

Chapter 1

Likelihood Analysis of SCR Models

In this book we mainly focus on Bayesian analysis of spatial capture-recapture models. And, in the previous chapters we learned how to fit some basic spatial capture-recapture models using a Bayesian formulation of the models analyzed in WinBUGS. Despite our focus on Bayesian analysis, it is instructive to develop the basic conceptual and methodological ideas behind classical analysis based on likelihood methods. In fact, simple SCR models can be analyzed fairly easily using classical likelihood methods. This has been the approach taken by Borchers and Efford (2008), Dawson and Efford (2009) and related papers.

In this chapter we provide some conceptual and technical footing for likelihood-based analysis of spatial capture-recapture models. We recognized earlier (Section xxxx) that SCR models are versions of binomial (or other) GLMs with random effects i.e., GLMMs, which are routinely analyzed by likelihood methods. In particular, likelihood analysis is based on the integrated likelihood in which the random effects are removed by integration from the likelihood. In SCR models, the random effect, \mathbf{s} , i.e., the 2-dimensional coordinate, is a bivariate random effect. In this chapter, we show that it is straightforward to compute the maximum likelihood estimates (MLE) for SCR models by integrated likelihood. We develop the MLE framework using R, and we also provide a basic introduction to an R package `secr` (Efford 2011) which is based on the stand-alone package `DENSITY` (Efford et al. 2004). To set the context we analyze the SCR model here when N is known because, in that case, it is precisely a GLMM and does not pose any difficulty at all. We generalize the model to allow for unknown N using both conventional ideas based on the “joint likelihood” (e.g., Borchers et al., 2002) and also using a formulation based on data augmentation. We consider likelihood analysis of SCR models in the context of the wolverine camera trapping study (Magoun et al., 2011) we analyzed in previous chapters

30 to compare/contrast the results.

31 1.1 Likelihood analysis

32 We noted in Chapter 4 that, with N known, the basic SCR model is a type
 33 of binomial regression with a random effect. For such models we can easily
 34 obtain maximum likelihood estimators of model parameters based on integrated
 35 likelihood. The integrated likelihood is based on the marginal distribution of the
 36 data y in which the random effects are removed by integration. Conceptually,
 37 our model is a specification of the conditional-on- \mathbf{s} model $[y|\mathbf{s}, \theta]$ and we have a
 38 “prior distribution” for \mathbf{s} , say $[\mathbf{s}]$, and the marginal distribution of the data y is

$$[y|\theta] = \int_{\mathbf{s}} [y|\mathbf{s}, \theta][\mathbf{s}]d\mathbf{s}.$$

39 When viewed as a function of θ for purposes of estimation, the marginal dis-
 40 tribution $[y|\theta]$ is often referred to as the *integrated likelihood*.

41 It is worth analyzing the simplest SCR model with known- N in order to
 42 understand the underlying mechanics and basic concepts. These are directly
 43 relevant to the manner in which many capture-recapture models are classically
 44 analyzed, such as model Mh, and individual covariate models (see chapt. 6 from
 45 Royle and Dorazio (2008)). To develop integrated likelihood for SCR models,
 46 we first identify the conditional likelihood.

47 The observation model for each encounter observation y_{ij} , specified condi-
 48 tional on \mathbf{s}_i , is

$$y_{ij}|\mathbf{s}_i \sim \text{Bin}(K, p_{\theta}(\mathbf{x}_j, \mathbf{s}_i)) \quad (1.1)$$

49 where we have indicated the dependence of p_{ij} on \mathbf{s} and parameters θ explicitly.
 50 For the random effect we have $\mathbf{s}_i \sim \text{Unif}(\mathcal{S})$. The joint distribution of the data
 51 for individual i is the product of J such terms (i.e., contributions from each of
 52 J traps).

$$[\mathbf{y}_i|\mathbf{s}_i, \theta] = \prod_j \text{Bin}(K, p_{\theta}(\mathbf{x}_j, \mathbf{s}_i))$$

53 We note that this assumes that encounter of individual i in each trap is indepen-
 54 dent of encounter in every other trap, conditional on \mathbf{s}_i , this is the fundamental
 55 property of SCR0 or “multi-catch” traps.

56 The so-called “marginal likelihood” is computed by removing \mathbf{s}_i , by integra-
 57 tion, from the conditional-on- \mathbf{s} likelihood. That is, we compute:

$$\mathcal{L}(\theta|\mathbf{y}_i) = \int_{\mathcal{S}} \mathcal{L}(\theta|\mathbf{y}_i|\mathbf{s}_i)g(\mathbf{s}_i)d\mathbf{s}_i$$

58 The joint likelihood for all N individuals, assuming independence of encounters
 59 among individuals, is the product of N such terms:

$$\prod_i f(y[i, j])$$

We emphasize that two independence assumptions are explicit in this development: independence of trap-specific encounters within individuals and also independence among individuals. In particular, this would only be valid when individuals are not physically restrained or removed upon capture, and when traps do not fill up.

