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# Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture–recapture data

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### Summary

1. Capture–recapture (CR) techniques are commonly used to gain information about population dynamics, demography and life-history traits of populations. However, traditional CR models cannot separate mortality from emigration. Recently developed spatial–capture–recapture (SCR) models explicitly incorporate spatial information into traditional CR models, thus allowing for individuals' movements to be modelled explicitly.

2. In this paper, we extend SCR models using robust-design data to allow for both processes in which individuals can disappear from the population, mortality and dispersal, to be estimated separately. We formulate a general robust-design spatial capture–recapture (RD-SCR) model, explore the properties of the model in a simulation study and compare the results to a Cormack–Jolly–Seber model and a non-spatial robust-design model with temporary emigration. In the case study, we fit several versions of the general model to data on field voles (*Microtus agrestis*) and compare the results with those from the non-spatial models fitted to the same data. We also evaluate assumptions of the fitted models with a series of simulation-based posterior predictive goodness-of-fit checks that are applicable to the SCR models in general and the RD-SCR model in particular.

3. The simulation results show that the model performs well under a wide range of dispersal distances. Our model outperforms the traditional CR models in terms of both accuracy and precision for survival. The case study showed that adult females have an *c.* 3.5 times higher mortality rate than adult males. Males have larger home ranges and disperse longer distances than females, but both males and females mostly move their activity centres within their previous home range between trapping sessions at 3-week intervals.

4. Our RD-SCR model has several advantages compared to other approaches to estimate 'true' survival instead of only 'apparent' survival. Additionally, the model extracts information about space use and dispersal distributions that are relevant for behavioural studies as well as studies of life-history variation, population dynamics and management. The model can be widely applied due to the flexible framework, and other variations of the model could easily be implemented.

**Key-words:** arvicoline (*Arvicolinae*) rodents, Bayesian analysis, competing risks, dispersal ecology, hierarchical modelling, individual random effects, life-history evolution, OpenBUGS/WinBUGS/JAGS, posterior predictive checks, spacing behaviour

### Introduction

Capture–recapture methods are primary tools for obtaining information about population dynamics, demography and life-history traits in wild populations (e.g. Lebreton *et al.* 1992; Williams, Nichols & Conroy 2002). These methods rely on marking individuals or in other ways individually identifying a sample of the population, which later may be recaptured or resighted, possibly in different life-history states or spatial locations. When individuals can be encountered multiple times

within a short period of time relative to the lifespan and movements of individuals, one may assume that mortality, recruitment and dispersal are negligible (i.e. that the population is 'closed') and estimates abundance through closed capture–recapture models (e.g. Otis *et al.* 1978). In contrast, when encounter occasions occur over longer time-scales, open capture–recapture models are used to estimate demographic rates (see Lebreton *et al.* 1992) and state transition probabilities (Brownie *et al.* 1993; Schwarz, Schweigert & Arnason 1993; Ergon, Yoccoz & Nichols 2009). 'Robust-design models' (Pollock 1982; Kendall, Pollock & Brownie 1995; Kendall, Nichols & Hines 1997) combine closed and open capture–recapture

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models to make use of data obtained from a hierarchical sampling design where there are several secondary encounter occasions within several short primary occasions spaced out in time.

In studies using open population capture–recapture models, survival is usually a key parameter of interest. However, traditional capture–recapture models cannot separate between the different sources of disappearance and hence only estimate the joint probability of surviving and not emigrating from the study area between primary sessions, often referred to as ‘apparent survival’. This confounding is highly unsatisfactory because mortality and emigration are fundamentally different processes, and a notion that either mortality or emigration is negligible, or even constant, is generally unjustified (e.g. Marshall *et al.* 2004; Zimmerman, Gutierrez & Lahaye 2007; Cooper, Daniels & Walters 2008). Even though it may not be necessary to distinguish between mortality and emigration to predict the dynamics of a population, this distinction is essential for understanding the population dynamics, whether the population is monitored for management purposes (Williams, Nichols & Conroy 2002) or purely scientific reasons. In life-history theory (Roff 1992; Stearns 1992), ‘apparent survival’ is not a meaningful quantity.

Recently, spatial–capture–recapture (SCR) models have been developed to make use of information about the spatial locations of individual encounters (Efford 2004; Borchers & Efford 2008; Royle & Young 2008; Gardner, Royle & Wegan 2009). These models provide more accurate estimates of population density compared to non-spatial models, because they account for individual heterogeneity in capture probabilities due to the location of the individuals’ home range relative to traps, and there is no need for an *ad hoc* definition of the sampling area to compute estimates of population density (Borchers & Efford 2008; Royle & Young 2008; Gardner, Royle & Wegan 2009). Other information, such as spatial variation in density and information about space use, can also be obtained. Recent work has extended SCR models to open populations to allow for the estimation of survival and/or recruitment (Gardner *et al.* 2010; Raabe, Gardner & Hightower 2014).

In this paper, we extend SCR models for robust-design data (Gardner *et al.* 2010) to allow both processes in which individuals can disappear from the population, mortality and dispersal, thus providing a model to estimate mortality rates separate from emigration. Like previous SCR models, we consider systems where individuals’ space use can be modelled with unique centres of activity and where probability of capture declines with the distance from this centre. In addition, we assume that movement direction and distance are independent of location within the study area and that behaviour outside the study area is identical to inside the study area. This situation is particularly relevant for the studies of small mammals and passerines with relatively small home ranges within a large homogenous landscape.

