Spatial capture–recapture models allowing Markovian transience or dispersal

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Abstract Spatial capture–recapture (SCR) models are a relatively recent development in quantitative ecology, and they are becoming widely used to model density in studies of animal populations using camera traps, DNA sampling and other methods which produce spatially explicit individual encounter information. One of the core assumptions of SCR models is that individuals possess home ranges that are spatially stationary during the sampling period. For many species, this assumption is unlikely to be met and, even for species that are typically territorial, individuals may disperse or exhibit transience at some life stages. In this paper we first conduct a simulation study to evaluate the robustness of estimators of density under ordinary SCR models when dispersal or transience is present in the population. Then, using both simulated and real data, we demonstrate that such models can easily be described in the BUGS language providing a practical framework for their analysis, which allows us to evaluate movement dynamics of species using capture–recapture data. We find that while estimators of density are extremely robust, even to pathological levels of movement (e.g., complete transience), the estimator of the spatial scale parameter of the encounter probability model is confounded with the dispersal/transience scale parameter. Thus, use of ordinary SCR models to make inferences about density is feasible, but interpretation of SCR model parameters in relation to movement should be avoided. Instead, when movement dynamics are of interest, such dynamics should be parameterized explicitly in the model.

Keywords Animal movement · Density estimation · Dispersal · Spatial capture–recapture · Spatially explicit capture–recapture · Transience

Introduction

Spatial capture–recapture models are a relatively new development in ecological statistics (Efford 2004; Borchers and Efford 2008; Royle and Young 2008; Efford et al. 2009; Borchers 2012; Royle et al. 2014). Such models resolve important technical problems of ordinary capture–recapture models such as relating estimates of population size, N, to density, D, and accounting for individual heterogeneity due to the juxtaposition of individuals with traps. A large number of extensions of SCR models have been developed for closed systems including acoustic sampling (Efford et al. 2009), incorporation of telemetry data for studying resource selection (Royle et al. 2013a), mark-resight SCR models (Chandler and Royle 2013; Sollmann et al. 2013), continuous time encounter models (Borchers et al. 2014) and integrating SCR with occupancy data (Chandler and Clark 2014). In addition, SCR models show promise in addressing a large number of ecological modeling problems related to spatial ecology, including studying movement and dispersal (Ergon and Gardner 2014; Schaub and Royle 2014) and modeling landscape connectivity (Royle et al. 2013b; Fuller et al. 2015; Sutherland et al. 2015).

Closure in the context of SCR models is a different manifestation of closure than in ordinary CR models. In particular, animals are allowed to move about in space, and thus a form of temporary emigration is admitted by the model, but their movements are assumed to be concentrated in the vicinity of a stationary point, referred to as the centroid of their home range, activity center, or home range center. Thus, closure in the context of closed SCR models is manifest as stationarity of the individual activity centers. While this may be reasonable for territorial animals, especially over short time periods, it is not always so. Many species exhibit territorial behavior and home ranges that can be defined (Borger et al. 2008), including carnivores such as Canada lynx (Fuller et al. 2007) and American marten (Fuller and Harrison 2005). Yet other species are better described by simple random walks or correlated movements around a central point (Moorcroft et al. 2006). Indeed, many biologists are skeptical of the relevance of SCR models for species that are distinctly non-territorial, or in situations when it is difficult to determine the exact timing of dispersal and subsequent territory establishment. Dispersal itself is a complex behavior which has received an enormous amount of attention in the literature and there are a continuous range of movement behaviors associated with dispersal (Clobert et al. 2012). As such, movement via dispersal is a key process in the dynamics of populations and has important implications for spatially explicit population ecology. One implication concerns populations that contain transient individuals, or "floaters", that for at least part of their life do not actively defend territories. Examples include humpback whales (Constantine et al. 2012), coyotes (Gehrt et al. 2009), migratory birds at stopover sites (Belda et al. 2007), great horned owls (Rohner 1997), loggerhead turtles (Sasso et al. 2006), cheetahs (Caro 1994), voles (Sutherland et al. 2013), and newts (Perret et al. 2003). Even for strictly territorial species, in applications of SCR models which assume closure, there is liable to be some portion of the population that does not possess stationary home ranges.

The purpose of this paper is to first evaluate the robustness of estimators of abundance and density using closed population SCR models in the presence of transience or dispersal. We devise a simulation study based on various forms of Markovian movement, in which the activity center **s** potentially changes *each* sampling occasion. We fit ordinary 'closed' SCR models to the resulting data, and summarize the bias of the maximum likelihood estimators (MLEs) of model parameters under non-stationarity of the activity centers. Next, we investigate the practicality of fitting SCR models with non-stationary activity centers to data from typical capture–recapture studies. We demonstrate, by way of several examples, that it is possible to fit Markovian models of non-stationary activity centers from ordinary SCR data. We fit such models with the BUGS language using the JAGS software (Plummer 2003). We provide an example using data from a black bear study (Gardner et al. 2010), and also simulated data sets.