The key operation for computing the likelihood is solving a 2-dimensional integration problem. There are some general purpose **R** packages that implement a number of multi-dimensional integration routines including **adapt** (REF) and **Rcuba** (REF XYZ). In practice, we won't rely on these extraneous **R** packages but instead will use perhaps less efficient methods in which we replace the integral with a summation over an equal area mesh of points on the state-space \mathcal{S} and explicitly evaluate the integrand at each point. Let $u = 1, 2, \dots, nG$ index a grid of nG points where the area of grid cell u is $a(u) \equiv a$ (for a regular grid). In this case, the trapezoidal rule for approximating the integral yields

$$f(y_{ij}) = \sum_{u=1}^{nG} f(\mathbf{y}_i|u)g(u) * area$$

This is a general expression that could be used for approximating the integral for any arbitrary bivariate distribution $g(u)$. In the present context note that $g(u) = (1/area(S)) = 1/[nG * a]$ and thus the grid-cell area cancels in the above expression and we have

$$f(y_{ij}) = \sum_{u=1}^{nG} f(\mathbf{y}_i|u)(1/nG)$$

Which not surprisingly is the same answer we get if S were inherently discrete, having nG unique values with equal probabilities $1/nG$. Then the marginal probability of y_{ij} , i.e., by the Law of Total probability, is precisely that last expression.

1.1.1 Implementation (simulated data)

Here we will illustrate how to carryout this integration and optimization based on the integrated likelihood using simulated data (i.e., following that from Chapter 4). Using **simSCR0.fn** we simulate data for 100 individuals and a 25 trap array layed out in a 5×5 grid of unit spacing. The specific encounter model is the half-normal model. The 100 activity centers were simulated on a state-space defined by a 8×8 square within which the trap array was centered (thus the trap array is buffered by 2 units). Therefore, the density of individuals in this system is fixed at $100/64$.

In the following set of R commands we generate the data and then harvest the required data objects:

```
data<-simSCR0.fn(discard0=FALSE,sd=2013)
y<-data$Y
```

```

95 traplocs<-data$traplocs
96 nind<-nrow(y)
97 X<-data$traplocs
98 J<-nrow(X)
99 K<-data$K
100 Xl<-data$xlim[1]
101 Yl<-data$ylim[1]
102 Xu<-data$xlim[2]
103 Yu<-data$ylim[2]

```

Now we need to define the integration grid, say **G**, which we do with the following set of **R** commands (here, `delta` is the grid spacing):

```

106 delta<- .2
107 xg<-seq(Xl+delta/2,Xu-delta/2,by=delta)
108 yg<-seq(Yl+delta/2,Yu-delta/2,by=delta)
109 npix<-length(xg)           # assumes xg and yg same dimension here
110 area<- (Xu-Xl)*(Yu-Yl)/((npix)*(npix)) # dont need area for anything
111 G<-cbind(rep(xg,npix),sort(rep(yg,npix)))
112 nG<-nrow(G)

```

In this case, the integration grid is set up as a grid with spacing $\delta = 0.2$ which produces a 40×40 grid of points for evaluating the integrand if the state-space buffer is set at 2.

We next create an **R** function that defines the likelihood as a function of the data objects y and X which were created above but, in general, you would read these files into **R**, e.g., from a .csv file. In addition to these data objects, we need to have defined the various quantities associated with the integration grid **G** and nG . However, instead of worrying about making all of these objects and keeping track of them we just put that code above into the likelihood function and pass δ as an additional (optional) argument and a few other things that we need such as the boundary of the state-space over which the integration (summation) is being done. Here is one reasonably useful variation of a function for estimation based on the integrated likelihood:

```

126
127 intlik1<-function(parm,y=y,delta=.2,X=traplocs,ssbuffer=2){
128
129   Xl<-min(X[,1]) - ssbuffer
130   Xu<-max(X[,1]) + ssbuffer
131   Yu<-max(X[,2]) + ssbuffer
132   Yl<-min(X[,2]) - ssbuffer
133
134   xg<-seq(Xl+delta/2,Xu-delta/2,,length=npix)
135   yg<-seq(Yl+delta/2,Yu-delta/2,,length=npix)
136   npix<-length(xg)
137
138   G<-cbind(rep(xg,npix),sort(rep(yg,npix)))

```

```

139 nG<-nrow(G)
140 D<- e2dist(X,G)
141
142 alpha0<-parm[1]
143 alpha1<-parm[2]
144 probcap<- plogis(alpha0)*exp(-alpha1*D*D)
145 Pm<-matrix(NA,nrow=nrow(probcap),ncol=ncol(probcap))
146           # all zero encounter histories
147 n0<-sum(apply(y,1,sum)==0)
148           # encounter histories with at least 1 detection
149 ymat<-y[apply(y,1,sum)>0,]
150 ymat<-rbind(ymat,rep(0,ncol(ymat)))
151 lik.marg<-rep(NA,nrow(ymat))
152 for(i in 1:nrow(ymat)){
153   Pm[1:length(Pm)]<- (dbinom(rep(ymat[i,],nG),K,probcap[1:length(Pm)],log=TRUE))
154   lik.cond<- exp(colSums(Pm))
155   lik.marg[i]<- sum( lik.cond*(1/nG))
156 }
157 nv<-c(rep(1,length(lik.marg)-1),n0)
158 -1*( sum(nv*log(lik.marg)) )
159 }

