AUTHOR QUERY FORM

ELSEVIER	**Book: Spatial Capture-Recapture** **Chapter: 13**	**Please e-mail your responses and any corrections to:** **E-mail:** **a.kittusamyramasamy@elsevier.com**

Dear Author,

Any queries or remarks that have arisen during the processing of your manuscript are listed below and are highlighted by flags in the proof. (AU indicates author queries; ED indicates editor queries; and TS/TY indicates typesetter queries.) Please check your proof carefully and answer all AU queries. Mark all corrections and query answers at the appropriate place in the proof (e.g., by using on-screen annotation in the PDF file http://www.elsevier.com/framework_authors/tutorials/ePDF_voice_skin.swf) or compile them in a separate list, and tick off below to indicate that you have answered the query.
Please return your input as instructed by the project manager.

Uncited references: References that occur in the reference list but are not cited in the text. Please position each reference in the text or delete it from the reference list.

Missing references: References listed below were noted in the text but are missing from the reference list. Please make the reference list complete or remove the references from the text.

Location in Chapter	Query / remark
AU:1, page 358	Please check the symbol "?" throughout the chapter is okay as typeset.

B978-0-12-405939-9.00013-X 10013

CHAPTER

13 Integrating Resource Selection with Spatial Capture-Recapture Models

p0005 In Chapter 5 we briefly discussed the notion of how SCR encounter probability models relate to models of space usage. When using symmetric and stationary encounter probability models, SCR models imply that space usage is a decreasing function of distance from an individual's home range center. This is not a very realistic model in most applications. In this chapter, we extend SCR models to incorporate models of resource selection, such as when one or more explicit landscape covariates are available which the investigator believes might affect how individual animals use space within their home range. This is what Johnson (1980) called *third-order* selection—a term emphasizing the hierarchical nature of resource selection.

p0010 An appealing feature of SCR models is that they provide a mechanism for modeling multiple levels of the resource selection hierarchy. For instance, Johnson (1980) defined *second-order* selection as the process determining the location of home ranges on a landscape, which is exactly the process being modeled using the methods presented in Chapter 11. Thus, SCR provides a way of studying the density and distribution of home range centers, while at the same time allowing for inferences about the use of resources within home ranges.

p0015 Our treatment follows Royle et al. (2012a) who integrated a standard family of resource selection models based on auxiliary telemetry data into the capture-recapture model for encounter probability. They argued that SCR models and resource selection models (Manly et al., 2002) are based on the same basic underlying model of space usage. The important distinction between SCR and RSF studies is that, in SCR studies, encounter of individuals is imperfect (i.e., "$p < 1$") whereas, with RSF data obtained by telemetry, encounter is perfect. SCR and telemetry data can therefore be combined in the same likelihood by formally recognizing this distinction in the model.

p0020 There are two important motives for considering a formal integration of RSF models with capture-recapture. The first is to integrate models of resource use by individuals with models of population size or density. There is relatively little in the literature on this topic, although Boyce and McDonald (1999) describe a procedure where (an estimate of) population size is used to scale resource selection functions to produce a population density surface. The second reason is because this allows for the integration of auxiliary data from telemetry studies with capture-recapture data. Telemetry studies are extremely common in animal ecology for studying movement and resource selection, and capture-recapture studies frequently involve a simultaneous

Spatial Capture-Recapture. http://dx.doi.org/10.1016/B978-0-12-405939-9.00013-X

978-0-12-405939-9 Royle

telemetry component. Telemetry data has been widely used in conjunction with capture-recapture data using standard non-spatial models. For example, White and Shenk (2001) and Ivan (2012) suggested using telemetry data to estimate the probability that an individual is exposed to capture-recapture sampling. However, their estimator requires that individuals are telemetry-tagged in proportion to this unknown quantity, which seems impossible to achieve in many studies. In addition, they do not directly integrate the telemetry data with the capture-recapture model so that common parameters are jointly estimated. Sollmann et al. (~~in revision~~) and Sollmann et al. (2013~~a~~) used telemetry data to directly inform the parameter σ from the bivariate normal SCR model in order to improve estimates of density, although these models do not include an explicit resource selection component.

Formal integration of capture-recapture with telemetry data for the purposes of modeling resource selection has a number of immediate benefits. For one, telemetry data provide direct information about σ (Sollmann et al., 2013a, ~~in revision~~). As a result, this leads to improved estimates of model parameters, and has design consequences (~~see~~ Section 10.7). In addition, active resource selection by animals induces a type of heterogeneity in encounter probability, which is misspecified by standard SCR encounter probability models. Animals that use more space due to the configuration of habitat or landscape features stand to be exposed to more traps than animals that use less space. As a result, estimates of population size or density under models that do not account for resource selection can be biased (Royle et al., 2012a). Finally, because the resource selection model translates directly to a model for encounter probability for spatial capture-recapture data, the implication of this is that it allows us to estimate resource selection model parameters directly from SCR data, i.e., *absent* telemetry data. This fact should broaden the practical relevance of spatial capture-recapture not just for estimating density, but also for directly studying movement and resource selection. p0025

