MT5751 Tutorials

David Borchers, Stephen Buckland, Eric Rexstad

January 19, 2017

Chapter 1

Distance Sampling

1. Show that if $n \sim \text{Binomial}(N, \pi_c)$, then

$$\widehat{Var}[\hat{N}] = \frac{n(1-\pi_c)}{\pi_c^2}$$

is an unbiased estimator of $Var[\hat{N}]$, where $\hat{N} = n/\pi_c$.

Solution: We have $Var[\hat{N}] = Var[n/\pi_c] = Var[n]/\pi_c^2 = N\pi_c(1-\pi_c)/\pi_c^2 = N(1-\pi_c)/\pi_c$.

$$\begin{aligned} E\left[\frac{n(1-\pi_c)}{\pi_c^2}\right] &= \frac{E[n](1-\pi_c)}{\pi_c^2} \\ &= \frac{N\pi_c(1-\pi_c)}{\pi_c^2} \\ &= \frac{N(1-\pi_c)}{\pi_c} \end{aligned}$$

and since this is $Var[\hat{N}]$, the estimator is unbiased.

2. As noted in class, it is usually not possible to get maximum likelihood estimators (MLEs) in closed form (i.e. get equations with the MLE on the left and a function of the data that we can evaluate on the right). A line transect survey with a half-normal detection function ($p(x) = \exp(-x^2/(2\sigma^2))$) and without any distance truncation (i.e. $w \to \infty$) is an exception.

(a) **Derive the MLE of σ^2:** On the above minke whale survey $n = 90$ detections at perpendicular distances $x_1, \ldots, x_{90}$ were made. Assuming that the detection function has a half-normal form, and using no perpendicular distance truncation, show that the maximum likelihood estimator of the half normal detection function scale parameter σ^2, from the **conditional likelihood** (given n) is

$$\widehat{\sigma^2} = \frac{\sum_{i=1}^n x_i^2}{n}$$

Hint: From the definition of a normal pdf, you can show that the effective strip half-width μ is

$$\mu = \int_0^\infty e^{-\frac{x^2}{2\sigma^2}}\,dx = \sqrt{\frac{\pi}{2}\sigma^2}.$$

Solution: The conditional likelihood (given n) is

$$\begin{aligned} L(\sigma^2) &= \prod_{i=1}^{n} \frac{\exp\left(-\frac{x_i^2}{2\sigma^2}\right)}{\int_0^\infty \exp\left(-\frac{x_i^2}{2\sigma^2}\right) dx} \\ &= \exp\left(-\frac{1}{2\sigma^2}\sum_{i=1}^{n} x_i^2\right)\left(\frac{\pi}{2}\sigma^2\right)^{-n/2} \end{aligned}$$

So the log-likelihood is

$$l(\sigma^2) = -\frac{1}{2\sigma^2}\sum_{i=1}^{n} x_i^2 - \frac{n}{2}\log(\sigma^2) + C \tag{1.1}$$

where C does not involve σ^2. Differentiating with respect to σ^2 and equating to zero gives

$$\begin{aligned} \frac{\sum_{i=1}^{n} x_i^2}{\sigma^2} &= n \\ \Rightarrow \widehat{\sigma^2} &= \frac{\sum_{i=1}^{n} x_i^2}{n} \end{aligned}$$

(b) **Calculate the MLE of σ^2:** Use the data in the object `minke` (see computing exercise below), to calculate the MLE of σ^2 for the minke whale survey, assuming that there was no perpendicular distance truncation. (You may find it useful to know that you can get rid of `NA`s when doing calculations in `R` by using the command `na.omit`. For example, `na.omit(c(1,NA,2)` returns `c(1,2)`.)

Solution:

```
> x=na.omit(minke$distance)
> sigma2.hat=sum(x^2)/length(x)
> sigma2.hat
[1] 0.4706733
```

(c) **Derive the full likelihood MLE of D and σ^2 under a Poisson model**: Assume that the number of whales detected (n) has a Poisson distribution with rate parameter Da, where D is density, $a = 2L\mu$ is the *effective area* surveyed, L is the total transect line length and μ the effective strip half-width. Assuming that there was no perpendicular distance truncation (as in the question above), do the following:

(i) Show that the log-likelihood function $l(D, \sigma^2)$ is

$$l(D,\sigma^2) = n\ln(D) - D\sqrt{2L^2\pi}\sqrt{\sigma^2} - \frac{\sum x_i^2}{2\sigma^2} + C$$

where C is some constant that does not involve D or σ^2.

Solution: The effective area of the survey is $a = 2\mu L = \sqrt{2L^2\pi\sigma^2}$ and hence the likelihood function is

$$L(D,\sigma^2) = \frac{\left(D\sqrt{2L^2\pi\sigma^2}\right)^n \exp\left(-D\sqrt{2L^2\pi\sigma^2}\right)}{n!} \exp\left(-\frac{1}{2\sigma^2}\sum_{i=1}^{n} x_i^2\right)\left(\frac{\pi}{2}\sigma^2\right)^{-n/2}$$

So the log-likelihood function is

$$\begin{aligned} l(D,\sigma^2) &= n\log(D) + \frac{n}{2}\log(\sigma^2) - D\sqrt{L^2 2\pi}\sqrt{\sigma^2} - \frac{\sum_{i=1}^{n} x_i^2}{2\sigma^2} - \frac{n}{2}\log(\sigma^2) + C \\ &= n\log(D) - D\sqrt{L^2 2\pi}\sqrt{\sigma^2} - \frac{\sum_{i=1}^{n} x_i^2}{2\sigma^2} + C \end{aligned}$$