```

The function accepts as input the encounter history matrix, y , the trap locations, X , and the state-space buffer. This allows us to vary the state-space buffer and easily evaluate the sensitivity of the MLE to the size of the state-space. Note that we have a peculiar handling of the encounter history matrix y . In particular, we remove the all-zero encounter histories from the matrix and tack-on a single all-zero encounter history as the last row which then gets weighted by the number of such encounter histories ($n0$). This is a bit long-winded and strictly unnecessary when N is known, but we did it this way because the extension to the unknown- N case is now transparent (as we demonstrate in the following section). The matrix Pm holds the log-likelihood contributions of each encounter frequency for each possible state-space location of the individual. The log contributions are summed up and the result exponentiated on the next line, producing `lik.cond`, the conditional-on- s likelihood (Eq. 1.1 above). The marginal likelihood (`lik.marg`) sums up the conditional elements weighted by $\Pr(s)$ (formula XXX above). Finally, this function assumes that K , the number of replicates, is constant for each trap. Further, it assumes that the state-space is a square. As an exercise, consider resolving these two issues by generalizing the code.

Here is the **R** command for maximizing the likelihood and saving the results into an object called `frog`. The output is a list of the following structure and these specific estimates are produced using the simulated data set:

```

181 # should take 15-30 seconds
182
183 > starting.values <- c(-2, 2)
184 > frog<-nlm(intlik1,starting.values,y=y,delta=.1,X=traplocs,ssbuffer=2,hessian=TRUE)

```

```

185 > frog
186
187 $minimum
188 [1] 297.1896
189
190 $estimate
191 [1] -2.504824  2.373343
192
193 $gradient
194 [1] -2.069654e-05  1.968754e-05
195
196 $hessian
197           [,1]      [,2]
198 [1,]  48.67898 -19.25750
199 [2,] -19.25750  13.34114
200
201 $code
202 [1] 1
203
204 $iterations
205 [1] 11

```

206 Details about this output can be found on the help page for `nlm`. We note
 207 briefly that `frog$minimum` is the negative log-likelihood value at the MLEs,
 208 which are stored in the `frog$estimate` component of the list. The hessian is
 209 the observed Fisher information matrix, which can be inverted to obtain the
 210 variance-covariance matrix using the commands:

```

211 solve(frog$hessian)

```

212 It is worth drawing attention to the fact that the estimates are different
 213 than the Bayesian estimates reported in the previous chapter (section XYZ)!!!
 214 How can that be?! There are several reasons for this. First Bayesian inference
 215 is based on the posterior distribution and it is not generally the case that the
 216 MLE should correspond to any particular value of the posterior distribution. If
 217 the prior distributions in a Bayesian analysis are uniform, then the mode of the
 218 posterior is the MLE, but note that Bayesians almost always report posterior
 219 means and so there will typically be a discrepancy there. Secondly, we have
 220 implemented an approximation to the integral here and there might be a slight
 221 bit of error induced by that. We will evaluate that shortly. Third, the Bayesian
 222 analysis by MCMC is subject to some amount of Monte Carlo error which the
 223 analyst should always be aware of in practical situations. All of these different
 224 explanations are likely responsible for some of the discrepancy. Accounting
 225 for these, as a practical matter, we see general consistency between the two
 226 estimates.

227 To compute the integrated likelihood we used a discrete representation of
 228 the state-space so that the integral could be approximated as a summation
 229 over possible values of `s` with each value being weighted by its probability of

occurring, which is $1/nG$ under the assumption that s is uniform on the state-space \mathcal{S} . In chapter 4 we used a discrete state-space in developing a Bayesian analysis of the model in order to be able to modify the state-space in a flexible manner. Bayesian analysis requires simulation of the point process conditional on the observations, and this can be a difficult task when the state-space is continuous but has irregular geometry. Conversely, if the state-space is a regular polygon then Bayesian analysis by MCMC is possibly more efficient with a continuous state-space. We emphasize that the state-space is a part of the model. In some cases there wont be a natural choice of state space beyond “some large rectangle containing the trap grid” and, in such cases, for regular detection functions the estimate of density is invariant to the size of the state-space (i.e., the buffer) as long as it is sufficiently large. However if there are good reasons to restrict the state-space, it will tend to have an influence on the likelihood and hence AIC and so forth. As an illustration, lets do that by changing the state space here.....Use my polygon clipping stuff

In summary, we note that, for the basic SCR model, integrated likelihood is a really easy calculation when N is known. Even for N unknown it is not too difficult, and we will do that shortly. However, if you can solve the known- N problem then you should be able to do a real analysis, for example by considering different values of N and computing the results for each value and then making a plot of the log-likelihood or AIC and choosing the value of N that produces the best log likelihood or AIC. As a homework problem we suggest that the reader take the code given above and try to estimate N without modifying the code by just repeatedly calling that code for different values of N and trying to deduce the best value. Nevertheless, we will formalize the unknown- N problem shortly. We note that the software package **DENSITY** (Efford et al., 2004) implements certain types of SCR models using integrated likelihood methods. **DENSITY** has been made into an **R** package called **secr** (Efford, 2011) and we provide an analysis of some data using **secr** shortly along with a discussion of its capabilities.

