

APPLICATION

Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models

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Summary

1. The advent of spatially explicit capture–recapture models is changing the way ecologists analyse capture–recapture data. However, the advantages offered by these new models are not fully exploited because they can be difficult to implement.
2. To address this need, we developed a user-friendly software package, created within the R programming environment, called SPACECAP. This package implements Bayesian spatially explicit hierarchical models to analyse spatial capture–recapture data.
3. Given that a large number of field biologists prefer software with graphical user interfaces for analysing their data, SPACECAP is particularly useful as a tool to increase the adoption of Bayesian spatially explicit capture–recapture methods in practice.

Key-words: abundance estimation, camera traps, carnivore conservation, carnivore monitoring, density estimation, faecal DNA sampling, hair snares, mark-recapture, marked animals, spatial models

Introduction

Capture–recapture (CR) sampling (Otis *et al.* 1978; Williams *et al.* 2002) has emerged as a powerful tool for estimating animal abundance by overcoming the key problem of imperfect detection. In such studies ‘capture histories’ of individually identifiable animals (tagged or naturally marked) obtained from repeated sampling across several occasions, typically presented in the ‘1’ (capture) or ‘0’ (no capture) format, comprise the basic data for analysis. As demographic closure is a critical model assumption (Otis *et al.* 1978; Williams *et al.* 2002), the survey period is kept short. Data are often analysed using several closed CR models (Amstrup *et al.* 2005) that incorporate heterogeneity in capture probabilities among individuals, trap response behaviour and time-varying capture probabilities. These analyses are performed using popular user-friendly software programs like CAPTURE (White *et al.* 1978) and MARK (White & Burnham 1999).

Such analyses incorporate statistical tests to select the best capture–recapture model for the data on hand, estimate capture probabilities, and the population size is estimated based

on the assumption that the population is ‘closed’. While these traditional methods provide reliable estimates of abundance, density estimation requires that one also estimates the sampled area. Typically, a buffer area is added around the trap array, based on some empirical, but ad hoc, approaches developed by Wilson & Anderson (1985) and Parmenter *et al.* (2003). Disadvantages of such approaches to sampled area estimation have been well-recognized statistically (Efford 2004; Efford *et al.* 2009) and empirically (Soisalo & Cavalcanti 2006; Sharma *et al.* 2010). Conventional CR analyses suffer from some other key disadvantages and deficiencies in estimating animal density. Foremost among them is the fact that although spatial information in the form of location of capture is available in field studies, the full potential of such critical information related to the animal’s home range and movement (and thus to abundance and density) is not meaningfully exploited in conventional CR analyses. Logistical problems, such as inability to adequately cover the entire array with traps without leaving any ‘holes’ (Karanth & Nichols 1998), the frequent need to sample the area in successive ‘blocks’ rather than in a single sweep, irregularly shaped trap arrays that are subsequently treated as circles while estimating variance of density or inclusion of habitats not used by the target species, may all combine and weaken inference under conventional CR analyses.

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The recent development of spatially explicit capture–recapture (SECR) models (Efford 2004; Borchers & Efford 2008; Royle *et al.* 2009a) has addressed several of these problems. Such models have been developed both under a maximum likelihood-based estimation framework (Borchers & Efford 2008) and under a Bayesian framework (Royle & Young 2008; Royle *et al.* 2009a, b; Gardner *et al.* 2009). Efford *et al.* (2009) provide a general review and describe various types of animal ‘captures’ or ‘detections’ that can generate data for such analyses.

In this study, we describe a free software program SPACECAP (Gopalaswamy *et al.* 2012), implementing a Bayesian SECR analysis of Royle *et al.* (2009a). Another software program called DENSITY (Efford *et al.* 2004) is already available and implements the maximum likelihood-based SECR analysis (Borchers & Efford 2008). The ‘SECR’ and the ‘SCRbayes’ in R (R Development Core Team 2009) implement more sophisticated maximum likelihood-based and Bayesian estimators, respectively. However, these R packages do not have Graphical User Interfaces (GUIs).

