

Chapter 1

Likelihood Analysis of SCR Models

X

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

30 camera trapping study (Magoun et al., 2011) we analyzed in previous chapters
 31 to compare/contrast the results.

32 1.1 Likelihood analysis

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

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

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

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

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

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

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

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

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

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

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

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

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

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

66 The key operation for computing the likelihood is solving a 2-dimensional in-
 67 tegration problem. There are some general purpose **R** packages that implement
 68 a number of multi-dimensional integration routines including **adapt** (REF) and
 69 **Rcuba** (REF XYZ). In practice, we wont rely on these extraneous **R** packages
 70 but instead will use perhaps less efficient methods in which we replace the inte-
 71 gral with a summation over an equal area mesh of points on the state-space \mathcal{S}
 72 and explicitly evaluate the integrand at each point. Let $u = 1, 2, \dots, nG$ index
 73 a grid of nG points where the area of grid cell u is $a(u) \equiv a$ (for a regular grid).
 74 In this case, the trapezoidal rule for approximating the integral yields

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

75 This is a general expression that could be used for approximating the integral
 76 for any arbitrary bivariate distribution $g(u)$. In the present context note that
 77 $g(u) = (1/area(\mathcal{S})) = 1/[nG * a]$ and thus the grid-cell area cancels in the above
 78 expression and we have

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

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

83 1.1.1 Implementation (simulated data)

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

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

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

```

96 traplocs<-data$traplocs
97 nind<-nrow(y)
98 X<-data$traplocs
99 J<-nrow(X)
100 K<-data$K
101 y<-rbind(y,matrix(0,nrow=(100-nrow(y)),ncol=J ) )
102 Xl<-data$xlim[1]
103 Yl<-data$ylim[1]
104 Xu<-data$xlim[2]
105 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):

```

108 delta<- .2
109 xg<-seq(Xl+delta/2,Xu-delta/2,by=delta)
110 yg<-seq(Yl+delta/2,Yu-delta/2,by=delta)
111 npix<-length(xg) # assumes xg and yg same dimension here
112 area<- (Xu-Xl)*(Yu-Yl)/((npix)*(npix)) # dont need area for anything
113 G<-cbind(rep(xg,npix),sort(rep(yg,npix)))
114 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:

```

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

```

```

140 G<-cbind(rep(xg,npix),sort(rep(yg,npix)))
141 nG<-nrow(G)
142 D<- e2dist(X,G)
143
144 alpha0<-parm[1]
145 alpha1<-parm[2]
146 probcap<- plogis(alpha0-alpha1*D)
147 Pm<-matrix(NA,nrow=nrow(probcap),ncol=ncol(probcap))
148           # all zero encounter histories
149 n0<-sum(apply(y,1,sum)==0)
150           # encounter histories with at least 1 detection
151 ymat<-y[apply(y,1,sum)>0,]
152 ymat<-rbind(ymat,rep(0,ncol(ymat)))
153 lik.marg<-rep(NA,nrow(ymat))
154 for(i in 1:nrow(ymat)){
155   Pm[1:length(Pm)]<- (dbinom(rep(ymat[i,],nG),K,probcap[1:length(Pm)],log=TRUE))
156   lik.cond<- exp(colSums(Pm))
157   lik.marg[i]<- sum( lik.cond*(1/nG))
158 }
159 nv<-c(rep(1,length(lik.marg)-1),n0)
160 -1*( sum(nv*log(lik.marg)) )
161 }

```

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 (n_0). 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 data set provided in the Online Supplement):

```

184
185 # should take 15-30 seconds

```

```

186 > starting.values <- c(a0=-2, a1=1) # just to make things clear
187 > frog<-nlm(intlik1,starting.values,y=y,delta=.1,X=traplocs,ssbuffer=2,hessian=TRUE)
188
189 Warning message:
190 In nlm(intlik1, c(-2, 1), y = y, delta = 0.1, X = traplocs, ssbuffer = 2, :
191   NA/Inf replaced by maximum positive value
192
193 > frog
194 $minimum
195 [1] 182.6882
196
197 $estimate
198 [1] -2.623456  1.658335
199
200 $gradient
201 [1] -1.867945e-06  1.587044e-06
202
203 $hessian
204           [,1]      [,2]
205 [1,]  69.16351 -72.13976
206 [2,] -72.13976 108.22528
207
208 $code
209 [1] 1
210
211 $iterations
212 [1] 12