13.1 A model of space usage s0005

Assume that the landscape is defined in terms of a discrete raster of one or more covariates, having the same dimensions and extent. Let $\mathbf{x}_1, \ldots, \mathbf{x}_G$ identify the center coordinates of G pixels that define a landscape, organized in the matrix $\mathbf{X}_{G\times 2}$. Let $C(\mathbf{x})$ denote a covariate defined for every pixel $\mathbf{x}$. We suppose that individual members of a population wander around space in some manner related to the covariate $C(\mathbf{x})$. p0030

As a biological matter, use is the outcome of individuals moving around their home range (Hooten et al., 2010), i.e., where an individual is at any point in time is the result of some movement process. However, to understand space usage, it is not necessary to entertain explicit models of movement, just to observe the outcomes, and so we don't elaborate further on what could be sensible or useful models of movement, but we imagine existing methods of hierarchical or state-space models are suitable for this purpose (Ovaskainen, 2004; Jonsen et al., 2005; Forester et al., 2007; Ovaskainen et al., 2008; Hooten et al., 2010; McClintock et al., 2012). We consider explicit p0035 movement models in the context of SCR models in the later chapters of this book (Chapters 15 and 16). Here we adopt more of a phenomenological formulation of space usage as follows: If an individual appears in pixel $\mathbf{x}$ at some instant, this is defined as a decision to "use" pixel $\mathbf{x}$. Thus, over any prescribed time interval, the percentage of time an individual spends in each pixel is theoretically knowable. Or, if we sample some number of points during that interval, say R, then the frequency of use decisions is, conceivably, observable by some omnipotent accounting mechanism (e.g., telemetry that doesn't malfunction). In this case, let m_{ij} be the *true* use frequency of pixel j by individual i—i.e., the number of times individual i used pixel j. We assume the vector of use frequencies $\mathbf{m}_i = (m_{i1}, \ldots, m_{iG})$ has a multinomial distribution:

$$\mathbf{m}_i \sim \text{Multinomial}(R, \boldsymbol{\pi}_i),$$

where $R = \sum_j m_{ij}$ is the total number of "use decisions" made by individual i and

$$\pi_{ij} = \frac{\exp(\alpha_2 C(\mathbf{x}_j))}{\sum_x \exp(\alpha_2 C(\mathbf{x}))},$$

for each $j = 1, 2, \ldots, G$ pixels. This is a standard RSF model (Manly et al., 2002) used to model telemetry data. In particular, this is "protocol A" of (Manly et al., 2002) where all available landscape pixels are censused (i.e., known without error), and used pixels are sampled randomly for each individual. The parameter α_2 is the effect of the landscape covariate $C(\mathbf{x})$ on the relative probability of use. Thus, if α_2 is positive, the relative probability of use increases as the covariate increases.

p0040 In practice, we don't ~~get to~~ observe m_{ij} for all individuals but, instead, only for a small subset which we capture and telemeter. For the telemetered individuals, we assume they use resources according to the same RSF model as the population as a whole. To extend this model to make it more realistic, and consistent with the formulation of SCR models, let $\mathbf{s}$ denote the center of an individual's home range and let $d_{ij} = ||\mathbf{x}_j - \mathbf{s}_i||$ be the distance from the home range center of individual i, $\mathbf{s}_i$, to pixel j, $\mathbf{x}_j$. We modify the space usage model to accommodate that space use will be concentrated around an individual's home range center:

$$\pi_{ij} = \frac{\exp\left(-\alpha_1 d_{ij}^2 + \alpha_2 C(\mathbf{x}_j)\right)}{\sum_x \exp\left(-\alpha_1 d_{ij}^2 + \alpha_2 C(\mathbf{x})\right)}. \tag{13.1.1}$$

The parameters α_1, α_2 and the activity centers $\mathbf{s}$ can be estimated directly from telemetry data, using standard likelihood methods based on the multinomial likelihood (Johnson et al., 2008b). Normally this model is expressed in terms of the scale parameter σ, $\alpha_1 = 1/(2\sigma^2)$, and the multinomial model Eq. (13.1.1) can be understood as a compound model of space usage governed by distance-based "availability" according to a Gaussian kernel, and "use," conditional on availability (Johnson et al., 2008b; Forester et al., 2009). In other words, the model suggests a kind of distance-based

B978-0-12-405939-9.00013-X 10013

availability in which a pixel is less available to an individual if it is located further away from $\mathbf{s}_i$.

Equation (13.1.1) resembles standard SCR encounter probability models that we have used previously, but here the model includes an additional covariate $C(\mathbf{x})$ (see Chapter 9). In particular, under this model for space usage or resource selection, if we have no covariates at all, or if $\alpha_2 = 0$, then the probabilities π_{ij} are directly proportional to the SCR model for encounter probability, *if ~~we have a~~ trap in every pixel*. Therefore, setting $\alpha_2 = 0$, the probability of use for pixel j is: p0045

$$p_{ij} \propto \exp\left(-\alpha_1 d_{ij}^2\right).$$

Clearly, whatever function of distance we use in the RSF model implies an equivalent model of space usage (Section 5.4) as an SCR model for encounter probability. In particular, for whatever model we choose for p_{ij} in an ordinary SCR model, we can modify the distance component in the RSF function in Eq. (13.1.1) to be consistent with that model by setting:

$$\pi_{ij} \propto \exp(\log(p_{ij}) + \alpha_2 C(\mathbf{x}_j))$$

(see Forester et al., 2009).