The reader is referred to the original article by Royle *et al.* (2009a) for technical details of the models implemented in SPACECAP. Although the models implemented in SPACECAP may suit spatial CR data originating from different types of non-invasive sources of data, such as from camera traps, hair snares or faecal DNA samples, they do not apply to some situations such as kill trapping (Efford *et al.* 2009).

Our primary motivation here is to enable practising biologists to reliably estimate animal densities using the flexible and powerful Bayesian SECR modelling approach of Royle *et al.*

(2009a) without having to decipher the underlying complexity of the original R code (Royle *et al.* 2009a, described below), thus meeting a key need of many species conservation initiatives involving rare and elusive animals that can only be studied using non-invasive survey methods (Hatler *et al.* 2009).

Materials and methods

PACKAGE DEVELOPMENT

SPACECAP was developed within programming environment R (R Development Core Team 2009), and is available within the library of R packages in the Comprehensive R Archive Network (CRAN; <http://cran.r-project.org>). We used the Tool Command Language (Tcl) with the Tk graphical user interface toolkit (<http://www.tcl.tk/>) to develop its GUI (Fig. 1). The software package includes a detailed Help file that is automatically downloaded with SPACECAP. The software can also be downloaded from the website of US Geological Survey, Patuxent Wildlife Research Center (PWRC) software archive (at <http://www.mbr-pwrc.usgs.gov/software/spacecap.html>).

MODEL DESCRIPTION

SPACECAP implements a hierarchical model whereby a *state* and an *observation* process are clearly defined. Here, the animal population size and their respective locations constitute the state process. Accordingly, the location of an animal i is defined by $s_i \sim \text{Uniform}(S)$. Here $s_i, i = 1, 2, \dots, N$, are the individual animal activity centres distributed randomly over some region S .

In well-designed CR experiments, investigators maintain a careful record of the individual animal i caught at a specific trap location j on a

