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LIKELIHOOD ANALYSIS OF SPATIAL CAPTURE-RECAPTURE MODELS

We have so far mainly focused 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 BUGS engines including **WinBUGS** and **JAGS**. Despite our focus on Bayesian analysis, it is instructive to develop the basic concepts and ideas behind classical analysis based on likelihood methods and frequentist inference for SCR models. This has been the approach taken by Borchers and Efford (2008); Dawson and Efford (2009) and related papers. Therefore, in this chapter, we provide some conceptual and technical foundation for likelihood-based analysis of spatial capture-recapture models. We recognized earlier (Chapt. 4) that SCR models are versions of binomial (or other) GLMs, but with random effects, i.e., GLMMs. These models 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 2-dimensional coordinate, $\mathbf{s}$, is a bivariate random effect. Beyond that, there is little difference between likelihood analysis of SCR models and ordinary GLMMs.

We will show here that it is straightforward to compute the maximum likelihood estimates (MLE) for SCR models by integrated or marginal likelihood. We develop the MLE framework using **R**, and we also provide a basic introduction to an **R** package `secr` (Efford, 2011) which mostly does likelihood analysis of SCR models (see also the the stand-alone package **DENSITY** (Efford et al., 2004)). To set the context for likelihood analysis of SCR models, we first 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 obtain the MLEs for the SCR model from the wolverine camera trapping study (Magoun et al., 2011) analyzed in previous chapters to compare/contrast the results.

6.1 MLE WITH KNOWN N

We noted in Chapt. 4 that, with N known, the basic SCR model is a type of binomial regression with a random effect. For such models we can obtain maximum likelihood estimators of model parameters based on integrated likelihood. The integrated likelihood is based on the marginal distribution of the data y in which the random effects are removed by integration from the conditional-on-$\mathbf{s}$ distribution of the observations. See Chapt. **??** for a review of marginal, conditional and joint distributions. Conceptually, any SCR model begins with a specification of the conditional-on-$\mathbf{s}$ model $[y|\mathbf{s}, \boldsymbol{\alpha}]$ and we have a "prior distribution" for $\mathbf{s}$, say $[\mathbf{s}]$. Then, the marginal distribution of the data y is

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

When viewed as a function of $\boldsymbol{\alpha}$ for purposes of estimation, the marginal distribution $[y|\boldsymbol{\alpha}]$ is often referred to as the *integrated likelihood*.

It is worth analyzing the simplest SCR model with known-N in order to understand the underlying mechanics and basic concepts. These are directly relevant to the manner in which many capture-recapture models are classically analyzed, such as model M_h, and individual covariate models (see Chapt. 3).

To develop the integrated likelihood for SCR models, we first identify the conditional-on-$\mathbf{s}$ likelhiood. The observation model for each encounter observation y_{ij}, specified conditional on $\mathbf{s}_i$, is

$$y_{ij}|\mathbf{s}_i \sim \text{Binomial}(K, p_\alpha(\mathbf{x}_j, \mathbf{s}_i)) \tag{6.1.1}$$

where we have indicated the dependence of p_{ij} on $\mathbf{s}$ and parameters $\boldsymbol{\alpha}$ explicitly. For example, p_{ij} might be the Gaussian model given by

$$p_{ij} = \text{logit}^{-1}(\alpha_0) \exp(\alpha_1 ||\mathbf{x}_j - \mathbf{s}_i||)$$

where $\alpha_1 = -1/(2\sigma^2)$. The joint distribution of the data for individual i is the product of J such terms (i.e., contributions from each of J traps).

$$[\mathbf{y}_i|\mathbf{s}_i, \boldsymbol{\alpha}] = \prod_{j=1}^{J} \text{Binomial}(K, p_\alpha(\mathbf{x}_j, \mathbf{s}_i))$$

We note this assumes that encounter of individual i in each trap is independent of encounter in every other trap, conditional on $\mathbf{s}_i$, this is the fundamental property of the basic model SCR0.

The marginal likelihood is computed by removing $\mathbf{s}_i$, by integration (hence also *integrated* likelihood), from the conditional-on-$\mathbf{s}$ likelihood and regarding the *marginal* distribution of the data as the likelihood. That is, we compute:

$$[y|\boldsymbol{\alpha}] = \int_{\mathcal{S}} [\mathbf{y}_i|\mathbf{s}_i, \boldsymbol{\alpha}][\mathbf{s}_i] d\mathbf{s}_i$$

In most SCR models, $[\mathbf{s}] = 1/A(\mathcal{S})$ where $A(\mathcal{S})$ is the area of the prescribed state-space $\mathcal{S}$ (but see Chapt. **??** for alternative specifications of $[\mathbf{s}]$).

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

$$\mathcal{L}(\boldsymbol{\alpha}|\mathbf{y}_1, \mathbf{y}_2, \ldots, \mathbf{y}_N) = \prod_{i=1}^{N} [\mathbf{y}_i|\boldsymbol{\alpha}]$$

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" (i.e., this is model SCR0, from Chapt. 4).

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` (Genz et al., 2007) and `R2cuba` (Hahn et al., 2010). In practice, we won't rely on these extraneous **R** packages (except see Chapt. **??** for an application of `R2cuba`) 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. We invoke the rectangular rule for integration here[1] in which we evaluate the integrand on a regular grid of points of equal area and compute the average of the integrand over that grid of points. Let $u = 1, 2, \ldots, nG$ index a grid of nG points, $\mathbf{s}_u$, where the area of grid cells is constant, say A. In this case, the integrand, i.e., the marginal pmf of $\mathbf{y}_i$, is approximated by

$$[\mathbf{y}_i|\boldsymbol{\alpha}] = \frac{1}{nG} \sum_{u=1}^{nG} [\mathbf{y}_i|\mathbf{s}_u, \boldsymbol{\alpha}] \tag{6.1.2}$$

This is a specific case of the general expression that could be used for approximating the integral for any arbitrary distribution $[\mathbf{s}]$. The general case is

$$[y|\boldsymbol{\alpha}] = \frac{A(\mathcal{S})}{nG} \sum_{u=1}^{nG} [y|\mathbf{s}_u, \boldsymbol{\alpha}][\mathbf{s}_u]$$

[1] e.g., `http://en.wikipedia.org/wiki/Rectangle_method`

Under the uniformity assumption, $[\mathbf{s}] = 1/A(\mathcal{S})$ and thus the grid-cell area cancels in the above expression to yield eq. 6.1.2. The rectangular rule for integration can be seen as an application of the Law of Total Probability for a discrete random variable $\mathbf{s}$, having nG unique values with equal probabilities $1/nG$.