Model description and simulation design

The standard SCR model posits that activity centers **s** for each of N individuals in the population are distributed uniformly over some region, $\mathcal{S}$, called the state-space. Further, most SCR models posit that the encounter probability in a trap with known coordinate, **x**, is a function of distance between the individual's activity center and the trap. In our simulation study we use one of the most commonly used encounter probability models, that based on the kernel of a Gaussian probability density function:

$$p(\mathbf{x}, \mathbf{s}) = p_0 \exp(-\mathrm{dist}(\mathbf{x}, \mathbf{s})^2 / (2\sigma_{scr}^2)).$$

Here the parameters of the encounter model are p_0, the baseline encounter probability, being the probability of encounter in a trap located precisely at the center of an animal's home range, and the parameter σ_{scr} which determines the rate of decrease in detection probability as a function of distance from **s** to **x**, $\mathrm{dist}(\mathbf{x}, \mathbf{s})$. Often we will express the parameters by the transformation $\alpha_0 = \mathrm{logit}(p_0)$ and $\alpha_1 = 1/(2\sigma_{scr}^2)$. A standard SCR model assumes that encounters $y_i(\mathbf{x}, \mathbf{s}_i)$ of individual i in trap **x** are Bernoulli outcomes with probability $p(\mathbf{x}, \mathbf{s}_i)$ (Borchers and Efford 2008).

We are interested in situations under which the activity centers are not static, so that encounter probability of an individual i depends on sampling occasion k through the *occasion*-specific activity center $\mathbf{s}_{i,k}$:

$$p(\mathbf{x}, \mathbf{s}_{i,k}) = p_0 \exp(-(1/(2\sigma_{scr}^2))\mathrm{dist}(\mathbf{x}, \mathbf{s}_{i,k})^2).$$

To study the effect of departures from the assumption of static activity centers, we require specific models that describe how $\mathbf{s}_{i,k}$ changes through time. For our simulation study, we consider three standard models to describe movement, dispersal or transience, identified as follows:

(A) *Partial transience* Some individuals in the population are transient individuals and do not establish

fixed home ranges. We assume that the initial value $\mathbf{s}_{i,1}$ is uniformly distributed over the state-space $\mathcal{S}$. We model transience by assuming that activity centers for some fraction of individuals are transient, moving according to a Gaussian random walk in 2-dimensions (Tufto et al. 2012):

$$\mathbf{s}_{i,k} \sim \text{Normal}(\mathbf{s}_{i,k-1}, \sigma_{rw}^2 \mathbf{I}) \qquad (1)$$

where $\mathbf{I}$ is the identity matrix. We denote the random walk variance by σ_{rw}^2 to distinguish it from the scale parameter of the SCR encounter probability model, σ_{scr}^2. In our simulation analysis we used a transience rate of 0.50, i.e., on average half of the population have fixed home ranges and half exhibit transience. This scenario is analogous to that situation considered by capture–recapture models allowing for transience in bird studies (Pradel et al. 1997; Hines et al. 2003; Saracco et al. 2010).

(B) *Complete transience* We consider the same basic model of transience as in the previous scenario (A) but we assume every individual in the population is transient. Thus, the core SCR assumption of stationary home ranges is not satisfied even for a segment of the population.

(C) *Dispersal* During a study period of some set interval, individuals may disperse to a new activity center $\mathbf{s}'$ according to some probability distribution (Ergon and Gardner 2014; Schaub and Royle 2014). We imagine the Gaussian distribution in Eq. 1 is a reasonable model for this kind of dispersal, although with larger values of σ_{rw}^2 reflecting that dispersal typically occurs over larger spatial scales than transience. In addition, we imagine that dispersal should only apply to some of the individuals in the population and only occur once, to some fraction of the population. Each individual in the population was determined to be a disperser with probability 0.50 so that, on average, half of the individuals in any simulated population would disperse.

The main difference between the first two situations and the last one is the potential scale of movements. For the transience situations (scenarios A and B) we imagine movements would typically be relatively small over short time periods (e.g., weekly trapping intervals). On the other hand, for the dispersal situations (scenario C), we imagine that movements could be sufficiently large so that individuals *may* move far enough from the trap array so as to be subsequently unobservable.

We defined a population distributed over the square $\mathcal{P} = [0, 31] \times [0, 31]$ with prescribed density D being the expected number of individuals per unit squared. For a simulated data set, we fix the population size N of the region at $D \times 31^2 =$

1153 individuals (i.e., $D = 1.2$) (Fig. 1) whose activity centers were simulated uniformly over $\mathcal{P}$ on occasion $k = 1$, and then generated activity centers for subsequent occasions $k = 2, \ldots, K = 5$ according to the models above. In cases in which subsequent activity center locations were generated outside of the square $\mathcal{P}$ we rejected those draws in order to preserve the total density of the state-space (density could be preserved equivalently by reflecting movements back into the state-space).