One difference between this multinomial observation model for resource use data and those that we have considered in previous chapters is that it includes the normalizing constant $\sum_x \exp(-\alpha_1 d_{ij}^2 + \alpha_2 C(\mathbf{x}_j))$, which ensures that the use distribution is a proper probability density function. In that sense, the model has the same form as the multinomial SCR model described in Chapter 9 except that, here, the probability density of use locations is distributed over the whole state-space $\mathcal{S}$, not just the subset of locations where we have traps. In a sense, we view telemetry data as a perfect sampling of space, equivalent to having a trap in each pixel, and the number of captures (uses by an individual) is fixed by design. p0050

13.1.1 A simulated example s0010

For a simulated landscape (shown in Figure 13.1), Royle et al. (2012a) depicted some typical space usage patterns under the model described above, which we reproduce here in Figure 13.2. The covariate in this case was simulated using a kriging model of correlated random noise with the following **R** commands: p0055

```
> set.seed(1234)                        o0005
> gr <- expand.grid(1:40,1:40)          o0010
> Dmat<-as.matrix(dist(gr))             o0015
> V <- exp(-Dmat/5)                     o0020
> C <- t(chol(V))%*%rnorm(1600)         o0025
```

The resulting covariate vector **C** is multivariate normal with mean 0 and variance-covariate matrix **V** which, here, has pairwise correlations ~~which~~ decay exponentially

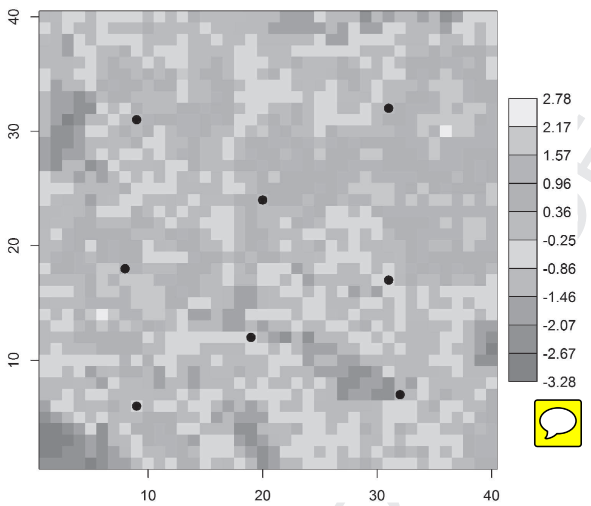

FIGURE 13.1

A typical habitat covariate reflecting habitat quality or hypothetical utility of the landscape to a species under study. Home range centers for 8 individuals are shown with black dots.

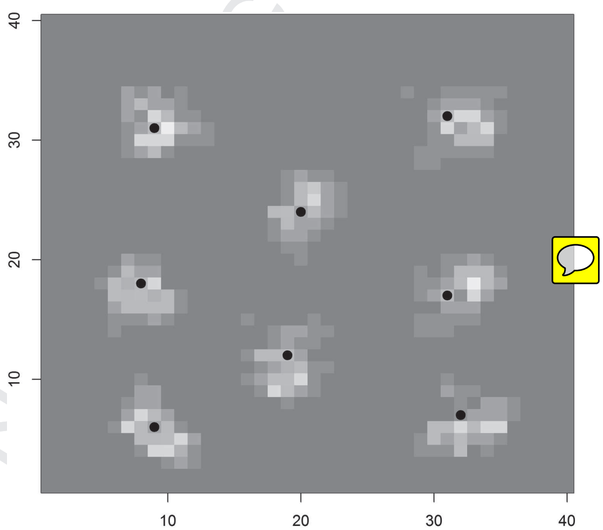

FIGURE 13.2

Space usage patterns of 8 individuals under a space usage model that contains a single covariate which is shown in Figure 13.1. The plotted value is the multinomial probability π_{ij} for pixel j under the model in Eq. (13.1.1).

with distance. The use densities shown in Figure 13.2 were simulated with $\alpha_1 = 1/(2\sigma^2)$, ~~with~~ $\sigma = 2$, and the coefficient on $C(\mathbf{x})$ set to $\alpha_2 = 1$. The resulting space usage densities—or "home ranges"—exhibit clear non-stationarity in response to the structure of the underlying covariate, and they are distinctly asymmetrical. We note that if α_2 were set to 0, the 8 home ranges shown here would be proportional to a bivariate normal kernel with $\sigma = 2$.[1] The commands for ~~the~~ kriging ~~model~~, and those to produce Figure 13.1 are in the package `scrbook` (see `?RSF_example`). AU:1

13.1.2 Poisson model of space use s0015

p0060 A natural way to motivate the multinomial model of space usage is to assume that individuals make a sequence of resource selection decisions so that the outcomes m_{ij} are *independent* Poisson random variables:

$$m_{ij} \sim \text{Poisson}(\lambda_{ij}),$$

where

$$\log(\lambda_{ij}) = a_0 - \alpha_1 d_{ij}^2 + \alpha_2 C(\mathbf{x}_j).$$

In this case, the number of visits to any particular cell is affected by the covariate $C(\mathbf{x})$ but has a baseline rate, $\exp(a_0)$, related to the amount (in an expected value sense) of movement occurring over some time interval. This is an equivalent model to the multinomial model given previously in the sense that, if we condition on the total sample size $R = \sum_j m_{ij}$, then the vector $\mathbf{m}_i$ has a multinomial distribution with probabilities given by Eq. (13.1.1) (see also Chapter 9).