We start by formulating a general robust-design SCR (RD-SCR) model and explore the properties of this model in a simulation study. We then fit various versions of the general model to data on field voles (*Microtus agrestis*) and compare the results with results from non-spatial models fitted to the same

data. We also evaluate assumptions of the fitted models with a series of simulation-based posterior predictive goodness-of-fit tests that are applicable to SCR models in general and to the RD-SCR model in particular. Finally, we discuss the suitability of this modelling framework in a wider context.

## Materials and methods

### MODEL FORMULATION

Our robust-design spatial capture–recapture (RD-SCR) model consists of three integrated components: a spatial capture–recapture (SCR) component within each primary sampling period, a model for survival between primary sampling periods and a model for dispersal from one primary sampling period to the next. The basic model includes two unobserved individual state variables: a binary alive/dead state and a bivariate location variable ( $x$  and  $y$  coordinates) for the centre of activity of each individual and primary sampling period. We formulate the model in a hierarchical manner (Royle & Dorazio 2008) by first deriving the likelihood conditional on the unobserved individual state variables and the model parameters, and subsequently defining the stochastic properties of these quantities. We fit the model in a Bayesian framework and obtain posterior distributions through Markov Chain Monte Carlo (MCMC) simulations in the computer program JAGS run through the R package ‘rjags’ (Plummer 2013).

### The spatial capture–recapture component

The capture component of our model is essentially the same model as has been used in a number of SCR models (Royle *et al.* 2014), except that we condition on individuals having been marked in the given primary sampling period or an earlier period. Our focus here is not to estimate abundance or population density, but rather to absorb information about the spatial location of the individuals at each primary sampling period which will inform (and be constrained by) the dispersal model. In addition, we obtain estimates of parameters describing individual space use.

We assume that an individual can be captured in at most one trap in a given secondary session, but that each trap can capture multiple individuals in the same session (Efford, Borchers & Byrom 2009; Royle *et al.* 2014). This corresponds to the sampling method used later in the case study. The data thus consist of indices of the traps at which each marked individual is captured at every trapping session. Let  $H_{ijk}$  denote the index of the trap where individual  $i$  is captured in secondary session  $j$  within primary session  $k$ . When a marked individual is not captured in a given session,  $H_{ijk}$  is set to zero. The observation likelihood is thus categorical,

$$H_{ijk} \sim \text{Cat}(\boldsymbol{\pi}_{ijk}), \quad \text{eqn 1}$$

where  $\boldsymbol{\pi}_{ijk}$  is a  $1 \times (R + 1)$  vector with the first element being the probability of not being captured and the subsequent elements are the probabilities of being captured in trap 1 to  $R$ .

An essential part of SCR modelling is to express the trap-and-individual-specific capture probabilities ( $\pi_{ijk}$ ) in terms of the latent centres of activity of the individuals and the location of the traps. The elements of  $\pi_{ijk}$  should sum to one, and the trap-specific probabilities should decline with distance between the activity centre of the individual and the trap. The trap-specific capture probabilities also depend on the locations of all other traps as an individual can only be captured once in a given trapping session. We may thus use competing risk theory to derive the trap-and-individual-specific capture probabilities (see Appendix S1 for details, Supporting Information). Denoting the capture hazard rate of individual ( $i$ ) during trapping session ( $jk$ ) in trap  $r$  as  $h_{ijkr}$ , and the total risk of being captured in any trap,  $h_{ijk*} = \sum_r h_{ijkr}$ , we find that the probability of not being captured in any trap is

$$\pi_{ijk}[1] = \exp(-h_{ijk*} z_{ik}) \quad \text{eqn 2}$$

where  $z_{ik}$  is the alive/dead state of the individual ( $z_{ik} = 1$  indicates that the individual is alive and  $z_{ik} = 0$  indicates that it is dead), and the probability of being captured in a given trap  $r$  is

$$\pi_{ijk}[r+1] = (1 - \pi_{ijk}[1]) \frac{h_{ijkr}}{h_{ijk*}} \quad \text{eqn 3}$$

Although this result is identical to the one derived by Royle & Gardner (2011), the competing risk formulation has the advantage that it can easily be generalized to situations where the trap hazard rates vary over continuous time and where individuals and/or traps are not exposed for capture over the same time intervals (e.g. if individuals are released after capture at different times or if traps are checked (or fail) at different times) – see Appendix S1 (Supporting Information) for details.

Finally, we define the trap-and-individual-specific capture hazard rates as a declining function of the Euclidean distance between the unobserved activity centre of the individual during the given primary session,  $s_{ik}$ , and the location of the trap,  $\mathbf{x}_r$ . Commonly used functions in SCR models are the half-normal (Gaussian kernel) or exponential (Efford, Borchers & Byrom 2009; Russell *et al.* 2012; Efford 2013); we use the generalized function

$$h_{ijkr} = \lambda_{ijk} \exp\left(-\left(\frac{\|\mathbf{s}_{ik} - \mathbf{x}_r\|}{\sigma_{ik}}\right)^{\kappa_{ik}}\right) \quad \text{eqn 4}$$

which is equivalent to the exponential when  $\kappa_{ik} = 1$  or the half-normal when  $\kappa_{ik} = 2$ . If  $\kappa_{ik}$  is higher, the capture hazard rate will decline more sharply around distance  $\|\mathbf{s}_{ik} - \mathbf{x}_r\|$  equal  $\sigma_{ik}$ . The individual and primary session-specific parameters  $\lambda_{ijk}$ ,  $\sigma_{ik}$  and  $\kappa_{ik}$  are all positive and should be constrained further to allow estimability.

