That's not the Mona Lisa! How to interpret spatial capture-recapture density surface estimates

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Appendix A   Bayesian models

Results presented in Section 4 in our manuscript were generated by fitting maximum-likelihood SCR models to simulated data. In this appendix we reproduce results from Section 4 using Bayesian models fitted via MCMC to demon-

strate that our conclusions are not simply a consequence of adopting a classical approach. We focus on reproducing Figures 7 and 9 from the manuscript; Figures 6 and 8 are based on averages over 100 simulations, which would require considerable computation time given that fitting SCR models via MCMC is more time consuming than maximum likelihood.

In Section A1 we describe our Baysian models, and in Section A2 we summarise our results.

A1   Model fitting

We fitted Bayesian versions of the maximum-likelihood models presented in Section 4 to each data set. Again, we used models with constant density to estimate realised AC and realised usage surfaces, and a model with inhomogeneous density characterised by a log-linear relationship with a spatial covariate to estimate expected AC density surfaces.

We fitted our models in NIMBLE (de Valpine, Turek, Paciorek, Anderson-Berman, Temple Lang & Bodik, 2017; Turek, Milleret, Ergon, Brøseth, Dupont, Bischof & de Valpine, 2021) using data augmentation (Tanner & Wong, 1987), which has become the prevailing way to fit SCR models under a Bayesian framework. This approach involves sampling a superpopulation of M activity centres, including those of the n animals detected on the SCR survey. We have an indicator variable z_i for the ith animal, denoting whether the ith animal in the augmented population is 'exists' in a given MCMC iteration. Rather than directly estimating N, the population size, we estimate the data augmentation parameter, ψ, the proportion of the animals in the superpopulation for which the indicator is equal to 1. For each MCMC iteration we obtain a sample from the posterior of N using $\sum_{i=1}^{M} z_i$. A sample from the posterior for animal density can be obtained by dividing by the area of the survey region. Further details on data augmentation can be found in Kéry & Schaub (2012, pp. 139–157).

We used the following uninformative priors for the detection function pa-

rameters, specifying a prior for $\log\{1/(2\sigma^2)\}$ rather than σ directly:

$$\lambda_0 \sim \text{Gamma}(0.001, 0.001)$$

$$\log\left(\frac{1}{2\sigma^2}\right) \sim \text{Uniform}(-10, 10)$$

For the constant density model, the activity centres were given a uniform prior distribution over the survey region and the data augmentation parameter was given a uniform prior from 0 to 1. For the inhomogeneous density model, animal density at location $\boldsymbol{x}$ is given by $D(\boldsymbol{x}) = \exp\{\beta_0 + \beta_1 y(\boldsymbol{x})\}$, where $y(\boldsymbol{x})$ is a measurement of a covariate at location $\boldsymbol{x}$. We used the following uninformative priors for the coefficients β_0 and β_1:

$$\beta_0 \sim \text{Uniform}(-10, 10)$$

$$\beta_1 \sim \text{Uniform}(-10, 10)$$

When we fit each constant density model, we ran $10\,000$ MCMC iterations, where we set M to be equal to 300. We also used an adapatation interval of 1000, and discarded 500 iterations as burn-in.

When fitting each inhomogeneous density model, we ran $100\,000$ MCMC iterations, and used a value of 9000 for M. We didn't use an adaptation interval, and disarded 2500 iterations as burn-in.

A2   Results

We created trace plots for all parameters across all models, and none of them indicated a lack of convergence. Although we do not present them here for brevity, the point estimates (calculated using the posterior mean) of all parameters were very similar to those obtained via maximum likelihood models fitted to the same data.

The plots based on our Bayesian models fitted via MCMC (Figures A1 and A2, respectively) were qualitatively similar to those based on maximum likeli-
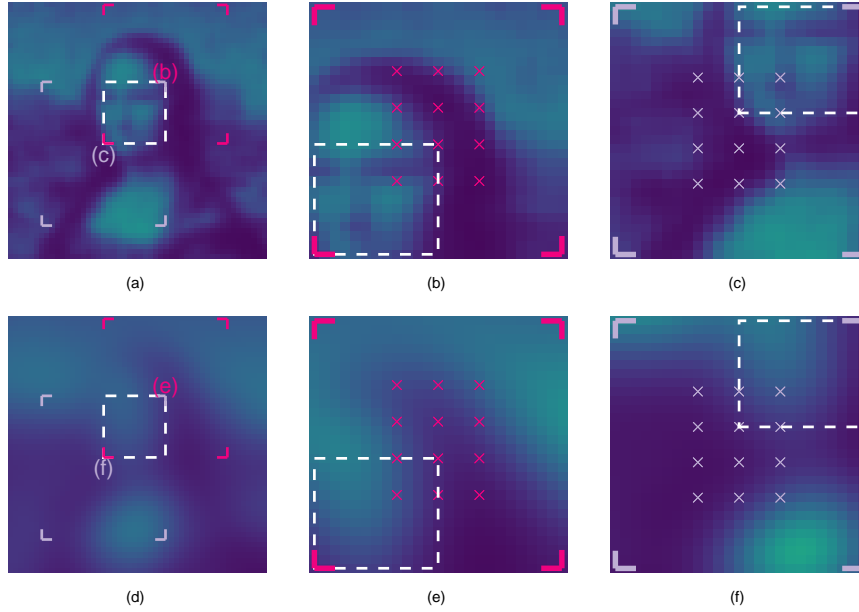
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Figure A1: A version of Figure 7 from the manuscript based on our Bayesian models fitted via MCMC.