p0065 In practice, we never observe "truth," i.e., the actual use frequencies m_{ij}. Instead, we observe a sample of the actual use outcomes by an individual. As formulated in Section 5.4, we assume a binomial ("random") sampling model:

$$y_{ij} \sim \text{Binomial}(m_{ij}, p_0).$$

We can think of these counts as arising by thinning the underlying point process (here, aggregated into pixels) where p_0 is the thinning rate of the point process. In this case, the marginal distribution of the observed counts y_{ij} is also Poisson but with mean

$$\log(\mathbb{E}(y_{ij})) = \log(p_0) + a_0 - \alpha_1 d_{ij}^2 + \alpha_2 C(\mathbf{x}_j).$$

Thus, the space-usage model (RSF) for the thinned counts y_{ij} is the same as the space-usage model for the original variables m_{ij}. This is because if we remove m_{ij} from the conditional model by summing over its possible values, then the vector $\mathbf{y}_i$ is *also* multinomial with cell probabilities

$$\pi_{ij} = \frac{\lambda_{ij}}{\sum_j \lambda_{ij}},$$

np005 [1]This is why we have always referred to the similar-looking model for encounter probability as the Gaussian or bivariate normal model, instead of half-normal.

B978-0-12-405939-9.00013-X 10013

where any constant (the intercept term a_0 and thinning rate p_0) cancels from the numerator and denominator. Thus, the underlying multinomial RSF model applies to the true unobserved count frequencies $\mathbf{m}_i$ and those produced from thinning or sampling, $\mathbf{y}_i$.

s0020 13.2 Integrating capture-recapture data

p0070 The key to combining RSF data with SCR data is to note that the Poisson model of space usage given above is exactly our Poisson encounter probability model from Chapter 9, only with a spatial covariate $C(\mathbf{x})$, and some arbitrary intercept off-set related to the sampling rate by the telemetry device. We've used exactly this model for ~~our~~ SCR data (Chapter 7), but with a different intercept, α_0, unrelated to the intercept of the Poisson use model for telemetry described above but, rather, to the efficiency of the capture-recapture encounter device. In other words, we view camera traps (or other devices) located in some pixel $\mathbf{x}$ (or multiple pixels) as being equivalent to being able to turn on a type of (less perfect) telemetry device only in that pixel. Therefore, data from ~~a~~ camera trapping are Poisson random variables for every pixel j where a trap is located:

$$y_{ij}|\mathbf{s}_i \sim \text{Poisson}(\lambda_{ij})$$

with

$$\log(\lambda_{ij}) = \alpha_0 - \alpha_1 d_{ij}^2 + \alpha_2 C(\mathbf{x}_j).$$

The parameters α_1 and α_2 are shared with the multinomial model for the telemetry data.

p0075 Alternatively, the SCR study can produce binary encounters depending on the type of sampling being done, where $y_{ij} = 1$ if the individual i visited the pixel containing a trap and was detected, then we imagine that y_{ij} is related to the latent variable m_{ij} being the event $m_{ij} > 0$, which occurs with probability

$$p_{ij} = 1 - \exp(-\lambda_{ij}) \tag{13.2.1}$$

and then the observed encounter frequencies for individual i and trap j, from sampling over K occasions, are binomial:

$$y_{ij}|\mathbf{s}_i \sim \text{Binomial}(K, p_{ij}).$$

p0080 A key point here is that if resource selection is happening, then it appears as a covariate on encounter rate (or encounter probability) in the same way as ordinary covariates which we discussed in Chapter 7.

p0085 To construct the likelihood for SCR data when we have direct information on space usage from telemetry data, we regard the two samples (SCR and RSF) as independent of one another, and we form the likelihood for each set of observations as a function of the same underlying parameters. The joint likelihood then is the product of the two components.

In particular, let $\mathcal{L}_{scr}(\alpha_0, \alpha_1, \alpha_2, N; \mathbf{y})$ be the likelihood for the SCR data in terms of the basic encounter probability parameters and the total (unknown) population size N, and let $\mathcal{L}_{rsf}(\alpha_1, \alpha_2; \mathbf{m})$ be the likelihood for the RSF data based on telemetry which, because the sample size of telemetered individuals is fixed, does not depend on N. Assuming independence of the two data sets, the joint likelihood is the product of these two pieces: p0090

$$\mathcal{L}_{rsf+scr}(\alpha_0, \alpha_1, \alpha_2, N; \mathbf{y}, \mathbf{m}) = \mathcal{L}_{scr}(\alpha_0, \alpha_1, \alpha_2, N; \mathbf{y}) \times \mathcal{L}_{rsf}(\alpha_1, \alpha_2; \mathbf{m}),$$

where the $\mathcal{L}_{scr}$ is the standard integrated likelihood (Chapter 6), and the RSF likelihood contribution is the multinomial telemetry likelihood having cell probabilities Eq. (13.1.1). The **R** code for maximizing the joint likelihood was given in the supplement to Royle et al. (2012a), and we include a version of this in the `scrbook` package, see `?intlik3rsf`, which also shows how to simulate data and fit the combined SCR + RSF model.