### The survival component

Since we condition on individuals that are marked, all individuals enter the data as 'alive' in the beginning of the primary sampling period in which they are marked. Like earlier robust-design models (Kendall, Nichols & Hines 1997), we assume that individuals can only die between, and not within, primary

sampling periods. An individual that is alive in primary sampling period  $k$  may remain alive in sampling period  $k + 1$  with probability  $\phi_{ik}$ , whereas an individual that has died will become alive with probability zero. Hence, the alive/dead state in primary sampling period  $k + 1$  is a Bernoulli trial with probability of success equal to the product  $z_{ik}\phi_{ik}$ ,

$$z_{ik+1} \sim \text{Bern}(z_{ik}\phi_{ik}) \quad \text{eqn 5}$$

The survival probabilities  $\phi_{ik}$  should be constrained as necessary and could potentially be functions of individual- or location-specific covariates (not considered in this paper).

### The dispersal component

Any RD-SCR model must necessarily include a model component for dispersal between primary sampling periods, and the formulation of this dispersal model affects the interpretation of the other model components. If there is little information about the dispersal distribution in the data or if dispersal distances appear uniform within the study area, one may assume that activity centres in one primary session are independent of the activity centres in the previous primary session (this model is the spatial parallel to a robust-design model with random emigration (*sensu* Kendall, Nichols & Hines 1997) where the emigration parameters are fixed to a value depending on the area of the spatial domain relative to the effective trapping area). Although such a model may be justifiable in some cases with a known spatial domain, a misspecification of the spatial domain may severely bias survival estimates (T. Ergon, unpublished results). A more realistic model in most cases would be to assume that an individual's centre of activity in one primary session depends on its centre of activity in the previous primary session. Gardner *et al.* (2010) suggested that one could allow individual activity centres to be perturbed randomly according to a bivariate normal distribution. In this paper, we use a more general model by assuming that movements between primary sessions take place in a random direction ( $\theta_{ik}$ ) and a random distance ( $d_{ik}$ ), such that the change in the  $x$ - and  $y$ -coordinates of the activity centre is given by trigonometric functions,

$$\begin{aligned} s_{ik}[1] &= s_{ik-1}[1] + \cos(\theta_{ik})d_{ik} \\ s_{ik}[2] &= s_{ik-1}[2] + \sin(\theta_{ik})d_{ik} \end{aligned} \quad \text{eqn 6}$$

We assume that the activity centres in the first primary session in which the individuals are captured are independent and uniformly distributed within a given spatial domain. Since we condition on the first capture of the individuals, the size of the spatial domain for the first capture has no practical implications as long as it includes all potential activity centres of individuals that have a non-negligible probability of being captured. Individual dispersal directions  $\theta_{ik}$  should be drawn independently from a circular distribution (e.g. a von Mises distribution; we use a uniform(0,  $2\pi$ ) throughout this paper), and dispersal distances  $d_{ik}$  can be drawn independently from any distribution of positive values. As individuals will typically either stay at their current location or disperse between primary sessions, zero-inflated distributions for dispersal distance are particularly attractive.

The crucial point here is to use a realistic model for dispersal that provides a mechanism for which individuals can leave the effective trapping area. Only then will the survival parameters ( $\phi_{ik}$ ) estimate true survival separated from emigration. Note, however, that we do not estimate emigration explicitly in this model. Any notion of emigration must necessarily be tied to a definition of a distinct area from which individuals disperse, and estimation of such quantities may be derived (analytically or numerically) from the fitted dispersal distribution in the specific model and sampling situation.

The dispersal model formulated here assumes that dispersal direction and distance are independent of each other and that both are independent of spatial location. Dispersal distance and direction could easily be made dependent, for example, by assuming that dispersal distance is proportional to a sine function of dispersal direction. Another approach could be to characterize the change in the  $x$ - and  $y$ -coordinates of the activity centres by a bivariate distribution. Future developments may also include dependencies between dispersal and spatial covariates (cf. Ovaskainen 2004 and Ovaskainen *et al.* 2008).

## SIMULATIONS

We conducted a simulation study to evaluate our model under a suite of mean dispersal distances using an exponential model for dispersal. We then compared the results from each scenario with those of the non-spatial Cormack–Jolly–Seber (CJS) and robust-design models. To do this, we set up a basic design of five primary periods each with five secondary periods. A  $10 \times 10$  grid of traps was operational at each period. We released 100 individuals in the first primary period and added 20 new individuals in each subsequent primary period. To evaluate the model under different levels of dispersal, we set  $\lambda = -\ln(0.4)$ ,  $\phi = 0.8$ ,  $\sigma = 1$  inter-trap distance and  $\kappa = 2$ , and then varied the mean dispersal distance from 0 to 10 by 2 trap distances, thus creating six different scenarios. For each of these scenarios, we simulated 100 data sets and then fitted the SCR model described above, as well as a non-spatial CJS and robust-design model with temporary emigration. We evaluated the 95% highest posterior density (HPD) interval coverage for  $\lambda$ ,  $\sigma$ , the estimated mean dispersal distance and  $\phi$  as well as the mortality rate,  $-\ln(\phi)$ . Even though point estimates are not

**Table 1.** Coverage rates of the 95% highest posterior density (HPD) intervals for 100 simulated data sets in each scenario. The first column indicates the true mean dispersal distance for each scenario. Values lower than 0.95 indicate higher than expected coverage failure rate

True mean dispersal distance	Mean dispersal distance	$\lambda$	$\sigma$	$\phi$	Mortality rate, $-\ln(\phi)$
0	NA	0.972	0.853	0.963	0.991
2	0.963	0.972	0.835	0.936	0.991
4	0.982	0.927	0.752	0.945	0.972
6	0.954	0.954	0.771	0.972	0.991
8	0.963	0.954	0.688	0.927	0.982
10	0.991	0.936	0.752	0.982	1.000

part of the Bayesian modelling philosophy, we also compute relative ‘bias’ as the mean difference between the posterior means and the simulation values of the parameters.