6.1.1 Implementation (simulated data)

Here we will illustrate how to carryout this integration and optimization based on the integrated likelihood using simulated data (i.e., see sec. **??**). Using `simSCR0` we simulate data for 100 individuals and a 25 trap array laid out in a 5×5 grid of unit spacing. The specific encounter model is the Gaussian 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:

```
  ## simulate a complete data set (perfect detection)
data<-simSCR0(discard0=FALSE,rnd=2013)
  ## extract the objects that we need for analysis
y<-data$Y
traplocs<-data$traplocs
nind<-nrow(y)  ## in this case nind=N
J<-nrow(traplocs)
K<-data$K
xlim<-data$xlim
ylim<-data$ylim
```

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):

```
delta<- .2
xg<-seq(xlim[1]+delta/2,xlim[2]-delta/2,by=delta)
yg<-seq(ylim[1]+delta/2,ylim[2]-delta/2,by=delta)
npix<-length(xg)          # valid for square state-space only
G<-cbind(rep(xg,npix),sort(rep(yg,npix)))
nG<-nrow(G)
```

In this case, the integration grid is set up as a grid with spacing $\delta = 0.2$ which produces, for our example, a 40×40 grid of points for evaluating the integrand if the state-space buffer is set at 2. We note that the integration grid is set-up here to correspond exactly to the state-space used in simulating the data. However, in practice, we wouldn't know this, and our estimate of N (for the unknown case, see below) would be sensitive to choice of the extent of the integration grid. As we've discussed previously, density, which is N standardized by the area of the state-space, will not be so sensitive in most cases.

We are now ready to compute the conditional-on-$\mathbf{s}$ likelihood and carry-out the marginalization described by Eq. 6.1.2. We need to do this by defining an **R**

function that computes the likelihood for the integration grid, as a function of the data objects `y` and `X` which were created above. However, it is a bit untidy to store the grid information in your workspace, and define the likelihood function in a way that depends on these things that exist in your workspace. Therefore, we build the **R** function so that it computes the integration grid *within* the function, thereby avoiding potential problems if our trapping grid locations change, or if we want to modify the state-space buffer easily. We therefore define the function, called `intlik1`, to which we pass the data objects and other information necessary to compute the marginal likelihood. This function is available in the `scrbook` package (use `?intlik1` at the **R** prompt). The code is reproduced here:

```
intlik1<-function(parm,y=y,delta=.2,X=traplocs,ssbuffer=2){

Xl<-min(X[,1]) - ssbuffer   ## these lines of code are setting up the
Xu<-max(X[,1]) + ssbuffer   ## support for the integration which is
Yu<-max(X[,2]) + ssbuffer   ## the same as the state-space of "s"
Yl<-min(X[,2]) - ssbuffer
xg<-seq(Xl+delta/2,Xu-delta/2,,length=npix)
yg<-seq(Yl+delta/2,Yu-delta/2,,length=npix)
npix<-length(xg)

G<-cbind(rep(xg,npix),sort(rep(yg,npix)))
nG<-nrow(G)
D<- e2dist(X,G)

alpha0<-parm[1]
alpha1<-exp(parm[2])  # alpha1 restricted to be positive here
                      # for convenience (it is negated below)
probcap<- plogis(alpha0)*exp(-alpha1*D*D)
Pm<-matrix(NA,nrow=nrow(probcap),ncol=ncol(probcap))
                    # all zero encounter histories
n0<-sum(apply(y,1,sum)==0)
                    # encounter histories with at least 1 detection
ymat<-y[apply(y,1,sum)>0,]
ymat<-rbind(ymat,rep(0,ncol(ymat)))
lik.marg<-rep(NA,nrow(ymat))
for(i in 1:nrow(ymat)){
 ## next line: log conditional likelihood for ALL possible values of s
Pm[1:length(Pm)]<- (dbinom(rep(ymat[i,],nG),K,probcap[1:length(Pm)],log=TRUE))
 ## next line: sum the log conditional likelihoods, exp() result
 ## same as taking the product
lik.cond<- exp(colSums(Pm))
 ## take the average value == computing marginal
lik.marg[i]<- sum( lik.cond*(1/nG))
}
 ## n0 = number of all-0 encounter histories
```

```
nv<-c(rep(1,length(lik.marg)-1),n0)
-1*( sum(nv*log(lik.marg)) )
}
```

The function `intlik1` 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. 6.1.1 above). The marginal likelihood (`lik.marg`) sums up the conditional elements weighted by the probabilities [**s**] (Eq. 6.1.2 above). This is a fairly primitive function which doesn't allow much flexibility in the data structure. For example, it assumes that K, the number of replicates, is constant for each trap. Further, it assumes that the state-space is a square. We generalize this to some extent later in this chapter.

Here is the **R** command for maximizing the likelihood using `nlm` (the function `optim` could also be used) 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:

```
# should take 15-30 seconds

starts<-c(-2,2)
frog<-nlm(intlik1,starts,y=y,delta=.1,X=traplocs,ssbuffer=2,hessian=TRUE)
frog

$minimum
[1] 297.1896

$estimate
[1] -2.504824  2.373343

$gradient
[1] -2.069654e-05  1.968754e-05

$hessian
          [,1]      [,2]
[1,]  48.67898 -19.25750
```

```
[2,] -19.25750  13.34114

$code
[1] 1

$iterations
[1] 11
```

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

```
> solve(frog$hessian)
```

It is worth drawing attention to the fact that the estimates are slightly different than the Bayesian estimates reported previously in sec. **??**. There are several reasons for this. First Bayesian inference is based on the posterior distribution and it is not generally the case that the MLE should correspond to any particular value of the posterior distribution. If the prior distributions in a Bayesian analysis are uniform, then the (multivariate) mode of the posterior is the MLE, but note that Bayesians almost always report posterior *means* and so there will typically be a discrepancy there. Secondly, we have implemented an approximation to the integral here and there might be a slight bit of error induced by that. We will evaluate that shortly. Third, the Bayesian analysis by MCMC is itself subject to some amount of Monte Carlo error which the analyst should always be aware of in practical situations. All of these different explanations are likely responsible for some of the discrepancy. Accounting for these, we see general consistency between the two estimates.

In summary, 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 applying it for different values of N in attempt to deduce the best value. We will formalize the unknown-N problem next.