13.3 SW New York black bear study s0025

Royle et al. (2012a) applied the integrated SCR + RSF model to data from a study of black bears (*Ursus americanus*) in a region of approximately 4, 600 km^2 in southwestern New York. These data come from a research project by Sun (in press) at Cornell University, and it is a different data set than our Fort Drum bear study data set which we've analyzed in previous chapters. The data can be loaded from the `scrbook` package with the command `data(nybears)`. We reproduce the findings of Royle et al. (2012a) in this section. p0095

The data are based on a noninvasive genetic capture-recapture study using 103 hair snares in June and July, 2011. Hair snares were baited and scented and checked weekly for hair (Sun, in press). The study yielded relatively sparse encounter histories of 33 individuals with a total of 14 recaptures and 27 individuals captured 1 time only. Telemetry data were collected on three telemetry-collared individuals, which produced locations for each bear approximately once per hour. Telemetry locations were thinned to once per 10 h to produce movement outcomes that might be more independent. This produced 195 telemetry locations used in the RSF component of the model. Elevation was used as ~~the~~ covariate for this model, a standardized version of which is shown in Figure 13.3 along with the number of individuals captured at each hair snare site. p0100

There are a number of models that could be fitted to these data based on the combination of SCR and RSF data as well as the elevation covariate. The models fit here are based on the Gaussian hazard trap encounter/space usage model, including an ordinary SCR model with no covariates or telemetry data, the SCR model with elevation affecting either λ_0 or density $D(\mathbf{x})$ (Chapter 11), and models that use telemetry data. The six models fitted were: p0105

Model 1, SCR: ordinary SCR model o0030

Model 2, SCR + p(C): ordinary SCR model with elevation as a covariate on baseline encounter probability λ_0. o0035

B978-0-12-405939-9.00013-X 10013

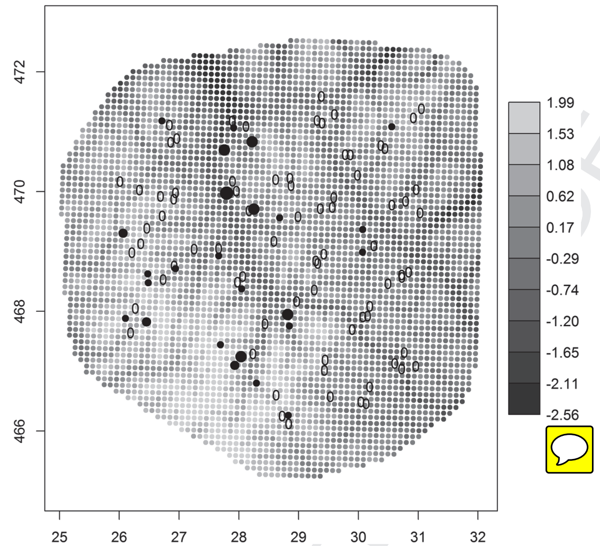

FIGURE 13.3

Elevation (standardized), hair snare locations are marked by the number of individuals captures at each site. The largest size solid mark corresponds to 4 individuals captured, the smallest to 1 individual. Hair snares that produced no individuals are given by "0."

o0040 Model 3, SCR + D(C): ordinary SCR model with elevation as a covariate on density only.

o0045 Model 4, SCR + p(C)+D(C): ordinary SCR model with elevation as a covariate on both baseline encounter probability and density.

o0050 Model 5, SCR + p(C)+RSF: SCR model including data from three telemetered individuals.

o0055 Model 6, SCR + p(C)+RSF + D(C): SCR model including telemetered individuals and with elevation as a covariate on density.

Parameter estimates for the six models are given in Table 13.1 (reproduced from Royle et al. (2012a), see also the help file `?nybears`). It is tempting to want to compare these different models by AIC but, because models 5 and 6 involve additional data, they cannot be compared with models 1–4.

p0110 By looking at Table 13.1, it is clear based on the negative log-likelihood for just Models 1–4, that those containing an elevation effect on density are preferred (Models 3 and 4). The parameter estimates indicate a positive effect of elevation on density, which seems to be consistent with the raw capture data shown in Figure 13.3. Despite this strong effect of elevation, the estimates of N under each of these models only ranged from 93 to 103 bears for the 4600 km^2 state-space, and so estimated density is pretty consistent across models. If we consider not just density, but space usage (i.e., looking at the parameter α_2), the effect of elevation is negative. Thus, elevation

Table 13.1 Summary of model-fitting results for the black bear study. Parameter estimates are for the intercept (α_0), logarithm of σ, the scale parameter of the Gaussian hazard encounter model, β is the coefficient of elevation on density, and the total population size N of the state-space. Standard errors are in parentheses. The SCR data are based on $n = 33$ individuals, and the telemetry data are based on 3 individuals. sp030