## CASE STUDY – SEX DIFFERENCES IN SPACE USE, SURVIVAL AND DISPERSAL OF FIELD VOLES

To illustrate the potential use of our RD-SCR model, we chose a data set on field voles (*Microtus agrestis*) from Kielder Forest area in northern England (Ergon & Lambin 2013) and aimed to describe sex differences in space use, survival and dispersal among adult, reproductively active individuals. We fitted the RD-SCR model with six different dispersal models (parameters  $d$  in eq. 6): exponential, gamma and log-normal, with zero-inflated versions for each of these distributions. The zero-inflated models also included an offset parameter, being the minimum dispersal distance given dispersal. Finally, we used simulation-based posterior predictive checks (Gelman *et al.* 2004, chap. 6) to assess goodness-of-fit of the three components of the model. For details on the data, modelling procedures and goodness-of-fit tests, see Appendix S2 (Supporting Information).

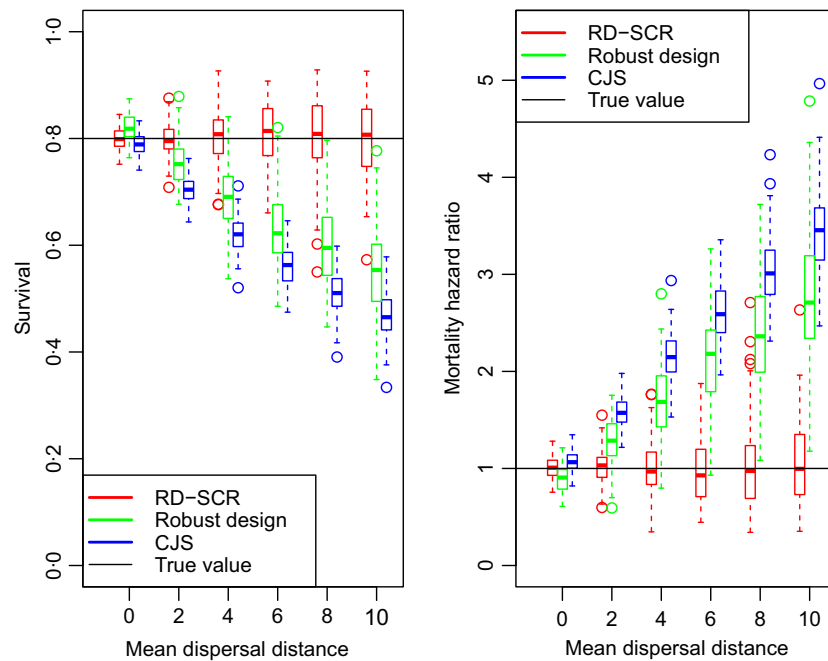
## ONLINE ENHANCEMENTS

An example, R script that simulates data and fits the RD-SCR model with the zero-inflated exponential dispersal distribution is included in Appendix S3 (Supporting Information), and the

**Table 2.** Relative ‘bias’ calculated as the mean relative difference between the posterior mean and the true simulation value for each parameter in the robust-design SCR (RD-SCR) model generated from 100 simulated data sets in each scenario. For comparison, relative ‘bias’ in the posterior means of mortality rate from the non-spatial robust-design model and the Cormack–Jolly–Seber (CJS) model are given in the two rightmost columns. Relative differences in mortality rates ( $-\ln(\phi)$ ) are, unlike relative differences in survival, invariant to the time-scale chosen for the  $\phi$ -parameter

True dispersal distance	Mean dispersal distance	RD-SCR model				Non-spatial RD model Mortality rate	CJS model Mortality rate
		$\lambda$	$\sigma$	$\phi$	Mortality rate		
0	NA	0.003	0.016	0.001	$-2e-4$	$-0.107$	0.066
2	0.019	0.003	0.019	$-3e-4$	0.008	0.266	0.571
4	0.050	$-1e-4$	0.026	0.006	$-0.009$	0.710	1.166
6	0.056	0.004	0.025	0.015	$-0.042$	1.067	1.617
8	0.048	0.002	0.034	0.005	0.023	1.365	2.042
10	0.066	0.004	0.032	0.003	0.041	1.769	2.439





**Fig. 1.** Distributions of posterior mean survival ( $\phi$ ; left panel) and mortality rate ( $-\ln(\phi)$ ) relative to true mortality (right panel) from 100 simulated data sets for each mean dispersal distance. Boxplots show median, 25th and 75th percentiles (boxes), ranges within 1.5 times the height of the box (whiskers) and outliers (points). Colours correspond to the robust-design SCR (RD-SCR) model (red), the non-spatial robust-design model with temporary emigration (green) and the standard non-spatial Cormack–Jolly–Seber model (blue).