6.2 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 known-N model is straightforward for the more general problem. The main distinction is that we don't 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 (that is, the number of individuals *not* encountered) as an unknown parameter of the model. Call that unknown quantity n_0. Then, $N = n_0 + n$. We will usually parameterize the likelihood in terms of n_0 because optimization over a parameter space in which $\log(n_0)$ is unconstrained is preferred to a parameter space in which N must be constrained $N \geq n$. With n_0 unknown, 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. In evaluating the *log*-likelihood, we have to compute terms such as the log-factorial $\log(N!) = log((n_0 + n)!)$. We do this in **R** by making use of the log-gamma function (`lgamma`) and the identity

$$\log(N!) = \texttt{lgamma}(N + 1).$$

Therefore, to compute the likelihood, we require the following 3 components: (1) the marginal probability of each $\mathbf{y}_i$ as before,

$$[\mathbf{y}_i|\boldsymbol{\alpha}] = \int_{\mathcal{S}} [\mathbf{y}_i|\mathbf{s}_i, \boldsymbol{\alpha}][\mathbf{s}_i] d\mathbf{s}_i.$$

(2) We compute the probability of an all-0 encounter history:

$$\pi_0 = [\mathbf{y} = \mathbf{0}|\boldsymbol{\alpha}] = \int_{\mathcal{S}} \text{Binomial}(\mathbf{0}|\mathbf{s}_i, \boldsymbol{\alpha})[\mathbf{s}_i] d\mathbf{s}_i$$

(3) The combinatorial term: $\binom{N}{n}$. Then, the marginal likelihood has this form:

$$\mathcal{L}(\boldsymbol{\alpha}, n_0|\mathbf{y}) = \frac{N!}{n! n_0!} \left\{ \prod_{i=1}^{n} [\mathbf{y}_i|\boldsymbol{\alpha}] \right\} (\pi_0)^{n_0}. \tag{6.2.1}$$

This is discussed in Borchers and Efford (2008, p. 379) as the conditional-on-N form of the likelihood – we might also call it the "binomial form" because of its appearance.

Operationally, things proceed much as before: We compute the marginal probability of each observed $\mathbf{y}_i$, i.e., by removing the latent $\mathbf{s}_i$ by integration. In addition, we compute the marginal probability of the "all-zero" encounter history $\mathbf{y}_{n+1}$, and make sure to weight it n_0 times. We accomplish this by "padding" the data set with a single encounter history having $y_{n+1,j} = 0$ for all traps $j = 1, 2, \ldots, J$. Then we be sure to include the combinatorial term in the likelihood or log-likelihood computation. We demonstrate this shortly. To analyze a specific case, we'll read in our fake data set (simulated using the parameters given above). To set some things up in our workspace we do this:

```
data<-simSCR0(discard0=TRUE,rnd=2013)  # obtain a simulated data set
  ## extract the items we need for analysis
y<-data$Y
nind<-nrow(y)
traplocs<-data$traplocs
J<-nrow(traplocs)
K<-data$K
```

Recall that these data were generated with $N = 100$, on an 8×8 unit state-space representing the trap locations buffered by 2 units.

As before, the likelihood is defined in the **R** workspace as an **R** function, `intlik2`, which takes an argument being the unknown parameters of the model and additional arguments as prescribed. In particular, we provide the encounter history matrix **y**, the trap locations `traplocs`, the spacing of the integration grid (argument `delta`) and the state-space buffer. Here is the new likelihood function:

```
intlik2<-function(parm,y=y,delta=.3,X=traplocs,ssbuffer=2){

Xl<-min(X[,1]) -ssbuffer
Xu<-max(X[,1])+ ssbuffer
Yu<-max(X[,2])+ ssbuffer
Yl<-min(X[,2])- ssbuffer

xg<-seq(Xl+delta/2,Xu-delta/2,delta)
yg<-seq(Yl+delta/2,Yu-delta/2,delta)
npix.x<-length(xg)
npix.y<-length(yg)
area<- (Xu-Xl)*(Yu-Yl)/((npix.x)*(npix.y))
G<-cbind(rep(xg,npix.y),sort(rep(yg,npix.x)))
nG<-nrow(G)
D<- e2dist(X,G)
    # extract the parameters from the input vector
alpha0<-parm[1]
alpha1<-exp(parm[2])
n0<-exp(parm[3])  # note parm[3] lives on the real line
probcap<- plogis(alpha0)*exp(-alpha1*D*D)
Pm<-matrix(NA,nrow=nrow(probcap),ncol=ncol(probcap))
ymat<-rbind(y,rep(0,ncol(y)))

lik.marg<-rep(NA,nrow(ymat))
for(i in 1:nrow(ymat)){
Pm[1:length(Pm)]<- (dbinom(rep(ymat[i,],nG),K,probcap[1:length(Pm)],log=TRUE))
lik.cond<- exp(colSums(Pm))
lik.marg[i]<- sum( lik.cond*(1/nG) )
}
nv<-c(rep(1,length(lik.marg)-1),n0)
 ## part1 here is the combinatorial term.
```

```
 ## math: log(factorial(N)) = lgamma(N+1)
part1<- lgamma(nrow(y)+n0+1) - lgamma(n0+1)
part2<- sum(nv*log(lik.marg))
 -1*(part1+ part2)
}
```

To execute this function for the data that we created with `simSCR0`, we execute the following command (saving the result in our friend `frog`). This results in the usual output, including the parameter estimates, the gradient, and the numerical Hessian which is useful for obtaining asymptotic standard errors (see below):

```
> starts<-c(-2.5,0,4)
> frog<-nlm(intlik2,starts,hessian=TRUE,y=y,X=traplocs,delta=.2,ssbuffer=2)

Warning message:
In nlm(intlik2, starts, hessian = TRUE, y = y, X = traplocs, delta = 0.2,  :
  NA/Inf replaced by maximum positive value

> frog
$minimum
[1] 113.5004

$estimate
[1] -2.538333  0.902807  4.232810

[... additional output deleted ...]
```

While usually produces one or more **R** warnings due to numerical calculations happening on extremely small or large numbers (calculation of p near the edge of the state-space), and they also happen if a poor parameterization is used which produces evaluations of the objective function beyond the boundary of the parameter space (e.g., $n_0 < 0$). You will see from the `nlm` output that can be reproduced that the algorithm performed satisfactory in minimizing the objective function. The estimate of population size for the state-space (using the default state-space buffer) is

```
nrow(y)+exp(4.2328)
[1] 110.9099
```

Which differs from the data-generating value ($N = 100$) as we might expect for a single realization. We usually will present an estimate of uncertainty associated with this MLE which we can obtain by inverting the Hessian. Note that $\text{Var}(\hat{N}) = n + \text{Var}(\hat{n}_0)$. Since we have parameterized the model in terms of $\log(n_0)$ we use the delta method[2] (Williams et al., 2002, Appendix F4) to obtain the variance on the

[2] We found a good set of notes on the delta approximation on Dr. David Patterson's ST549 notes: `http://www.math.umt.edu/patterson/549/Delta.pdf`

scale of n_0 as follows:

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

Therefore, the asymptotic "Wald-type" confidence interval for N is $110.91 \pm 1.96 \times 16.125 = (79.305, 142.515)$. To report this in terms of density, we scale appropriately by the area of the prescribed state-space which is 64 units of area (i.e., an 8×8 square).