Model	α_0	$\log(\sigma)$	α_2	N	β	−loglik
SCR(elev)	−2.860 (0.390)	−1.117 (0.139)	0.175 (0.248)	95.8 (22.99)		122.738
SCR	−2.729 (0.345)	−1.122 (0.140)	–	93.9 (22.06)		122.990
SCR + D(elev)	−2.715 (0.353)	−1.133 (0.139)	–	94.2 (21.90)	1.247 (0.408)	118.007
SCR(elev) + D(elev)	−2.484 (0.391)	−1.157 (0.142)	−0.384 (0.276)	103.5 (26.56)	1.571 (0.463)	117.075
SCR(elev) + RSF	−3.068 (0.272)	−0.814 (0.036)	−0.281 (0.118)	81.6 (17.65)		1271.739
SCR(elev) + RSF + D(elev)	−3.070 (0.272)	−0.810 (0.037)	−0.371 (0.124)	89.1 (20.55)	1.273 (0.411)	1266.700

appears to affect density and space usage differently. It was suggested that density operates at the second-order scale of resource selection and "....is largely related to the spacing of individuals and their associated home ranges across the landscape. On the other hand, our RSF was defined based on selection of resources within the home range (third-order)." (Royle et al., 2012a) The positive effect of density on elevation is consistent with some other studies on black bears (e.g., Frary et al., 2011), and the negative effect of elevation on space usage can be attributed to seasonal variation in food availability, usage of corridors, or environmental conditions.

Models 5 and 6 include the additional telemetry data, thus the negative log-likelihoods are not directly comparable to the first four models, but we can still make a few important observations. First is that the parameter estimates under these two models are consistent with Model 4 in that elevation had a strong effect on both density and space usage. In comparing Models 5 and 6, the latter model which includes elevation as an effect on density reduces the negative log-likelihood by 5 units. Additionally, including the telemetry data reduces the standard errors (SE) of the density and space usage parameters and as we would expect, the incorporation of telemetry data also reduces the SE for σ. The increased precision for the estimated population size (N) is negligible with the use of telemetry data in this case. However, that may be different if more telemetry information were available. Model 6 (SCR + p(C) + RSF + D(C)) was used to produce maps of density (Figure 13.4) and space usage (Figure 13.5) showing the effect of elevation on both components of the model. The map of space usage shows the relative probability of using a pixel $\mathbf{x}$ relative to one having the mean elevation, given a constant distance to the individual's activity center. p0115

B978-0-12-405939-9.00013-X 10013

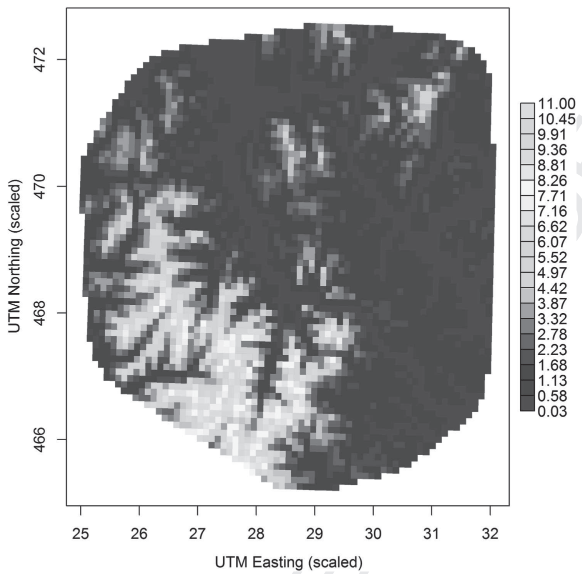

FIGURE 13.4

Predicted density of black bears (per 100 km^2) in southwestern New York study area.

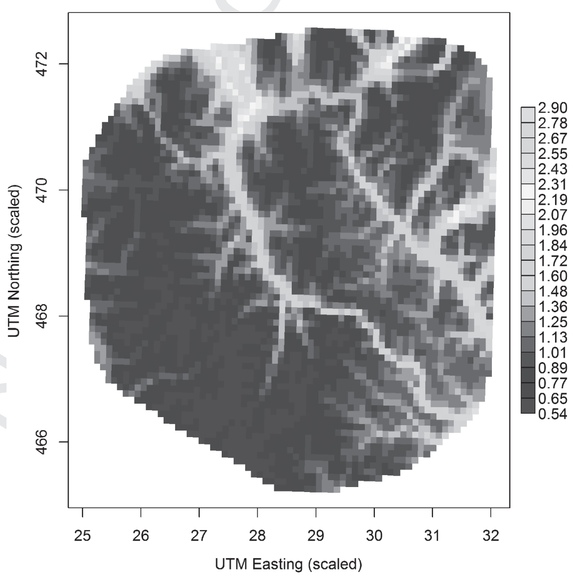

FIGURE 13.5

Relative probability of use of pixel **x** compared to a pixel of mean elevation, at a constant distance from the activity center.

