and the true value. (b) Standard errors summarising the precision of the simulation estimates. (c) Log of the mean squared error of the simulation estimates from the true value. Each panel column represents one of the four scenarios for combinations of high and low abundance and encounter rates. Each panel row shows results for the estimates of expected abundance: $E[N]$, expected encounter rate at the activity centre: λ_0, and the range parameter: σ.

TABLE 2 Estimates and standard errors (*SE*) from the SCR and SCR-2 models for both the sites. *CV*, the coefficient of variation, is *SE*/Estimate. ΔEst and Δ*CV* are the relative differences in the parameter estimates and *CV*s of the SCR and SCR-2 models with respect to the SCR-2 model.

| Site | Parameter | Estimate (*SE*) | | CV | | | |
		SCR	SCR-2	SCR	SCR-2	ΔEst(%)	ΔCV(%)
Munkhkhairkhan	$E[N]$	33.06 (8.76)	26.58 (10.49)	0.26	0.39	24.38	−32.86
	λ_0	0.011 (0.0024)	0.013 (0.0031)	0.23	0.24	−16.67	−6.56
	σ	5491.24 (575.79)	5758.48 (657.8)	0.10	0.11	−4.64	−8.21
Tost	$E[N]$	23.99 (5.13)	22.15 (5.11)	0.21	0.23	8.34	−7.47
	λ_0	0.016 (0.0018)	0.017 (0.002)	0.12	0.12	−7.44	−0.91
	σ	7826.52 (431.34)	7684.95 (421.48)	0.06	0.05	1.84	0.49

Estimated σ from both models were similar, with the absolute difference between both models being < 5. With the exception of the σ estimate in Tost, dropping individuals with a single detection resulted in higher coefficients of variation for the estimates in the SCR-2 model. There was no loss in the precision on σ in Tost.

4 | DISCUSSION

Non-invasive methods used in surveys for abundance estimation by SCR generate raw data such as photographs or genetic samples that have to be converted into capture histories for the model. The step of converting the raw data to capture histories is seldom error-free, irrespective of whether it is done manually or is automated. Errors in data processing leading to single detection 'ghost' individuals are the most common in capture histories derived from both genetic as well as camera trap data (Johansson et al., 2020; Yoshizaki, 2007). We propose the SCR-2 method which we have demonstrated reduces the bias resulting from this common misidentification error across a number of sampling scenarios. The SCR-2 likelihood disregards all single captures (and therefore, it is assumed, all ghosts) and is parameterised in terms of the probability of being detected at least twice, rather than at least once.

Our simulation study shows the effect of ghosts in the capture history on parameter estimates. Johansson et al. (2020) reported a splitting error probability of 0.11 for each detection that led to up to four ghosts (25% of detected individuals) by experts in their experiment. However, they did not investigate whether this probability was affected by the total number of detections or individuals detected. More detections could lead to more ghosts or alternatively provide more reference images to reduce splitting errors. We therefore chose a conservative approach of introducing ghosts as a proportion of the number of individuals detected rather than a proportion of the total number of detections. Even at 10% of the detected individuals introduced as ghosts, there was a significant bias in the SCR abundance estimate. In contrast, estimates from the SCR-2 method were less biased under all scenarios of introduced ghosts.

Dropping single detections and fitting the SCR-2 model lead to a loss in precision of the parameter estimates. With regards to MSE, SCR-2 outperformed the SCR method at 10% of the detected individuals being introduced as ghosts under the high encounter rate scenarios suggesting that the reduction in bias outweighed the loss in precision. Under the low encounter rate scenarios, SCR-2 had comparable MSE to that of SCR only at 20% of the detected individuals being introduced as ghosts. If error rates are expected to generate 10% or more ghost capture histories, we recommend using the SCR-2 method over SCR for abundance estimation. In cases of low encounter rates, the modeller can choose between prioritising reduction in bias or variance, or alternatively given low sample sizes revisit the identification of the individuals from raw data. Within our case study, where the rates and types of misidentifications are not known, we show that there is a relative difference of 24% in abundance estimates in the site we suspected to be prone to identification errors. Based on the results from the simulation study, at 24% difference in the abundance estimates between the SCR and SCR-2 methods, it is likely that Munkhkhairkhan has identification errors that bias the abundance estimates from SCR.

Apart from camera trap surveys and genetic sampling, ghost recaptures have been shown to be the most common misidentification error in other non-invasive sampling methods (Stevick et al., 2001), making the SCR-2 method applicable in a larger range of surveys. Furthermore, SCR conditioned on at least *K* detections can also be used to deal with transient animals in a similar way to the CR method used by Conn et al. (2011). In cases where transients are expected to be detected more than once, given enough detections, higher numbers of detections can be dropped to estimate the resident population. The specific SCR-2 model, where *K*=2, has been independently developed and used to deal with potential false-positive detections of bowhead whale (*Baleana mysticetus*) calls in an acoustic spatial capture–recapture study (Petersma et al., 2023). The Petersma et al. (2023) model is specified for a binomial detection process and the conditional probability of an individual being detected at least twice is computed numerically, making it hard to scale for larger values of *K*.