6.2.1 Integrated Likelihood using the model under data augmentation

The likelihood analysis developed in the previous sections is based on the likelihood in which N (or n_0) is an explicit parameter. This is usually called the "full likelihood" or sometimes "unconditional likelihood" (Borchers et al., 2002) because it is the likelihood for all individuals in the population, not just those which have been captured, i.e., not that which is *conditional on capture*. It is also possible to express an alternative unconditional likelihood using data augmentation, replacing the parameter N with ψ (e.g., see Sec. 7.1.6 Royle and Dorazio, 2008, for an example). We don't go into detail here, but we note that the likelihood under data augmentation is a zero-inflated binomial mixture – precisely an occupancy type model (Royle, 2006). Thus, while it is possible to carryout likelihood analysis of models under data augmentation, we primarily advocate data augmentation for Bayesian analysis.

6.2.2 Extensions

We have only considered basic SCR models with no additional covariates. However, in practice, we are interested in other types of covariate effects including "behavioral response", sex-specificity of parameters, and potentially other effects. Some of these can be added directly to the likelihood if the covariate is fixed and known for all individuals captured or not. An example is a behavioral response, which amounts to having a covariate $x_{ik} = 1$ if individual i was captured prior to occasion k and $x_{ik} = 0$ otherwise. For uncaptured individuals, $x_{ik} = 0$ for all k. Royle et al. (2011) called this a global behavioral response because the covariate is defined for all traps, no matter the trap in which an individual was captured. We could also define a *local* behavioral response which occurs at the level of the trap, i.e., $x_{ijk} = 1$ if individual i was captured in trap j prior to occasion k, etc.. Trap-specific covariates such as trap type or status, or time-specific covariates such as date, are easily accommodated as well. As an example, Kéry et al. (2010) develop a model for the European wildcat *Felis silvestris* in which traps are either baited or not (a trap-specific covariate with only 2 values), and also encounter probability

varies over time in the form of a quadratic seasonal response. We consider models with behavioral response or fixed covariates in Chapt. 9. The integrated likelihood routines we provided above can be modified directly for such cases, which we leave to the interested reader to investigate.

Sex-specificity is more difficult to deal with since sex is not known for uncaptured individuals (and sometimes not even for all captured individuals). To analyze such models, we do Bayesian analysis of the joint likelihood using data augmentation (Gardner et al., 2010; Russell et al., 2012), discussed further in Chapt. 9. For such covariates (i.e., that are not fixed and known for all individuals), it is somewhat more challenging to do MLE for these based on the joint likelihood as we have developed above. Instead it is more conventional to 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, 2011) which we describe in sec. 6.5 below. This idea is motivated by thinking about unequal probability sampling methods known as Horvitz-Thompson sampling (e.g., see Overton and Stehman, 1995).

6.3 CLASSICAL MODEL SELECTION AND ASSESSMENT

In most analyses, one is interested in choosing from among various potential models, or ranking models, or something else to do with assessing the relative merits of a set of models. A good thing about classical analysis based on likelihood is we can apply AIC methods (Burnham and Anderson, 2002) without difficulty. There are two distinct contexts for model-selection that we think are relevant to SCR models. First is, and AIC selecting among models that represent distinct biological hypotheses (e.g., covariates affecting encounter probability or density). AIC is convenient for assessing the relative merits of these different models although if there are only a few models it is not objectionable to use hypothesis tests or confidence intervals to determine importance of effects. The second model selection context has to do with choosing among various detection functions although, as a general rule, we don't recommend this application of model selection. This is because there is hardly ever (if at all) a rational subject-matter based reason motivating specific distance functions. As a result, we believe that doing too much model selection will invariably lead to over-fitting and thus over-statement of precision. This is the main reason that we haven't loaded you down with a basket of models for detection probability so far, although we discuss many possibilities in Chapt. 9.

Goodness-of-fit – For many standard capture-recapture models, it is possible to identify goodness-of-fit statistics based on the multinomial likelihood and evaluate model adequacy using formal statistical tests. Similar strategies can be applied to SCR models using expected cell-frequencies based on the marginal distribution of the observations. Also, because computing MLEs is somewhat more efficient in many cases compared to Bayesian analysis, it is also sometimes easy to use bootstrap methods although, at the present time, we don't know of any applications of

goodness-of-fit testing for SCR models based on likelihood inference[3].

6.4 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 $\mathbf{K} = (K_1, \ldots, K_J)$), which requires also a modification to the construction of the likelihood. In addition, we accommodate 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 **R** package `scrbook`. Incidentally, this function also returns the area of the state-space for a given set of parameter values, as an attribute to the function value, which will be used in converting $\hat{N}$ to $\hat{D}$. To use this function to obtain the MLEs for the wolverine camera trap study, we execute the following commands (note: these are in the help file and will execute if you type `example(intlik3)`:

```
library("scrbook")
data("wolverine")

traps<-wolverine$wtraps
traplocs<-traps[,2:3]/10000
K.wolv<-apply(traps[,4:ncol(traps)],1,sum)

y3d<-SCR23darray(wolverine$wcaps,traps)
y2d<-apply(y3d,c(1,3),sum)

starts<-c(-1.5,0,3)

frog<-nlm(intlik3,starts,hessian=TRUE,y=y2d,K=K.wolv,X=traplocs,delta=.2,ssbuffer=2)

frog
$minimum
[1] 220.4313

$estimate
[1] -2.8176120  0.2269395  3.5836875

[.... output deleted ....]
```

Of course we're interested in obtaining an estimate of population size for the prescribed state-space, or density, and associated measures of uncertainty which we do using the delta method (Williams et al., 2002, Appendix F4). To do all of that

[3]WE NEED TO LOOK INTO THIS!!

we need to manipulate the output of `nlm` since we have our estimate in terms of `log(n0)`. We execute the following commands:

```
frog<-nlm(intlik3,starts,hessian=TRUE,y=y2d,K=K.wolv,X=traplocs,delta=.2,ssbuffer=2)
Nhat<-nrow(y2d)+exp(frog$estimate[3])
area<-attr(intlik3(starts,y=y2d,K=K.wolv,X=traplocs,delta=.2,ssbuffer=2),"SSarea")
Dhat<- Nhat/area

Dhat
[1] 0.5494947

SE<- (1/area)*exp(frog$estimate[3])*sqrt(solve(frog$hessian)[3,3])

SE
[1] 0.1087073
```

So our estimate of density is 0.55 individuals per "standardized unit" which is 100 km^2, because we divided UTM coordinates by 10000. So this is about 5.5 individuals per 1000 km^2, with a SE of around 1.09 individuals. This compares closely with 5.77 reported in sec. **??** based on Bayesian analysis of the model.

