13

INTEGRATING RESOURCE SELECTION WITH SPATIAL CAPTURE-RECAPTURE MODELS

In Chapt. 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 individuals home range center. This is not a very realistic model of space usage 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).

Our treatment follows Royle et al. (2012b) which 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 are 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 on resource selection can be combined in the same likelihood by formally recognizing this distinction in the model.

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 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 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 sampling. However, their estimator requires that individuals are sampled 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) 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., 2013, in revision). As a result, this leads to improved estimates of model parameters, and also has design consequences (see Sec. 10.4). In addition, active resource selection by animals induces a type of heterogeneity in encounter probability, which is misspecified by standard SCR encounter probability models. As a result, estimates of population size or density under models that do not account for resource selection can be biased (Royle et al., 2012b). 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.

13.1 A MODEL OF SPACE USAGE

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 $C(\mathbf{x})$.

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; Patterson et al., 2008; Hooten et al., 2010; McClintock et al., 2012). We consider explicit movement models in the context of SCR models later chapters of this book (Chapts. 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 $\mathbf{x}$. This also induces a definition of "truth" – that is, over any prescribed time interval, the percentage of time 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

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

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 pixels are censused, 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.

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 their behavior is 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 individuals 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 individuals home range center:

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

where $\alpha_1 = 1/(2\sigma^2)$ describes the rate at which capture probability declines as a function of distance. 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., 2008). Sometimes in RSF modeling activities there are continuous covariates and so the denominator in Eq. 13.1.1 involves integration over a distribution for the covariate, which is the conditional intensity of observed point locations in a point process model.

The 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 also "use", conditional on availability (Johnson et al., 2008; Forester et al., 2009). Further, Eq. 13.1.1 resembles standard SCR encounter probability models that we have used previously, but here with an additional covariate $C(\mathbf{x})$ (and see Chapt. 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. Therefore, setting $\alpha_2 = 0$, the probability of use for pixel j is:

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

Clearly, whatever function of distance we use in the RSF model implies an equivalent model of space usage (Sec. 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 accordingly to be consistent with that model by using whatever function p_{ij} we choose according to

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

(see Forester et al. (2009)). One difference between this observation model 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 Chapt. 9 except that, here, the density is with respect to the whole state space $\mathcal{S}$, not just the subset of trap locations. 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.

Royle et al. (2012b) depict some typical space usage patterns under this model for a single simulated covariate (reproduced here in Fig. 13.1). These home ranges were

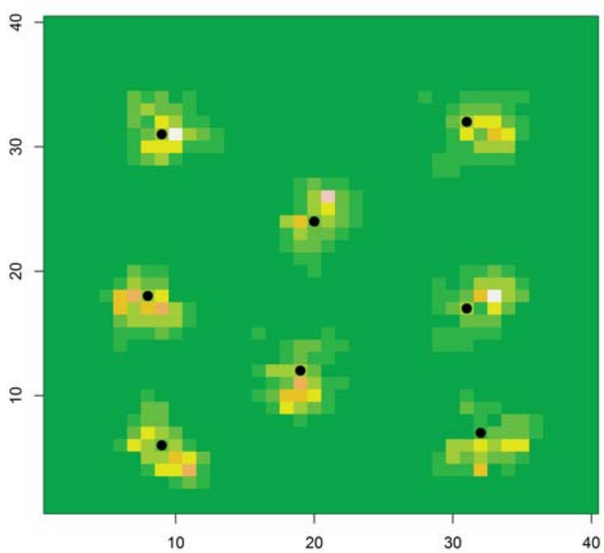

Figure 13.1. Space usage patterns of 8 individuals under a space usage model that contains a single covariate which is shown in Fig. 13.2. The plotted value is the multinomial probability π_{ij} for pixel j under the model in Eq. 13.1.1.

simulated with $\alpha_1 = 1/(2\sigma^2)$ with $\sigma = 2$ and the coefficient on $C(\mathbf{x})$ set to $\alpha_2 = 1$. The covariate in this case was simulated by using a kriging model with the following **R** commands:

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

These space usage densities – "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 bivariate normal kernels with $\sigma = 2$. These commands, and those to produce Fig. 13.2 are in the package `scrbook` (see `?RSF_example`).

