Spatially explicit capture–recapture models for relative density

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Abstract

Spatially explicit capture–recapture (SECR) methods are used widely to estimate animal population density and related parameters. Maximum likelihood has been applied to two flavors of SECR model - a full model that includes absolute density as a spatially varying parameter, and a model conditional on the number of detected individuals that assumes uniform density. We show how the conditional model may be extended to estimate relative density as a function of habitat and other spatial variables. The conditional model has the major advantage of seamlessly including individual covariates of detection. It is also faster to fit than the full model and more robust with an 'identity' link. The spatial absolute density surface may be derived from the conditional model fit. We demonstrate this with a spline surface fitted to data on American black bears (*Ursus americanus*). The relative density formulation also allows an adjustment for spatially selective prior marking. The problem arises when fish are caught and implanted with transponders, such as acoustic tags, and later monitored intensively with passive recorders. The confounding spatial effect of undocumented initial sampling may be removed from spatial analyses of the monitoring data by including an offset proportional to the smoothed sampling effort.

Introduction

Capture–recapture is used to estimate parameters of animal populations from detections of marked individuals. In spatially explicit capture–recapture (SECR) the population is conceived as a spatial distribution of activity centers (AC) and inference includes both the absolute density of the distribution and variation with respect to spatial covariates. The method is well-suited to data

from automatic cameras, given that individuals can be distinguished from natural marks, and from passive DNA samplers such as hair snares.

SECR modeling of spatial variation in density was introduced by Borchers & Efford (2008) and has been further discussed by Efford & Fewster (2013), Royle et al. (2014) and Borchers & Fewster (2016). Density is modeled as the intensity of an inhomogeneous Poisson process for AC. AC are assumed to be located independently of each other i.e. there is no clustering or spacing (cf Reich et al., 2016); breaches of the independence assumption particularly affect variance estimates (cf Bischof et al., 2020; Efford & Fletcher, 2024). We do not consider here the illustrations sometimes described as 'density surfaces' that result from aggregating the estimated sampling distributions of AC for detected individuals (Durbach et al., 2024).

The elegance of SECR for estimating absolute density has overshadowed its potential for modeling density with respect to spatial covariates. A spatial covariate may be any known attribute of points in the potentially occupied habitat. Candidates include vegetation type, disturbance history, distance to human habitation, and the spatial coordinates themselves. The pattern of animal density with respect to such predictors provides important data for population management (e.g., Boulanger, Neilsen & Stenhouse, 2018; Lamb et al., 2018).

The fitting of SECR models with spatial variation in density has previously been assumed to require maximization of the full likelihood (Borchers & Efford, 2008; Borchers & Fewster, 2016), or an equivalent Bayesian method (Royle et al., 2014). We show how relative density can instead be estimated by maximizing the simpler likelihood conditional on n, the number of detected individuals. Modeling of relative density is sufficient to answer ecological questions such as whether there is evidence that density varies with a particular environmental factor.

Location-specific absolute density may be estimated as a derived parameter. Conditioning on n has the further advantage of allowing detection parameters to be modeled as a function of individual covariates, thereby reducing potential heterogeneity bias.

Conditional estimation of relative density opens up further possibilities. We describe one arising from the acoustic tagging and telemetry of fish in a river system. Fish are caught and implanted with acoustic transponders and then monitored with stationary acoustic recorders (Whoriskey et al., 2019). It is common for the initial capture-and-implantation phase to be informal and to lack the detailed documentation of effort and capture locations needed for SECR. Whether documented or not, the tagged population is likely to differ in distribution from the population as a whole. Analyses of fish distribution that use data from the acoustic monitoring phase alone will therefore be misleading. An ad hoc measure of spatial variation in tagging probability may be incorporated in the conditional estimation of relative density. Simulations show this is effective for describing variation in AC density of the population as a whole.

Theory

Full SECR likelihood

The SECR likelihood has the form

$$L(\phi, \theta|\Omega) = \Pr(n|\phi, \theta)\,\Pr(\mathbf{\Omega}|n, \phi, \theta), \tag{1}$$

where Ω is the set of n observed spatial detection histories, ϕ is a vector of density parameters and θ is a vector of detection parameters (Borchers & Efford, 2008). The first factor on the right of

Equation (1) concerns the number of detected animals n, which is expected to be Poisson for sampling from an inhomogeneous Poisson distribution of AC. The second factor on the right concerns the probability of their detection histories, conditional on n. Assuming that individuals are detected independently of each other, the second factor may be expanded to

$$\Pr(\mathbf{\Omega}|n, \phi, \theta) \propto \prod_{i=1}^{n} \int \Pr(\boldsymbol{\omega}_i|\theta, \mathbf{x})\, f(\mathbf{x}|\boldsymbol{\omega}_i > 0, \phi, \theta)\; d\mathbf{x}. \tag{2}$$

A multinomial coefficient is omitted because it does not depend on the parameters and therefore does not affect their maximum likelihood estimates. In words, for each detection history $\boldsymbol{\omega}_i$ we integrate over possible AC locations $\mathbf{x}$ the probability of observing $\boldsymbol{\omega}_i$ given that the activity center was at $\mathbf{x}$ (i.e. $\Pr(\boldsymbol{\omega}_i|\theta, \mathbf{x})$), weighted by the probability density for an AC at $\mathbf{x}$ given that the individual was observed (i.e. $f(\mathbf{x}|\boldsymbol{\omega}_i > 0, \phi, \theta)$). Integration here is typically over 2-D space and $\mathbf{x}$ is a vector comprising the x- and y-coordinates, but the same mathematics applies in linear networks. Integration is achieved in practice by summing the integrand over a set of pixels for which its value is non-negligible, known as the habitat mask.