**Table 3.** Summary statistics for the six model fits. See text for explanation of posterior predictive goodness-of-fit tests

Dispersal model	Number of distributional parameters	Deviance posterior mean (standard deviation)	Effective number of parameters, $p_D^1$	Deviance Information Criterion, DIC <sup>2</sup>	Posterior predictive goodness-of-fit tests. Posterior $\Pr(P > 0.05)$		
					Capture	Dispersal	Survival
Exponential	11	6532.69 (47.65)	1135.48	7668.17	0.83	0.90	0.96
Gamma	13	6558.12 (51.56)	1329.21	7887.33	0.86	0.96	0.97
Log-normal	13	6562.59 (47.60)	1132.72	7695.31	0.82	0.97	0.97
Zero-inflated exponential	15	6660.09 (42.93)	921.65	7581.74	0.91	0.62	0.97
Zero-inflated Gamma	17	6696.53 (44.39)	985.13	7681.67	0.89	0.70	0.97
Zero-inflated log-normal	17	6642.51 (45.44)	1032.40	7674.91	0.91	0.67	0.97

<sup>1</sup>Effective number of parameters,  $p_D$ , estimated as half the posterior variance of the deviance, Gelman *et al.* (2004).

<sup>2</sup>Deviance Information Criterion, calculated as Deviance posterior mean + Effective number of parameters ( $p_D$ ).

case study data is available in the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.r17n5>).

## Results

### SIMULATIONS

The results of our simulation study showed that under the specified set of conditions, the estimates were accurate and had good coverage. The 95% coverage was close to 0.95 for all parameters except  $\sigma$ , which had values between 0.69 and 0.85 for the different dispersal distances (Table 1). However, the mean difference between the posterior mean and the parameter value used in the simulations was always <7%, including that for  $\sigma$  (Table 2). In looking at the posterior distributions of  $\sigma$ , the lower HPD interval border was in most cases <1% above

the parameter value used in the simulations. For the standard CJS and robust-design models, the posterior mean for survival becomes increasingly more biased as the mean dispersal distance becomes larger, while the RD-SCR model remains accurate (Fig. 1, Table 2). Even with no dispersal, the RD-SCR model gives the most accurate estimates of mortality rate (Table 2). Interestingly, with no dispersal, the mean of the posterior means of the mortality rate from the non-spatial robust-design model was 11% lower than true mortality (Table 2).

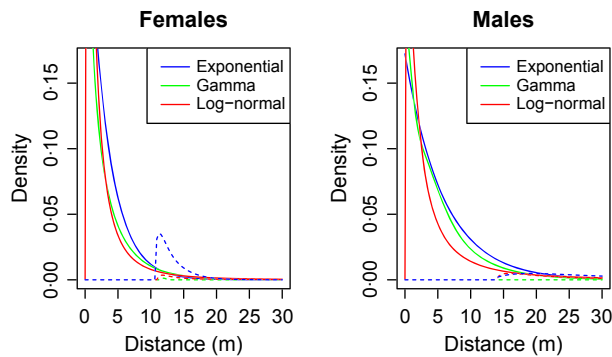
### CASE STUDY

Summary statistics for the six RD-SCR models fitted to the data are given in Table 3, and summaries of the posterior distributions from these models as well as the two non-spatial models are given in Table 4.

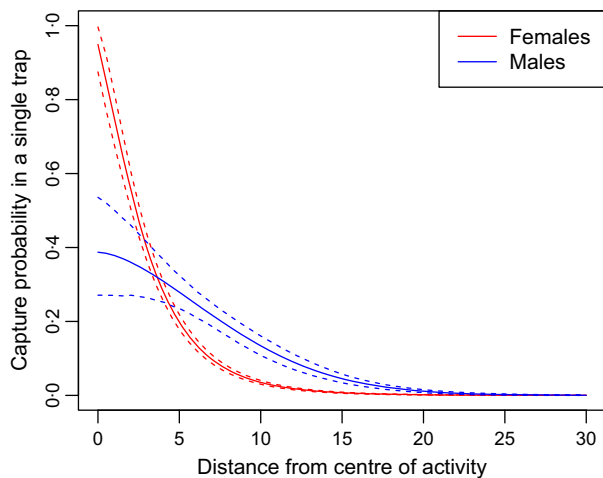
**Table 4.** Summaries of the posterior distributions from each of the six robust-design SCR (RD-SCR) models (A), as well as the two non-spatial models (B) fitted to the field vole data. Values are posterior means with 95% high posterior density (HPD) intervals in parentheses. Upper values in each cell represent females and lower values represent males