As the purpose of the simulation is to evaluate different transience and dispersal patterns, we imagine that the part of this region that we sample by traps should be small relative to $\mathcal{P}$ so that individuals may effectively leave the vicinity of the trap array permanently, which is to say disperse to a distant part of the region so as to become uncaptureable, or emigrate from distant parts of the region to some location where they are observable. As such, we subject the population to sampling by a grid of traps located in the central 1/9th quadrant of the study area, bounded by the square $[11, 20] \times [11, 20]$ (Fig. 1). To subject this population to sampling, we placed 100 traps on the integer coordinates. Any specified level of density primarily affects the expected sample size (i.e., of observed individuals), and so we considered only a single value of $D = 1.2$ ($N = 1153$ individuals in the 961 units squared state-space) and varied other of the model parameters as described subsequently to achieve variable
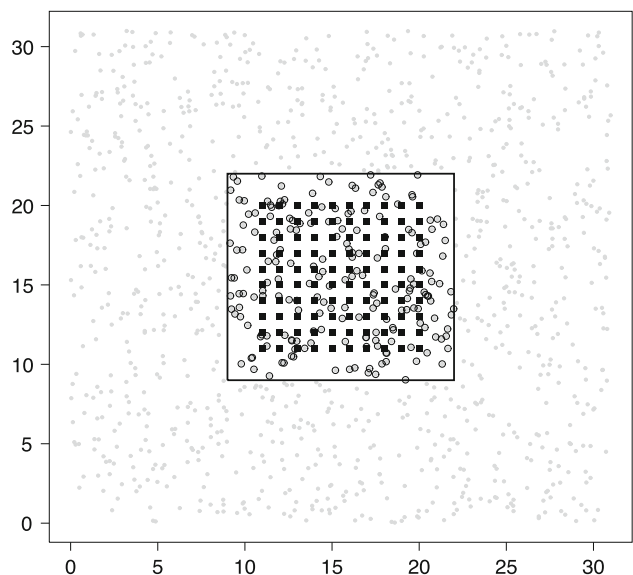

Fig. 1 Configuration of the simulation trap array (*black squares*), and the state-space $\mathcal{P} = [0, 31] \times [0, 31]$ used to simulate a constant density of 1.2 individuals per area squared. One realization of the population is shown as the *gray dots* (shown as *open circles* in the vicinity of the trap array). To obtain the MLEs of model parameters a localized state-space was used for computing the marginal likelihood, shown here by the *inner bounded square*

expected sample sizes (of individuals captured), encounter frequency, and expected number of traps encountered per individual (spatial recaptures). We simulated two levels of baseline encounter probability $logit(p_0) \equiv \alpha_0 = -2$ (low p) and $\alpha_0 = -1$ (high p), crossed with 3 different levels of $\sigma_{rw} \in \{0.4, 0.7, 1.4\}$ for each of the transience simulation scenario (6 simulation cases for simulation cases A and B), and $\sigma_{rw} \in \{0.7, 1.4, 2.8\}$ for the dispersal scenario (C), and we held σ_{scr} constant at $\sigma_{scr} = 0.7$ for all situations.

For each of scenarios A, B and C, we simulated 200 data sets and fit an ordinary SCR model by maximizing the "full likelihood" which contains the parameter N (Borchers and Efford 2008; ch. 6 in Royle et al. 2014, 2015). To carry out the numerical integration we have to specify the bounds of integration. We could use the square $\mathcal{P}$ for this purpose, but more efficient computation is possible by defining the state-space $\mathcal{S}$ for purposes of this integration to be more local to the trap array. Under the Gaussian encounter probability model, individuals beyond about $2–3 \times \sigma_{scr}$ have negligible encounter probability and thus contribute nothing to the likelihood (see Royle et al. 2014, chapter 6) so we constructed the numerical integration grid by buffering the trap grid boundary by the maximum of $(3, 3\sigma_{scr})$ (the 3 unit buffer is shown in Fig. 1). The R script for carrying out the simulations is given in Electronic Supplementary Material (ESM) S1.

Results: assessing bias in N

For the "partial transience" scenario (scenario A) in which on average 50 % of the population has a non-stationary activity center, we see negligible bias (<1 %) in estimating D across all levels of p_0 and σ_{rw} considered (Table 1).