The probability density $f(\mathbf{x})$ has components for (i) the spatial distribution of the population, modeled with the density function $D(\mathbf{x}|\phi)$, and (ii) the probability $p_{\cdot}(\mathbf{x}|\theta)$ that an individual with AC at $\mathbf{x}$ appears in the sample. Formally:

$$f(\mathbf{x}|\boldsymbol{\omega}_i > 0, \phi, \theta) = \frac{D(\mathbf{x}|\phi)p_{\cdot}(\mathbf{x}|\theta)}{\int D(\mathbf{x}|\phi)p_{\cdot}(\mathbf{x}|\theta)d\mathbf{x}}. \tag{3}$$

The probability $p_{\cdot}(\mathbf{x}|\theta)$ combines the probabilities of detection at each detector, each possibly compounded from probabilities of detection over multiple occasions. For further details see Borchers & Efford (2008), Efford et al. (2009) and Appendix S1.

Density submodels

The intensity of the inhomogeneous Poisson process for AC is commonly modeled as a log-linear function of covariates, viz.

$$\log D(\mathbf{x}|\phi) = \beta_0 + \sum_{v=1}^{V} \beta_v c_v(\mathbf{x}), \tag{4}$$

where the $c_v(\mathbf{x})$ are spatial covariates and the βs are coefficients to be estimated that together comprise the vector ϕ. A spatial covariate is any habitat or other characteristic measured at point $\mathbf{x}$, possibly including the spatial coordinates themselves. The bases of regression splines may be used as covariates in the linear predictor, the right-hand side of Equation (4), and this is especially useful in SECR for fitting trend surfaces (Borchers & Kidney, 2014). The logarithmic transformation ensures that the modeled density is always positive. The transformation is analogous to the 'link' function in generalized linear models (McCullagh & Nelder, 1989) and we use that term for convenience.

A log link is used widely for density in SECR, but it has a major defect. SECR models usually include an unsampled region peripheral to the detectors; AC there are detected with low probability, but ignoring them altogether causes bias in estimates of density. Extrapolation of a fitted log-linear density model to the periphery often results in biologically implausible values, and this is almost inevitable when the covariates are spatial coordinates or a regression spline.

An alternative 'identity' link was used by Efford and Fewster (2013) in a model of skink density. The identity link uses the linear predictor truncated at zero:

$$D(\mathbf{x}|\phi) = \max[\beta_0 + \sum_{v=1}^{V} \beta_v c_v(\mathbf{x}), 0]. \tag{5}$$

Extrapolation of a linear density model gives less extreme predictions in the periphery, and the

coefficients are more easily interpreted than those of the log-linear model.

Conditional likelihood

If density is uniform then $D(\mathbf{x}|\phi)$ cancels out of Equation (3) and maximizing the likelihood conditional on n in Equation (2) provides an estimate of θ. The effective sampling area a is a function of θ that may include individual covariates $\mathbf{z}$, so this leads to a Horvitz-Thompson-like estimate of the uniform density $\hat{D} = \sum_{i=1}^{n} 1/a(\hat{\theta}, \mathbf{z}_i)$ (Borchers & Efford, 2008). The conditional form has some practical uses: models for θ may be evaluated more rapidly as maximization is over fewer parameters, and modeling the effect of individual covariates on detection can be beneficial (Huggins, 1989). The derived estimate of density is numerically identical to that from maximization of the full likelihood when AC are assumed to follow a Poisson distribution. However, if density is not uniform then $D(\mathbf{x}|\phi)$ does not cancel out of Equation (3) and the spatial variation in density (i.e. relative density) must be modeled to obtain an unbiased estimate of θ. This is not as onerous as it sounds.

We define relative density by $D'(\mathbf{x}|\phi^-) \equiv k^{-1}D(\mathbf{x}|\phi)$ where ϕ^- is a vector with one fewer coefficients than ϕ and k^{-1} is a constant of proportionality. For the log link, $k = \exp(\beta_0)$ and ϕ^- is simply ϕ without the intercept. For the identity link, $k = \beta_0$ and ϕ^- is ϕ with the intercept removed and remaining coefficients divided by β_0.