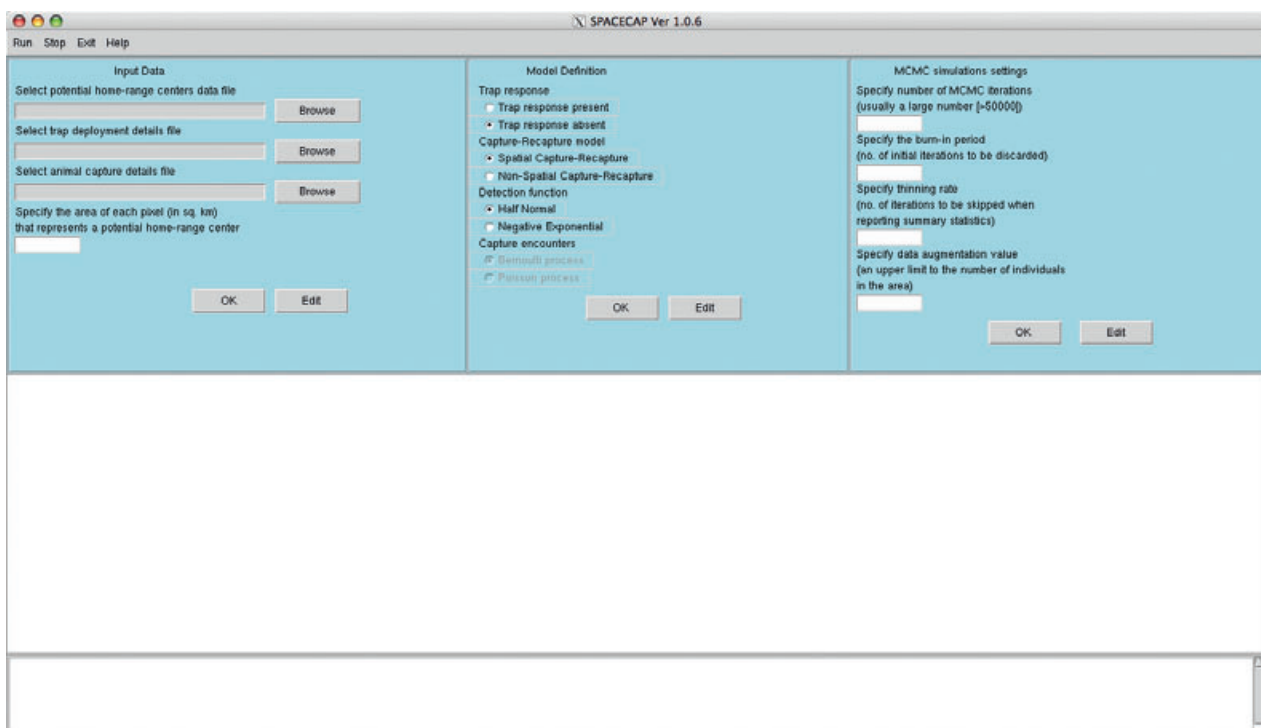


Fig. 1. The Graphic User Interface (GUI) of SPACECAP.

specific sampling occasion (e.g. a night, or a week) k . Thus, in SPACECAP, binary observations (i.e. 1 s and 0 s) y_{ijk} are recorded for an individual animal i caught at trap location j on sample occasion k .

The model is a type of binary regression model, similar to logistic regression, in which, $y_{ijk} \sim \text{Bernoulli}(p_{ijk})$. Here p_{ijk} is the probability of detecting an individual i , at trap j on sample occasion k . The probability p_{ijk} may be related to covariates of interest by applying a suitable transformation. In SPACECAP, we make use of the complementary log–log link transformation. Thus, the simplest possible model is expressed as

$$\text{cloglog}(p_{ijk}) = b_0$$

where b_0 is a parameter to be estimated. By taking the inverse of the cloglog transformation:

$$p_{ijk} = 1 - e^{-e^{b_0}}$$

This particular function arises by considering the binary observations to be formally reduced from a Poisson encounter frequency model (see Royle *et al.* 2009a, for details). That is, p_{ijk} is the Pr (that animal i makes at least one encounter with trap j on occasion k) under the Poisson model. The most general model that SPACECAP presently allows is a model in which $\text{cloglog}(p_{ijk}) = \beta_0(1 - x_{ijk}) + \beta_1 x_{ijk} + \beta_2 f[\text{dist}(s_i, u_j)]$. In this expression x_{ijk} is an indicator of previous capture of individual i in trap j and f is the function that describes the mechanism of decline of detection probability as the distance between trap j and location of individual i increases, that is, a function to make p_{ijk} have a half-normal or negative exponential form in SPACECAP. Thus, β_0 and β_1 are measures of capture probabilities (refer to Royle *et al.* 2009a, for details) until and after the first capture, respectively. The parameter β_2 is a regression coefficient on the effect of distance between individual activity centre s_i and the location of trap j , u_j . β_2 is constrained to be <0 implying that the probability of encountering an individual in a trap decreases as the distance between the individual and the trap increases. However, there may be situations where this is not true, for example, when animals spend a lot of time patrolling territory borders (Borchers & Efford 2008).

MODELS IMPLEMENTED

SPACECAP draws data for analysis in the form of spreadsheet files (such as from Microsoft Excel or OpenOffice) created by the user. The user also defines the specific type of spatial capture–recapture model to be run. Currently, SPACECAP can analyse the Bernoulli encounter process model with the following options (see Royle *et al.* 2009a, for a discussion):

- 1 Spatially explicit OR Non-spatially explicit model.
- 2 Behavioural OR Non-behavioural response model.
- 3 Half-normal OR Negative exponential detection function model.

The detection function model specifies the mechanism by which the regression coefficient β_2 , in the complementary log–log link function, decreases as distance between an animal and a trap increases. Further detail on how the detection function is linked to the observation process is described elsewhere (Borchers & Efford 2008; Royle *et al.* 2009a).

PARAMETERS REPORTED

In SPACECAP, the parameter $N(S)$ or N_{super} is the population size of individuals – the estimated number of activity centres located in S and density is calculated as $D = \frac{N_{\text{super}}}{\|S\|}$, where $\|S\|$ is the area of the state-space. Note that $N(S)$ is the population size for the prescribed state-space (see Royle *et al.* 2009a, for a description of the

Bayesian estimation procedure) and should not be interpreted as the population size in some sampled area. λ_0 is the intercept, which is the expected encounter rate of an individual i in trap location j at sampling occasion k , whose activity centre is exactly at the trap location. For a non-behavioural response model, whereby $\beta_0 = \beta_1$, $\lambda_0 = e^{\beta_0}$.