To evaluate the effect of the integration grid density, we obtained the MLEs for a state-space buffer of 2 (standardized units) and for integration grid with spacing $\delta = .3, .2, .1, .05$. The MLEs for these 4 cases including the relative runtime are given in Table 6.1. We see the results change only slightly as the fineness of the integration grid increases. Conversely, the runtime on the platform of the day for the 4 cases increases rapidly. These runtimes could be regarded in relative terms, across platforms, for gaging the decrease in speed as the fineness of the integration grid increases. The effect of this is that we anticipate some numerical error in approximating the integral on a mesh of points, and that error increases as the coarseness of the mesh increases.

Table 6.1. Run time and MLEs for different integration grid resolutions for the wolverine camera trapping data.

δ		Estimates		
	runtime	$\hat{\alpha}_0$	$\hat{\alpha}_1$	$\widehat{\log(n_0)}$
0.30	9.9	-2.819786	1.258468	3.569731
0.20	32.3	-2.817610	1.254757	3.583690
0.10	115.1	-2.817570	1.255112	3.599040
0.05	407.3	-2.817559	1.255281	3.607158

We studied the effect of the state-space buffer on the MLEs, using a fixed $\delta = .2$ for all analyses. The results are show in Table 6.2. We used state-space buffers of 1 to 4 units stepped by .5. As we can see in Table 6.2, the estimates of D stabilize rapidly and the incremental difference is within the numerical error associated with approximating the integral.

Table 6.2. Results of the effect of the state-space buffer on the MLE. Given here are the state-space buffer (buff), area of the state-space (area), the MLE of N ($\hat{N}$) for the prescribed state-space and the corresponding MLE of density ($\hat{D}$).

buff	area	$\hat{N}$	$\hat{D}$
1.0	66.98212	37.73338	0.5633352
1.5	84.36242	46.21008	0.5477567
2.0	103.74272	57.00617	0.5494956
2.5	125.12302	69.03616	0.5517463
3.0	148.50332	82.17550	0.5533580
3.5	173.88362	96.44018	0.5546249
4.0	201.26392	111.83524	0.5556646

6.4.1 Using a habitat mask (Restricted state-space)

In sec. **??** we used a discrete representation of the state-space in order to have control over its extent and shape. This makes it easy to do things like clip out non-habitat, or create a *habitat mask* which defines suitable habitat. Clearly that formulation of the model is relevant to the calculation of the marginal likelihood in the sense that the discrete state-space is equivalent to the integration grid. Thus, for example, we could easily compute the MLE of parameters under some model with a restricted state-space merely by creating the required state-space at whatever grid resolution is desired, and then inputting that state-space into the likelihood function above, instead of computing it in the function itself. We can easily create an explicit state-space grid for integration from arbitrary polygons or GIS shapefiles which we demonstrate here. Our approach is to create the integration grid (or state-space grid) outside of the likelihood evaluation, and then determine which points of the grid lie in the polygon defined by the shapefile using functions in the **R** packages `sp` and `maptools` . For each point in the state-space grid (object `G` in the code below which is assumed to exist), we deterimine whether it is inside the polygon[4], identifying such points with a value of `mask=1` and `mask=0` for points that are *not* in the polygon. We load the shapefile which originates by an application of the `readShapeSpatial` function. We have saved the result into an **R** data object called `SSp` which is in the `scrbook` package. Here are the **R** commands for doing this (see the helpfile `?intlik4`):

```
library(maptools)
library(sp)
library(scrbook)
```

[4]We perform this check using the `over` function. This function takes as its second argument (among others) an object of the class "SpatialPolygons" or "SpatialPolygonsDataFrame", which can hold additional information for each polygon, and the output value of the function differs slightly for these two classes: if using a "SpatialPolygons" object, the function returns a vector of length equal to the number of points (e.g., in the example above), but if using a SpatialPolygonsDataFrame it returns a data frame (e.g., see sec. **??** in Chapt. 7). If you use the `over` function, make sure you know the class of your second argument so that when processing the function output you index it correctly.

```
data("fakeshapefile")
#### replaces this:
#####SSp<-readShapeSpatial('Sim_Polygon.shp')
Pcoord<-SpatialPoints(G)
PinPoly<-over(Pcoord,SSp)  ### determine if each point is in polygon
mask<-as.numeric(!is.na(PinPoly[,1]))  ## convert to binary 0/1
G<-G[mask==1,]
```

We created the function `intlik4` which accepts the integration grid as an explicit argument, and this function is also available in the package `scrbook`.

We apply this modification to the wolverine camera trapping study. Royle et al. (2011) created 2, 4 and 8 km state-space grids so as to remove "non-habitat" (mostly ocean, bayes, and large lakes). We previously analyzed the model using **JAGS** and **WinBUGS** in Chapt. 4. To set up the wolverine data and fit the model we execute the following commands

```
library("scrbook")
data("wolverine")

traps<-wolverine$wtraps
traplocs<-traps[,2:3]/10000
K.wolv<-apply(traps[,4:ncol(traps)],1,sum)

y3d<-SCR23darray(wolverine$wcaps,traps)
y2d<-apply(y3d,c(1,3),sum)
G<-wolverine$grid2/10000

starts<-c(-1.5,0,3)
frog<-nlm(intlik4,starts,hessian=TRUE,y=y2d,K=K.wolv,X=traplocs,G=G)

frog
$minimum
[1] 225.8355

$estimate
[1] -2.9955424  0.2350885  4.1104757

[... some output deleted ...]
```

Next we convert the parameter estimates to estimates of total population size for the prescribed state-space, and then obtain an estimate of density (per 1000 km^2) using the area computed as the number of pixels in the state-space grid `G` multiplied by the area per grid cell. In the present case (the calculation above) we used a state-space grid with 2km $\times$ 2km pixels. Finally, we compute a standard errors using the delta approximation: **XXXX Check these commands and compare with whats in the table XXXXXX**

Table 6.3. MLEs for the wolverine camera trapping data using 2, 4 and 8 km state-space grids.

grid	α_0	α_1	$log(n_0)$	N	SE	D(1000)	SE
2	-3.00	1.27	4.11	81.98	16.31	8.31	1.65
4	-2.99	1.34	4.16	84.88	16.76	8.57	1.69
8	-3.05	1.08	4.06	78.89	15.31	7.85	1.52

```
area<- nrow(G)*4
Nhat<- 21+exp(frog$estimate[3])
SE<-  exp(frog$estimate[3])*sqrt(solve(frog$hessian)[3,3])
D<- (Nhat/(nrow(G)*area))*1000
SE.D<- (SE/(nrow(G)*area))*1000
```

We did this for each the 2 km, 4 km and 8 km state-space grids which produced the estimates summarized in Tab. 6.3. These estimates compare with the 8.6 (2 km grid) and 8.2 (8 km grid) reported in Royle et al. (2011) based on a clipped state-space as described in sec. **??**.