We simplify and maximize the conditional likelihood in Equation (2) to estimate both the detection parameters θ and the coefficients of relative density ϕ^-. Cancelling the constant k and

allowing the overall probability of detecting individual i to vary with covariates $\mathbf{z}_i$ yields

$$\Pr(\mathbf{\Omega}|n, \phi^-, \theta) \propto \prod_{i=1}^{n} \frac{\int \Pr(\boldsymbol{\omega}_i|\theta, \mathbf{x})\, D'(\mathbf{x}|\phi^-)\, p_{\cdot}(\mathbf{x}|\theta, \mathbf{z}_i)\, d\mathbf{x}}{\int D'(\mathbf{x}|\phi^-)\, p_{\cdot}(\mathbf{x}|\theta, \mathbf{z}_i)\, d\mathbf{x}}. \tag{6}$$

Observe that when $p_{\cdot}(\mathbf{x}|\theta)$ does not depend on covariates, $\mathrm{E}(n) = k \int D'(\mathbf{x}|\phi^-) p_{\cdot}(\mathbf{x}|\theta)\, d\mathbf{x}$. This suggests the estimate

$$\hat{k} = \sum_{i=1}^{n} 1 / \int D'(\mathbf{x}|\hat{\phi}^-) p_{\cdot}(\mathbf{x}|\hat{\theta}, \mathbf{z}_i)\, d\mathbf{x}, \tag{7}$$

where $\hat{k}$ provides the missing intercept of the absolute density model (e.g., $\hat{\beta}_0 = \log \hat{k}$ for a log link).

For uniform density $D'(\mathbf{x}|\phi^-)$ takes the value 1 and $\int D'(\mathbf{x}|\phi^-) p_{\cdot}(\mathbf{x}|\theta, \mathbf{z}_i)\, d\mathbf{x}$ collapses to the effective sampling area of individual i ($a(\theta, \mathbf{z}_i) = \int p_{\cdot}(\mathbf{x}|\theta, \mathbf{z}_i)\, d\mathbf{x}$). Equation (7) is then the usual Horvitz-Thompson-like estimate of uniform density. This justifies calling $\int D'(\mathbf{x}|\phi^-) p_{\cdot}(\mathbf{x}|\theta, \mathbf{z}_i)\, d\mathbf{x}$ the 'density-weighted effective sampling area'. Further, an estimate of the absolute density at a point $\mathbf{x}$ is

$$\hat{D}(\mathbf{x}|n, \hat{\phi}^-, \hat{\theta}) = \sum_{i=1}^{n} \frac{D'(\mathbf{x}|\hat{\phi}^-)}{\int D'(\mathbf{x}|\hat{\phi}^-) p_{\cdot}(\mathbf{x}|\hat{\theta}, \mathbf{z}_i)\, d\mathbf{x}}. \tag{8}$$

Relative density and 2-phase sampling

For acoustic telemetry we must allow for distinct tagging and monitoring phases. In concept, each phase is a spatially explicit capture–recapture experiment with a shared population process $D(\mathbf{x}|\phi)$, but differing sampling processes (detection parameters θ_1, θ_2). For the notional detection

histories Ω_1 from Phase 1, and the observed histories Ω_2 from Phase 2,

$$\begin{aligned} L(\phi, \theta_1|\Omega_1) &= \Pr(n_1|\phi, \theta_1)\Pr(\Omega_1|n_1, \phi, \theta_1), \text{ and} \\ L(\phi, \theta_2|\Omega_2) &= \Pr(n_2|\phi, \theta_2)\Pr(\Omega_2|n_2, \phi, \theta_2). \end{aligned} \tag{9}$$

However, we lack the data to fit the idealized model in Equation (9) and thereby to estimate ϕ, θ_1 and θ_2. We have only the n_2 detection histories from Phase 2, represented by Ω_2, and possibly the total number marked in Phase 1 (n_1). Further, the only fish at risk of detection in Phase 2 are those marked in Phase 1, and these have a spatial distribution that confounds the underlying density and the Phase-1 detection process.

If we limit ourselves to fitting a model for *relative* density to the Phase 2 data then some progress is possible. The population at risk of detection in Phase 2 has density at $\mathbf{x}$ proportional to $D'(\mathbf{x}|\phi^-)p_1(\mathbf{x}|\theta_1)$, using $p_1(\mathbf{x}|\theta_1)$ for the location-specific probability of detection in Phase 1, and similarly for Phase 2 (we assume no covariate effects on indiivdual detection). That is also true if $p_1(\mathbf{x}|\theta_1)$ is substituted by any proportional variable $q(\mathbf{x}) \propto p_1(\mathbf{x}|\theta_1)$. This leads to

$$\Pr(\mathbf{\Omega}_2|n_2, \phi^-, \theta_2) \propto \prod_{i=1}^{n_2} \frac{\int \Pr(\boldsymbol{\omega}_{2i}|\theta_2, \mathbf{x})\, D'(\mathbf{x}|\phi^-)\, q(\mathbf{x})\, p_2(\mathbf{x}|\theta_2) d\mathbf{x}}{\int D'(\mathbf{x}|\phi^-)\, q(\mathbf{x})\, p_2(\mathbf{x}|\theta_2) d\mathbf{x}}. \tag{10}$$

The good news here is that maximizing the likelihood from Equation (10) allows us to estimate coefficients of the relative density function ϕ^- and the acoustic detection process θ_2. The bad news is that this depends on knowledge of the original detection process summarized as $q(\mathbf{x})$. If we ignore the factor $q(\mathbf{x})$ then the results may be misleading because the tagged animals are a spatially biased sample of the larger population.