The rate of decline in detection probability as the distance between the animal centre and the trap increases is indicated by the parameter β_2 in the complementary log–log link function. SPACECAP reports the parameter $\sigma = (1/\beta_2)$. This may also be viewed as a ‘range parameter’ of an animal if the animal movement about its activity centre has a distribution similar to the detection function used. Thus, for a highly mobile animal, this value will tend to be large (e.g. tigers will have a higher σ value compared to civets). We note here that the σ estimated in SPACECAP is scaled according to the standard detection function implemented in the study by Borchers & Efford (2008) and not according to the alternative scaling used in the study by Royle *et al.* (2009a).

When the ‘behavioural response’ option is chosen, SPACECAP estimates two more derived parameters:

$p_1 = 1 - e^{-\beta_0}$ is the encounter probability of an individual before initial encounter.

$p_2 = 1 - e^{-\beta_1}$ is the encounter probability of an individual after initial encounter.

All parameters are estimated using the Markov chain Monte Carlo (MCMC) estimation process using the Metropolis algorithm (Gelman *et al.* 1996). The current version of SPACECAP only runs one MCMC chain and multiple chains can be analysed by running SPACECAP sequentially. The user is provided with the option of setting the basic MCMC parameters before analysis. These include the number of iterations to be run, the number of iterations to be discarded (called the ‘burn-in period’), thinning rate of the MCMC samples and the data augmentation value (the maximum allowable number of animals possible within the state-space S). Precautions must be taken when setting the data augmentation value. If a very low value is set, then there may be a possibility of underestimating the population size by truncating the posterior distribution of the population size estimate. Similarly, if a very high value is set, it may result in high computational time. SPACECAP reports the parameter ψ , which is the fraction of the maximum allowable number (set by the user during data augmentation), that actually represents the true population. We recommend users to set the data augmentation value at about 5–10 times the expected population size in the larger state-space.

ASSESSMENT OF MODEL ADEQUACY

SPACECAP implements an assessment of model adequacy by computing the Bayesian P -value based on individual encounter frequencies

Table 1. Posterior density estimates of parameters estimated on tiger data set (Royle *et al.* 2009a)

Parameter	Posterior mean	Posterior SD	95% Lower HPD level	95% Upper HPD level
σ	1.975	0.2166	1.5801	2.412
λ_0	0.016	0.0034	0.0096	0.023
ψ	0.4307	0.0822	0.2799	0.5936
N_{super}	210.60	38.915	137	284
Density D	13.03	2.4079	8.5388	17.6344

See *Methods and Materials* – Parameters reported for definitions of parameters. D is measured per 100 sq km.