(ii) By differentiating $l(D,\sigma^2)$ with respect to D and then with respect to σ^2 (not σ), show that the MLEs of D and σ^2 are

$$\hat{D} = \frac{n}{2L\hat{\mu}} = \frac{n}{2L\sqrt{\frac{\pi}{2}\widehat{\sigma^2}}} \quad \text{and}$$
$$\widehat{\sigma^2} = \frac{\sum_{i=1}^n x_i^2}{n}$$

Solution: correction

$$\frac{\partial l(D,\sigma^2)}{\partial D} = \frac{n}{D} - \sqrt{2L^2\pi}\sqrt{\sigma^2}$$
$$\frac{\partial l(D,\sigma^2)}{\partial \sigma^2} = -D\sqrt{2L^2\pi}\frac{1}{2}\frac{1}{\sqrt{\sigma^2}} + \frac{\sum_{i=1}^n x_i^2}{2(\sigma^2)^2}$$

Setting both of these to zero, we get

$$\frac{n}{D} = \sqrt{2L^2\pi}\sqrt{\sigma^2}$$
$$\Rightarrow D = \frac{n}{\sqrt{2L^2\pi}\sqrt{\sigma^2}} \quad \text{and}$$
$$D\sqrt{2L^2\pi}\frac{1}{2}\frac{1}{\sqrt{\sigma^2}} = \frac{\sum_{i=1}^n x_i^2}{2}\frac{1}{(\sigma^2)^2}.$$

Substituting the second of these equations for D in the third equation gives correction

$$\frac{n}{2}\frac{1}{\sqrt{\sigma^2}} = \frac{\sum_{i=1}^n x_i^2}{2}\frac{1}{(\sigma^2)^2}$$
$$\Rightarrow \frac{n}{2} = \frac{\sum_{i=1}^n x_i^2}{2\sigma^2}$$
$$\Rightarrow \widehat{\sigma^2} = \frac{\sum_{i=1}^n x_i^2}{n}.$$

And substituting this back into the equation for D above, we get

$$\hat{D} = \frac{n}{\sqrt{2L^2\pi}\sqrt{\widehat{\sigma^2}}} = \frac{n}{2L\sqrt{\frac{\pi}{2}\widehat{\sigma^2}}}.$$

(iii) Using these estimators, calculate the full likelihood MLE of density D from the minke whale survey data.

Solution: Using $\hat{\sigma} = 0.4706733$ as calculated above:

```
> L=sum(unique(minke$Effort)) # this works because no two transects are
                              # the same length in this dataset
> L
[1] 1842.79
> D.hat=length(x)/(2*L*sqrt(pi*sigma2.hat/2))
> D.hat
[1] 0.02839991
```

Chapter 2

Capture-Recapture

Notation used here is the same as that used in lectures.

1. Consider a two-sample mark-recapture survey in which all animals have a constant probability of being captured, and this is the same on all occasions.

(a) Write down the likelihood for abundance, N, given the data (n_1, n_2, m_2).

Solution:

$$L(N,p) \quad = \quad \binom{N}{n_1} p^{n_1}(1-p)^{N-n_1} \times \binom{N-n_1}{u_2} p^{u_2}(1-p)^{N-n_1-u_2} \times \binom{n_1}{m_2} p^{m_2}(1-p)^{n_1-m_2}$$

where $u_2 = n_2 - m_2$ is the number of unmarked individuals caught on occasion 2. Collecting terms and cancelling appropriately, this gives

$$L(N,p) \quad = \quad \left(\frac{N!}{n_1!(n_2-m_2)!m_2!(N-n)!}\right) p^{n_1+n_2}(1-p)^{2N-(n_1+n_2)}$$

where $n = n_1 + n_2 - m_2$, the number of individuals caught in total

(b) Maximise the log-likelihood with respect to N and p and hence show that the maximum likelihood estimator of N is $[(n_1+n_2)/2]^2/m_2$.

Solution: Logging the equation above, and absorbing terms without parameters into a constant C, we get the log-likelihood

$$l(N,p) = \log\{L(N,p)\} \quad = \quad \ln\left(\frac{N!}{(N-n)!}\right) + (n_1+n_2)\ln(p) + [2N-(n_1+n_2)]\ln(1-p) + C$$

Differentiating with respect to N (remembering that $\frac{d\log(N!)}{dN} \approx \log(N)$) and p and setting the derivatives to zero: correction

$$\begin{aligned}
\frac{\partial l}{\partial N} = 0 \Rightarrow \ln\left(\frac{(N-n)}{N}\right) &= \ln\{(1-p)^2\} \\
\Rightarrow 1 - \frac{n}{N} &= 1 - p(2-p) \\
\Rightarrow \frac{n}{N} &= p(2-p) \qquad (2.1) \\
\frac{\partial l}{\partial p} = 0 \Rightarrow \frac{(n_1+n_2)}{p} &= \frac{2N-(n_1+n_2)}{1-p} \\
\Rightarrow \frac{1}{p} - 1 &= \frac{2N}{(n_1+n_2)} - 1 \\
\Rightarrow N &= \frac{(n_1+n_2)}{2p} \qquad (2.2)
\end{aligned}$$

Substituting (2.2) into (2.1) gives

$$\begin{aligned}
\frac{2pn}{(n_1+n_2)} &= p(2-p) \\
\Rightarrow \hat{p} &= \frac{2(n_1+n_2)-2n}{(n_1+n_2)} = \frac{2(n_1+n_2)-2[(n_1+n_2)-m_2]}{(n_1+n_2)} \\
\Rightarrow \hat{p} &= \frac{2m_2}{(n_1+n_2)} = \frac{m_2}{(n_1+n_2)/2} \qquad (2.3)
\end{aligned}$$

And substituting into (2.1) gives

$$\hat{N} = \frac{\left(\frac{(n_1+n_2)}{2}\right)^2}{m_2} \qquad (2.4)$$

(c) Show that the likelihood in (a) above is a multinomial likelihood in which the frequencies with which capture histories 11, 10, 01 and 00 are observed are the random variables. (It may help to start with a likelihood written in terms of (u_1, u_2, m_2) rather than (n_1, n_2, m_2).)