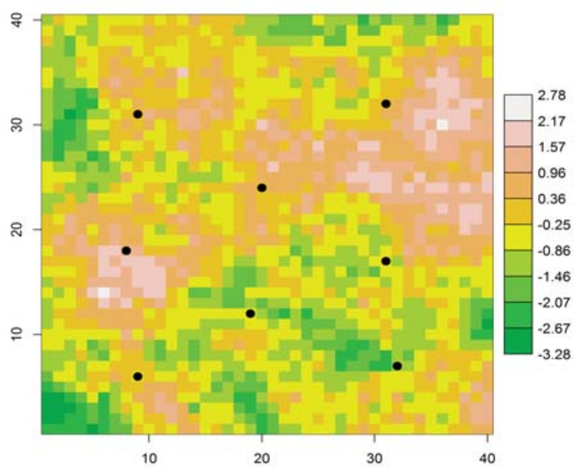

Figure 13.2. A typical habitat covariate reflecting habitat quality or hypothetical utility of the landscape to a species under study. Home range centers for 8 individuals are shown with black dots.

13.1.1 Poisson use model

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 occuring 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 Chapt. 9). Also note that if use frequencies are summarized over individuals for each pixel, i.e., create the totals $m_{\cdot j} = \sum_i m_{ij}$, then a standard Poisson regression model for the resulting "quadrat counts" is reasonable. This is "Design I" in Manly et al. (2002).

In practice, we never observe "truth", i.e., the actual use frequencies m_{ij}. Instead, we observe a sampling of the actual use outcomes by an individual. As formulated in Sec. 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

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

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

13.2 INTEGRATING CAPTURE-RECAPTURE DATA

The key to combing RSF data with SCR data is to note that the Poisson model of space usage given above is exaactly our Poisson encounter probability model from Chapt. 9, but with some arbitrary intercept off-set related to the sampling rate by the telemetry device, and with a spatial covariate $C(\mathbf{x})$. We've used exactly this model for our SCR data (Chapt. 7), but with a different intercept, α_0, unrelated to the intercept of the Poisson use model for trelemetry 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.

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

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

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

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

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 were discussed in Chapt. 7.

13.2.1 The Joint RSF/SCR Likelihood

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 and form the joint likelihood as 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 such individuals is fixed, does not depend on N. Assuming independence of the two datasets, the joint likelihood is the product of these two pieces:

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

Where the $\mathcal{L}_{scr}$ is the standard integrated likelihood (Chapt. 6), and the RSF likelihood contribution is the multinomial telemetry likelihood having cell probabilities Eq. 13.1.1. The **R** code for this was given in the supplement to Royle et al. (2012b), 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

Royle et al. (2012b) applied the integrated SCR+RSF model to data from a study of black bears in a region of approximately 4,600 km^2 in southwestern New York (Sun, in prep)[1]. The data can be loaded from the `scrbook` library with the command `data(nybears)`. We reproduce the findings of Royle et al. (2012b) in this section.

The data are based on a noninvasive, genetic, mark-recapture study using 103 hair snares in June and July, 2011. Hair snares were baited and scented and checked weekly for

[1] This is different from our Fort Drum bear study data set which we've analyzed in previous chapters

hair (Sun, in prep). The study yielded relatively sparse encounter histories of 33 individuals and a total of 14 recaptures (27 individuals captured 1 time only. Data were collected on 3 radio-telemetered individuals, which produced locations for each bear approximately once per hour. We thinned these data to once per 10 hours 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 Fig. 13.3 along with the locations of each capture at hair snare sites.

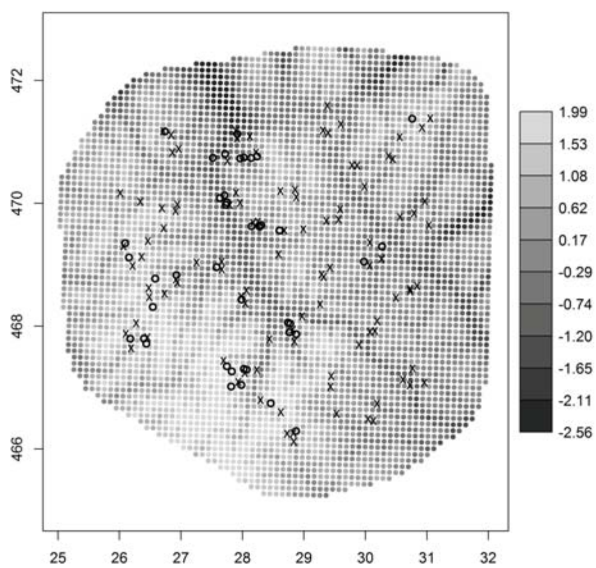

Figure 13.3. Elevation (standardized), hair snare locations (indicated by "x") and location of bear captures (open circles). Multiple captures at a trap location are offset by adding random noise.