It is straightforward to address heterogeneity in how ghosts are introduced. If individuals that are difficult to identify are more likely to generate ghosts, this heterogeneity can be modelled by adding individual-based covariates to λ_0 to model encounter rates. This could be the case in species where identifying individuals of

one sex is harder than the other, or if juveniles have less distinct markings than adults. The SCR-2 method can be used to avoid bias from ghosts in other common SCR extensions such as the M_t model where detection probability depends on trapping occasion and M_h models where there is heterogeneity in capture probabilities of different individuals (Borchers & Efford, 2008). While it is unbiased in the absence of misidentifications, the SCR-2 method, however, cannot be used to remove bias caused by ghost capture histories for M_b models where detection probability changes with repeated detections. Baiting to lure animals to detectors such as camera traps or hair snares is common in surveys (Gardner et al., 2010; Green et al., 2020). This can elicit a behavioural response in individuals resulting in them being 'trap-happy', more likely to be recaptured, or 'trap-shy', less likely to be recaptured. If misidentification has led to ghost individuals, the SCR-2 method cannot resolve the order of detections to model their appropriate detection probabilities. The ghost detection split from the true capture history may have been the first capture or one of the many recaptures, and estimates in this scenario may therefore be biased.

The hypothesis test we developed (Supporting Information S2), had low power and was different under each of the simulation scenarios. Running the hypothesis test to check for presence of ghosts would need to be accompanied by a power analysis of the test under the specific survey design and estimated parameters to interpret the results of the hypothesis test appropriately.

While ghosts are the result of the most common misidentification errors, other misidentification errors also occur and further investigation is required to understand how they affect SCR and SCR-2 estimates. Choo et al. (2020) review common errors in identifying camera trap images and outline best practices for teams to avoid them. Meanwhile, machine learning and deep learning methods for individual identification are areas of active research (Petso et al., 2022; Wang et al., 2022) and are becoming more accessible to practitioners. Similarly, model-based approaches to incorporate uncertainty in individual identities by leveraging partial identity (Augustine, 2018) and spatial information (Augustine et al., 2020) of detection illustrate effective frameworks for bypassing deterministic identification of individuals and the associated identification errors. Alongside these advances, there is a need to develop end-to-end integrated workflows which are able to take detections as input, classify individuals and incorporate the uncertainty of individual identities into the abundance estimates.

Conversely, a large number of single detection individuals need not indicate large number of identification errors or the presence of ghosts. The expected number of single captures is a function of the encounter function parameters, the trap layout and the state space. Low encounter rates yield lower detections and fewer recaptures. Small home ranges relative to the distance between traps can lead to greater numbers of single detections and traps placed further away from suitable habitats are likely to have fewer detections. SCR survey design and the trade-off between maximising the number of individuals detected or the number of recaptures is an active area of research (Efford & Boulanger, 2019; Durbach et al., 2021).

In summary, we extend the standard SCR model to condition on at least K detections. The new likelihood can be used to estimate abundance and detection parameters on a subset of the capture histories if there may be ghosts in the data. Our work shows that despite the loss in precision, it may be preferable to use the SCR-2 method rather than the SCR method when ghosts may be present. The standard SCR model is a special case of the more general method developed, the spatial capture–recapture conditioned on at least K detections, where $K = 1$. SCR conditioned on at least K detections lends itself to many extensions of SCR, is easily implementable in existing software and adds little additional computation time, making it accessible to both researchers and practitioners.

AUTHOR CONTRIBUTIONS

Abinand Reddy Kodi, Jasmin Howard, David Louis Borchers and Koustubh Sharma conceived the idea. Abinand Reddy Kodi and Jasmin Howard conducted the analysis and wrote the manuscript. David Louis Borchers, Hannah Worthington, Orjan Johansson and Koustubh Sharma reviewed and provided critical feedback for the manuscript. Justine Shanti Alexander, Purevjav Lkhagvajav, Gantulga Bayandonoi and Koustubh Sharma designed and organised camera trap surveys and managed the data. Justine Shanti Alexander, Purevjav Lkhagvajav, Gantulga Bayandonoi, Choidogjamts Byambasuren, Munkhtogtokh Ochirjav, Sergelen Erdenebaatar and Nyamzav Battulga conducted the camera trap surveys and classified individuals in the camera trap images.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

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.14326.

DATA AVAILABILITY STATEMENT

The data and code used in this study can be found on Zenodo https://zenodo.org/doi/10.5281/zenodo.10829662.

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SUPPORTING INFORMATION

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

Supporting Information S1. Presence-absence detection process simulation.

Supporting Information S2. Diagnosing ghosts-hypothesis test.