Alternatively, we might treat $q(\mathbf{x})$ as known and plug the values into Equation (10). A possible candidate for $q(\mathbf{x})$ is a smoothed measure of the sampling effort. The bandwidth of the smoother

will be arbitrary. It determines the 'edge effect' of initial tagging - the risk of becoming tagged for AC at some distance from the locations of sampling effort. It is convenient for our motivating case that edge effects are much reduced in linear riverine systems compared to two dimensional habitats. If the relative density model uses a log link then $\log q(\mathbf{x})$ is effectively an offset in GLM terms (a covariate with known coefficient 1.0; McCullagh & Nelder, 1989).

A simulated example in Appendix S2 shows that inference on covariate effects may be very poor when the spatial bias from Phase 1 is ignored, and that this may be corrected with a suitable plug-in value $q(\mathbf{x})$.

Implementation

The number of identifiable coefficients for relative density in the conditional model (ϕ^{-}) is one less than the number for absolute density in the full model (ϕ). This is achieved in software for maximizing the full likelihood by fixing the intercept coefficient at either zero (log link) or 1.0 (identity link), and omitting the likelihood component for n. For the log link, estimated coefficients of the Poisson relative density model are identical to the corresponding coefficients of the full model. For the identity link, the estimated coefficients equal those from the full model divided by its intercept. The density intercept on the natural scale may be derived from the density-weighted effective sampling areas of Equation (7).

Estimation of relative density by maximizing the conditional likelihood is included in recent versions of the R package 'secr' (R Core Team, 2024; Efford, 2025a). The conditional likelihood in Equation (6) is maximized numerically whenever the CL argument of function 'secr.fit' is

TRUE and a model formula is specified for density. Functions ‘derivedDcoef’ and ‘derivedDsurface’ implement Equations (7) and (8) respectively.

The suggested extension for two-phase tagging and acoustic monitoring presumes that the spatial selectivity of tagging can be represented by $q(\mathbf{x})$. This may be included as an offset in the model for relative density by fixing the coefficient of the corresponding covariate to 1.0 (log link only) or more generally by maximizing the conditional likelihood Equation (10). The more general route is taken in ‘secr.fit’ when the covariate is named in the ‘details’ argument ‘externalqx’.

Example

American black bears *Ursus americanus* were surveyed with 65 baited hair snags in the Great Smoky Mountains National Park, Tennessee, over 10 weeks in the summer of 2003; individuals were identified from their microsatellite DNA (Settlage et al., 2008; Laufenberg, van Manen & Clark, 2013; Efford, 2025a). We fitted a regression-spline trend surface model with 5 df for density using both the full and conditional likelihoods. A habitat mask (pixels 0.25 km $\times$ 0.25 km) extended 6 km beyond the outermost hair snags except where truncated at the park boundary. Bears showed a tendency to return to snags they had visited previously, and this effect was included in all models. R code and additional results are in Appendix S3.

The derived density surface from the regression-spline relative density model is shown in Fig. 1. Coefficients of the relative density were identical within numerical precision to the scaled coefficients from the full likelihood model (Appendix S3).

In the bear example with location-specific learned response, the conditional (relative density)

model fit much faster than the full model (93 s vs 327 s). The speed advantage of the conditional model is more typically on the order of 25–50% (see simulations in Appendix S4).

Simulations

Simulations were performed to compare the performance of full likelihood and conditional likelihood density models when the covariate effect on density was known, and to demonstrate the effect of heterogeneous detection.

Sampling was simulated for a 10 x 10 square grid of multi-catch traps spaced s units apart. The population density declined radially and linearly from $2.0s^{-2}$ in the grid center to $0.0s^{-2}$ at $12.5s$ units from the center ($\beta_1 = -0.16$) within a region that extended $5s$ beyond the grid (Fig. 2). The population was assumed to comprise two equal groups that differed in movement scale ($\sigma_1 = 0.5s$, $\sigma_2 = 1.0s$) but not in the intercept of the hazard half-normal detection function ($\lambda_0 = 0.5$).

The distribution of AC may be viewed as an inhomogenous Poisson process (IHPP) or as an IHPP conditional on a fixed number N_A within an area of interest A. The conditional IHPP approach leads to a binomial model for n, in contrast to the usual Poisson model. We do not repeat here the arguments against routine use of the conditional IHPP approach (e.g. Efford & Fletcher, 2024). However, for interest we contrasted the fixed (binomial-n) and Poisson approaches. The number of AC simulated within the region was either drawn from a Poisson distribution with mean 302.3 or fixed to approximate that mean (randomly 302 or 303 in proportions 0.7, 0.3).

Three models were fitted to each simulated dataset for each AC distribution by numerically maximizing the likelihood: a full likelihood model, a conditional likelihood model, and a

conditional likelihood model with group as a covariate of σ. All used radial distance as a linear covariate of density and estimated the coefficient of decline β_1. The identity link was used for all fits. For the full likelihood model this required tuning of the maximization algorithm to allow for differences in the scale of the coefficients (argument 'typsize' of the R function nlm (R Core Team 2024)). For conditional fits the density intercept β_0 was derived using Equation (7). The distribution of n for the full model was appropriate to the generating distribution (Poisson or binomial). R code, sample sizes and detailed results are given in Efford (2025b).