1.2 MLE when N is Unknown

Here we build on the previous introduction to integrated likelihood but we consider now the case in which N is unknown. We will see that adapting the analysis based on the N -known model is really straightforward for the more general problem. The main distinction is that we dont observe the all-zero encounter history so we have to make sure we compute the probability for that encounter history which we do by tacking a row of zeros onto the encounter history matrix. In addition, we include the number of such all-zero encounter histories as an unknown parameter of the model. Call that unknown quantity n_0 . In addition, we have to be sure to include a combinatorial term to account for the fact that of the n observed individuals there are $\binom{N}{n}$ ways to realize a sample of size n . The combinatorial term involves the unknown n_0 and thus it must be included in the likelihood.

273 DETAILS NEEDED HERE

274 To summarize, when N is unknown, the n observed encounter histories have
 275 a multinomial distribution with probabilities $\pi(i)$ and sample size N^1 . The last
 276 cell the “zero cell” is computed by carrying out the integral in expression XYZ
 277 above for the all-zero encounter history and we have to account for the fact that
 278 there are $n_0 = N - n$ such encounter histories.

279 To analyze a specific case, we'll read in our fake data set (simulated using the
 280 parameters given above). To set some things up in our workspace we do this:

```
281 data<-simSCRO.fn(discard0=TRUE,sd=2013)
282 y<-data$Y
283 nind<-nrow(y)
284 X<-data$traplocs
285 J<-nrow(X)
286 K<-data$K
287 Xl<-data$xlim[1]
288 Yl<-data$ylim[1]
289 Xu<-data$xlim[2]
290 Yu<-data$ylim[2]
291
```

292 Recall that these data were generated with $N = 100$, on an 8×8 unit
 293 state-space representing the trap locations (\mathbf{X}) buffered by 2 units. As before,
 294 the likelihood is defined in the **R** workspace as an **R** function which takes an
 295 argument being the unknown parameters of the model and additional arguments
 296 as prescribed. In particular, as before, we provide the encounter history matrix
 297 \mathbf{y} , the trap locations traplocs , the spacing of the integration grid (δ) and the
 298 state-space buffer. Here is the new likelihood function:

```
299 intlik2<-function(parm,y=y,delta=.3,X=traplocs,ssbuffer=2){
300
301   Xl<-min(X[,1]) -ssbuffer
302   Xu<-max(X[,1]) + ssbuffer
303   Yu<-max(X[,2]) + ssbuffer
304   Yl<-min(X[,2]) - ssbuffer
305
306   #delta<- (Xu-Xl)/npix
307   xg<-seq(Xl+delta/2,Xu-delta/2,delta)
308   yg<-seq(Yl+delta/2,Yu-delta/2,delta)
309   npix.x<-length(xg)
310   npix.y<-length(yg)
311   area<- (Xu-Xl)*(Yu-Yl)/((npix.x)*(npix.y))
312   G<-cbind(rep(xg,npix.y),sort(rep(yg,npix.x)))
313   nG<-nrow(G)
```

¹Maybe you could show an alternative simulation script to generate data using the `rmulti-`
`nom` function. This would make it a little more clear for people


```

314 D<- e2dist(X,G)
315
316 alpha0<-parm[1]
317 alpha1<-parm[2]
318 n0<-exp(parm[3])
319 probcap<- plogis(alpha0)*exp(-alpha1*D*D)
320 Pm<-matrix(NA,nrow=nrow(probcap),ncol=ncol(probcap))
321 ymat<-rbind(y,rep(0,ncol(y)))
322
323 lik.marg<-rep(NA,nrow(ymat))
324 for(i in 1:nrow(ymat)){
325   Pm[1:length(Pm)]<- (dbinom(rep(ymat[i,],nG),K,probcap[1:length(Pm)],log=TRUE))
326   lik.cond<- exp(colSums(Pm))
327   lik.marg[i]<- sum( lik.cond*(1/nG) )
328 }
329 nv<-c(rep(1,length(lik.marg)-1),n0)
330 part1<- lgamma(nrow(y)+n0+1) - lgamma(n0+1)
331 part2<- sum(nv*log(lik.marg))
332   -1*(part1+ part2)
333 }

```

334 To execute this function for the data that we created with `simSCRO.fn`, we
335 execute the following command (saving the result in our friend `frog`). This
336 results in the usual output, including the parameter estimates, the gradient,
337 and the numerical Hessian which is useful for obtaining asymptotic standard
338 errors (see below):

```

339 > frog<-nlm(intlik2,c(-2.5,2,log(4)),hessian=TRUE,y=y,X=X,delta=.2,ssbuffer=2)
340 There were 50 or more warnings (use warnings() to see the first 50)
341 >
342 >
343 > frog
344 $minimum
345 [1] 113.5004
346
347 $estimate
348 [1] -2.538334  2.466515  4.232810
349
350 [. Additional output deleted .]