6.5 DENSITY AND THE R PACKAGE SECR

DENSITY is a software program developed by Efford (2004) for fitting spatial capture-recapture models based mostly on classical maximum likelihood estimation and related inference methods. Efford (2011) has also released an **R** package called `secr`, that contains much of the functionality of **DENSITY** but also incorporates new models and features. Here, we briefly introduce the `secr` package which we prefer to use instead of **DENSITY** because it allows us to remain in the **R** environment for data processing and summarization.

To install and run models in `secr`, you must download the package and load it in **R**.

```
install.packages("secr")
library(secr)
```

`secr` allows the user to simulate data and fit a suite of models with various detection functions and covariate responses. It also contains a number of helpful constructor functions for creating objects of the proper class that are recognized by other `secr` functions. We provide a brief overview of the capabilities here, but the `secr` help manual can be accessed with the command:

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

We note that `secr` has many capabilities that we will not cover or do so only sparingly. We encourage you to read through the manual to get a better understanding of what the package is capable of.

The main model-fitting function in `secr` is called `secr.fit`, which makes use of the standard **R** model specification framework with tildes. As an example, the equivalent of the basic model SCR0 is fitted as follows: **XXXX need centered tildes here XXXXX**

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

where `capturedata` is the object created by `secr` containing the encounter history data and the trap information, and the model expression `g0~1` indicates the intercept-only (i.e., constant) model. 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. For example, to include a global behavioral response, this would be written as `g0~b`. The discussion of this (global versus local trap-specific behavioral response) and other covariates is developed more in Chapt. 9.

Before we can fit the models, the data must first be packaged properly for `secr`. We require data files that contain two types of information: trap layout (location and identification information for each trap), which is equivalent to our trap deployment file (TDF) described in sec. **??** and the capture data file containing sampling *session*, animal identification, trap day, and trap location, equivalent in information content to our encounter data file (EDF). Sample session can be thought of as primary period identifier in a robust design like framework – it could represent a yearly sample or multiple sample periods within a year, each of them producing data on a closed population. We discuss "multi-session" models in more detail below, in sec. 6.5.5.

There are three important constructor functions that help package-up your data for use in `secr`: `read.traps`, `make.capthist` and `read.mask`. We provide a brief description of each here, but apply them to our wolverine camera trapping data in the next section:

(1) `read.traps`: This function points to an external file *or* **R** data object containing the trap coordinates, and other information, and also requires specification of the type of encounter devices (described in the next section). A typical application of this function looks like the following, invoking the `data=` option when there is an existing **R** object containing the trap information:

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

(2) `make.capthist`: This function takes the EDF and combines it with trap information, and the number of sampling occasions. A typical application looks like this:

```
capturedata<-make.capthist(enc.data,trapfile,fmt="trapID",noccasions=165)
```

See `?make.capthist` for definition of distinct file formats. Specifying `fmt = trapID` is equivalent to our EDF format.

(3) `read.mask`: If there is a habitat mask available (as described in sec. 6.4.1), then this function will organize it so that `secr.fit` knows what to do with it. The function accepts either an external file name (see `?read.mask` for details of the structure) or a $nG \times 2$ **R** object, say `mask.coords`, containing the coordinates of the mask. A typical application looks like the following:

```
grid<-read.mask(data=mask.coords)
```

These constructor functions produce output that can then be used in the fitting of models using `secr.fit`.

6.5.1 Encounter device types and detection models

The `secr` package requires that you specify the type of encounter device. Instead of describing models by their statistical distribution (Bernoulli, Poisson, etc..), `secr` uses certain operational classifications of detector types including 'proximity', 'multi', 'single', 'polygon' and 'signal'. For camera trapping/hair snares we might consider 'proximity' detectors or 'count' detectors. The 'proximity' detector type allows, at most, one detection of each individual at a particular detector on any occasion (i.e., it is equivalent to the Bernoulli or binomial encounter process model, or model SCR0). 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 (Royle and Young, 2008) which we discuss further in Chapt. **??**, and 'signal' detector which allows for traps that have a strength indicator, e.g., acoustic arrays (Dawson and Efford, 2009). The detector types 'single' and 'multi' 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 (single-catch traps), while 'multi' indicates traps that may catch more than one animal at a time (multi-catch). These are both variations of the multinomial encounter models described in Chapt. **??**.

As with all 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 as of version 2.3.1 (see Tab. **??** in Chapt. 9), but some are only available for simulating data. 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.

Most of the detection functions available in `secr` contain some kind of a scale parameter which is usually labeled σ. The units of this parameter default to meters in the `secr` output. We caution that the meaning of this parameter depends on the specific model being used and it should not be directly compared as a measure of home-range size across models. Instead, as we noted in sec. **??** every encounter probability model implies a model of space-usage and fitted encounter models should be converted to a common currency such as "area used."

6.5.2 Analysis using the `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 sec. **??**. To use the `secr` package, the data need to be formatted in a similar but slightly different manner than we use in **WinBUGS**.

For example, in sec. **??** we introduced a standard data format for the encounter data file (EDF) and trap deployment file (TDF). The EDF shares the same format as that used by the `secr` package with 1 row for every encounter observation and 4 columns representing trap session ('Session'), individual identity ('ID'), sample occasion ('Occasion'), and trap identity ('trapID'). For a standard closed population study that takes place during a single season, the 'Session' column in our case is all 1s, to indicate a single primary sampling occasion. In addition to providing the encounter data file (EDF), we must tell `secr` information about the traps, which is formated as a matrix with column labels 'trapID', 'x' and 'y', the last two being the coordinates of each trap, with additional columns representing the operational state of each trap during each occasion (1=operational, 0=not).