Full and conditional likelihood approaches gave almost identical estimates of the density model coefficients for Poisson N_A (Table 1). Estimates of the intercept parameter β_0 were negatively biased, as expected, when the model did not allow for heterogeneous σ. Intercept estimates from the conditional model were virtually unbiased when the model included a group effect on σ. The group effect cannot be included directly in the full likelihood model. Full (binomial-n) and conditional likelihood gave noticeably different estimates of the coefficients when N_A was fixed (Table 1).

Fitting the Poisson conditional model took on average 1.07 s (SE 0.01 s) compared to 2.53 s (SE 0.01 s) for the full model. Post hoc calculation of $\hat{\beta}_0$ was fast (0.01 s). Inclusion of a group effect on σ slowed fitting of the conditional model (3.07 s, SE 0.02 s).

Discussion

Although density models lie at the heart of SECR, they have received only limited statistical attention. Recent papers have called for greater care in the modeling of density surfaces from

capture–recapture data. Durbach et al. (2024) questioned the misleading use of the term ‘density surface’ in many papers. Zhang & Shen (2024) emphasized that their method for estimating density dependence required rigorous control of density-independent variation in density.

Maximization of the conditional likelihood has practical advantages. Estimating one fewer parameters than in the full model leads to faster maximization and potentially reduces the frequency of numerical issues. Models with the identity link are easier to fit by maximizing the conditional likelihood because coefficients are automatically scaled by the intercept. An important feature of the relative density model is that it may include the effect of individual covariates on detection, as in the uniform-density conditional likelihood model (Borchers & Efford, 2008) and its nonspatial equivalent (Huggins 1989). This facilitates the joint investigation of detection and density, and inclusion of individual covariates of detection removes a potential source of bias as in the simulated example.

The present approach clarifies the relationship between the conditional and full likelihoods: the former captures all information on relative density, while the latter simultaneously scales this to absolute density by modeling n. Coefficients for log-linear covariate effects on density are numerically identical between the full and conditional likelihood models for IHPP data. This follows from the S-ancillarity of n in a Poisson model (Schofield & Barker, 2016). Conversely the binomial-n full likelihood estimates diverged from the conditional likelihood estimate when N_A was fixed, and n is not ancillary in this case. The conditional likelihood model assumes k to be constant rather than varying with individual characteristics as proposed by Borchers & Efford (2008 p. 380). However, the Horvitz–Thompson-like estimator in Equation (7) may be computed for arbitrarily defined subsets of the detected individuals.

The effectiveness of the conditional model for estimating spatial variation in relative density has a direct equivalent in the Pradel–Link–Barker (PLB) open population model that also conditions on n (Schofield & Barker, 2016; Efford & Schofield, 2020). Temporal variation of the finite population growth rate in PLB models is analogous to spatial variation in relative density. Spatial implementations of the PLB model (e.g., Efford & Schofield, 2020) have not so far included spatial variation in density. This would be a useful extension, although it is a challenge to parameterize temporally varying spatial variation in density.

Some implementation issues have yet to be resolved. Certain models do not fit neatly into the framework. These include models in which the spatial scale of detection σ is treated as a function of absolute density (Efford et al., 2016). Models for relative density in which the likelihood is a product over independent samples ('sessions') require special care: all coefficients are estimable in a model for session-specific trend of the form D ~ session:x because it does not include an intercept, whereas the implied intercept in D ~ session*x is not.

The utility of the suggested application of the offset method for 2-phase sampling remains to be explored in practise. It has the limitation that uncertainty in $q(\mathbf{x})$ is not propagated to the final estimates. Consequences for the model of relative density might be examined by simulation.

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Table 1: Coefficients of radial density model estimated from simulated data ($\beta_0 = 2.0, \beta_1 = -0.16$).

	Poisson N_A		Fixed N_A	
Model	$\hat{\beta}_0$ (SE)	$\hat{\beta}_1$ (SE)	$\hat{\beta}_0$ (SE)	$\hat{\beta}_1$ (SE)
Full	1.9406 (0.0101)	-0.1612 (0.0020)	1.9682 (0.0101)	-0.1684 (0.0021)
CL, $\sigma \sim 1$	1.9406 (0.0101)	-0.1612 (0.0020)	1.9324 (0.0098)	-0.1599 (0.0020)
CL, $\sigma \sim g$	2.0087 (0.0099)	-0.1616 (0.0019)	1.9995 (0.0098)	-0.1597 (0.0020)

The conditional likelihood (CL) model with $\sigma \sim g$ includes a group effect that causes bias in $\hat{\beta}_0$ when not modeled. Results are shown for an unconstrained IHPP distribution of activity centers (Poisson N_A) and for a conditional IHPP distribution (Fixed N_A). Mean of 1000 replicates

Figure captions

Figure 1. Derived density surface for American black bears in Great Smoky Mountains National Park, Tennessee, USA, in 2003. Contour labels indicate the number of bears per km^2. Hair snag locations are shown as white dots. Bear activity centers were not believed to occur outside the northern park boundary as shown.

Figure 2. Scenario for simulated density of AC centered on a 10 x 10 grid of multi-catch traps. Grey dots along the line in the right-hand plot correspond to pixels on the left.