Table 1 Summary of simulation results for scenario A (partial transience)

α_0	σ_{scr}	σ_{rw}	n	$E(\hat{\sigma})$	$E(\hat{D})$	Relbias	95 % cover
-1	0.7	0.4	150.110	0.743	1.198	-0.186	0.840
-1	0.7	0.7	154.265	0.821	1.200	0.018	0.890
-1	0.7	1.4	164.415	1.049	1.205	0.425	0.820
-2	0.7	0.4	115.425	0.743	1.205	0.435	0.885
-2	0.7	0.7	117.105	0.822	1.210	0.798	0.915
-2	0.7	1.4	119.575	1.051	1.201	0.081	0.915

The data-generating parameters are shown by the first four columns, n is the average number of unique individuals encountered, $E(\hat{\sigma})$ is the sampling mean of the MLE of the 'effective' SCR scale parameter σ when fitting a model to the data generated with true SCR scale σ_{scr} and transience scale parameter σ_{rw}, and $E(\hat{D})$ is the mean of the sampling distribution of the MLE of D under the SCR model assuming static activity centers ($D = 1.2$ in all cases). Relbias is the percent bias in $\hat{D}$, "95 % cover" is the coverage of a 95 % Wald-type confidence interval

However, we see that coverage of 95 % confidence intervals is less than the nominal level. This makes sense given that the misspecification of the model assumes independence of encounters which is clearly violated under the transience model. In addition, we see that the MLE of the scale parameter of the SCR encounter model σ is positively biased in all cases. Intuitively, the scale parameter of the SCR model, σ, is confounding the true value of σ_{scr} with the parameter governing the scale of transience, σ_{rw}.

For the "complete transience" scenario (scenario B) where all individuals in the population are transient, we see (Table 2) mild bias creeping into the estimator of D as σ_{rw} increases to 1.4 (twice the value of σ_{scr} governing the encounter probability model). In the $\sigma_{rw} = 1.4$ case, we see only about 3 % bias in the estimator of D in the high-p case ($\alpha_0 = -1$) and 5 % bias in the low-p case ($\alpha_0 = -2$) and the bias in σ is more pronounced. Once again we confirm the less-than-nominal coverage of the intervals in this case.

In the "Dispersal" scenario (scenario C) we see negligible (less than about 1 %) bias in the estimator of D, even for the largest value of the dispersal standard deviation $\sigma_{rw} = 2.8$ (Table 3). There is relatively less bias in the MLE of σ. While it is estimating some combination of σ_{scr} and the dispersal parameter σ_{rw}, there is only 1 dispersal event happening over the study and this induces little bias in σ compared with scenarios A and B. The coverage is slightly better for this case, although still clearly less than nominal 95 %.

Fitting SCR models with transience and dispersal

We saw that the MLE of D is very robust to the Markovian models of transience and dispersal. Despite this, it is desirable to consider fitting explicit models of transience or dispersal for two reasons: First, we sometimes have a direct

Table 2 Results of scenario B (complete transience)

α_0	σ_{scr}	σ_{rw}	n	$E(\hat{\sigma})$	$E(\hat{D})$	Relbias	95 % cover
-1	0.7	0.4	152.020	0.787	1.1959	-0.35	0.840
-1	0.7	0.7	160.415	0.940	1.205	0.413	0.820
-1	0.7	1.4	179.905	1.373	1.232	2.665	0.780
-2	0.7	0.4	117.920	0.792	1.224	1.979	0.910
-2	0.7	0.7	119.348	0.937	1.212	0.963	0.902
-2	0.7	1.4	126.778	1.369	1.259	4.902	0.944

The data-generating parameters are shown by the first four columns, n is the average number of unique individuals encountered, $E(\hat{\sigma})$ is the sampling mean of the MLE of the 'effective' SCR scale parameter σ when fitting a model to the data generated with true SCR scale σ_{scr} and transience scale parameter σ_{rw}, and $E(\hat{D})$ is the mean of the sampling distribution of the MLE of D under the SCR model assuming static activity centers ($D = 1.2$ in all cases). Relbias is the percent bias in $\hat{D}$, "95 % cover" is the coverage of a 95 % Wald-type confidence interval

Table 3 Summary of simulation results for scenario C (dispersal) where the probability of an individual dispersing is 0.50 at some time during a study based on $K = 5$ occasions

α_0	σ_{scr}	σ_{rw}	n	$E(\hat{\sigma})$	$E(\hat{D})$	Relbias	95 % cover
−1	0.7	0.7	150.260	0.727	1.192	−1.03	0.880
−1	0.7	1.4	151.285	0.790	1.176	−2.036	0.915
−1	0.7	2.8	158.439	0.913	1.191	−0.760	0.855
−2	0.7	0.7	117.600	0.725	1.196	−0.347	0.900
−2	0.7	1.4	117.880	0.800	1.187	−1.069	0.880
−2	0.7	2.8	120.600	0.905	1.216	1.306	0.900