Solution: Rewriting the likelihood in terms of (u_1, u_2, m_2) gives

$$L(N,p) = \binom{N}{u_1} p^{u_1}(1-p)^{N-u_1} \times \binom{N-u_1}{u_2} p^{u_2}(1-p)^{N-u_1-u_2} \times \binom{u_1}{m_2} p^{m_2}(1-p)^{u_1-m_2}$$

Looking at the combinatorial terms and canceling we get:

$$\begin{aligned}
\binom{N}{u_1}\binom{N-u_1}{u_2}\binom{u_1}{m_2} &= \frac{N!}{u_1!(N-u_1)!}\frac{(N-u_1)!}{u_2!(N-u_1-u_2)!}\frac{u_1!}{m_2!(u_1-m_2)!} \\
&= \frac{N!}{u_2!(N-u_1-u_2)!m_2!(u_1-m_2)!} \\
&= \frac{N!}{u_2!(N-n)!m_2!(u_1-m_2)!}
\end{aligned}$$

This is the combinatorial term for a multinomial with u_2 animals with capture histories (01), $(N-n)$ animals with capture histories (00), m_2 with capture histories (11), and (u_1-m_2) with capture histories (10). The corresponding probabilities are $[(1-p)p]^{u_2}$, $[(1-p)^2]^{N-n}$, $[p^2]^{m_2}$ and $[p(1-p)]^{u_2}$. So we need to see if

$$[(1-p)p]^{u_2}[(1-p)^2]^{N-n}[p^2]^{m_2}[p(1-p)]^{u_1-m_2}$$

is equal to

$$p^{u_1}(1-p)^{N-u_1}p^{u_2}(1-p)^{N-u_1-u_2}p^{m_2}(1-p)^{u_1-m_2}.$$

In the first case p appears with a power $u_2+2m_2+u_1-m_2 = u_1+u_2+m_2$, while in the second case p appears with a power $u_1+u_2+m_2$. So the powers of p are the same in the two cases.

What about the powers of $(1-p)$? In the first case $(1-p)$ appears with a power $u_2+2N-2n+u_1-m_2 = u_2+2N-2(u_1+u_2)+u_1-m_2 = 2N-u_2-u_1-m_2$, while in the second cases $(1-p)$ appears with a power $N-u_1+N-u_1-u_2+u_1-m_2 = 2N-u_1-u_2-m_2$. So the powers of $(1-p)$ are the same in the two cases.

Hence the multinomial likelihood

$$L(N,p) = \frac{N!}{u_2!(N-n)!m_2!(u_1-m_2)!}[(1-p)p]^{u_2}[(1-p)^2]^{N-n}[p^2]^{m_2}[p(1-p)]^{u_1-m_2}$$

is equal to the likelihood in (a) above.

(d) Show that when the data are reduced to the frequencies of animals caught 0, 1, or 2 times, the likelihood is also a multinomial likelihood.

Solution: The frequencies are $f_1 = u_1+u_2$, $f_2 = m_2$, and $f_0 = N-(f_1+f_2)$. Also, $n = f_1+f_2$. When only frequencies are observed, the cells for u_1 and u_2 are combined into a single cell. And since the two capture histories involved are mutually exclusive, it has cell probability $[p(1-p)] + [(1-p)p] = 2p(1-p)$. To get the correct combinatorial term, we need to divide the likelihood by the number of ways that f_1 individuals can be split into a set of u_1 and another of u_2, i.e. divide by $f_1!/(u_1!u_2!)$. This gives

$$\begin{aligned} L(N,p) &= \left(\frac{u_1!u_2!}{f_1!}\right)\left(\frac{N!}{u_1!u_2!f_2!(N-(f_1+f_2))!}\right)[2p(1-p)]^{f_1}[p^2]^{f_2}[(1-p)^2]^{N-(f_1+f_2)} \\ &= \left(\frac{N!}{f_1!f_2!f_0!}\right)[2p(1-p)]^{f_1}[p^2]^{f_2}[(1-p)^2]^{f_0} \end{aligned}$$

which is a multinomial pmf.

2. There are known to be 60 marked animals in a population of unknown size, N. A survey is conducted to estimate N. On it 50 animals are detected and 20 of them are found to have marks.

(a) Assuming that marked and unmarked animals are equally catchable, and that animals are detected independently of each other, write down an expression for the probability of detecting 50 animals on the survey if there are N animals in the population.

Solution:

$$L(N,p) = \left(\frac{N!}{50!(N-50)!}\right)p^{50}(1-p)^{N-50}$$

(b) Estimate the probability (p) that an animal is detected on the survey.

Solution: The number of marked individuals that are captured can be modelled as a binomial random variable with parmaters 60 (number of "trials") and p. Of the $n_1 = 60$ "trials", $m_2 = 20$ are "successes" (i.e., were captured on the second occasion), and the MLE for p from a binomial with 60 "trials" 20 "successes" is $\hat{p} = 20/60 = 1/3$.

(c) Consider the expression in (a) to be a likelihood function for N. Using the estimate of p from (b), show that the MLE for N, given the estimate of p and the data, is 150.

Solution: Replacing p by $\hat{p} = 1/3$ in the likelihood in (a), we have a binomial with parameters N (unknown) and $p = 1/3$, and number of "successes" $n_1 = 50$. The MLE of N is $\hat{N} = 50/(1/3) = 150$.