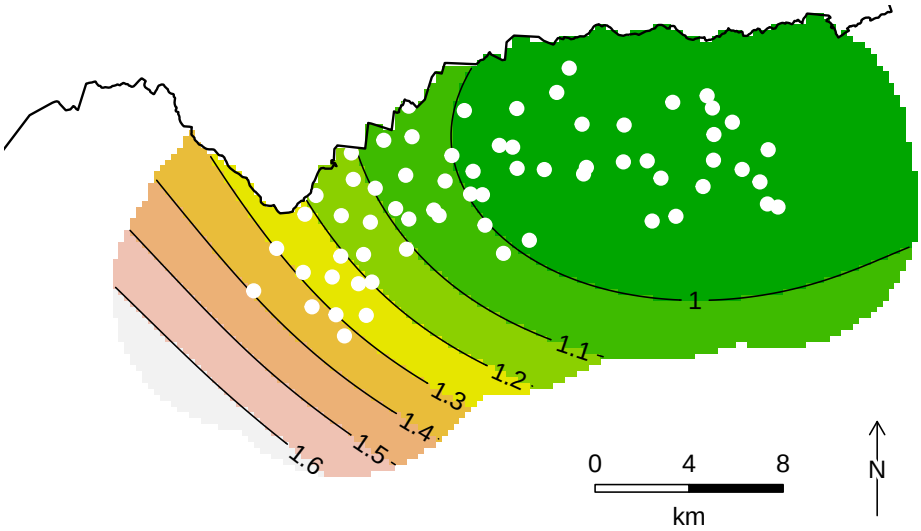

Figure 1

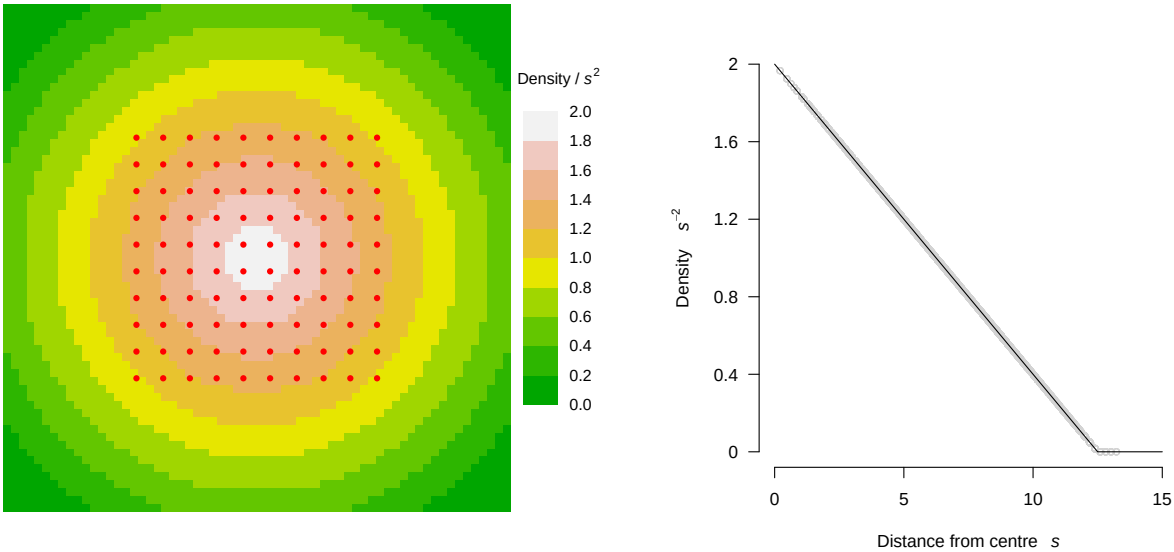
Density / s^2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Density s^{-2}
2
1.6
1.2
0.8
0.4
0
0
5
10
15
Distance from centre s

Figure 2

Appendix S1. Model for overall probability of detection

For independent events,

$$p_{\cdot}(\mathbf{x}|\theta) = 1 - \prod_{k}^{k=K} \prod_{j}^{j=J} [1 - p_{jk}(\mathbf{x}|\theta)], \tag{1}$$

where $p_{jk}(\mathbf{x}|\theta)$ is the probability of detection on occasion j at detector k given the vector of parameters θ. For present purposes we assume the p_{jk} are all governed by a distance-detection function such as the halfnormal $p_k(\mathbf{x}|\theta) = g_0 \exp[-d_k^2/(2\sigma^2)]$ where d_k is the distance between AC location $\mathbf{x}$ and detector k, and parameter vector $\theta = (g_0, \sigma)$. Then

$$p_{\cdot}(\mathbf{x}|\theta) = 1 - \prod_{k}^{k=K} [1 - p_k(\mathbf{x}|\theta)]^J. \tag{2}$$

Other distance-detection functions are the negative exponential, hazard halfnormal and hazard negative exponential.

Appendix S2. Simulation of two-phase sampling

Failure to account for the spatial distribution of sampling effort can heavily bias models for the effect of covariates on fish density. The risk is demonstrated here with simulations of a fish population along a linear reach using code in Efford (2025).

Density of activity centers (AC) varies in a log-linear fashion along the reach: $\log D = \beta_0 + \beta_1 d$ where d is the distance in kilometers from the start. We use $\beta_0 = \log(100)$ and $\beta_1 = 1.0$. Localized tagging (Phase 1) leads to a tagged population with the spatial distribution shown in light blue in Fig. 1. The per capita probability of being tagged (dashed line in Fig. 1) is unknown, but we assume its relative magnitude can be approximated from the distribution of sampling effort (light blue bar), appropriately smoothed.