We demonstrate these differences now by walking through an analysis of the wolverine camera trapping data using `secr`. To read in the trap locations and other related information, we make use of the constructor function `read.traps` which also requires that we specify the detector type. The detector type is important because it will determine the likelihood that `secr` will use to fit the model. Here, we have selected "proximity" which corresponds to the Bernoulli encounter model in which individuals are captured at most once in each trap during each sampling occasion:

```
library("secr")
library("scrbook")
data("wolverine")

traps<-as.matrix(wolverine$wtraps)
dimnames(traps)<-list(NULL,c("trapID","x","y",paste("day",1:165,sep="")))
traps1<-as.data.frame(traps[,1:3])
trapfile1<-read.traps(data=traps1,detector="proximity")
```

Here we note that trap coordinates are extracted from the wolverine data but we do *not* standardize them. This is because `secr` defaults to coordinate scaling of meters which is the extant scaling of the wolverine trap coordinates. Note that

we add a 'trapID' column to the trap coordinates and provide appropriate column labels to the 'traps' matrix. An important aspect of the wolverine study is that while the camera traps were operated over a 165 day period, each trap was operational during only a portion of that period. We need to provide the trap operation information which is contained in the columns to the right of the trap coordinates in our standard trap deployment file (TDF). Unfortunately, this is less easy to do in `secr`, which requires an external file with a single long string of 1's and 0's indicating the days in which each trap was operational (1) or not (0). The `read.traps` function will not allow for this information on trap operation if the data exists as an **R** object – instead, we can create this external file and then read it back in with `read.traps` using these commands:

```
hold<-rep(NA,nrow(traps))
for(i in 1:nrow(traps)){
hold[i]<-paste(traps[i,4:ncol(traps)],collapse="")
}
traps1<- cbind(traps[,1:3],"usage"=hold)

write.table(traps1, "traps.txt", row.names=FALSE, col.names=FALSE)
trapfile2<-read.traps("traps.txt",detector="proximity")
```

These operations can be accomplished using the function `scr2secr` which is provided in the **R** package `scrbook`.

After reading in the trap data, we now need to create the encounter matrix or array using the `make.capthist` command, where we provide the capture histories in EDF format, which is the existing format of the data input file `wcaps`. In creating the capture history, we provide also the trapfile created previously, the format (e.g., here EDF format is `fmt= ''trapID''`), and finally, we provide the number of occasions. We also set up a habitat mask using the 2×2 km grid which we used previously in the analysis of the wolverine data and then pass the relevant objects to `secr.fit` as follows:

```
#
# grab the encounter data file and format it:
#
wolv.dat<-wolverine$wcaps
dimnames(wolv.dat)<-list(NULL,c("Session","ID","Occasion","trapID"))
wolv.dat<-as.data.frame(wolv.dat)
wolvcapt2<-make.capthist(wolv.dat,trapfile2,fmt="trapID",noccasions=165)

# grab the habitat mask (2 x 2 km) and format it:
#
gr2<-(as.matrix(wolverine$grid2))
dimnames(gr2)<-list(NULL,c("x","y"))

# To fit the model we use secr.fit:
```

```
#
wolv.secr2<-secr.fit(wolvcapt2,model=list(D~1, g0~1, sigma~1), buffer=20000,mask=gr2)
```

We are using the basic "proximity detector" model (SCR0), so we do not need to make any specifications in the command line because we have specified the detector type using the constructor function `read.traps`, except to provide 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. We provide all of these commands and additional analyses in the `scrbook` package with the function called `secr_wolverine`. Printing the output object produces the following (slightly edited):

```
wolv.secr2

secr 2.3.1, 15:52:45 29 Aug 2012

Detector type     proximity
Detector number   37
Average spacing   4415.693 m
x-range           593498 652294 m
y-range           6296796 6361803 m
N animals       :  21
N detections    :  115
N occasions     :  165
Mask area       :  987828.1 ha

Model           :  D~1 g0~1 sigma~1
Fixed (real)    :  none
Detection fn    :  halfnormal
Distribution    :  poisson
N parameters    :  3
Log likelihood  :  -602.9207
AIC             :  1211.841
AICc            :  1213.253

Beta parameters (coefficients)
           beta    SE.beta       lcl       ucl
D     -9.390124 0.22636698 -9.833795 -8.946452
g0    -2.995611 0.16891982 -3.326688 -2.664535
sigma  8.745547 0.07664648  8.595323  8.895772

Variance-covariance matrix of beta parameters
                   D            g0        sigma
D      0.0512420110 -0.0004113326 -0.003945371
g0    -0.0004113326  0.0285339045 -0.006269477
sigma -0.0039453711 -0.0062694767  0.005874683
```

```
Fitted (real) parameters evaluated at base levels of covariates
       link     estimate  SE.estimate          lcl          ucl
D       log 8.354513e-05 1.915674e-05 5.360894e-05 1.301982e-04
g0    logit 4.762453e-02 7.661601e-03 3.466689e-02 6.509881e-02
sigma   log 6.282651e+03 4.822512e+02 5.406315e+03 7.301037e+03
```

The object returned by `secr.fit` provides extensive default output when printed. Much of this is basic descriptive information about the model, the traps, or the encounter data. We focus here on the parameter estimates. Under the fitted (real) parameters, we find D, the density, given in units of individuals/hectare (1 hectare = 10000 m^2). To convert this into individuals/1000 km^2, we multiply by 100000, thus our density estimate is 8.35 individuals/1000 km^2. The parameter σ is given in units of meters, and so this corresponds to 6.283 km. Both of these estimates are very similar to those obtained in our likelihood analysis summarized in Tab. **??** which, for the 2×2 km grid, we obtained $\hat{D} = 8.31$ with a SE of $100000 \times 1.915674e-05 = 1.9156$ and, accounting for the scale difference (1 unit = 10000 m in the previous analysis), $\hat{\sigma} = \sqrt{1/(2\hat{\alpha}_1)} * 10000 = 6.289$ km. The difference in the MLE between Tab. **??** and those produced by `secr` are likely due to subtle differences in internal tuning of optimization algorithms, starting values or other numerical settings. In addition, see the next section. On the other hand, the SE is slightly larger based on `secr` which is due to a subtle difference in the interpretation of D under the `secr` model (See below).

6.5.3 Likelihood Analysis in the `secr` Package

The `secr` package does likelihood analysis of SCR models for most classes of models as developed by Borchers and Efford (2008). Their formulation deviates slightly from the binomial form we presented in sec. 6.2 above (though Borchers and Efford (2008) mention the binomial form). Specifically, the likelihood that `secr` implements is that based on removing N from the likelihood by integrating the binomial likelihood (Eq. 6.2.1 above) over a Poisson prior for N – what we will call the *Poisson-integrated likelihood* as opposed to the conditional-on-N (*binomial-form*) considered previously.