hood mdoels presented in the manuscript (Figures 7 and 9, respectively). We observed that the locations with the highest AC densities in Figure A2 were shifted slightly further from the detectors, relative to Figure 9. A potential explanation for subtle differences is that our Bayesian plots are constructed based on entire posterior distributions, whereas the maximum likelihood alternatives only use point estimates.

Appendix B Realised usage density

Estimation of realised usage density is a similar process for both maximum likelihood and Bayesian approaches: we sum usage densities for each individual animal, each of which is calculated by convolving the posterior probability density function of its activity centre with an individual usage distribution.
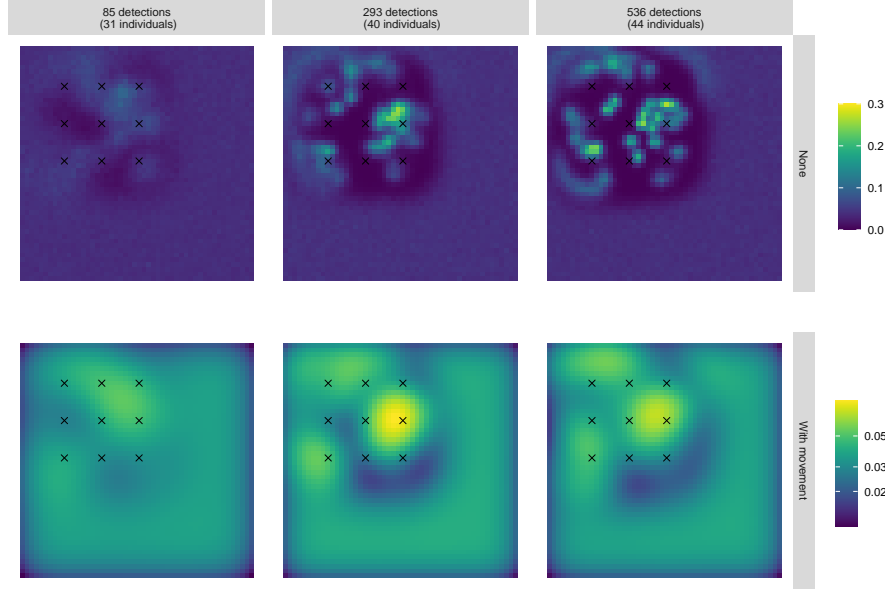
Figure A2: A version of Figure 7 from the manuscript based on our Bayesian models fitted via MCMC.

B1   The maximum likelihood approach

For maximum likelihood, the estimated usage density for the ith animal, with capture history $\boldsymbol{\omega}_i$, is given by

$$f_{\boldsymbol{s}|\boldsymbol{\omega}}(\boldsymbol{s} \mid \boldsymbol{\omega}_i; \widehat{\boldsymbol{\theta}}) = \int f_{\boldsymbol{x}|\boldsymbol{\omega}}(\boldsymbol{x} \mid \boldsymbol{\omega}_i; \widehat{\boldsymbol{\theta}}) f_{\boldsymbol{s}|\boldsymbol{x}}(\boldsymbol{s} \mid \boldsymbol{x}; \widehat{\boldsymbol{\theta}}) d\boldsymbol{x}, \tag{1}$$

where

- $\widehat{\boldsymbol{\theta}}$ is a vector containing the maximum likelihood estimates of the encounter function parameters;

- $f_{\boldsymbol{s}|\boldsymbol{\omega}}(\boldsymbol{s} \mid \boldsymbol{\omega}_i; \widehat{\boldsymbol{\theta}})$ is the estimated usage distribution, providing the probability density of finding an individual with capture history $\boldsymbol{\omega}_i$ at location $\boldsymbol{s}$ at a randomly selected point in time;

- $f_{\boldsymbol{x}|\boldsymbol{\omega}}(\boldsymbol{x} \mid \boldsymbol{\omega}_i; \widehat{\boldsymbol{\theta}})$ is the estimated PDF of the activity centre of an individual with capture history $\boldsymbol{\omega}_i$ (see Section 3); and

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84 • $f_{\boldsymbol{s}|\boldsymbol{x}}(\boldsymbol{s} \mid \boldsymbol{x}; \widehat{\boldsymbol{\theta}})$ is the estimated usage distribution of the individual con-

85   ditional on the activity centre, providing the probability density of the

86   individual being at location $\boldsymbol{s}$ given that its activity centre is at $\boldsymbol{x}$.