3. Consider a mark-recapture model of type M_{tb}. A "full" M_{tb} model allows capture probability to change between capture occasions and to depend on whether or not an animal has been captured before. Such a model has the probability of catching a previously uncaught animal on occasion s as p_s (for $s = 1, \ldots, S$). This model has $2S+1$ parameters ($2S$ capture probability parameters in addition to N). But a mark-recapture survey with S occasions generates only $2S-1$ bits of data (the number of unmarked animals on occasion 1 and the number of marked and unmarked animals on each of the remaining $S-1$ occasions). You can't sensibly estimate $2S+1$ parameters from $2S-1$ bits of data - the parameters are said to be "unidentifiable".

Now consider a model in which the capture probability for marked animals on occasion s (c_s, say) is equal to a constant multiple of the capture probability p_s, for unmarked animals on this occasion: $c_s = \beta p_s$ for some unknown β. (Call this a "reduced" M_{tb} model.)

(a) How many parameters does the reduced M_{tb} model have?

Solution: It has $S+1$ parameters: p_s for $s = 1, \ldots, S$ and β.

(b) Write down these parameters for the case in which $S = 3$, and say what each is.

Solution:

$0 \le p_1 \le 1$ is the probability of capture of unmarked animals on occasion 1.
$0 \le p_2 \le 1$ is the probability of capture of unmarked animals on occasion 2.
$0 \le p_3 \le 1$ is the probability of capture of unmarked animals on occasion 3.
$0 \le \beta \le 1$ is the effect on capture probability, of having been captured before.

(c) Write down the likelihood for abundance, N, given the data $(n_1, u_2, m_2, u_3, m_3)$ for a survey with $S = 3$.

Solution: Let n_c be the number of individuals with capture history c. The likelihood is then

$$L(N, \{p_s\}, \beta) = \prod_{s=1}^{S} \left(\frac{U_s!}{u_s!(U_s - u_s)!} \right) p_s^{u_s} [1 - p_s]^{U_s - u_s} \times \left(\frac{M_s!}{m_s!(M_s - m_s)!} \right) (\beta p_s)^{m_s} [1 - \beta p_s]^{M_s - m_s}$$

where $U_1 = N$, $u_1 = n_1$, $M_1 = m_1 = 0$, $U_s = N - \sum_{t=1}^{s} u_t$ and $M_s = \sum_{t=2}^{s} u_{t-1}$.

(d) Write down the likelihood for abundance, N, given the capture history frequencies: n_c, the number of individuals with capture history c $(s = 1, 2, 3)$.

Solution: Let n_c be the number of individuals with capture history c. The likelihood is then

$$\begin{aligned} L(N, \{p_s\}, \beta) = & \left(\frac{N!}{n_{100}!n_{110}!n_{101}!n_{111}!n_{010}!n_{011}!n_{001}!(N-n)!} \right) \\ & \times [p_1(1 - \beta p_2)(1 - \beta p_3)]^{n_{100}} [p_1 \beta p_2 (1 - \beta p_3)]^{n_{110}} [p_1(1 - \beta p_2)\beta p_3]^{n_{101}} \\ & \times [p_1 \beta p_2 \beta p_3]^{n_{111}} [(1 - p_1)p_2(1 - \beta p_3)]^{n_{010}} [(1 - p_1)p_2 \beta p_3]^{n_{011}} \\ & \times [(1 - p_1)(1 - p_2)p_3]^{n_{001}} [(1 - p_1)(1 - p_2)(1 - p_3)]^{N-n} \end{aligned}$$

(e) By finding the S at which there are at least as many bits of data as parameters, find the minumum number of surveys required for the parameters of the reduced M_{tb} to be identifiable.

Solution: The model has $S+1$ parameters. There are $2S-1$ independent bits of data gathered on the survey. So for the parameters to identifiable, we need $S + 1 \le 2S - 1$, i.e. $S \ge 2$.

Chapter 3

SECR

You can take this general likelihood function for SECR surveys with constant animals density, as given:

$$L(D,\boldsymbol{\theta}) \quad = \quad \frac{(Da)^n e^{-Da}}{n!}\prod_{i=1}^{n}\frac{\int P(\mathbf{c}_i|\mathbf{x})d\mathbf{x}}{a}. \tag{3.1}$$

Notation is the same as that used in notes.

1. Consider an SECR survey with **count detectors**, in which animal density is assumed to be constant in space and animals are detected independently with a mean detection rate $\lambda_k(\mathbf{x})$ at detector k, that depends only on the distance of the detector from animal activity centre, $\mathbf{x}$.

(a) Write down an expression for the probability that at least one detector detects an animal with activity centre at $\mathbf{x}$ on at least one occasion.

Solution: Count detectors have independent detections at each trap (conditional on animal activity centre, $\mathbf{x}$), and they detect individuals multiple times. We can model the number of detections of an individual at detector k as a Poisson random variable (τ_k, say). Hence $p_k(\mathbf{x}) = 1 - \mathbb{P}(\tau_k = 0|\mathbf{x}) = 1 - \exp(-\lambda_k(\mathbf{x})$. The probability that at least one detector detects an animal with activity centre at $\mathbf{x}$ is therefore

$$p_\cdot(\mathbf{x}) \quad = \quad 1 - \prod_{s=1}^{S}\prod_{k=1}^{K}\left[1 - \left(1 - e^{-\lambda_k(\mathbf{x})}\right)\right] \;=\; 1 - \prod_{s=1}^{S}\prod_{k=1}^{K} e^{-\lambda_k(\mathbf{x})}$$

(b) Assuming that the number of detected animals has a Poisson distribution, write down the likelihood function for a survey with S occasions and K detectors each occasion, on which individual i is detected τ_{iks} times by detector k on occasion S ($k = 1,\ldots,K; s = 1,\ldots,S$).