```

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

```

218 solve(frog$hessian)

```

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

233 To compute the integrated likelihood we used a discrete representation of
 234 the state-space so that the integral could be approximated as a summation
 235 over possible values of \mathbf{s} with each value being weighted by its probability of
 236 occurring, which is $1/nG$ under the assumption that \mathbf{s} is uniform on the state-
 237 space S . In chapter 4 we used a discrete state-space in developing a Bayesian
 238 analysis of the model in order to be able to modify the state-space in a flexible
 239 manner. Bayesian analysis requires simulation of the point process conditional
 240 on the observations, and this can be a difficult task when the state-space is
 241 continuous but has irregular geometry. Conversely, if the state-space is a regular
 242 polygon then Bayesian analysis by MCMC is possibly more efficient with a
 243 continuous state-space. We emphasize that the state-space is a part of the
 244 model. In some cases there wont be a natural choice of state space beyond some
 245 large rectangle containing the trap grid and, in such cases, for regular detection
 246 functions the estimate of density is invariant to the size of the state-space (i.e.,
 247 the buffer) as long as it is sufficiently large. However if there are good reasons
 248 to restrict the state-space, it will tend to have an influence on the likelihood
 249 and hence AIC and so forth. As an illustration, lets do that by changing the
 250 state space here Use my polygon clipping stuff.

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

266 1.2 MLE when N is Unknown

267 Here we build on the previous introduction to integrated likelihood but we
 268 consider now the case in which N is unknown. We will see that adapting the
 269 analysis based on the N -known model is really straightforward for the more
 270 general problem. The main distinction is that we dont observe the all-zero
 271 encounter history so we have to make sure we compute the probability for that
 272 encounter history which we do by tacking a row of zeros onto the encounter
 273 history matrix. In addition, we include the number of such all-zero encounter
 274 histories as an unknown parameter of the model. Call that unknown quantity
 275 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 N choose 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 (we have already done that in the previous likelihood construction even though we didnt need it).

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

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

```

287  simSCR0.fn( blah blah blah)
288
289  > y<-read.csv("ind_by_trap.csv")[, -1]
290  > y<-as.matrix(y)
291  >
292  > X<-read.csv("traplocs.csv")[, -1]
293  > X<-as.matrix(X)
294  >
295

```

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

```

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

```

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


```

317 nG<-nrow(G)
318 D<- e2dist(X,G)
319
320 alpha0<-parm[1]
321 alpha1<-parm[2]
322 n0<-exp(parm[3])
323 probcap<- plogis(alpha0-alpha1*D)
324 Pm<-matrix(NA,nrow=nrow(probcap),ncol=ncol(probcap))
325 ymat<-rbind(y,rep(0,ncol(y)))
326
327 lik.marg<-rep(NA,nrow(ymat))
328 for(i in 1:nrow(ymat)){
329   Pm[1:length(Pm)]<- (dbinom(rep(ymat[i,],nG),K,probcap[1:length(Pm)],log=TRUE))
330   lik.cond<- exp(t(Pm)%*%rep(1,nrow(probcap)))
331   lik.marg[i]<- sum( lik.cond*(1/nG) )
332 }
333 nv<-c(rep(1,length(lik.marg)-1),n0)
334 part1<- lgamma(nrow(y)+n0+1) - lgamma(n0+1)
335 part2<- sum(nv*log(lik.marg))
336   -1*(part1+ part2)
337 }

```

338 To execute this function for the data that we just read into the workspace,
 339 we execute the following command (saving the result in our friend **frog**).

```

340 > frog<-nlm(intlik2,c(-2.5,2,log(4)),hessian=TRUE,y=y,X=traplocs,delta=.2,ssbuffer=2)

```

341 This results in the usual output, including the parameter estimates, the
 342 gradient, and the numerical Hessian which is useful for obtaining asymptotic
 343 standard errors (omitted here).

```

344 > frog
345 $minimum
346 [1] 181.4657
347
348 $estimate
349 [1] -2.629342  1.790849  3.997268
350
351 [. Additional output deleted .]