There are a number of such models that could be fitted to these data based on the combination of SCR and RSF data as well as the elevation covariate. Here, the various models are based on the Gaussian hazard model including an ordinary SCR model with no covariates or telemetry data, the SCR model with elevation affecting either λ_0 or density $D(\mathbf{x})$ (Chapt. 11), and models that use telemetry data. The 6 models fitted were:

Model 1, SCR: ordinary SCR model
Model 2, SCR+p(C): ordinary SCR model with elevation as a covariate on baseline encounter probability λ_0.
Model 3, SCR+D(C): ordinary SCR model with elevation as a covariate on density only.
Model 4, SCR+p(C)+D(C): ordinary SCR model with elevation as a covariate on both

baseline encounter probability and density.
Model 5, SCR+p(C)+RSF: SCR model including data from 3 telemetered individuals.
Model 6, SCR+p(C)+RSF+D(C): SCR model including telemetered individuals and with elevation as a covariate on density.

Its 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. Parameter estimates for the six models are given in Table 13.1 (reproduced from Royle et al. (2012b), see also the help file `?nybears`).

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 (Model 3 and 4). The parameter estimates indicates a positive effect of elevation on density, which seems to be consistent with the raw capture data shown in Fig. 13.3. Despite this strong, significant effect of elevation, the estimate of N under each of these models only ranged from $93-103$ bears for the 4600 km^2 state-space. If we consider not just density, but space usage(i.e., looking at the parameter α_2), the effect of elevation is negative. The covariate, elevation, appears to affect density and space usage differently. It was suggested that density is operating 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., 2012b) The positive effect of density to elevation is consistent with some other studies (e.g. Frary et al., 2011), and the negative effect of elevation on space usage was 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 4 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 (Fig. 13.4) and space usage (Fig. 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.

13.4 SIMULATION STUDY

Using the simulated landscape shown in Fig. 13.2, (Royle et al., 2012b) presented results of a simulation study considering populations of $N = 100$ and $N = 200$ individuals using the Gaussian hazard mode:

$$\text{cloglog}(p_{ij}) = -2 - \frac{1}{2\sigma^2} d_{ij}^2 + 1 \times C(\mathbf{x}_j).$$

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 rae in parentheses. The SCR data are based on $n = 33$ individuals, and the telemetry data are based on 3 individuals.

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

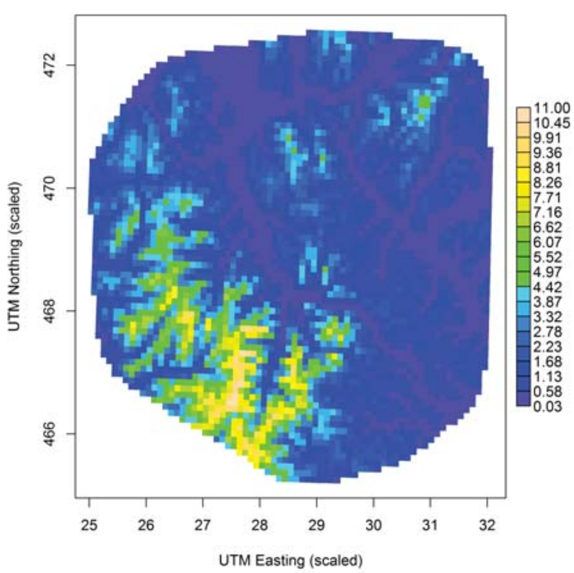

Figure 13.4. Predicted density of black bears (per 100 km^2) in southwestern New York study area.

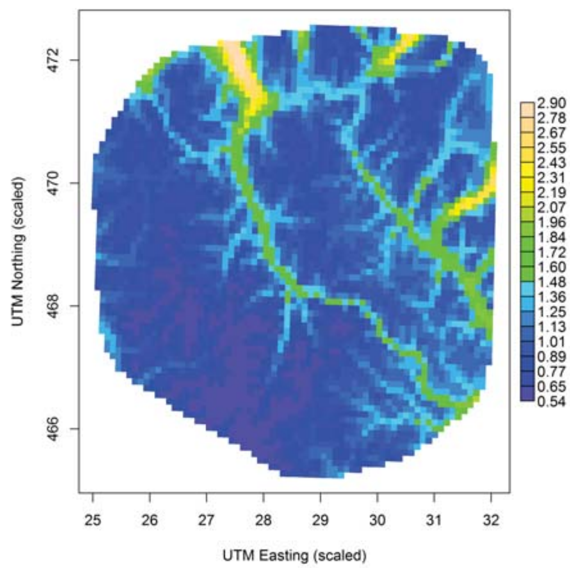

Figure 13.5. Relative probability of use of pixel $\mathbf{x}$ compared to a pixel of mean elevation, at a constant distance from the activity center.