13.4 Simulation study s0030

p0120 Using the simulated landscape shown in Figure 13.1, Royle et al. (2012a) presented results of a simulation study considering populations of $N = 100$ and $N = 200$ individuals exposed to encounter by a 7×7 array of trapping devices, with $K = 10$ sampling occasions, using the Gaussian hazard model (Eq. (13.2.1)) with

$$\log(\lambda_{ij}) = -2 - \frac{1}{2\sigma^2} d_{ij}^2 + 1 * C(\mathbf{x}_j),$$

where $\sigma = 2$. They looked at the effect of misspecification of the resource selection model with an ordinary model SCR0 (i.e., no habitat covariates affecting the trap encounter model), and the performance of the MLEs, under SCR + telemetry designs having 2, 4, 8, 12, and 16 telemetered individuals (with 20 independent telemetry fixes *per* individual). Three models were fitted: (i) the SCR only model, in which the telemetry data were not used; (ii) the integrated SCR/RSF model which combined all of the data for jointly estimating model parameters; and (iii) the RSF only model which just used the telemetry data alone (and therefore the parameters α_0 and N are not estimable). An abbreviated version of the results from Royle et al. (2012a) is summarized in Table 13.2. We provide an **R** script (see `?RSFsim`) that can be modified for further analysis and exploration.

One thing we see is a pretty dramatic negative bias in estimating N if the model SCR0 is fitted (interestingly, there is much less bias in estimating σ). Overall, though, when either the SCR model with covariate or the joint SCR + RSF model is fitted, the MLEs exhibit little bias for the parameter values simulated here. In terms of RMSE, there is only a slight ≈5–10% reduction in RMSE of the estimator of N when we have at least 2 telemetered individuals. Thus, estimating N benefits only slightly from the addition of telemetry data, which is because information about the intercept, α_0, comes only from the capture-recapture data. However, there is a large improvement in precision (50–60%) for estimating the scale parameter σ. While this doesn't translate much into improved estimation of N, it suggests that it should be relevant to the design of SCR studies for which trap spacing is one of the main considerations (Chapter 10). In terms of study design these results also suggest that, perhaps, spatial recaptures are not needed if some telemetry data are available (in Chapter 19, in the context of mark-resight models, we show a case study of raccoons where additional telemetry data allows estimating model parameters in spite of a very low number of spatial recaptures (Sollmann et al., 2013a)). The resource selection parameter α_2 is well estimated even *without* telemetry data. The fact that parameters of resource selection can be estimated from ~~ordinary~~ capture-recapture data should have considerable practical relevance in the study of animal populations and landscape ecology. For the highest sample size of telemetered individuals ($n = 16$), the RMSE for estimating this parameter only decreases from about 0.09 to 0.07.

sp035 **Table 13.2** This table summaries the sampling distribution of the MLE of model parameters for models fitted to data generated under a resource selection model. The models fitted include the misspecified model, which is a basic model SCR0 (with no covariate), the SCR model with the covariate on encounter probability, and the SCR model including the covariate and a sample of telemetered individuals (n is the number of individuals telemetered). Data were simulated with $N = 200$ individuals, $\alpha_2 = 1$ and $\sigma = 2$.

	$\hat{N}$	RMSE	$\hat{\alpha}_2$	RMSE	$\hat{\sigma}$	RMSE
***n* = 2**						
SCR + C(x)	199.11	14.28	0.99	0.09	2.00	0.090
SCR + RSF	199.11	13.80	0.99	0.09	2.00	0.079
SCR0	161.48	39.98	–	–	1.84	0.180
***n* = 4**						
SCR only	199.67	13.87	1.00	0.09	2.00	0.090
SCR/RSF	199.65	13.59	1.00	0.09	2.00	0.072
SCR0	161.32	40.00	–	–	1.83	0.191
***n* = 8**						
SCR only	199.24	15.49	0.99	0.10	2.01	0.093
SCR/RSF	199.55	14.17	0.99	0.08	2.00	0.063
SCR0	161.46	40.06	–	–	1.84	0.184
***n* = 12**						
SCR only	200.41	15.16	0.99	0.10	2.00	0.086
SCR/RSF	200.95	13.04	1.00	0.08	2.00	0.051
SCR0	162.40	38.95	–	–	1.84	0.185
***n* = 16**						
SCR only	199.16	15.62	1.00	0.09	2.00	0.095
SCR/RSF	199.63	13.38	1.00	0.07	2.00	0.052
SCR0	160.93	40.44	–	–	1.84	0.190

s0035 13.5 Relevance and relaxation of assumptions

p0125 In constructing the combined likelihood for RSF and SCR data, we assumed the data from capture-recapture and telemetry studies were independent of one another. This implies that whether or not an individual enters into one of the data sets has no effect on whether it enters into the other data set. We cannot foresee situations in which violation of this assumption should be problematic or invalidate the estimator under the independence assumption. In some cases it might so happen that some individuals appear in *both* the RSF and SCR data sets. In this case, ignoring that information should entail only an incremental decrease in precision because a slight bit of information about an individuals activity center is disregarded.