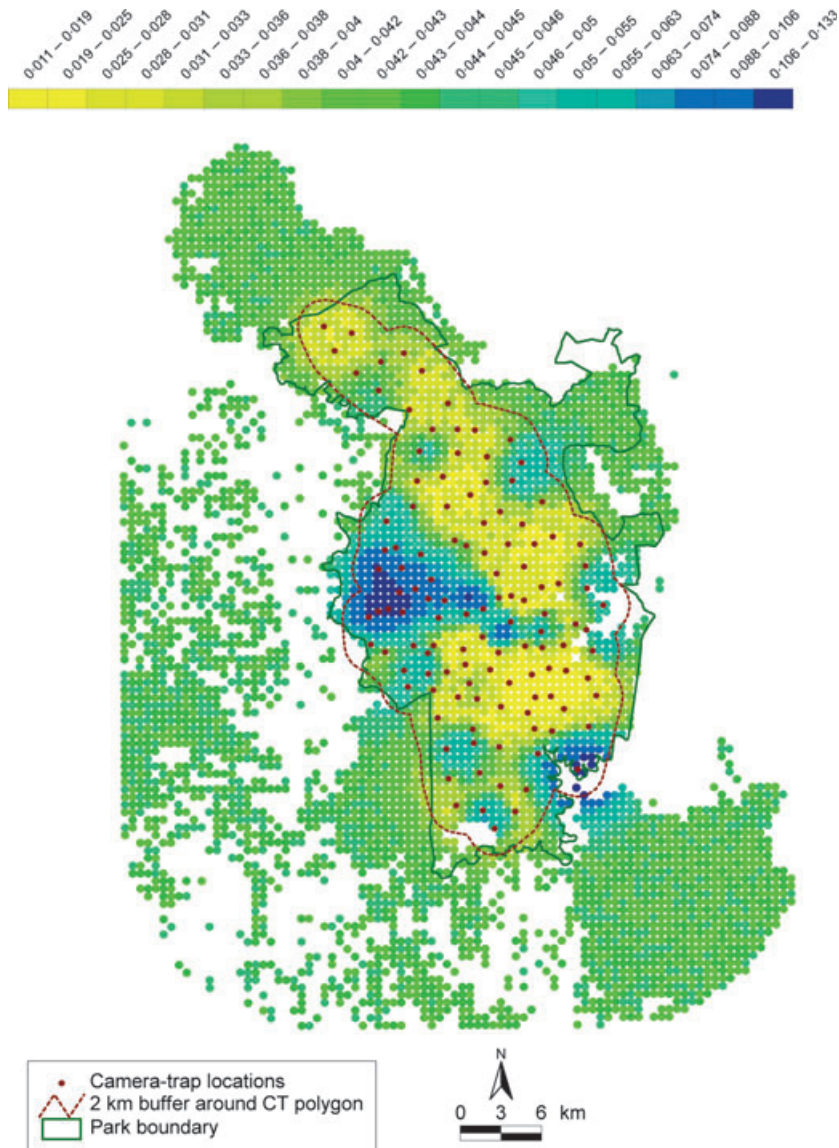


Fig. 2. A pixellated density map produced in SPACECAP showing relative animal densities. This map reports estimated tiger densities per pixel of size 0.336 km². White regions represent unsuitable habitat.

(see Royle *et al.* 2011, for details on the implementation). In this approach, a fit-statistic, D , is constructed based on individual encounter frequencies, n_i , by using a Freeman-Tukey type statistic (Freeman & Tukey 1950).

$$D(\text{data}, \theta) = \sum_{i=1}^N (\sqrt{n_i} - \sqrt{e_i})^2$$

where we define n_i to be the encounter frequency for individual i conditional on s_i , e_i is the expected value under the model and θ are the model parameters. A Bayesian P -value estimate close to 0 or 1 would imply model *inadequacy*. We note that DENSITY utilizes the Akaike's Information Criteria as a means to facilitate model selection.

SUMMARY STATISTICS AND OUTPUT

The approach for parameter estimation in SPACECAP is Bayesian. Therefore, the package produces a summary of parameter estimates comprising of the posterior mean, posterior standard deviation and the

Table 2. Comparison of parameter estimates (posterior means and standard deviations) in SPACECAP, DENSITY and M_h -jackknife

Parameter	SPACECAP	DENSITY	M_h -jackknife
σ	1.975 (0.217)	1.977 (0.226)	NA
λ_0/g_0	0.016 (0.00)	0.015 (0.00)	NA
ψ	0.43 (0.08)	NA	NA
N_{super}	210.60 (38.92)	NA	NA
N_{hat}	NA	99.69 (19.19)	100 (18.15)
Density(/100 km ²)	13.03 (2.41)	13.23 (2.62)	20.3(3.80)

See *Methods and Materials* – Parameters reported for definitions of parameters. The parameter g_0 is estimated in DENSITY and is analogous to λ_0

95% highest posterior density intervals (for examples, see Table 1). Thus, for a basic user, SPACECAP provides only all the details relating to the parameter estimates. In addition, SPACECAP also outputs files

to allow the user to generate a pixellated map showing fine-scale variation in density (Fig. 2).

All the prior distributions of parameters defined in SPACECAP are improper uniform priors. So, for all positive parameters, the prior distribution would be $\text{Uniform}(0, \infty)$ and for all other parameters, the prior distribution would be $\text{Uniform}(-\infty, \infty)$.