Dispersal model	Sex	Mean dispersal distance (m)	90th quantile of dispersal distribution (m)	Monthly probability of dispersal >10 m	Recapture parameters						
					Mean conditional dispersal distance	Monthly survival probability ( $\phi$ )	$\kappa$	$\sigma$	$\lambda_{morning}$	$\lambda_{evening}$	
A. RD-SCR models											
Exponential	F	3.0 (2.3, 3.7)	6.9 (5.3, 8.6)			0.75 (0.68, 0.82)	0.76 (0.66, 0.87)	1.43 (0.89, 2.02)	2.98 (1.84, 4.45)	1.64 (1.01, 2.45)	
	M	5.8 (3.9, 8.0)	13.4 (9.1, 18.5)			0.92 (0.84, 0.99)	1.62 (1.17, 2.20)	8.84 (6.11, 11.58)	0.49 (0.31, 0.75)	0.27 (0.17, 0.41)	
Gamma	F	2.5 (1.7, 3.5)	6.7 (4.7, 8.9)			0.75 (0.68, 0.82)	0.77 (0.67, 0.87)	1.46 (0.94, 2.04)	2.93 (1.83, 4.36)	1.63 (1.02, 2.42)	
	M	5.0 (2.8, 7.2)	11.3 (5.5, 16.3)			0.92 (0.83, 0.99)	1.72 (1.18, 2.42)	9.36 (6.48, 12.26)	0.45 (0.26, 0.70)	0.25 (0.15, 0.39)	
Log-normal	F	2.9 (1.7, 4.8)	6.4 (3.9, 9.7)			0.76 (0.69, 0.83)	0.77 (0.68, 0.87)	1.47 (0.95, 2.04)	2.91 (1.84, 4.32)	1.61 (1.02, 2.39)	
	M	6.4 (1.6, 36.0)	13.3 (4.8, 31.5)			0.94 (0.85, 1.00)	1.71 (1.17, 2.41)	9.38 (6.47, 12.35)	0.45 (0.27, 0.69)	0.25 (0.15, 0.38)	
Zero-inflated exponential	F	2.0 (1.1, 3.1)	10.7 (0, 12.3)	0.15 (0.08, 0.24)	13.1 (10.5, 16.4)	0.75 (0.68, 0.82)	0.80 (0.70, 0.91)	1.63 (1.06, 2.28)	2.63 (1.59, 3.88)	1.46 (0.89, 2.17)	
	M	5.8 (1.0, 16.7)	14.8 (0, 24.7)	0.16 (0.04, 0.31)	35.6 (14.8, 98.2)	0.94 (0.85, 1.00)	1.82 (1.25, 2.59)	10.17 (7.26, 13.10)	0.40 (0.25, 0.60)	0.22 (0.14, 0.33)	
Zero-inflated Gamma	F	1.8 (0.9, 2.8)	11.2 (0, 13.1)	0.15 (0.07, 0.25)	11.8 (10.1, 13.8)	0.75 (0.68, 0.82)	0.80 (0.70, 0.91)	1.65 (1.10, 2.29)	2.55 (1.61, 3.74)	1.43 (0.90, 2.08)	
	M	3.2 (0.8, 6.0)	14.5 (0, 29.1)	0.14 (0.02, 0.37)	24.0 (10.3, 35.4)	0.92 (0.83, 0.99)	1.88 (1.32, 2.61)	10.39 (7.72, 13.03)	0.37 (0.24, 0.55)	0.21 (0.13, 0.31)	
Zero-inflated log-normal	F	" $\infty$ " (0.6, " $\infty$ ") <sup>1</sup>	10.9 (10, 13.1)	0.27 (0.12, 0.41)	" $\infty$ " (10.5, " $\infty$ ") <sup>1</sup>	0.86 (0.73, 0.98)	0.80 (0.69, 0.91)	1.61 (1.04, 2.27)	2.66 (1.63, 4.00)	1.48 (0.90, 2.22)	
	M	" $\infty$ " (0.3, " $\infty$ ") <sup>1</sup>	13.9 (0, 22.3)	0.23 (0.07, 0.43)	" $\infty$ " (10.4, " $\infty$ ") <sup>1</sup>	0.95 (0.86, 1.00)	1.76 (1.21, 2.51)	9.80 (6.95, 12.81)	0.42 (0.26, 0.63)	0.23 (0.14, 0.35)	
B. Non-spatial models											
CJS	F										
	M										
Robust-design with temporary emigration	F	0.05 (0.00, 0.21)		0.22 (0.00, 0.88)			0.98 (0.95, 1.00)				
	M	0.13 (0.02, 0.24)		0.44 (0.09, 0.87)			0.92 (0.85, 0.98)				
								0.70 (0.67, 0.74)		0.48 (0.44, 0.52)	
								0.78 (0.73, 0.83)		0.66 (0.59, 0.72)	

<sup>1</sup> ' $\infty$ ' means 'very high compared to the size of the trapping array', in all cases >600 m.



**Fig. 2.** Median posterior probability density for dispersal distance of female (left) and male (right) field voles. Colours refer to dispersal model (see legend); stippled lines are zero-inflated models with a minimum dispersal distance of  $> 10$  m, solid lines are models without zero inflation. The densities at zero dispersal distance for the zero-inflated models can be read as the complement of the probability of dispersal in Table 4.



**Fig. 3.** Capture probability during the morning trapping sessions for female (red) and male (blue) field voles in a single trap at different distances from the (unobserved) centre of activity of the individual. The plot shows the predicted probability of capture if only one trap is being used ( $1 - \exp(-h_{ijkl})$ , where  $h_{ijkl}$  is the trap hazard rate given by equation 4). When there are more traps within the home range of the individual (we used 7 m spacing in a regular grid was), per-trap capture probability will decrease. Predictions are obtained by sampling from all the posterior distributions from the six robust-design SCR (RD-SCR) models (Table 3) with equal probability. Solid lines show the posterior median, and the dashed lines show the 95% highest posterior density (HPD) intervals. During evening trapping sessions, the trap hazard rate is 45% lower than in the morning (95% HPD interval: 37–52% lower; assuming additive effects of sex and time of day).

### Dispersal and survival

It is evident that the individuals in this study population (adult individuals during the main reproductive season) mostly dispersed only short distances during the 3-week intervals between primary trapping sessions (Fig. 2 and Table 4). Consequently, most of the RD-SCR models yielded very similar estimates of survival (Table 4 and Fig. S1, Supporting Information). An exception is the zero-inflated log-normal model, which produced both higher dispersal probabilities and higher, and more uncertain, survival probabilities (Table 4).

This model converged on a dispersal distribution with a very high mean, but with a median, and even 90th quantile, in the same range as the other models (Table 4). The other models showed a large difference in survival of females and males. For example, the exponential model showed that the mortality rate of males was only 28% (posterior median; 95% HPD interval 2.7–64%) of the mortality rate of females.