Solution: The likelihood is as given above, but we need to specify $\mathbb{P}(\mathbf{c}_i|\mathbf{x})$. We can write the capture history for animal i as $\mathbf{c}_i = \{\tau_{iks}\}$, where τ_{iks} is the number of times animal i was detected by detector k on occasion s (and the curly brackets indicate the set of all τ_{iks}). Then, assuming that τ_{iks} has a Poisson distribution:

$$\mathbb{P}(\mathbf{c}_i|\mathbf{x}) \quad = \quad \prod_{s=1}^{S}\prod_{k=1}^{K}\frac{\lambda_k(\mathbf{x})^{\tau_{iks}} e^{-\lambda_k(\mathbf{x})}}{\tau_{iks}!}$$

(c) Hence show that in this case occasion is irrelevant, i.e., that (aside from a constant that does not involve parameters) the above likelihood is identical to that for the case in which only the summed capture frequencies across all occasions ($\tau_{i\cdot k} = \sum_s \tau_{isk}$) and not the frequencies within each occasion, are available.

Solution:

$$\begin{aligned}\mathbb{P}(\mathbf{c}_i|\mathbf{x}) &= \prod_{s=1}^{S}\prod_{k=1}^{K}\frac{\lambda_k(\mathbf{x})^{\tau_{iks}} e^{-\lambda_k(\mathbf{x})}}{\tau_{iks}!} \\ &= \prod_{k=1}^{K}\frac{\lambda_k(\mathbf{x})^{\sum_k \tau_{iks}} e^{-S\lambda_k(\mathbf{x})}}{\prod_{s=1}^{S}\tau_{iks}!} \;=\; \prod_{k=1}^{K}\frac{\lambda_k(\mathbf{x})^{\tau_{i\cdot k}} e^{-S\lambda_k(\mathbf{x})}}{\prod_{s=1}^{S}\tau_{iks}!}\end{aligned}$$

So ignoring the denominator, which does not involve parameters, the likelihood using all the τ_{iks}s is identical to that using only the $\tau_{i\cdot k}$s, i.e. the likelihood does not change when you ignore occasion and deal only with the total number of captures across all occasions.

2. Consider an SECR survey of birds using S occasions, each with the same K mist nets to catch birds, in which the probability of catching a bird with activity centre at $\mathbf{x}$ in net k, on any one occasion, in the absence of any other nets, is $1 - e^{\lambda_k(\mathbf{x})}$.

(a) Write down an expression for the probability that on any single occasion, the bird is caught in none of the K nets used in the survey.

Solution:

$$\begin{aligned} 1 - p.(\mathbf{x}) &= \prod_{k=1}^{K} \left[1 - \left(1 - e^{-\lambda_k(\mathbf{x})}\right)\right] \\ &= \prod_{k=1}^{K} e^{-\lambda_k(\mathbf{x})} = e^{-\sum_k \lambda_k(\mathbf{x})} \end{aligned}$$

(b) Hence obtain an expression for the probability that on any single occasion, the bird is caught by at least one of the K nets.

Solution:

$$p.(\mathbf{x}) = 1 - e^{-\sum_k \lambda_k(\mathbf{x})}$$

(c) Obtain an expression for the probability that the bird is caught by at least one of the K nets on at least one of S occasions.

Solution: On occasion s:

$$p._s(\mathbf{x}) = 1 - \prod_{s=1}^{S} e^{-\sum_k \lambda_k(\mathbf{x})} = 1 - e^{-S\sum_k \lambda_k(\mathbf{x})}$$

(d) Using the above probability, show that in this case the effective area covered in the survey is

$$a = A - \int \exp\left\{-\sum_k S\lambda_k(\mathbf{x})\right\} d\mathbf{x}.$$

where A is the area of the region from which birds could be caught in the nets and the integral is over this region.

Solution:

$$\begin{aligned} a &= \int 1 - e^{-S\sum_k \lambda_k(\mathbf{x})} d\mathbf{x} \\ &= \int 1 d\mathbf{x} - \int e^{-S\sum_k \lambda_k(\mathbf{x})} d\mathbf{x} \\ &= A - \int \exp\left\{-\sum_k S\lambda_k(\mathbf{x})\right\} d\mathbf{x} \end{aligned}$$

(e) (*Difficult question*) If the conditional probability that a bird is caught in net k on occasion s, given that it was caught in one of the nets on this occasion, is $\lambda_k(\mathbf{x})/\sum_k \lambda_k(\mathbf{x})$, show that the appropriate likelihood for this survey is

$$L(D,\boldsymbol{\theta}) = \frac{D^n e^{-Da}}{n!} \prod_{i=1}^{n} \int \prod_{s=1}^{S} \left[e^{\sum_k \lambda_k(\mathbf{x})}\right]^{1-\delta_{i\cdot s}} \prod_{k=1}^{K} \left[\frac{\lambda_k(\mathbf{x})}{\sum_{k=1}^{K} \lambda_k(\mathbf{x})} \left(1 - e^{\sum_k \lambda_k(\mathbf{x})}\right)\right]^{\delta_{iks}} d\mathbf{x},$$

where n is the number of birds caught, $\delta_{iks} = 1$ if bird i was caught in net k on occasion s, and $\delta_{iks} = 0$ otherwise, $\delta_{i\cdot s} = 1$ if bird i was caught in any net on occasion s, and $\delta_{i\cdot s} = 0$ otherwise, D is bird density, and $\boldsymbol{\theta}$ is the parameter vector of $\lambda_k(\mathbf{x})$.

Solution: The key is working out what $P(\mathbf{c}_i|\mathbf{x})$ is. We know from above the following:

- The probability of a bird at $\mathbf{x}$ going uncaptured on occasion s is $e^{-\sum_k \lambda_k(\mathbf{x})}$.
- The probability of being caught at all on occasion s is $1 - e^{-\sum_k \lambda_k(\mathbf{x})}$ and
- The conditional probability of being caught in net k, give capture in some net on occasion s is $\lambda_k(\mathbf{x})/\sum_k \lambda_k(\mathbf{x})$.