The data-generating parameters are shown by the first four columns, n is the average number of unique individuals encountered, $E(\hat{\sigma})$ is the sampling mean of the MLE of the 'effective' SCR scale parameter σ when fitting a model to the data generated with true SCR scale σ_{scr} and transience scale parameter σ_{rw}, and $E(\hat{D})$ is the mean of the sampling distribution of the MLE of D under the SCR model assuming static activity centers ($D = 1.2$ in all cases). Relbias is the percent bias in $\hat{D}$, "95 % cover" is the coverage of a 95 % Wald-type confidence interval

ecological interest in the aspects of movement, dispersal or transience. And, as a practical matter, the estimated scale parameter of the SCR encounter probability model is not interpretable as being relevant to home range size in the presence of non-stationarity of the home range. By doing a better job of separating components of variation in space usage we might be able to more accurately characterize home range size from SCR data. Second, the transience model allows for non-independence of detections that might result from an animal using only portions of its home range during each occasion, thus forming clusters of detections. Thus, even if animals do have stationary home ranges, non-independence of detections violates one of the assumptions of SCR models which the transience model accounts for.

The models described above can be easily described in the BUGS language using data augmentation (Royle et al. 2007, 2014) and therefore we can fit models with non-stationary activity centers in the various BUGS engines such as WinBUGS or JAGS. For example, the ordinary SCR model with static activity centers is shown in Fig. 2 and the extension which includes transience is shown in Fig. 3. In both cases the models are described in terms of the most basic observation, the individual-, trap-, and occasion-specific encounter. Therefore, expanding the BUGS model specification to include other effects (e.g., a behavioral response) is easily done (see Royle et al. 2014). We demonstrate the fitting of an SCR model allowing for transience using simulated data and also data from a study of black bears conducted on Fort Drum New York (NY) (Gardner et al. 2010).

Simulated transience data

To investigate the effectiveness of Bayesian estimators of model parameters under an SCR model allowing for transience, we conducted a small simulation study where 100

Fig. 2 BUGS model specification for an ordinary closed SCR model with static activity centers

```
model {
  # Prior distributions
  p0 ~ dunif(0,1)
  sigma.scr ~ dunif(0,20)
  alpha1<- 1/(2*sigma.scr*sigma.scr)
  psi~dunif(0,1)  # Data augmentation parameter (see Royle et al. 2007)

  for(i in 1:M){
    # Latent variables
    z[i] ~ dbern(psi)    # Data augmentation variables
    s[i,1]~dunif(xlim[1],xlim[2])   # Activity centers
    s[i,2]~dunif(ylim[1],ylim[2])

  for(j in 1:J){
    # Model for observations
    for(k in 1:K){
      d[i,j,k]<- pow(pow(s[i,1]-X[j,1],2) + pow(s[i,2]-X[j,2],2),0.5)
      p[i,j,k]<- z[i]*p0*exp(- alpha1*d[i,j,k]*d[i,j,k])
      y[i,j,k] ~ dbin(p[i,j,k],1)
  }
 }
}
N<-sum(z[])   # N and D are derived parameters
D<- N/area
}
```

data sets were simulated for each of 4 degrees of transience $\sigma_{rw} \in \{0.01, 0.50, 1.0, 1.5\}$, i.e., with increasingly large spatial displacement of activity centers between sampling occasions. The lowest setting of σ_{rw} is effectively "no transience." In each case, data were simulated with a constant density of $D = 1.20$ (as in our simulation study described previously). We used $\sigma_{scr} = 0.7$. We also used $\text{logit}(p_0) \equiv \alpha_0 = -1.5$ which corresponds to a baseline detection probability of $p_0 = 0.1824$. The R script for simulating the data sets and fitting the models is given in ESM S2.

The models were fitted in the JAGS package using the R package rjags (Plummer 2003). Posterior summaries are based on 3 Markov chains of 22000 MCMC iterations with 2000 discarded as burn-in for a total of 60000 posterior samples. We assessed convergence using the Gelman-Rubin statistic (Brooks and Gelman 1998). The simulation results are summarized in Table 4. In general the SCR model parameters, including density, are accurately estimated for all values of σ_{rw} (relative bias is generally 0-3 %). In addition to the SCR model parameters, the random walk variance component is generally well estimated with the exception of the $\sigma_{rw} = 0.01$ case where the parameter is nearly on the boundary of the parameter space, where poor mixing causes frequentist bias in the posterior mean which is a necessary implication of the boundary case combined with a diffuse prior distribution. This case indicates poor mixing, which would suggest, in practice, that the additional parameter is poorly identified and, indeed, probably not necessary. Despite this, the key parameters of the model for the $\sigma_{rw} = 0.01$ case are well estimated. The Rhat statistics suggest adequate mixing in the other cases, for $\sigma_{rw} > 0.01$ ($Rhat < 1.10$ on average). Despite the accuracy of posterior means, Bayesian credible intervals for the parameter density (D) based on the 0.025 nad 0.975 percentiles of the posterior distribution indicate less-than-nominal coverage varying between 0.67 and 0.85 (Table 4) although, except for the $\sigma_{rw} = 0.01$ case, coverage for the other parameters averages 0.94.