Additionally, SPACECAP evaluates the Geweke's diagnostic (Geweke 1992) on the MCMC analysis and provides the user with the z -score of the diagnostic. Values of the z -score statistic of $|z\text{-score}| > 1.6$ implies lack of convergence. Future versions of SPACECAP will permit users to define their own priors and incorporate more model variants.

Results

We report results of a re-analysis of a tiger camera trap data set, originally used in the study by Royle *et al.* (2009a), using SPACECAP (see Table 1). In Table 2, we compare density estimates using software packages SPACECAP and DENSITY (Efford 2004). We also estimate density using conventional CR approaches implementing the general heterogeneity CR model, M_h -jackknife (Otis *et al.* 1978), in conjunction with the 1/2 MMDM approach (Wilson & Anderson 1985) for abundance and area estimation, respectively.

These comparisons show that:

1 Densities estimated from both the SECR approaches (Bayesian and maximum likelihood) were less than those obtained from conventional CR approaches.

2 Both Bayesian and maximum likelihood-based inferences from packages SPACECAP and DENSITY, respectively, produced similar estimates of animal density.

The overall conclusion is that as the sample size increases (a combination of number of individuals caught, and their recaptures over multiple locations), there does not appear to be any major difference in density estimates derived using programs SPACECAP or DENSITY. Conventional CR model M_h -jackknife estimates derived from program CAPTURE appear to over-estimate tiger densities if the sampled area is defined using the *ad hoc* Wilson & Anderson (1985) approach using 1/2 MMDM as buffer. It results in underestimates of densities if the buffer is defined using the Parmenter *et al.* (2003) full MMDM approach.

Discussion

In ecological inquiries, the use of Bayesian inference methods (Gelman *et al.* 1996; Bolker 2008; Royle & Young 2008) is becoming popular because of their inherent capacity to solve complex problems with powerful MCMC algorithms (Tierney 1994), computational power (Venables & Ripley 2002) and flexibility to tailor the modelling to account for particular ecological and sampling situations (e.g. Gardner *et al.* 2010; Sollmann *et al.* 2011). We visualize the present and future advantages of the SECR models presented by Royle *et al.* (2009a) implemented in SPACECAP within this context. Although a typical analysis using SPACECAP now takes much longer than a comparable analysis using DENSITY, we do not view this as a serious practical disadvantage because

such analyses are typically performed only once in a season or a year following 45–65 days of field work and several weeks of organizing and checking the data prior to analysis.

We envisage that the modelling framework of Royle *et al.* (2009a) used in SPACECAP for analysing animal detection data, especially from camera trap surveys, provides the opportunity to incorporate auxiliary information in the form of 'capture' data on the same individuals in the form of photographs taken by tourists, animals killed in conflicts or by poachers and even live tracking of animals tagged by radio-frequency identification tags, radio-collars or satellite-collars to improve accuracy and precision of density estimates. The explicit recognition of the fact that most animals have biologically defined home ranges in the statistical modelling allows for a more realistic characterization of the spatial ecology of the constituent individuals within a population. This realistic biological treatment, in turn, is likely to provide more reliable estimates of animal abundance and density. Further, SPACECAP also permits for inference about the locations of uncaught animals of a study, which is not possible with DENSITY, and therefore can be easily extended to modelling demographically open populations. Currently such open model analysis is available with program MARK (White & Burnham 1999) using modelling approaches developed by Jolly (1965); Seber (1965); Pollock *et al.* (1990); Lebreton *et al.* (1992); Kendall & Pollock (1992) to derive estimates of critical vital rates such as apparent survival, temporary immigration, transience, recruitment, in addition to the changes in population size and density (see Karanth *et al.* 2006, for an example of such an analyses with tiger photo-capture data collected over a decade). Recent work by Gardner *et al.* (2010) has demonstrated the use of SECR approaches to analyse open population models. We hope to incorporate several such developments in SPACECAP during future releases, keeping in view our fundamental goal of making these modern statistical tools available to practitioners. For users, there is a SPACECAP user group email forum where frequently asked questions are answered. Emails to this group can be sent to spacecapforum@googlegroups.com.

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