We aim to estimate the relationship between AC density and distance along the river d. For the relative measure of tagging probability $q(\mathbf{x})$ we use the Phase-1 $p_.(\mathbf{x})$; this is a 'best case' scenario. We compare three SECR relative density models fitted to simulated Phase 2 data:

1. A naive model with d as a predictor
2. A model including adjustment $q(\mathbf{x})$
3. A model with $\log q(\mathbf{x})$ as an offset

The naive model estimated a covariate relationship that was not only the wrong magnitude but also the wrong direction, whereas both implementations of the adjustment resulted in unbiased estimates of the relationship (Table 1). This is an extreme case, and assumes a suitable adjustment is available.

Efford, M. G. 2025. Simulations of spatially selective prior marking in capture-recapture analyses (1.0.0). Zenodo. https://doi.org/10.5281/zenodo.14714959

Table S1: Estimates of coefficient β_1 in model $\log D = \beta_0 + \beta_1 d$ from three models described in the text. True $\beta_1 = 1.0$. 1000 simulations.

Model	Mean ($\hat{\beta}_1$)	SE ($\hat{\beta}_1$)
naive	–0.2131	0.0044
$q(\mathbf{x})$	0.9999	0.0086
offset	1.0135	0.0089

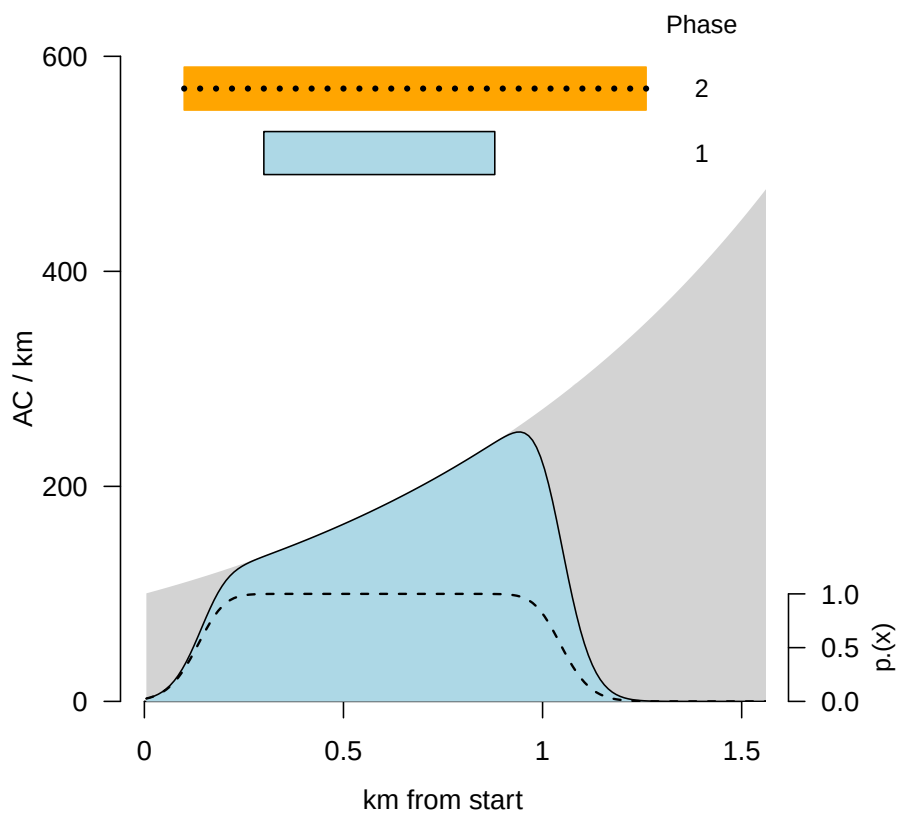

Fig. S1: Scenario for simulation of 2-phase sampling. Population density (gray shading) increases log-linearly from left to right. Informal sampling in Phase 1 (light blue bar) results in a spatially localized tagged population (light blue hill). The probability of an individual being tagged ($p.(\mathbf{x})$) is shown by the dashed line. The extent of acoustic monitoring (Phase 2) is shown by the orange bar.