```

352 The estimate of population size for the state-space (using the default state-
 353 space buffer) is

```

354 > nrow(y)+exp(3.997)
355 [1] 113.4346

```

356 Which differs from the data-generating truth (N=100) as we might expect.

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 probcap there, and add the relevant parameters to the argument that gets passed to the intlik 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 $n0$) 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 . See Royle et al. (2007); Royle and Dorazio (2008, distance sampling example), etc.. Briefly, we note that the likelihood under data augmentation looks like a zero-inflated binomial mixture precisely as an occupancy type model (see Royle 2006). We think 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. Despite that we can carry-out likelihood analysis of models under data augmentation, we primarily advocate data augmentation for Bayesian analysis.

1.2.3 Extensions and Classical model selection and assessment

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). .

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.

1.3 Likelihood analysis of the wolverine camera trapping data

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

The data were read into our R session and manipulated using the following commands. Note that we use the utility R function SCR2darray.fn which we defined in section XYZ.XYZ.

```
> wcaps<-source("wcaps.R")$value
```

```

440 > wtraps<-source("wtraps.R")$value
441 > K.wolv<-apply(wtraps[,4:ncol(wtraps)],1,sum)
442 >
443 > xx<-SCR23darray.fn(wcaps,ntraps=37,nperiods=165)
444 > y.wolv<- apply(xx,c(1,3),sum)
445 > traplocs.wolv<-wtraps[,2:3]
446 > traplocs.wolv<-traplocs.wolv/10000
447 >
448 > nlm(lik,c(-1.5,1.2,log(4)),hessian=TRUE,y=y.wolv,K=K.wolv,X=traplocs.wolv,
449 delta=.1,ssbuffer=2)$estimate
450
451 [1] -1.646692  3.128712  3.761974
452

```

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

```

456
457 > nlm(intlik3,c(-1.5,1.2,log(4)),hessian=TRUE,y=y.wolv,K=K.wolv, X=traplocs.wolv,delta=
458
459 [1] -1.654535  3.108126  3.723244
460
461 > nlm(lik,c(-1.5,1.2,log(4)),hessian=TRUE,,delta=.2,ssbuffer=2)$estimate
462
463 [1] -1.643023  3.133985  3.749195
464
465 > nlm(lik,c(-1.5,1.2,log(4)),hessian=TRUE,,delta=.1,ssbuffer=2)$estimate
466
467 [1] -1.646692  3.128712  3.761974
468
469 > nlm(lik,c(-1.5,1.2,log(4)),hessian=TRUE,,delta=.05,ssbuffer=2)$estimate
470
471 [1] -1.647191  3.128308  3.769455
472

```

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

478 Next we studied the effect of the state-space buffer on the MLEs, using a fixed
 479 $\delta=.1$ for all analyses. We used state-space buffers of 1 to 4 units stepped by
 480 .5. This produced the following results, given here are the state-space buffer,
 481 area of the state-space, the MLE of N for the prescribed state-space and the
 482 corresponding MLE of density:

```

483
484 ### REDO ANALYSES
485
486      ssbuff      Ass      Nhat      Dhat
487 [1,]      1.0 66.98212 42.18630 0.6298144
488 [2,]      1.5 84.36242 52.12473 0.6178667
489 [3,]      2.0 103.74272 64.03329 0.6172317
490 [4,]      2.5 125.12302 77.36792 0.6183348
491 [5,]      3.0 148.50332 91.99139 0.6194568
492 [6,]      3.5 173.88362 107.87487 0.6203855
493 [7,]      4.0 201.26392 125.01359 0.6211426
494

```

495 The estimates of D stabilize rapidly² and the results suggest that wolverine
496 density is around 0.62 individuals per 100 square km (recall that a unit is 10 x
497 10 km). This is about 6.2 individuals per thousand square km which compares
498 with XYZ reported in Royle et al. (2011) based on a clipped state-space as
499 described in section XYZ.