Our model pretends that we do not know anything about the telemetered individuals in terms of their encounter history in traps. In principle it should not be difficult to admit a formal reconciliation of individuals between the two lists. In that case, we just combine the two conditional likelihoods before we integrate **s** from the conditional likelihood. This would be almost trivial to do if *all* individuals were reconcilable (or none, as in the case we have covered here). But, in general, we think you will often have an intermediate case, i.e., either none will be or at most a subset of telemetered ~~guys~~ will be known and there will be some individuals of unknown mark status. In that case, basically a type of marking uncertainty or misclassification is clearly more difficult to deal with (see Chapter 19 for some additional context). p0130

We developed the model in a discrete landscape which regarded potential trap locations and the covariate $C(\mathbf{x})$ as being defined on the same set of points. In practice, trap locations may be chosen independent of the definition of the raster and this does not pose any challenge or novelty to the model as it stands. In that case, the covariate(s) need to be defined at each trap location. The model should be applicable also to covariates that are naturally continuous (e.g., distance-based covariates) although, in practice, it will usually be sufficient to work with a discrete representation of such covariates. p0135

The multinomial RSF model for telemetry data assumes independent observations of resource selection. This would certainty be reasonable if telemetry fixes are made far apart in time (or thinned). However, as noted by Royle et al. (2012a), the independence assumption is *not* an assumption of spatially independent movement outcomes in geographic space. Active resource selection should probably lead to the appearance of spatially dependent outcomes, regardless of how far apart in time the telemetry locations are. Even if resource selection observations are dependent, use of the independence model probably yields unbiased estimators while understating the variance. Development of integrated SCR + RSF models that accommodate more general models of movement is needed. p0140

13.6 Summary and outlook s0040

How animals use space is of fundamental interest to ecologists and is important in the conservation and management of many species. Investigating space use is normally done using telemetry and models referred to as resource selection functions (Manly et al., 2002) but in all of human history, animal resource selection has *never* been studied using capture-recapture models. Instead, essentially all applications of SCR models have focused on density estimation. It is intuitive, however, that space usage or resource selection should affect encounter probability and thus it should be highly relevant to density estimation in SCR applications, and, vice versa, SCR applications should yield data relevant to resource selection questions. The development in this chapter shows clearly that these two ideas can be unified within the SCR methodological framework so that classical notions of resource selection modeling can be addressed simultaneous to modeling of animal density. What we find is that if p0145 animal resource selection is occurring, this can be modeled as covariate on encounter probability, with or without the availability of auxiliary telemetry data. If telemetry data do exist, we can estimate parameters jointly by combining the two likelihood components—that of the SCR data and that of the telemetry data.

p0150 Active resource selection by individuals induces a type of heterogeneous encounter probability, and this induces (possibly severe) bias in the estimated population size for a state-space when default symmetric encounter probability models are used. As such, it is important to account for resource selection when relevant covariates are known to influence resource selection patterns. Aside from properly modeling this selection-induced heterogeneity, integration of RSF data from telemetry with SCR models achieves a number of useful advances: First, it leads to an improvement in our ability to estimate density, and an improvement in our ability to estimate parameters of the RSF function. As many animal population studies have auxiliary telemetry information, the incorporation of such information into SCR studies has broad applicability to many studies. It seems possible even to estimate density now, with no spatial recaptures, provided telemetry data are available. Secondly, the integrated model allows for the estimation of RSF model parameters directly from SCR data *alone*. This establishes clearly that SCR models *are* explicit models of resource selection. In our view, this greatly broadens the utility and importance of capture-recapture studies beyond their primary historical use of estimating density or population size. Finally, we note that telemetry information provide direct information about the home range shape parameter, σ, in our analyzes above, and its estimation is greatly improved with even moderate amounts of telemetry data (see also Sollmann et al. (2013a) and Sollmann et al. (~~in revision).~~ This should have some consequences in terms of the design of capture-recapture studies (Chapter 10), especially as it relates to trap spacing.

p0155 Simultaneously conducting telemetry studies with capture-recapture is extremely common in field studies of animal populations. However, the simultaneous, integrated analysis of the two sources of data is uncommon. The new class of integrated SCR/RSF models based on Royle et al. (2012a) allows researchers to model how the landscape and habitat influence the movement and space use of individuals around their home range, using non-invasively collected capture-recapture data that can be augmented with telemetry data. This should improve our ability to understand, and study, aspects of space usage and it might, ultimately, aid in addressing conservation-related problems such as reserve or corridor design. This should greatly expand the relevance and utility of spatial capture-recapture beyond its use for density estimation.

This page is intentionally left blank

Non Print Items

sp005 **Abstract:** In this chapter, we extend SCR models to incorporate models of resource selection, such as when one or more explicit landscape covariates are available which the investigator believes might affect how individual animals use space within their home range. We present a method that integrates a standard family of resource selection models based on auxiliary telemetry data into the capture-recapture model for encounter probability. The important distinction between SCR and resource selection function (RSF) studies is that, in SCR studies, encounter of individuals is imperfect (i.e., "$p < 1$") whereas, with RSF data obtained by telemetry, encounter is perfect. Thus in this chapter, we argue that SCR and telemetry data can therefore be combined in the same likelihood by formally recognizing this distinction in the model. We demonstrate a model for integrating capture-recapture data with RSF data under a Poisson model of space usage. We present and analyze data from a study of black bears in southwest NY, USA to which we fit a variety of models that highlight the differences between models including only SCR data or models that include both SCR and RSF data. We also provide a simulation study to validate the model and for the reader to become more familiar with the models and data. This integration of SCR and RSF models wil allow researchers to model how the landscape and habitat influence the movement and space use of individuals around their home range, using non-invasively collected capture-recapture data that can be augmented with telemetry data.

st075 **Keywords:** Black bears, Habitat selection, Landscape structure, Multiple data sources, Resource selection functions, RSF, Telemetry, Utilization distribution