```

351 While this produces some **R** warnings, these happen to be harmless in this case,
352 and we will see from the `nlm` output that the algorithm performed satisfactory
353 in minimizing the objective function. The estimate of population size for the
354 state-space (using the default state-space buffer) is

```

355 > nrow(y)+exp(4.2328)
356 [1] 110.9099

```

Which differs from the data-generating value ($N = 100$) as we might expect. We usually will present an estimate of uncertainty associated with this MLE which we can obtain by inverting the Hessian. Note that $Var(\hat{N}) = n + Var(\hat{n}_0)$. Since we have parameterized the model in terms of $\log(n_0)$ we use a delta approximation to obtain the variance on the scale of n_0 as follows:

```
> (exp(4.2328)^2)*solve(frog$hessian)[3,3]
[1] 260.2033
> sqrt(260)
[1] 16.12452
```

1.2.1 Exercises

1. Run the analysis with different state-space buffers and comment on the result.
2. Conduct a brief simulation study using this code by simulating 100 data sets and obtain the MLEs for each data set. Do things seem to be working as you expect?
3. Further extensions: It should be straightforward to generalize the integrated likelihood function to accommodate many different situations. For examples, if we want to include more covariates in the model we can just add stuff to the object `probcap`, and add the relevant parameters to the argument that gets passed to the main function. For the simulated data, make up a covariate by generating a Bernoulli covariate (“trap type” perhaps baited or not baited) randomly and try to modify the likelihood to accommodate that.
4. We would probably be interested in devising the integrated likelihood for the full 3-d encounter history array so that we could include temporally varying covariates. This is not difficult but naturally will slow down the execution substantially. The interested reader should try to expand the capabilities of this basic **R** function.

1.2.2 Integrated Likelihood using the model under data augmentation

Note that this likelihood analysis is based on the standard likelihood in which N (or n_0) is an explicit parameter. This is usually called the “joint likelihood” or “unconditional likelihood”. We could also express the joint likelihood using data augmentation, replacing the parameter N with ψ (e.g., Royle and Dorazio, 2008, chapt. xyz). We don’t go into detail here, but we do note that the likelihood under data augmentation is a zero-inflated binomial mixture precisely as an occupancy type model (Royle, 2006). The interested reader could adapt the material from Royle and Dorazio (2008) with the **R** code given above for the likelihood and implement the likelihood analysis based on the model under data augmentation. While we can carryout likelihood analysis of models under data augmentation, we primarily advocate data augmentation for Bayesian analysis.

1.2.3 Extensions

There are other types of covariates of interest: behavioral response, sex-specificity of parameters and all of these things. Some of these can be added directly to the likelihood if the covariate is fixed and known for all individuals captured or not. This excludes most covariates but it does include behavioral response. Sex-specificity is more difficult since sex is not known for uncaptured individuals. Trap-specific covariates such as trap type or status, or time-specific covariates such as date, are relatively easy to deal with (we leave these as exercises). We apply these various models in Chapter XXXX. To analyze such models, we do Bayesian analysis of the joint likelihood facilitated by the use of data augmentation. For covariates that are not fixed and known for all individuals, it is hard to do MLE for these based on the joint likelihood as we have developed above. Instead what people normally do is use what is colloquially referred to as the “Huggins-Alho” type model which is one of the approaches taken in the software package `secr` (Efford XYZ; see chapter XYZ).

1.3 Classical model selection and assessment

In most analyses, one is interested in choosing from among various potential models. A good thing about classical analysis based on likelihood is we can do rote application of AIC without thinking about anything. With distance as a covariate (e.g., distance sampling) this is usually applied to some arbitrary selection of distance functions. We don't recommend this. Given there is hardly ever (if at all) a rational science-based reason for choosing some particular distance function we believe that this standard approach will invariably lead to over-fitting. The fact that AIC is easy to compute does not mean that it should be abused in such fashions. Further discussion is made in chapters XYZ.

Goodness-of-fit In many analyses based on likelihood methods it is possible to cook-up fit statistics for which asymptotic distributions are known. In general, however, applied statisticians tend to adopt bootstrapping based on heuristically appealing fit statistics. An omnibus global GoF statistic is not so obvious but we can apply bootstrapping principles to SCR models directly which we discuss in chapter XYZ. Bayesian goodness-of-fit is almost always addressed with Bayesian p-values or some other posterior predictive check (REF XXX). Thus the approach whether Bayesian or classical is the same. We identify a fit statistic, we do a bootstrap (classical) or a Bayesian p-value. Royle et al. (2011) decomposed the fit problem into separate evaluations of the CSR hypothesis and the encounter process model. We discuss all of this in Chapter XYZ.

434 1.4 Likelihood analysis of the wolverine camera 435 trapping data

436 Here we compute the MLEs for the wolverine data using an expanded version
437 of the function we developed in the previous section. To accommodate that
438 each trap might be operational a variable number of nights, we provided an
439 additional argument to the likelihood function (allowing for a vector K), which
440 requires also a modification to the construction of the likelihood (see Online
441 Supplement). In addition, we had to accommodate that the state-space is a
442 general rectangle, and we included a line in the code to compute the state-space
443 area which we apply below for computing density. The more general function
444 (intlik3) is given in the online supplement (shall we provide it here?).