Black bear hair snare data

We fitted the complete transience model (see scenario B) to data from a black bear study conducted on Fort Drum, New York (Gardner et al. 2010). We don't expect that bears would be dispersing at a significant rate at the time of the study and over such a short period (8 weeks) but, as we noted above, the model accommodates non-independence of spatial captures in the form of clustering about the transient home range centers which may be a concern in any SCR study. In particular, individuals of either sex may use very large areas over a season or yearly and thus our expectation is that home ranges are used in a transient fashion as individuals move about their range slowly relative to the time scale of the capture–recapture study (weekly). We thus investigate the fitting of a transience model here to account for non-independence of detections due to bears using their home range in a non-independent manner.

For the Fort Drum data, we fitted both the ordinary SCR model and the complete transient (random walk) SCR models to these data. The results are shown in Table 5. The occasions are weekly so we think the best interpretation of the σ_{scr} parameter corresponds to typical space usage patterns on a weekly time interval. We note that σ_{scr} is estimated smaller under the random walk model as apparent movement is being partitioned between transient space usage and movement about the activity center. The model was fitted to a standardized coordinate system (1 unit = 1 km). This estimate of σ_{scr} translates to 72.3 km^2 under the ordinary SCR model and 53 km^2 under the transient model, which is within the range of typical values.[1] The conversion to a 95 % area used is $A_{0.95} = \pi r_{0.95}^2$ where $r_{0.95} = \sigma_{scr}\sqrt{5.99}$ (see Royle et al. 2014, section 5.4). The main point is that the area used shrinks when non-stationarity is accounted for and clearly the variance of the random walk is not negligible for these data, which suggests non-independence of space usage.

Discussion

Despite the prominence of the stationary home range assumption in SCR models, the effect of departures from stationarity of the home range on estimates of population size and density has not been addressed. But see Borchers et al. (2014) who showed that a continuous time SCR model could adequately model dependence due to movement of individuals about their stationary home range center. Our simulation study found that, under models of Markovian transience or dispersal which are routinely used for modeling such processes in animal populations, estimators of abundance or density appear to be robust to even substantial non-stationarity of the home range centers. However, there is some evidence that coverage of 95 % confidence intervals is less than nominal, due to unaccounted for dependence in the individual encounters under the movement scenarios considered. In addition, it appears that the scale parameter of the SCR model effectively accounts for the increasing spatial movement, and this

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[1] This compares to estimates of home range size derived from telemetry at a different site in New York (over a longer time period) of 155–253 km^2 for males and 36 km^2 for females.

Fig. 3 BUGS model specification for a SCR model with transient activity centers that follow a 2-dimensional random walk

```
model {
 # Prior distributions
 p0 ~ dunif(0,1)
 sigma.scr ~ dunif(0,20)
 alpha1<- 1/(2*sigma.scr*sigma.scr)
 psi~dunif(0,1)   # Data augmentation parameter
 sigma.ar ~ dunif(0,5)
 tau<- 1/(sigma.ar*sigma.ar)

 for(i in 1:M){
   # Latent variables
   z[i] ~ dbern(psi)   # Data augmentation variables
   s[i,1,1]~dunif(xlim[1],xlim[2])  # Initial activity centers
   s[i,2,1]~dunif(ylim[1],ylim[2])

   # Observation model for occasion 1
 for(j in 1:J){   # Compute distance and detection probability
   d[i,j,1]<- pow(pow(s[i,1,1]-X[j,1],2) + pow(s[i,2,1]-X[j,2],2),0.5)
   p[i,j,1]<- z[i]*p0*exp(- alpha1*d[i,j,1]*d[i,j,1])
   y[i,j,1] ~ dbin(p[i,j,1],1)
 }

 for(k in 2:K){
     # Activity centers for occasions 2,...,K
     s[i,1,k]~dnorm(s[i,1,k-1],tau)T(xlim[1],xlim[2])
     s[i,2,k]~dnorm(s[i,2,k-1],tau)T(ylim[1],ylim[2])
     # Observation model for occasions 2, ..., K
     for(j in 1:J){ # Distance and detection probability
        d[i,j,k]<- pow(pow(s[i,1,k]-X[j,1],2) + pow(s[i,2,k]-X[j,2],2),0.5)
        p[i,j,k]<- z[i]*p0*exp(- alpha1*d[i,j,k]*d[i,j,k])
        y[i,j,k] ~ dbin(p[i,j,k],1)
      }
  }
 }
N<-sum(z[])  # N and D are derived parameters
D<- N/area
}
```

happens even when animals leave permanently due to dispersal. This suggests that, generally speaking, one should be careful when interpreting σ_{scr} as being related to home range size. In fact, in the black bear data set, we observed a 36 % increase in home range size when we assumed stationary home range centers rather than allowing for transient space usage. It is clear that the *effective* SCR scale parameter σ_{scr}^2 estimated under the misspecified model absorbs the additional variance due to transience of the activity center. This further emphasizes the home range has temporal context which is especially true in SCR models where we expect it to increase in size over time.