Hence the probability of being caught *and* being in trap k on occasion s is

$$p_{ks}(\mathbf{x})) = \frac{\lambda_k(\mathbf{x})}{\sum_k \lambda_k(\mathbf{x})} \left(1 - e^{-\sum_k \lambda_k(\mathbf{x})}\right).$$

Assuming that captures are independent between occasions, $P(\mathbf{c}_i|\mathbf{x}) = \prod_{s=1}^{S} P(c_{is}|\mathbf{x})$, where $c_{is} = (\delta_{i\cdot s}, \delta_{i1s}, \ldots, \delta_{iKs})$ is the spatial "capture history" on occasion s. (Note that at most one of $\delta_{i1s}, \ldots, \delta_{iKs}$ can be equal to 1 and all the others must be zero, since birds can only be caught in one trap on any occasion.)

If $\delta_{i\cdot s} = 0$ then the bird was not captured on occasion s and so $P(c_{is}|\mathbf{x}) = e^{-\sum_k \lambda_k(\mathbf{x})}$. Otherwise exactly one of $\delta_{i1s}, \ldots, \delta_{iKs}$ is 1 (the others being zero), and if it is δ_{ik^*s} that is 1 then $P(c_{is}|\mathbf{x}) = \frac{\lambda_{k^*}(\mathbf{x})}{\sum_k \lambda_k(\mathbf{x})} \left(1 - e^{-\sum_k \lambda_k(\mathbf{x})}\right)$. We can write this all succinctly as follows:

$$P(c_{is}|\mathbf{x}) = \left[e^{\sum_k \lambda_k(\mathbf{x})}\right]^{1-\delta_{i\cdot s}} \prod_{k=1}^{K} \left[\frac{\lambda_k(\mathbf{x})}{\sum_{k=1}^{K} \lambda_k(\mathbf{x})} \left(1 - e^{\sum_k \lambda_k(\mathbf{x})}\right)\right]^{\delta_{iks}} \tag{3.2}$$

Substitution into $P(\mathbf{c}_i|\mathbf{x}) = \prod_{s=1}^{S} P(c_{is}|\mathbf{x})$ and then into Equation (3.1) gives the required likelihood.

(f) Suppose now that a bird's sex (z say, with $z = 0$ for males, $z = 1$ for females) affects $\lambda_k(\mathbf{x})$ as follows:

$$\lambda_k(\mathbf{x}, z) = \lambda_k(\mathbf{x}) + \phi^z$$

and that π_1 is the probability of a bird being female.

(i) Show that in this case

$$a(z) = \begin{cases} a; & z = 0 \\ A - e^{SK\phi} \int \exp\{-\sum_k S\lambda_k(\mathbf{x})\}\, d\mathbf{x} & z = 1. \end{cases}$$

Solution: For males $\lambda_k(\mathbf{x}, z = 0) = \lambda_k(\mathbf{x}) + \phi^0 = \lambda_k(\mathbf{x})$ and so $a(z = 0)$ is equal to the a from the earlier parts of this question.

For females,

$$\begin{aligned} a(z = 1) &= \int 1 - e^{-S\sum_k[\lambda_k(\mathbf{x})+\phi]} d\mathbf{x} \\ &= \int 1 d\mathbf{x} - \int e^{-S\sum_k \lambda_k(\mathbf{x})+SK\phi} d\mathbf{x} \\ &= A - e^{SK\phi} \int \exp\left\{-\sum_k S\lambda_k(\mathbf{x})\right\} d\mathbf{x} \end{aligned}$$

(ii) Hence show that the effective area for the survey is

$$a = A - \int \exp\left\{-\sum_k S\lambda_k(\mathbf{x})\right\} d\mathbf{x} \times \left[1 - \pi_1\left(1 - e^{SK\phi}\right)\right].$$

Solution: The pmf of z is $f(z) = \pi_1^z(1-\pi_1)^{1-z}$ (it is a Bernoulli random variable). Before we do the survey, we don't know what any zs are and so to calculate the effective area we take expectation over z:

$$\begin{aligned}
a &= \sum_{z=0}^{1} a(z)f(z) \\
&= \left[A - \int \exp\left\{-\sum_k S\lambda_k(\mathbf{x})\right\} d\mathbf{x}\right](1-\pi_1) + \left[A - e^{SK\phi}\int \exp\left\{-\sum_k S\lambda_k(\mathbf{x})\right\} d\mathbf{x}\right]\pi_1 \\
&= A - \left[\int \exp\left\{-\sum_k S\lambda_k(\mathbf{x})\right\} d\mathbf{x}\right]\left[(1-\pi_1) + e^{SK\phi}\pi_1\right] \\
&= A - \int \exp\left\{-\sum_k S\lambda_k(\mathbf{x})\right\} d\mathbf{x} \times \left[1 - \pi_1\left(1 - e^{SK\phi}\right)\right].
\end{aligned}$$

3. Below is output from an SECR model fit using the package `secr`, that was obtained using this command: `secr.fit(capthist = data, buffer = 1000, detectfn = 0)`.
Five numbers have been deleted from the output and replaced by `<MISSING1>` to `<MISSING5>`.

```
Detector type     proximity
Detector number   94
Average spacing   250 m
x-range           -1500 1500 m
y-range           -1500 1500 m
N animals       :  20
N detections    :  30
N occasions     :  7
Mask area       :  2416.992 ha

Model           :  D~1 g0~1 sigma~1
Fixed (real)    :  none
Detection fn    :  halfnormal
Distribution    :  poisson
N parameters    :  3
Log likelihood  :  -145.7055
AIC             :  297.4109
AICc            :  298.9109

Beta parameters (coefficients)
           beta   SE.beta       lcl       ucl
D     -3.706471 0.2962042 -4.287021 -3.125921
g0    -3.047745 0.4504881 -3.930685 -2.164804
sigma  5.540604 0.1721173  5.203260  5.877947

Variance-covariance matrix of beta parameters
                 D          g0        sigma
D      0.087736926 -0.04812886 -0.006317331
g0    -0.048128858  0.20293955 -0.055537147
sigma -0.006317331 -0.05553715  0.029624348
```

```
Fitted (real) parameters evaluated at base levels of covariates
       link    estimate  SE.estimate         lcl         ucl
D       log  <MISSING1>  0.007438526  <MISSING4>  <MISSING5>
g0    logit  <MISSING2>  0.019488786  0.01925229  0.10295588
sigma   log  <MISSING3> 44.187805675 181.86419237 357.07557098
```