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

503 1.3.1 Exercises

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

508 1.4 Program DENSITY and the R package secr

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

```

517 >install.packages(secr)
518 >library(secr)

```

²not very convincing

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

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

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

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

```
>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

1.4.1 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 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.

```
>wolv.dat <- wcaps[,c(2, 3, 1)] #NEED TO UPDATE THIS WHEN I GET THE FILES, I JUST GUESSED AT TH
>wolv.dat <- cbind(rep(1, dim(wolv.dat)[1], wolv.dat)
>colnames(wolv.dat) <- c("Session", "ID", "Occasion", "trapID")
>wolvcapt=make.caphist(wolv.dat, trapfile, fmt = "trapID", nooccasions = 165)
```

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 doesnt explain this, does he? In some sections in chapter 4 or possibly 6 we get into this issue.

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

```
601 > wolv.secr=secr.fit(wolvcapt, model = list(D~1, g0~1, sigma~1), buffer = 20000)
602
603 >wolv.secr
604
605 secr.fit( capthist = wolvcapt, buffer = 20000, binomN = 1 )
606 secr 2.0.0, 18:26:39 05 Jul 2011
607
608 Detector type      proximity
609 Detector number    37
610 Average spacing    4415.693 m
611 x-range            593498 652294 m
612 y-range            6296796 6361803 m
613 N animals          : 21
614 N detections        : 115
615 N occasions         : 165
616 Mask area          : 1037069 ha
617
618 Model              : D~1 g0~1 sigma~1
619 Fixed (real)        : none
620 Detection fn        : halfnormal
621 Distribution         : poisson
622 N parameters        : 3
623 Log likelihood      : -746.754
624 AIC                 : 1499.508
625 AICc                : 1500.920
626
627 Beta parameters (coefficients)
628           beta      SE.beta      lcl      ucl
629 D      -9.749576 0.23027860 -10.200913 -9.298238
630 g0      -4.275736 0.15846104  -4.586313 -3.965158
631 sigma   8.699202 0.07868944   8.544973  8.853430
632
633 Variance-covariance matrix of beta parameters
634           D           g0          sigma
635 D      0.053028233 0.000546922 -0.005226926
636 g0      0.000546922 0.025109900 -0.005885213
637 sigma -0.005226926 -0.005885213 0.006192027
638
639 Fitted (real) parameters evaluated at base levels of covariates
640           link      estimate SE.estimate      lcl      ucl
```



```

641 D      log 5.831941e-05 1.360973e-05 3.713638e-05 9.158548e-05
642 g0     logit 1.371121e-02 2.142902e-03 1.008756e-02 1.861207e-02
643 sigma  log 5.998124e+03 4.727205e+02 5.140849e+03 6.998355e+03

```

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

654 1.5 Summary and Outlook

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

665 To compute the integrated likelihood we have to precisely describe the state-
666 space of the underlying point process. In practice, this leads to a buffer around
667 the trap array. We note that this is not really a buffer strip in the sense of
668 Wilson et al. (XYZ) which is a feature of the analysis but it is somewhat more
669 general here. In particular, it establishes the support of the integrand which
670 we generally require to compute any integral. It might be that the integrand
671 itself is finite even if the support is infinity but that may or may not be the
672 case depending on the choice of detection function. As a practical matter then,
673 it will typically be the case that, while estimates of N increase with the size of
674 the buffer, estimates of density stabilize. This is not a feature of the classical
675 methods based on using model M0 or model Mh and buffering the trap array.

676 Why or why not use likelihood inference exclusively? For certain specific
677 models, it is probably more computationally efficient to produce MLEs. How-
678 ever, WinBUGS is extremely flexible in terms of describing models, although
679 it sometimes can be quite slow. We can devise models in WinBUGS easily
680 that we cannot fit in secr. E.g., random individual effects of various types
681 (see next chapter), we can handle missing covariates in complete generality and
682 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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