There are two theoretical cases to help understand the bias that is present in the estimated effective scale parameter. The first derives from the variance of a random walk process which is $\sigma^2 T$, where T is the number of time steps. Thus we expect the effective (estimated) SCR scale parameter to grow with the length of the study under the pure random walk

model. That is, when all individuals are transient. However, this theoretical variance will not be realized in practice because data on the activity center trajectory is restricted to be in the vicinity of the trapping array and thus truncation of trajectories due to sampling should serve to keep the effective SCR scale parameter somewhat less than this theoretical value. The second theoretical result is that which occurs under the limiting model in which transient activity centers are *independently* distributed around a central point $\boldsymbol{\mu}_i$ and, further, movements within periods t are independently distributed about $\mathbf{s}_{it}$ (see below). This compound bivariate-normal model has total variance $\sigma_{clust}^2 + \sigma_{scr}^2$, and accounts for clustering of space usage by individuals. Under our random walk model of transience or dispersal, and over short time-periods, this meta-home range center model may be a good approximation to the random walk and therefore we might expect the effective SCR scale parameter to be less than $\sigma_{clust}^2 + \sigma_{scr}^2$, as we observed in our simulation study.

The transience models (scenarios A and B) can be thought of as models that allow for non-independent use of an individual's home range. In particular, if home ranges are relatively large so that individuals are only using portions of the home range during each trapping occasion, then resulting encounters will appear spatially clustered around the centroid of the home range portion being used during that occasion. A variation on (A) that could also be used for this phenomenon, and which we did not consider in our simulation study, is a spatial autoregressive model which is centered on some meta-home range center, say $\boldsymbol{\mu}_i$:

$$\mathbf{s}_{i,k} \sim \text{Normal}(\boldsymbol{\mu}_i - \rho(\mathbf{s}_{i,k-1} - \boldsymbol{\mu}_i), \sigma_{ar}^2\mathbf{I}).$$

(Royle et al. 2014, sec. 15.4.1) used this to describe movements about a stationary home range center and they fitted the model to simulated data using the JAGS software. A variation of this model is that (described in the previous paragraph) in which transient activity centers are scattered independently about the meta-home range center so that home range centers form clusters about $\boldsymbol{\mu}_i$:

$$\mathbf{s}_{i,k} \sim \text{Normal}(\boldsymbol{\mu}_i, \sigma_{clust}^2\mathbf{I}).$$

We didn't consider these cases (random walk or clusters) because it seems obvious that the effect will be to produce a composite scale parameter (i.e., $\sigma_{scr}^2 + \sigma_{ar}^2$ or $\sigma_{scr}^2 + \sigma_{clust}^2$) but not biased estimates of N. And, misspecification of this model by an ordinary SCR model should perform no worse than the random walk situation (Eq. 1) which we do simulate.

While we have shown there is little adverse effect on estimating density, it is clear that non-stationarity strongly influences the interpretation of the scale parameter of the encounter probability model. Thus, our study supports the view that the estimated σ parameter is only strictly interpretable as relevant to home range size when home range centers are strictly stationary and space within the home range is used independently. As a result, it is practically advantageous to be able to develop and fit explicit models of transience and dispersal. We have shown that it is feasible to model departures from home range stationarity and we demonstrated this by fitting the flexible random walk model to real and simulated data sets using the JAGS software. Our simulation study summarized in Table 4 was based on a model in which no individuals in the population possess stationary home ranges. However, we have recently established that it is possible to allow for an unknown proportion of transient individuals *and* to estimate the unknown transience fraction (we provide this

Table 4 Simulation results of fitting an SCR model with complete Markovian transience to 100 simulated data sets with $\sigma_{rw} \in \{0.01, 0.50, 1.00, 1.50\}$