445 The data were read into our R session and manipulated using the following
446 commands. Note that we use the utility R function SCR23darray.fn which we
447 defined in section XYZ.XYZ.

```
448 > wcaps<-source("wcaps.R")$value
449 > wtraps<-source("wtraps.R")$value
450 > K.wolv<-apply(wtraps[,4:ncol(wtraps)],1,sum)
451 >
452 > xx<-SCR23darray.fn(wcaps,ntraps=37,nperiods=165)
453 > y.wolv<- apply(xx,c(1,3),sum)
454 > traplocs.wolv<-wtraps[,2:3]
455 > traplocs.wolv<-traplocs.wolv/10000
456 >
457 > nlm(lik,c(-1.5,1.2,log(4)),hessian=TRUE,y=y.wolv,K=K.wolv,X=traplocs.wolv,
458 delta=.1,ssbuffer=2)$estimate
459
460 [1] -1.646692  3.128712  3.761974
461
```

462 We obtained the MLEs for a state-space buffer of 2 (standardized units) and
463 for integration grid with spacing $\delta = .3, .2, .1, .05$. The MLES for these 4
464 cases are as follows:

```
465
466 > nlm(intlik3,c(-1.5,1.2,log(4)),hessian=TRUE,y=y.wolv,K=K.wolv, X=traplocs.wolv,delta=
467
468 [1] -1.654535  3.108126  3.723244
469
470 > nlm(lik,c(-1.5,1.2,log(4)),hessian=TRUE,,delta=.2,ssbuffer=2)$estimate
471
472 [1] -1.643023  3.133985  3.749195
473
474 > nlm(lik,c(-1.5,1.2,log(4)),hessian=TRUE,,delta=.1,ssbuffer=2)$estimate
475
```

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```

476 [1] -1.646692  3.128712  3.761974
477
478 > nlm(lik,c(-1.5,1.2,log(4)),hessian=TRUE,,delta=.05,ssbuffer=2)$estimate
479
480 [1] -1.647191  3.128308  3.769455
481

```

482 We see the results change only slightly as the fineness of the integration grid
 483 increases. Conversely, the runtime on the platform of the day for the 4 cases was
 484 approximately 19s, 40s, 169s, and 723s which as we have suggested before could
 485 probably be regarded as relative to each other, across platforms, for gaging the
 486 decrease in speed as the fineness of the integration grid increases.

487 Next we studied the effect of the state-space buffer on the MLEs, using a fixed
 488 $\text{delta}=.1$ for all analyses. We used state-space buffers of 1 to 4 units stepped by
 489 .5. This produced the following results, given here are the state-space buffer,
 490 area of the state-space, the MLE of N for the prescribed state-space and the
 491 corresponding MLE of density:

```

492
493 ### REDO ANALYSES
494
495      ssbuff      Ass      Nhat      Dhat
496 [1,]      1.0 66.98212 42.18630 0.6298144
497 [2,]      1.5 84.36242 52.12473 0.6178667
498 [3,]      2.0 103.74272 64.03329 0.6172317
499 [4,]      2.5 125.12302 77.36792 0.6183348
500 [5,]      3.0 148.50332 91.99139 0.6194568
501 [6,]      3.5 173.88362 107.87487 0.6203855
502 [7,]      4.0 201.26392 125.01359 0.6211426
503

```

504 The estimates of D stabilize rapidly² and the results suggest that wolverine
 505 density is around 0.62 individuals per 100 square km (recall that a unit is 10 x
 506 10 km). This is about 6.2 individuals per thousand square km which compares
 507 with XYZ reported in Royle et al. (2011) based on a clipped state-space as
 508 described in section XYZ.

509 In a later chapter analysis by MLE is done with an irregular state-space.
 510 Therefore we will have to extend the R function again to accept as possible
 511 input a pre-defined state-space grid.

512 1.4.1 Exercises

- 513 1. Compute the 95% confidence interval for wolverine density, somehow.
- 514 2. Compute the AIC of this model and modify `intlik3` to consider alternative
- 515 link functions (at least one additional) and compare the AIC of the different
- 516 models and the estimates. Comment. [should we do that here?].

²not very convincing

517 1.5 Program DENSITY and the R package secr

518 DENSITY is a software program developed by Efford et al. (2004) for fitting
 519 spatial capture-recapture models based mostly on classical maximum likelihood
 520 estimation and related inference methods. Efford (2011) has also released an
 521 R package named secr, that contains many of the functions within DENSITY
 522 but also incorporates new models and features. Here, we will focus on secr as
 523 it will continue to be developed, contains more functionality and is based in R.
 524 To install and run models in secr, you must download the package and load it in
 525 R.