To develop the Poisson-integrated likelihood we compute the marginal probability of each $\mathbf{y}_i$ and the probability of an all-0 encounter history, π_0, as before, to arrive at the marginal likelihood in the binomial-form:

$$\mathcal{L}(\boldsymbol{\alpha}, n_0|\mathbf{y}) = \frac{N!}{n!n_0!}\left\{\prod_i [\mathbf{y}_i|\boldsymbol{\alpha}]\right\}\pi_0^{n_0}$$

Now, what Borchers and Efford (2008) do is assume that $N \sim \text{Poisson}(\Lambda)$ and they

do a further level of marginalization over this prior distribution:

$$\sum_{n_0=0}^{\infty} \frac{N!}{n!n_0!} \left\{ \prod_i [\mathbf{y}_i|\boldsymbol{\alpha}] \right\} \pi_0^{n_0} \frac{\exp(-\Lambda)\Lambda^N}{N!}$$

Carrying-out the summation above produces exactly this marginal likelihood:

$$\mathcal{L}_2(\boldsymbol{\alpha}, \Lambda|\mathbf{y}) = \left\{ \prod_i [\mathbf{y}_i|\boldsymbol{\alpha}] \right\} \Lambda^n \exp(-\Lambda\pi_0)$$

which is Eq. 2 of Borchers and Efford (2008) except for notational differences. It also resembles the binomial-form of the likelihood in Eq. 6.2.1 except with $\Lambda^n \exp(-\Lambda\pi_0)$ replacing the combinatorial term and the $\pi_0^{n_0}$ term. We emphasize there are two marginalizations going on here: (1) the integration to remove the latent variables $\mathbf{s}$; and, (2) summation to remove the parameter N. We provide a function for computing this in the `scrbook` package called `intlik3Poisson`. The help file for that function shows how to conduct a small simulation study to compare the MLE under the Poisson-integrated likelihood with that from the binomial form.

The essential distinction between our MLE and Borchers and Efford as implemented in `secr` is whether you keep N in the model or remove it by integration over a Poisson prior. If you have prescribed a state-space explicitly with a sufficiently larger buffer, then we imagine there should be hardly any difference at all between the MLEs obtained by either the Poisson-integrated likelihood or the binomial-form of the likelihood which retains N. There is a subtle distinction in the sense that under the binomial form, we estimate the realized population size N for the state-space whereas, for the Poisson-integrated form we estimate the *prior* expected value which would apply to a hypothetical new study of a similar population.

Both models (likelihoods) assume $\mathbf{s}$ is uniformly distributed over space, but for the binomial model we make no additional assumption about N whereas we assume N is Poisson using the formulation in `secr` from (Borchers and Efford, 2008). Using data augmentation we could do a similar kind of integration but integrate N over a binomial (M, ψ) prior – which we referred to as the binomial-integrated likelihood in sec. **??**. So obviously the two approaches (data augmentation and Poisson-integrated likelihood) are approximately the same as M gets large. However, doing a Bayesian analysis by MCMC, we obtain an estimate of both N, the *realized population size*, and the parameter controlling its expected value ψ which are, in fact, both identifiable from the data even using likelihood analysis (Royle et al., 2007). That said we can integrate N out completely and just estimate ψ as we noted in sec. 6.2.1 above. And we could make a prediction for a new study which would be based on the posterior distribution of $M\psi$ which, we imagine, should have slightly larger uncertainty associated with it.

6.5.4 Other stuff secr does

secr has a function called `region.N` for estimating the realized value of N and not its expectation.

We can also model covariates on density, allowing that the activity centers $\mathbf{s}$ are a realization of an inhomogeneous point process. We cover such models in Chapt. 10.

mapping, and other things???

6.5.5 Multi-Session Models in `secr`

In practice we will often deal with SCR data that have some meaningful stratification or group structure. For example, we might conduct mist-netting of birds on K consecutive days, repeated, say, T times during a year, or perhaps over T years. Or we might collect data from R distinct trapping grids. In these cases, we have T or R groups which we might reasonably regard as being samples of indepdent populations. While the groups might be distinct sites, year, or periods within years, they could also be other biological groups such as sex or age. Conveniently, `secr` fits a specific model for stratified populations – referred to as *multi-session* models. These models build on the Poisson assumption which underlies the integrated likelihood used in `secr` (as described in the previous section). To understand the technical framework, let N_g be the population size of group g and *assume*

$$N_g \sim \text{Poisson}(\Lambda_g).$$

Naturally, we model group-specific covariates on Λ_g:

$$\log(\Lambda_g) = \beta_0 + \beta_1 z_g$$

where z_g is some group-specific covariate such as a categorical index to the group, or a trend variable, or a spatial covariate, such as treatment effect or habitat structure, if the groups represent spatial units. Under this model, we can marginalize *all* N_g parameters out of the likelihood to concentrate the likelihood on the parameters β_0 and β_1 precisely as discussed in the previous section. This Poisson hierarchical model is the basis of the multi-session models in `secr`.

To implement a multi-session model (or stratified population model) in `secr`, we provide the relevant stratification information in the 'Session' variable of the input encounter data file (EDF). If 'Session' has multiple values then a "multi-session" object is created by default and session-specific variables can be described in the model. For example, if the session has 2 values for males and females then we have sex-specific densities , and baseline encounter probability p_0 (named g_0 in `secr`) by just doing this: **XXXXX need centered tildes here XXXXX**

```
out<-secr.fit(wolvcapt,model=list(D~session, g0~session, sigma~1), buffer=20000)
```

More detailed analysis is given in sec. **??** where we fit a number of different models and apply methods of model selection to obtain model-averaged estimates of density.

We can also easily implement stratified population models in the various **BUGS** engines using data augmentation (Converse and Royle, 2012, 2013) which we address, with examples, in Chapt. **??**.

6.6 SUMMARY AND OUTLOOK

In this chapter, we discussed basic concepts related to classical analysis of SCR models based on likelihood methods. Analysis is based on the so-called integrated or marginal 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 using the **R** library `secr` (Efford, 2011) which we provided a brief introduction to. In later chapters we provide more detailed analyses of SCR data using likelihood methods and the `secr` package.

Why or why not use likelihood inference exclusively? For certain specific models, it is probably more computationally efficient to produce MLEs (for an example see Chapt. **??**). However, **BUGS** is extremely flexible in terms of describing models, although it sometimes can be quite inefficient. We can devise models in the **BUGS** language easily that we cannot fit in `secr`. E.g., random individual effects of various types (Chapt. 9), 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 **BUGS** 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, although you should be able to do this with the tools we have provided here. Later we consider open population models which are straightforward to develop in **BUGS** but, so far, there is no available platform for doing MLE of such models, although we imagine one could develop this. On the other hand, likelihood analysis makes it easy to do model-selection by AIC and in some cases compute standard errors or carry-out goodness-of-fit evaluations.

7

MCMC DETAILS

8

GOODNESS OF FIT AND STUFF

9

COVARIATE MODELS

10

INHOMOGENEOUS POINT PROCESS

11

OPEN MODELS

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