Even though long dispersal distances within the trapping grid were rare (Fig. 2), survival estimates from the CJS model were somewhat lower than for the spatial models, particularly for males (Table 4 and Fig. S1, Supporting Information). The survival estimates from the non-spatial robust-design model with temporary emigration were closer to the estimates from the spatial models, but were much less precise (Table 4 and Fig. S1 Supporting Information). Consequently, the sex difference in survival was less evident from the non-spatial robust-design model; the 95% HPD interval for the hazard ratio ranges from  $2.3e-6$  to 0.99 (compared with estimates from the exponential model above).

### Space use and capture probabilities

The capture parameters were widely different between males and females and varied only slightly between the different models (Table 4). As expected, the posterior predictions of capture probability (Fig. 3) indicated a much smaller home range for females than for males. In males, capture probability declined gradually with distance from the centre of activity and became virtually zero at around 25 m. Note, however, that the model does not account for individual heterogeneity in the capture parameters (it only accounts for individual heterogeneity in capture probability depending on the activity centres in relation to the location of the traps). Hence, we do not know whether these results indicate that all males have 'soft borders' of their home ranges or whether there is large individual heterogeneity in home range size (see however the goodness-of-fit assessments below).

### Goodness-of-fit

A summary of the three global goodness-of-fit tests is given in Table 3. The test for the dispersal component of the model indicated that the zero-inflated (and offset) dispersal models fit the data less well than the models without zero inflation (the posterior mass of the  $P$ -values  $< 0.05$  was  $> 30\%$ ). However, plots of the posterior quantiles of the changes in mean capture locations against the quantiles of the same quantity in the observed data (Fig. S2, Supporting Information) showed that the zero-inflated models failed only slightly in generating enough small changes in mean capture positions compared to the data. In part, this may also be due to a lack of fit of the capture model. In contrast, the test for the capture component of the model, comparing the distributions of the number of unique traps each individual was captured in, indicated a slightly better fit of the zero-inflated models. A closer inspection of the proportions of individuals that were captured in a given number of unique traps (Table S1, Supporting Informa-

tion) showed that there are more individuals captured in only one unique trap than expected from the model. For primary session 3, it also appeared that more individuals than expected were captured in the maximum number of unique traps than expected. This over-dispersion suggests behavioural individual heterogeneity, or heterogeneity in the capture success of traps, that may be addressed in future model developments.

## Discussion

### APPROACHES TO SEPARATING MORTALITY AND EMIGRATION

The inability of standard capture–recapture models to separate between mortality and emigration has long been recognized as a potentially severe problem (Marshall *et al.* 2004; Zimmerman, Gutierrez & Lahaye 2007; Cooper, Daniels & Walters 2008). Our RD-SCR model provides a tool for estimating mortality, separated from emigration, in cases where movement direction and distance are independent of location within the study area and where behaviour outside the study area is identical to inside the study area. Like previous SCR models, we consider systems where individuals' space use can be modelled with unique centres of activity and where probability of capture declines with the distance from this centre. This situation is perhaps most relevant for studies of small mammals and passerines with relatively small home ranges within a large homogenous landscape.

Considering similar situations, Glazer (2005) and Gilroy *et al.* (2012) also used data on individual capture locations and observed movements to estimate true survival from capture–recapture data. They did this in a two-step approach where they first obtained the estimates of individual emigration probabilities depending on the location of last capture and subsequently used this to obtain estimates of survival adjusted for emigration. In contrast, we treat the activity centres of the individuals at each primary sampling period as unobserved random variables in a unified hierarchical model and hence ensure correct propagation of uncertainty. Unlike the approaches of Gilroy *et al.* (2012) and Glazer (2005), and also Schaub & Royle (2014), our RD-SCR model does not require a demarcation of the study area. We do not attempt to estimate emigration rates, which depend on the (often rather arbitrary) size and shape of the trapping array. A further difference with the approach by Glazer (2005) and Gilroy *et al.* (2012) is that they assume that emigration is always permanent, whereas in our model, individuals can move in and out of the area in which they are available for capture (similar to Schaub & Royle 2014).

Several non-spatial capture–recapture models include 'temporary emigration' (i.e. emigration conditional on probability of return not being zero): the robust-design models of Kendall, Nichols & Hines (1997), Barker's joint data model (Barker 1997; Kendall *et al.* 2013) and multistate models that include unobservable states (Kendall & Nichols 2002; Schaub *et al.* 2004). Note that also in these models, there is always a nonzero probability for an individual to emigrate and never return within the duration of the study even if probability of return is not zero. However, these models assume that the probability of re-entering the observable population is independent of time since emigration. These models may yield accurate estimates of true survival in some situations, but, as our simulation study shows, estimates can also be severely biased when the model assumptions are not met (Horton & Letcher 2008). In our model, the probabilities of leaving and re-entering the effective trapping area are random individual quantities that depend on the spatial location of the individual and the fitted dispersal

distribution. Thus, individuals that live in the peripheral parts of study area are more likely to become unavailable for capture in the next primary session than individuals closer to the centre of the study area, and the probability that an emigrated individual will re-enter the trappable population, given survival, decreases with the length of time the individual has been away from the population (as it will tend to disperse further away from the trapping array in a random walk fashion). In many situations, this may be a more realistic model for emigration and hence yield more accurate survival estimates.