(a) Write down an expression for $p_{ks}(\mathbf{x})$, the probability of detector k detecting an individual with location $\mathbf{x}$ on occasion s.

Solution:

$$p_{ks}(\mathbf{x}) \quad = \quad g_0 \exp\left(-\frac{d_k(\mathbf{x})^2}{2\sigma^2}\right) \tag{3.3}$$

where $d_k(\mathbf{x})$ is the distance from $\mathbf{x}$ to detector k.

(b) Write down an expression for the likelihood function for this survey.

Solution: From the output you see that the detector type is `proximity`, which means that detections of animals are independent between detectors (given $\mathbf{x}$) and that capture data are contained in binary variables (δ_{iks}, for animal i in detector k on occasion s: 1 for detection, 0 for non-detection). The likelihood is therefore as in Equation (3.1), with

$$\mathbb{P}(\mathbf{c}_i|\mathbf{x}) \quad = \quad \prod_{s=1}^{S}\prod_{k=1}^{K} p_{ks}(\mathbf{x})^{\delta_{iks}}[1-p_{ks}(\mathbf{x})]^{1-\delta_{iks}}$$

where δ_{iks} is as in part (a).

(c) Explain what each of the parameters in the "`Fitted (real)`" table is.

Solution:

- `D` is the animal density (number of animals per unit area).
- `g0` is the probability that an animal with activity centre at a distanze zero from a detector is detected by the detector.
- `sigma` is the scale parameter that controls the detection range (larger `sigma` implying longer range).

(d) Calculate `<MISSING1>` to `<MISSING5>`.

Solution:

- `<MISSING1>`$=\exp(-3.706471) = 0.02456406$
- `<MISSING2>`$=\exp(-3.047745)/[1+\exp(-3.047745)] = 0.04531493$
- `<MISSING3>`$=\exp(5.540604) = 254.8319$
- `<MISSING4>`$=\exp(-4.287021) = 0.01374581$
- `<MISSING5>`$=\exp(-3.125921) = 0.04389649$

(e) Explain why the `buffer` used in fitting is or is not adequate.

Solution: It seems adequate. The buffer is 1,000m, which is almost 4σ, by which distance the half-normal detection function is very close to zero, implying that any animal beyond this distance has virtually zero chance of being detected. So the area inside the outer limit of the buffer region includes the activity centres of all the animals that did, or could have, appeared in the survey data.

Chapter 4

Occupancy

Notation used here is the same as that used in lectures.

1. Show that

$$L(\Psi, p) \quad = \quad \left[\Psi^n p^{\delta_{\cdot\cdot}} (1-p)^{nT-\delta_{\cdot\cdot}}\right] [1 - \Psi p_{\cdot}]^{N-n}$$

can be written as

$$L(\Psi, p) \quad = \quad [\Psi p_{\cdot}]^n [1 - \Psi p_{\cdot}]^{N-n} \left[\left(\frac{p}{1-p}\right)^{\delta_{\cdot\cdot}} \left\{\frac{(1-p)^T}{p_{\cdot}}\right\}^n \right]$$

Solution: Write $(1-p)^{nT-\delta_{\cdot\cdot}}$ in the first equation as $\frac{\{(1-p)^T\}^n}{(1-p)^{\delta_{\cdot\cdot}}}$ and then multiply by $\frac{p_{\cdot}^n}{p_{\cdot}^n}$. This gives the desired result.

2. Explain why you do or do not need to multiply the above likelihood equation by the binomial coefficient $\binom{N}{n}$ in order to obtain maximum likelihood estimates of Ψ and p from this equation.

Solution: The term $\binom{N}{n}$ does not involve any parameters and so does not affect which parameter values correspond to the maximum of the likelihood.

3. Write down the likelihood for an occupancy model with constant detection probability p for a (rather artificially simple) 3-occasion survey of 10 sites in which 7 sites have capture history 000 and the other three capture histories are 011, 1·0 and ··1, where "·" indicates that the site was not surveyed on the given occasion.

Solution: The probability of observing 000 is the probability that the site is unoccupied, $(1-\Psi)$, plus the probability that it is occupied but occupancy went undetected on all three occasions, $(1-p)^3 \times \Psi$. So the probability of 7 sites having this capture history is $\left[(1-\Psi) + (1-p)^3\Psi\right]^7$.

The probability of observing 011 is the probability that the site is occupied (Ψ) multiplied be the probability of missing occupancy on the first occasion and detecting it on the next two, $(1-p)p^2$, i.e., $(1-p)p^2\Psi$.

The probability of observing $1 \cdot 0$ is just the probability of observing 10 if you had only two occasions (not three): $p(1-p)\Psi$.

Similarly, the probability of observing $\cdot \cdot 1$ is $p\Psi$.

The likelihood is the product of the above:

$$L(\Psi, p) = \left[(1-\Psi) + (1-p)^3\Psi\right]^7 \times (1-p)p^2\Psi \times p(1-p)\Psi \times p\Psi$$

And with some rearranging you see that $\left[(1-\Psi) + (1-p)^3\Psi\right] = [1 - p.\Psi]$, where $p. = 1-(1-p)^3$, so after collecting the other terms together we get

$$L(\Psi, p) = [1 - p.\Psi]^7 (1-p)^2 p^4 \Psi^3$$

.