Appendix 3. Code and results for black bear example

The black bear example uses the dataset 'blackbearCH' included in recent versions of the R package 'secr' (Efford 2025; J. Laufenberg and J. Clark pers. comm.). The models fitted here use the hazard negative exponential detection function (HEX) because this has been shown to provide a better fit than the usual halfnormal and because it is robust to occasional long-distance movements. Model comparisons (not reported here) show a small difference in detection parameters between males and females; these are not included in the comparison reported here because they cannot be accommodated in the direct full-likelihood equivalent of the relative density model. The effect 'bk' represents a tendency of bears to return to hair snags they visited previously.

```
library(secr)

# generate a habitat mask
msk <- make.mask(traps(blackbearCH), buffer = 6000, spacing = 250,
    type = 'trapbuffer', poly = GSM, keep.poly = FALSE)

# fit model
baseargs <- list(
    capthist = blackbearCH,
    model    = list(D~s(x,y, k = 5), lambda0~bk),
    detectfn = 'HEX',
    mask     = msk,
    link     = list(D = 'identity'),
    details = list(fastproximity = FALSE),
    ncores   = 8,
    trace    = FALSE)

# fit full and conditional models, most arguments shared
fitboth <- list.secr.fit(CL = c(FALSE, TRUE), constant = baseargs)

# plot
plot(derivedDsurface(fitboth[[2]], mask = msk), title = 'Density / km2',
    scale = 1e4, legend = FALSE)
plot(derivedDsurface(fitboth[[2]], mask = msk),  plottype = "contour",
    poly = FALSE, breaks = seq(0,22,2), add = TRUE, scale = 1e2,
    labcex = 1)
plot(traps(blackbearCH), add = TRUE, detpar = list(pch=16, fg = 'white',
    cex = 1.2))
plot(GSM, add = TRUE, lwd = 1.5)
```

Table S1: Coefficients of black bear SECR model fitted by maximizing the full and conditional likelihoods. The identity link was used for density (D) and a log link for λ_0 (lambda0) and σ (sigma).Also shown are the coefficients of the full density model divided by the intercept (0.0113).

	Full		Full (scaled)		Conditional	
	beta	SE.beta	beta	SE.beta	beta	SE.beta
D	0.0113	0.0018	1.0000	0.1582	–	–
D.s(x,y).1	0.0006	0.0021	0.0503	0.1864	0.0504	0.1869
D.s(x,y).2	–0.0057	0.0099	–0.5035	0.8753	–0.5036	0.8422
D.s(x,y).3	–0.0014	0.0017	–0.1218	0.1520	–0.1217	0.1546
D.s(x,y).4	–0.0008	0.0024	–0.0738	0.2081	–0.0737	0.2022
lambda0	–3.0992	0.2053	–	–	–3.0992	0.2053
lambda0.bkTRUE	2.0295	0.2122	–	–	2.0296	0.2121
sigma	6.9953	0.1013	–	–	6.9952	0.1011

References

Efford, M. G. 2025. secr: Spatially Explicit Capture–Recapture models. R package version 5.2.0. https://CRAN.R-project.org/package=secr.

Appendix 4. Execution time for full and conditional models

The time required to fit conditional (relative density) and full (absolute density) models was checked for a range of trend surface models fitted to each of two datasets builtin to the R package 'secr' (Efford 2025a): 'captdata', an artificial dataset of 235 captures of 76 individuals on a notional 10 × 10 array of single-catch traps, and 'blackbearCH', the Great Smoky Mountains National Park black bear dataset used in the main text. The fitted density models are listed in Table S1. R code is provided in Efford (2025b).

Table S1: Scenarios for simulating execution time

Code	Model	Description
a	D~1	constant density
b	D~x	log-linear E-W trend
c	D~s(x, y, k = 3)	regression spline 3 df
d	D~s(x, y, k = 5)	regression spline 5 df
e	D~s(x, y, k = 7	regression spline 7 df

Average execution time for a conditional fit was 29% less than the time for the full fit with 'captdata' and 51% less than the time for the full fit with 'blackbearCH'. Times are plotted in Fig. S1.

References

Efford, M. G. 2025a. secr: Spatially Explicit Capture–Recapture models. R package version 5.2.0. https://CRAN.R-project.org/package=secr.

Efford, M. G. 2025b. Comparative timing of conditional and full-likelihood density models (1.0.0). Zenodo. https://doi.org/10.5281/zenodo.14715036

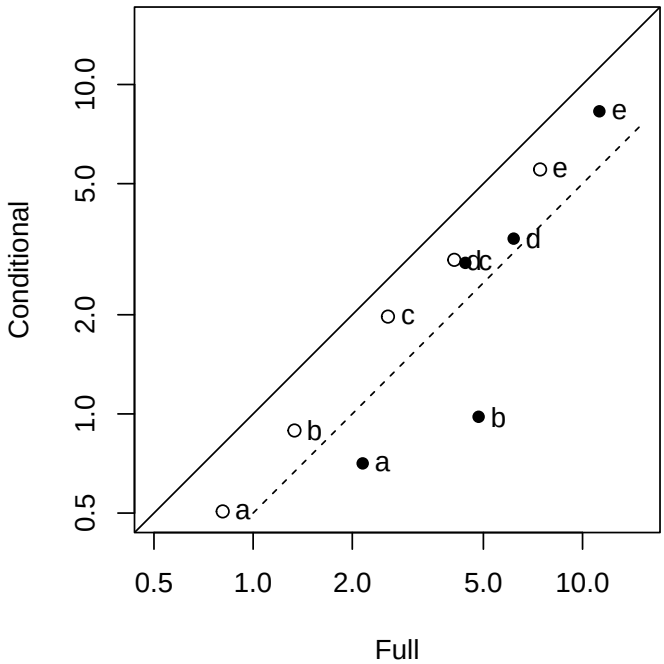

Fig. S1: Execution times (seconds) for fitting density surface models by maximizing the full or conditional (relative density) likelihoods. 'captdata' open circles; 'blackbearCH' closed circles. Solid line indicates equality, dashed line indicates time for conditional fit was 50% of full fit.