with $\sigma = 2$. Recall, that $\text{cloglog}(u) = \log(-\log(1-u))$ is the complementary log-log function. In the absence of selection (omitting the covariate $C(\mathbf{x})$), this model corresponds to a space usage model that is bivariate normal with standard deviation 2 (Sec. 5.4).

Using this model, Royle et al. (2012b) looked at the effect of misspecification of the resource selection model with an ordinary model SCR0, and the peformance of the MLEs, under SCR+telemetry designs having 2, 4, 8, 12, and 16 telemetered individuals (with 20 independent telemetry fixes *per* individual). We summarize some of the results here, but provide an **R** script (see `?RSFsim`) that can be modified for further analysis and exploration. They fitted 3 models: (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 α_0 and N are not estimable parameters). An abbreviated version of the results from Royle et al. (2012b) is summarized in Table 13.2 below.

One thing we see is a pretty dramatic bias in estimating N if the normal 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 $\approx 5\%$ reduction in RMSE of the estimator of N when we have at least 2 telemtered individuals, and as much as a 10% reduction as in the $N = 200$ situations. This makes sense because we nail down the parameters and still don't know where guys are, and get info about mean p, i.e. α_0, only from the SCR data. Thus estimating N benefits only slightly from the addition of telemetry data. However, there is a large improvement (50-60%) in estimating the home range 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 (Chapt. 10) where spatial recaptures are need to estimate σ. These results suggest that, perhaps, spatial recaptures are not needed if some telemetry data are available. The resource selection parameter α_2 is well-estimated even *without* telemetry data. The fact that parameters of resrouce selection can be estimated from ordinary capture-recapture data should have considerable practical relevance in the study of animal populations and in 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.

13.5 RELEVANCE AND RELAXATION OF ASSUMPTIONS

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

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 telemtered). 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

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 $\mathbf{s}$ 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 always have an intermediate case, i.e., either none will be or at most a subset of telemetered guys will be known. More likely you have variations of "well, that individual looks telemetered but we are not sure which one it is....hmmm" and in that case, basically a type of marking uncertainty or misclassification, is clearly more difficult to deal with although its possible that this can be dealt with in some cases (see Chapt. 19 for models that make use of marked, unmarked, and unknown mark status of individuals).

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 pratice, it will usually be sufficient to work with a discrete representation of such covariates.

The multinomial RSF model for telemetry data assumes independent observations of resource selection. This would certaintly be reasonable if telemetry fixes are made far apart in time (or thinned). However, as noted by Royle et al. (2012b), 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, but probably under-states the variance. Development of integrated SCR+RSF models that accommodate more general models of movement is needed.

13.6 SUMMARY AND OUTLOOK

How animals use space is a fundamental interest to ecologists and is important in the conservation and management of many species. Normally this is done by 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. However, it is intuitive that space usage should affect encounter probability and thus it should be highly relevant to density estimation in SCR applications. 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 addresssed simultaneous to modeling of animal density. What we find is that if 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 cominbing the two likelihood components – that of the SCR data and that of the telemetry data.

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 space usage when relevant covariates are known to influence space use 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 also 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 space usage. 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 analyses above, and its estimation is greatly improved with even moderate amounts of telemetry data (see also Sollmann et al. (2013) and Sollmann et al. (in revision). This should have some consequences in terms of the design of capture-recapture studies (Chapt. 10), especially as it relates to trap spacing.

Simultaneously conductingt elemetry studies with capture-recapture is extremely common in field studies of animal populations. However, the simultaneous, integrated analysis of the two sources of data has not been done. The new class of integrated SCR/RSF models based on the Royle et al. (2012b) model allows researchers to model how the landscape and habitat influence the movement and use of individuals around their home range, using non-invasively collected capture-recapture data or capture-recapture data 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 development should greatly expand the relevance and utility of spatial capture-recapture beyond simply its use for density estimation.