```
526 >install.packages(secr)
527 >library(secr)
```

528 SECR allows the user to simulate data and fit a suite of models with various
 529 detection functions and covariate responses. SECR uses the standard R model
 530 specification framework using tildes. E.g., the model command is secr.fit and is
 531 generally written as

```
532 >secr.fit(capturedata, model = list(D~1, g0~1, sigma~1), buffer = 20000)
```

533 where we have `g0 1` indicating the intercept model. To include covariates,
 534 this would be written as `g0 b` where `b` is a behavioral covariate. Possible pre-
 535 dictors for detection probability include both pre-defined variables (e.g., `t` and
 536 `b` corresponding to time and behavior), and user-defined covariates of several
 537 kinds. The discussion of covariates is developed in chapter XX(8).

538 Before we can fit the models, the data must first be entered into SECR. Two
 539 input files are required: trap layout (location and identification information for
 540 each trap) and capture data (e.g., sampling session, animal identification, trap
 541 day, and trap location). SECR requires that you specify the trap type, the
 542 two most common for camera trapping/hair snares are proximity detectors and
 543 count detectors. The ‘proximity’ detector type allows, at most, one detection
 544 of each individual at a particular detector on any occasion. The count detector
 545 designation allows repeat encounters of each individual at a particular detector
 546 on any occasion. There are other detector types that one can select such as:
 547 ‘polygon’ detector type which allows for a trap to be a sampled polygon, e.g.,
 548 scat surveys, and ‘signal’ detector which allows for traps that have a strength
 549 indicator, e.g., acoustic arrays. The detector types `single` and `multi` can be
 550 confusing as `multi` seems like it would appropriate for something like a camera
 551 trap, but instead these two designations refer to traps that retain individuals,
 552 thus precluding the ability for animals to be captured in other traps during
 553 the sampling occasion. The `single` type indicates trap that can only catch one
 554 animal at a time, while `multi` indicates traps that may catch more than one
 555 animal at a time. For a full review of the detector types, one should look at the
 556 help manual, which can be accessed in R after installing the SECR package by
 557 using the command:

```
558 >RShowDoc("secr-manual", package = "secr")
```

As with all of the `scr` models, SECR fits a detection function relating the probability of detection to the distance of a detector from an individual activity center. SECR allows the user to specify one of a variety of detection functions including the commonly used half-normal, hazard rate, and exponential. There are 12 different functions, but some are only available for simulating data, and one should take caution when using different detection functions as the interpretation of the parameters, such as `sigma`, may not be consistent across formulations. The different detection functions are defined in the `secr` manual and can be found by calling the help function for the detection function:

```
> ?detectfn
```

It is useful to note that `secr` requires the buffer distance to be defined in meters and density will be returned as number of animals per hectare. Thus to make comparisons between `secr` and other models, we will often have to convert the density to the same units. Also, note that `sigma` is returned in units of meters.

3

1.5.1 Analysis using `secr` package

To demonstrate the use of the `secr` package, we will show how to do the same analysis on the wolverine study as shown in section 4.6. To use the `secr` package, the data need to be formatted in a similar but slightly different manner than we use in WinBUGS. After installing the `secr` package, we first have to read in the trap locations and other related information, such as if the trap is operational during a sampling occasion. The `secr` package reads in the trap data through a command called `read.traps`, which requires the detector type as input. The detector type is important because it will determine the likelihood that `secr` will use to fit the model. Here, we have selected proximity since individuals are captured at most once in each trap during each sampling occasion.

```
>traps= read.csv(wtraps.csv)
>colnames(traps)[1:3]<- c("trapID","x", "y") #name the first 3 columns
# to match the secr nomenclature

>trapfile <- read.traps(data = traps, detector = "proximity")
```

After reading in the data, we now need to create the encounter matrix or array. The `secr` package does this through the use of the `make.caphist` command, where we provide the capture histories in raw data format (each line contains the session, identification number, occasion, and trap id for only 1 individual). This is the format that was shown in the data input file `wcaps`, and we only need a line or two to organize the data into the order that the `make.caphist`

³One question: SECR only ever reports `sigma`. What exactly is `sigma`? It is a scale parameter of a detection function and all detection functions have a scale parameter. But in what sense is this `sigma` parameter related to home range diameter? Efford doesn't explain this, does he? In some sections in chapter 4 or possibly 6 we get into this issue.

command wants. In creating the capture history, we provide also the trapfile with the trap information, and the format (e.g., here `fmt= trapID`) so that `secr` knows how to match the encounters to the trap, and finally, we provide the number of occasions.

```

600 >wolv.dat <- wcaps[,c(2, 3, 1)] #NEED TO UPDATE THIS WHEN I GET THE FILES, I JUST GU
601 >wolv.dat <- cbind(rep(1, dim(wolv.dat)[1]), wolv.dat)
602 >colnames(wolv.dat) <- c("Session", "ID", "Occasion", "trapID")
603
604 >wolvcapt=make.caphist(wolv.dat, trapfile, fmt = "trapID", noccasions = 165)

```

Calling the `secr.fit` command, will run the model. We are using the basic model (SCR0), so we do not need to make any specifications in the command line except for the providing the buffer size (in m). To specify different models, you can change the default `D 1`, `g0 1`, `sigma 1`, which the interested reader can do with very little difficulty.