σ_{rw}	Mean	RMSE	Rhat	95 % CRI coverage
Parameter: D				
0.01	1.20	0.10	1.07	0.79
0.50	1.18	0.10	1.01	0.81
1.00	1.17	0.09	1.00	0.85
1.50	1.26	0.13	1.00	0.67
Parameter: p_0				
0.01	0.20	0.02	1.06	0.91
0.50	0.19	0.03	1.03	0.94
1.00	0.18	0.03	1.01	0.94
1.50	0.17	0.03	1.00	0.89
Parameter: σ_{rw}				
0.01	0.16	0.15	1.79	0.09
0.50	0.49	0.08	1.10	0.97
1.00	0.99	0.09	1.02	0.93
1.50	1.47	0.12	1.01	0.91
Parameter: σ_{scr}				
0.01	0.68	0.03	1.08	0.95
0.50	0.70	0.05	1.04	0.93
1.00	0.70	0.05	1.01	0.97
1.50	0.71	0.05	1.00	0.95

Data generating parameter values were $\alpha_0 = -1.5$ ($p_0 = 0.1824$), $\sigma_{scr} = 0.7$ ($\alpha_1 = 1.02$), and $D = 1.2$. Summary statistics are posterior means and mean value of the Gelman-Rubin diagnostic of convergence (Rhat), and 95 % posterior credible interval coverage for density, D. RMSE is the root mean-squared error of the maximum likelihood estimator (MLE)

Table 5 Analysis of Fort Drum black bear SCR data using an ordinary SCR model which assumes stationary activity centers and a model of complete transience allowing non-stationary movement of the activity center

Parameter	Ordinary SCR model					SCR model with transience				
	Mean	SD	2.5 %	50 %	97.5 %	Mean	SD	2.5 %	50 %	97.5 %
D	0.175	0.018	0.143	0.175	0.214	0.166	0.017	0.136	0.166	0.202
N	77.067	7.758	63.000	77.000	94.000	73.067	7.257	60.000	73.000	89.000
α_1	0.130	0.016	0.010	0.130	0.164	0.179	0.029	0.127	0.177	0.242
p_0	0.108	0.014	0.082	0.107	0.137	0.150	0.026	0.105	0.147	0.208
σ_{scr}	1.972	0.126	1.746	1.964	2.241	1.689	0.138	1.439	1.681	1.982
σ_{rw}						1.066	0.262	0.606	1.056	1.609

Results are based on 3 Markov chains run for 42000 iterations each and discarding the first 2000 as burn-in, for a total of 120000 iterations

JAGS model specification in ESM S3). At the present time the computational efforts to fit such models and conduct simulation studies has proved to be prohibitive although the development of more efficent custom MCMC algorithms in R or other languages should increase the practicality of such general models.

Several authors have considered "open" SCR models involving some form of dispersal, movement or population dynamics. Tufto et al. (2012) studied dispersal of butterflies using 2-dimensional Brownian motion (continuous time version of our scenario A) with exponential survival. Schaub and Royle (2014) considered modeling dispersal in open capture–recapture models with individuals subject to natural mortality. Their model was an "area search" type of observation model (Royle and Young 2008) with a Cormack–Jolly–Seber state model for survival. They modeled dispersal using a Markovian dispersal model consistent with our dispersal scenario. Ergon and Gardner (2014) fitted a type of Jolly–Seber model under a robust design. While their spatially-explicit version of a Jolly–Seber model does produce estimates of population size or density, as with Schaub and Royle (2014), they were interested in the biasing effect of dispersal on survival and attempting to disentangle those effects, and did not address robustness or the effect of model misspecification on density estimates. The main distinctions between our work here and these earlier papers are that (1) we studied the bias in estimating N that arises as a result of misspecifying the movement dynamics and (2) our models address the situation of spatial dynamics in the context of *demographic* closure (absent recruitment or mortality), thus establishing that SCR-type models permit a sort of intermediate dynamics between demographically closed and open models.

An important applied aspect of our work is that random walk models of dispersal for closed populations are easy to describe in the BUGS language and we fitted such models using JAGS to both simulated data and a real data set from a study of black bears (Gardner et al. 2010). To the best of our knowledge, no likelihood formulation of the models has been proposed. However, we think that such models could be analyzed using likelihood methods if the state-space was approximated by a discrete set of points. In this case, such models should be closely related to classical multi-state models (Arnason 1973; Hestbeck et al. 1991; Kéry and Schaub 2012, chapt. 9). Such a formulation might be advantageous because Bayesian analysis of the model is, at the present time, computationally expensive as a result of having many latent variables, and requiring the full 3-dimensional (individuals by traps by occasions) data structure.

The random walk model that we used to describe transient dispersal also provides a reasonable model of correlated space usage within individual home ranges. In practice, this produces non-independent and clustered encounters of individuals (e.g., in nearby traps) during a sample occasion. Although departures from the assumption of independent encounters has not been addressed in the literature, our results suggest that estimates of N or density should be robust to spatial clustering of encounters due to non-independence. However, the price paid is understatement of uncertainty when models of movement are misspecified by an ordinary SCR model, and concomitant under-coverage of confidence intervals.

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