4. The `RMark` dataset `Donovan.7` contains data from a 5-occasion occupancy survey of some species.

(a) Obtain an estimate of probability of occupancy per site (Ψ), together with an approximate 95% confidence interval for this probability, assuming perfect detection of the species within each site.

Solution: `R` code:

```
library(RMark, quietly=TRUE)
data(Donovan.7)
N.total <- dim(Donovan.7)[1]
T.occ <- nchar(Donovan.7$ch[1])
n.occupied <- sum(Donovan.7$ch!="00000")
Psi.0 <- n.occupied/N.total
Psi.0.ci <- Psi.0 + c(-1.96,1.96)*sqrt(Psi.0*(1-Psi.0)/N.total) # assuming normality
```

This gives an estimate $\Psi = 0.85$ with 95% confidence interval (CI) $(0.694; 1.006)$. The fact that the CI goes above 1 indicates that the normal approximation is not adequate. We can use the `R` function `pbinom` to get an exact confidence interval, by evaluating it with various ps, $n = 17$ (the observed number of "successes") and $N = 20$ (the number of "trials"). Since `pbinom(17,20,0.603)`≈ 0.975 and `pbinom(17,20,0.9679)`≈ 0.025, an exact 95% CI is (0.603; 0.9679).

(b) Without fitting a model, decide whether or not the maximum likelihood estimates of an occupancy model fitted to these data assuming constant detection probability p, satisfy these equations:

$$\hat{\Psi} = \frac{n}{N\hat{p}.} \qquad \frac{\hat{p}}{\hat{p}.} = \frac{\delta_{..}}{nT}.$$

Solution: `R` code to do the calculation:

```
line <- paste(Donovan.7$ch,collapse="")
d.. <- 0
for(i in 1:nchar(line)) if(substr(line,i,i)=="1") d..=d..+1
p.hat <- d../(N.total*T.occ)
inequality1 <- (1-n.occupied/N.total)
inequality2 <- (1-d../(N.total*T.occ))^T.occ
Donovan.7.null <- mark(Donovan.7,model="Occupancy", output=FALSE)
```

```
p <- get.real(Donovan.7.null, "p")[1] # p same for all occasions,
                                      # so just use first here
pdot <- 1-(1-p)^T.occ
Psi <- get.real(Donovan.7.null, "Psi")
psi.satisfy <- n.occupied/(N.total*pdot)
satisfy1 <- p/pdot
satisfy2 <- d../(n.occupied*T.occ)
```

Guillera-Arroita *et al.* (2010) showed that MLEs satisfy the equations above providing that $\left(1-\frac{1}{N}\right) \geq \left(1-\frac{\delta_{..}}{NT}\right)^T$. The above calculations have $\left(1-\frac{1}{N}\right) = 0.15$ and $\geq \left(1-\frac{\delta_{..}}{NT}\right)^T = 0.009$. So the inequality is satisfied and hence the MLEs satisfy the equations above.

(c) Using the `RMark` function `mark`, fit occupancy models to these data that assume (i) that there is no heterogeneity in detection probability, (ii) that detection probabilities arise as a are each one of a finite number of underlying unobserved detection probabilities, and (ii) that detection probability depends on (unobserved) abundance at the site, which is assumed to follow a Poisson distribution.

Solution: `R` code to do this:

```
Donovan.7.het <- mark(Donovan.7,model="OccupHet", output=FALSE, silent=TRUE)
Donovan.7.poisson <- mark(Donovan.7,model="OccupRNPoisson", output=FALSE, silent=TRUE)
models.for.7 <- collect.models(c("Donovan.7.null","Donovan.7.het","Donovan.7.poisson"))
```

The ΔAICs are 0, 4.634 and 7.428 for models `Donovan.7.poisson`, `Donovan.7.null` and `Donovan.7.het`, respectively.

(d) Use one of these fitted models to verify your answer to part (b) of this question.

Solution: Part (b) has constant p and constant Ψ so we need to use the model `Donovan.7.null` to verify the answer to part (b).

Now $\hat{\Psi} = 0.85156$ and $\frac{n}{N\hat{p}.} = 0.85156$, so the first likelihood equation is satisfied.

Also $\frac{\hat{p}}{\hat{p}.}0.71765$ and $\frac{\delta_{..}}{nT}0.71765$, so the second likelihood equation is satisfied.

(e) Using the best of your fitted models, estimate the probability of presence at each of the 20 sites in the survey.

Solution: Using `Donovan.7.poisson` to do this because it has the smallest AIC, the relevant `R` code is:

```
r <- get.real(Donovan.7.poisson, "r")
D <- get.real(Donovan.7.poisson, "Lambda")
# see what max z is sensible:
z <- 0:20
plot(z,ppois(z,D),type="l", main="Plot to determine maximum abundance \nover which to sum\n
# denominator of Bayes Theorem:
pmiss <- sum((1-r)^z*dpois(z,D))
# numerator of Bayes Theorem:
num.bayes <- sum((1-r)^z[-1]*dpois(z[-1],D))
Pr.presence <- num.bayes/pmiss
# Check that it is less than the unconditional prob present:
uncond.Pr.presence <- 1-dpois(0,D)
```

This gives parameter estimates $\hat{r} = 0.462$ SE$(\hat{r}) = 0.409$ and $\hat{\lambda} = 2.089$ with SE$(\hat{\lambda})$0.295.

The probability of presence on sites on which presence has been observed is obviously 1. Applying Bayes theorem, Pr(presence—observed absence)=0.675 for all sites without observed presence. This contrasts with the unconditional Pr(presence)=0.876.