Under the conditions of our simulation study, the RD-SCR model gave accurate survival estimates even when mean dispersal distance was equal to the dimensions of a square trapping grid. The simulation study also showed that it is important to account for dispersal even when dispersal distances are generally short relative to the size of the trapping arrays. Even when mean dispersal distance was only 20% of the dimensions of a square trapping grid, the non-spatial models severely overestimated the mortality rate (by 27% and 57% for the robust-design and CJS models, respectively; Table 2). In the case study, where mean dispersal distances were very short compared to the size of the trapping array (particularly for females), the non-spatial and the spatial robust-design model results were similar, but precision was considerably worse for the non-spatial model. This is likely due to the RD-SCR model making use of spatial information to inform individual heterogeneity in capture and emigration probabilities, whereas non-spatial models do not use this information and thus effectively use less data to estimate the parameters. Interestingly, the simulation study revealed a negative bias in the non-spatial robust-design estimates of mortality when dispersal distance was fixed to zero. This is presumably because spatial heterogeneity in capture probability is not accounted for in the non-spatial model. Instead, some of the individual heterogeneity in capture probability is interpreted as temporary emigration by the non-spatial model. This leads to overestimation of the probability of emigration and never returning within the duration of the study, and hence also an overestimation of survival.

### LIMITS TO THE RD-SCR MODEL AND POSSIBLE EXTENSIONS

The accuracy of the survival estimates from the RD-SCR model is obviously contingent on a realistic model for dispersal away from the trapping array. We can only say something about the distribution of dispersal distances within the area covered by the trapping array, and if we fit the wrong weight of the dispersal distribution outside the trapping array, significant bias may result. It is obviously most important to account for dispersal when the study area is small relative to dispersal distances, but when this is the case, we have little information about the shape of the dispersal function. Even when the trapping array is large compared to mean dispersal distance, one may find that alternative dispersal distributions with quite different tail-weight fit the data equally well. This is illustrated in our case study, where we found that the zero-inflated log-normal distribution for dispersal distance gave higher estimates of survival than the other models even though dispersal distances generally were very short. Thus, inferences about true survival will always be model dependent to some degree. To get better information about individual dispersal distributions, it would be valuable to combine trapping studies with telemetry, particularly when the trapping grids are small (see Sollmann *et al.* (2013) and Ivan, White & Shenk (2013) for approaches to using telemetry with CR data).

We also assume that dispersal direction and distance, as well as survival and capture probabilities, are independent of location. This must also be the case for the area surrounding the trapping array. It should,



however, be straightforward to let the model parameters be functions of spatial covariates (cf. Ovaskainen (2004) and Ovaskainen *et al.* (2008)). It should also be possible to use habitat masks to restrict the state space for the activity centres (Borchers & Efford 2008; Royle *et al.* 2009; Sollmann *et al.* 2013) and hence deny migration into uninhabitable areas.

The goodness-of-fit tests suggested possible individual heterogeneity in spacing behaviour. It would therefore be particularly interesting to incorporate individual heterogeneity on the capture parameters to study variation in spacing behaviour.

## GOODNESS-OF-FIT

Goodness-of-fit assessment is generally seen as an important part of capture–recapture modelling (Lebreton *et al.* 1992; Choquet *et al.* 2009), but so far has received less attention for SCR models. We developed a series of simulation-based posterior predictive goodness-of-fit tests that are applicable to SCR models in general and to the RD-SCR model in particular. In the case study, these tests revealed a small lack of fit in the zero-inflated dispersal models and a more substantial lack of fit in the capture model. This approach may be expanded further to address, for example, heterogeneity in capture success among traps, or other aspects of interest for a particular model and data. Such tests can be used to assess whether it is necessary or justified to fit more complex models to the data, which is of particular interest when it is computationally difficult or time-consuming to fit complex models.

## CASE STUDY

In arvicoline rodents, such as voles, dispersal fractions and distances do not only vary largely among species, but there is also large variation within species and populations depending on environmental factors, age, body condition and social status (Le Galliard *et al.* 2012). Despite the strong interest in both dispersal ecology and population dynamics of small rodents (e.g. Stenseth 1999), reports of dispersal distributions almost never account for the usually decreasing recapture probabilities with dispersal distance (Le Galliard *et al.* 2012).

We found that adult field voles during the summer season in our study population changed their activity centres short distances within the trapping grid, mostly within their previous home range. This is a common observation in small rodent populations at high densities, presumably due to high costs of dispersal and settlement at high regional population densities (Solomon 2003). Density estimates from the case study data were around 200 voles per hectare, which is moderately high in this system (Ergon *et al.* 2011).

It should be noted that voles are capable of dispersing several kilometres (Le Galliard *et al.* 2012). If such long distance dispersal is common, we will get biased estimates of dispersal unless one has means to detect such long distance movements. Clearly, even though the size of the trapping grid in the case study was more than three times larger than what is often used, the sampling design is not optimal for studying dispersal. To be able to estimate dispersal probability densities at longer distances, one could use an array of smaller trapping grids, possibly combined with telemetry and molecular methods.

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## Data accessibility

Case study data on field voles: DRYAD entry doi:10.5061/dryad.r17n5.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Derivation of trap and individual specific capture probabilities by competing risk theory.

**Appendix S2.** Details of the Case study; Data, modelling procedure and posterior predictive goodness-of-fit tests.

**Appendix S3.** Example R script, including JAGS model specification.

**Table S1.** Posterior predictive *P*-values for the capture model.

**Fig. S1.** Posterior median and 95% HPD intervals for monthly survival.

**Fig. S2.** Goodness-of-fit plot for dispersal distance.