87 Estimated usage density at location $\boldsymbol{s}$ is then given by $\widehat{D}_u(\boldsymbol{s}) = \sum_i f_{\boldsymbol{s}|\boldsymbol{\omega}}(\boldsymbol{s} \mid$

88 $\boldsymbol{\omega}_i; \widehat{\boldsymbol{\theta}})$, noting that the sum is over individuals that were not detected, with

89 capture histories $(0, \cdots, 0)$, along with those that were.

90   Here we constructed the individual usage distribution under the assumption

91 that the density of an individual being at location $\boldsymbol{s}$ given its activity centre is

92 at $\boldsymbol{x}$ is proportional to the encounter function $h\{d(\boldsymbol{s}, \boldsymbol{x}); \widehat{\boldsymbol{\theta}}\}$, where $d(\boldsymbol{s}, \boldsymbol{x})$ is the

93 Euclidean distance between $\boldsymbol{s}$ and $\boldsymbol{x}$, and so

$$f_{\boldsymbol{s}|\boldsymbol{x}}(\boldsymbol{s} \mid \boldsymbol{x}; \widehat{\boldsymbol{\theta}}) = \frac{h\{d(\boldsymbol{s}, \boldsymbol{x}); \widehat{\boldsymbol{\theta}}\}}{\int h\{d(\boldsymbol{s}', \boldsymbol{x}); \widehat{\boldsymbol{\theta}}\}d\boldsymbol{s}'}, \tag{2}$$

94 where the denominator is a normalising constant.

B2   The Bayesian approach

96 Bayesian models fitted via MCMC can directly sample activity centres of de-

97 tected individuals, and also of undetected individuals using data augmentation,

98 thus obtaining samples from $f_{\boldsymbol{x}|\boldsymbol{\omega}}(\boldsymbol{x} \mid \boldsymbol{\omega})$ for each individual. We can use these

99 samples directly to obtain the following approximation of the ith individual's

100 usage distribution:

$$f_{\boldsymbol{s}|\boldsymbol{\omega}}(\boldsymbol{s} \mid \boldsymbol{\omega}_i) \approx \frac{1}{J} \sum_{j=1}^{J} f_{\boldsymbol{s}|\boldsymbol{x}}(\boldsymbol{s} \mid \boldsymbol{x}_{(j)}, \boldsymbol{\theta}_{(j)}), \tag{3}$$

101 where $\boldsymbol{x}_{(j)}$ and $\boldsymbol{\theta}_{(j)}$ are the activity centre and a vector of encounter function

102 parameters that were sampled on the jth of J total MCMC iterations, respec-

103 tively. The estimated usage distribution is therefore not conditional on one

104 particular set of estimated parameter values, but instead considers the range of

105 values across the posterior distribution of $\boldsymbol{\theta}$.

B3   Discussion

I'm not sure that this is the best place for the discussion below, but leaving it here for now.

We constructed individual usage distributions using the encounter function from our SCR model, but this may not always be appropriate. For example, if individuals cannot fully explore their home range within the duration of the survey, then we would not expect the spatial range of the detection function to match the extent of an animal's usage distribution.

Even for longer surveys, it may not be sensible to relate the range of the encounter function to the size of the region used by an individual even for longer surveys, so care should be taken when this practice is used. For example, Tenan, Pedrini, Bragalanti, Groff & Sutherland (2017) found that the spatial scale of the encounter rate function for brown bears (*Ursus arctos*) estimated using SCR was not consistent with spatial usage parameters estimated from other data sources, although Popescu, de Valpine & Sweitzer (2014) did not detect any such inconsistency for a population of fishers (*Pekania pennanti*). If alternative data sources are available (e.g., telemetry, or opportunistic data such as hair or scat samples) they may be incoporated for improved estimation of individual usage distributions (Tenan *et al.*, 2017).

Our method also assumes that home ranges are circular, however their shapes are likely to be modified by variables relating to population and landscape connectivity (see Drake, Lambin & Sutherland, in press, for a review).

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