```

610 > wolv.secr=secr.fit(wolvcapt, model = list(D~1, g0~1, sigma~1), buffer = 20000)
611
612 >wolv.secr
613
614 secr.fit( caphist = wolvcapt, buffer = 20000, binomN = 1 )
615 secr 2.0.0, 18:26:39 05 Jul 2011
616
617 Detector type      proximity
618 Detector number    37
619 Average spacing    4415.693 m
620 x-range            593498 652294 m
621 y-range            6296796 6361803 m
622 N animals          : 21
623 N detections        : 115
624 N occasions         : 165
625 Mask area          : 1037069 ha
626
627 Model              : D~1 g0~1 sigma~1
628 Fixed (real)        : none
629 Detection fn         : halfnormal
630 Distribution         : poisson
631 N parameters         : 3
632 Log likelihood      : -746.754
633 AIC                  : 1499.508
634 AICc                 : 1500.920
635
636 Beta parameters (coefficients)
637      beta    SE.beta      lcl      ucl
638 D      -9.749576 0.23027860 -10.200913 -9.298238
639 g0     -4.275736 0.15846104  -4.586313 -3.965158

```



```

640 sigma 8.699202 0.07868944 8.544973 8.853430
641
642 Variance-covariance matrix of beta parameters
643           D           g0          sigma
644 D      0.053028233 0.000546922 -0.005226926
645 g0      0.000546922 0.025109900 -0.005885213
646 sigma -0.005226926 -0.005885213 0.006192027
647
648 Fitted (real) parameters evaluated at base levels of covariates
649           link      estimate SE.estimate          lcl          ucl
650 D      log 5.831941e-05 1.360973e-05 3.713638e-05 9.158548e-05
651 g0     logit 1.371121e-02 2.142902e-03 1.008756e-02 1.861207e-02
652 sigma  log 5.998124e+03 4.727205e+02 5.140849e+03 6.998355e+03

```

Under the fitted (real) parameters, we find D, the density, given in units of individuals/hectare (1 hectare = 100 m²). To convert this into individuals/1000km², we multiply by 100000, thus our density estimate is 5.83 individuals/1000 km². Sigma is given in units of meters, to convert to kilometers, we divide by 1000, which puts sigma at 5.99 km. Both of these estimates are very similar to those provided in section 4.6 for the buffer size equal to 20 km. As an exercise, run this analysis for 30 and 40 km buffers and compare those found in section 4.6 under WinBUGS. NOTE: The secr.fit will return a warning when the buffer size appears to be too small. This is useful particularly with the different units being used between programs and packages.

1.6 Summary and Outlook

In this chapter, we showed that classical analysis of SCR models based on likelihood methods is a relatively simple proposition. Analysis is based on the so-called integrated likelihood in which the individual activity centers (random effects) are removed from the conditional-on-s likelihood by integration. We showed how to construct the integrated likelihood and fit some simple models in the R programming language. In addition, likelihood analysis for some broad classes of SCR models can be accomplished in the software package DENSITY (and other packages such as ADMB) or in the equivalent R library secr which we provided an illustration of here. In later chapters we provide more detailed analyses of SCR data using the secr package.

To compute the integrated likelihood we have to precisely describe the state-space of the underlying point process. In practice, this leads to a buffer around the trap array. We note that this is not really a buffer strip in the sense of Wilson et al. (XYZ) which is a feature of the analysis but it is somewhat more general here. In particular, it establishes the support of the integrand which we generally require to compute any integral. It might be that the integrand itself is finite even if the support is infinity but that may or may not be the case depending on the choice of detection function. As a practical matter then,

it will typically be the case that, while estimates of N increase with the size of the buffer, estimates of density stabilize. This is not a feature of the classical methods based on using model M_0 or model M_h and buffering the trap array.

Why or why not use likelihood inference exclusively? For certain specific models, it is probably more computationally efficient to produce MLEs. However, WinBUGS is extremely flexible in terms of describing models, although it sometimes can be quite slow. We can devise models in WinBUGS easily that we cannot fit in secr. E.g., random individual effects of various types (see next chapter), we can handle missing covariates in complete generality and seamlessly, and impose arbitrary distributions on random variables. Moreover, models can easily be adapted to include auxiliary data types. For example, we might have camera trapping and genetic data and we can describe the models directly in WinBUGS and fit a joint model. For the MLE we have to write a custom new piece of code for each model or hope someone has done it for us. Later we consider open population models which are straightforward to develop in WinBUGS but, so far, there is no available platform for doing MLE although we imagine one could develop this. . Another thing that is more conceptual here is non-CSR point processes (see chapter XYZ) and generating predictions of how many individuals have home range centers in any particular polygon. Basic benefits of Bayesian analysis have been discussed elsewhere (Chapter 2? BPA book? Link and Barker?) and we believe these are compelling. On the other hand, likelihood analysis makes it easy to do model-selection by AIC. Goodness-of-fit is probably no more difficult or easy under either paradigm (see next chapter?).

In summary, basic SCR models are easy to implement by either likelihood or Bayesian methods but we feel that the typical user will realize much more flexibility in model development using existing platforms for Bayesian analysis. While these tend to be slow (sometimes excruciatingly slow), this will probably not be an impediment in most problems, especially at some near point in the future. Since we spent a lot of time here talking about specific technical details on how to implement likelihood analysis of SCR models, we provided a corresponding treatment in the next chapter on how to devise MCMC algorithms for SCR models. This is a bit more tedious and requires more coding, but is not technically challenging (except perhaps to develop highly efficient algorithms which we don't excel at).

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