

Non-Spatial Closed Population Capture-Recapture Models for Estimating N



Outline

Part I

- Basic design and data structure
- “Model M0” – likelihood analysis
- Bayesian analysis of Model M0 – Data augmentation
 - Converts Model M0 to “site occupancy” model
 - Model M0 in BUGS

Part II

- Model Mb (behavioral response), Model Mt and related....
- Model selection in BUGS

Transition to spatial capture-recapture

Part III

- Model Mh
- Discrete class models (stratified populations)

Part IV

- Model Mx (individual Covariates)

Closed populations

- Simplest conceptual model of a population is that it is “closed”. This has two components:
 - (a) Demographic closure. No recruitment and no mortality
 - (b) Geographic closure. Animals don't leave the population (no emigration) or enter the population (no immigration).
- Model is that of a **fish bowl** or other spatially constrained population over a short period of time
- Closure cannot possibly hold in real populations.

Sampling a closed population

- Sampling model: individuals are **randomly selected** from a population with probability p == *per sample encounter or capture or detection probability*
- Conceptually this is a Bernoulli sampling model: whether each individual appears in the sample is a “coin toss”:

$$y[i] \sim \text{Bernoulli}(p) \quad \text{for } i = 1, 2, \dots, N$$

N = population size

- CR models: many different ways that p can vary (later...)

Closed populations: data structure

- We estimate p by obtaining replicate samples from the population. Let K = number of replicate samples. Individuals are released after each sample, may be recaptured.
- Produces **individual encounter histories** ($n \times K$ matrix)

	sample 1	sample 2	sample 3	TOTAL
Individual 1	1	0	1	$y_1 = 2$
Individual 2	0	0	1	$y_2 = 1$
Individual 3	1	1	1	$y_3 = 3$
etc..				
Individual n	0	1	0	$y_n = 1$

Closed population models

- We need to estimate p in order to estimate N

Under random sampling:

$$n \sim \text{Binomial}(N, \bar{p})$$

This is the probability that an individual appears in the sample over the K occasions.

$$\bar{p} = 1 - (1 - p)^K$$

The **heuristic estimator** of N :

$$E(n) = \bar{p} * N$$

$$N = n / \bar{p}$$

(“moment estimator”, equate the 1st moment of our statistic n to its expected value and solve)

Closed population models

- Estimating p is really important!
- How do we estimate p ?
- Dozens of models have been proposed that differ mainly in how p varies by individuals, time, etc..

Otis et al (1978) characterization of closed models

- The standard models:
 - M_0 = “the null model”, p is constant in all dimensions
 - M_t = p is a function of sample occasion , $p(t)$
 - M_b = behavioral response model. Trap happiness or shyness
 - M_h = individual heterogeneity
 - M_{bt} = time + behavior, or time*behavior
 - M_{bh} , M_{th} , M_{bth}
- See Kery and Schaub (2012) Ch. 6 for how to do all of these in WinBUGS/JAGS

MODEL M0

Model M0 is a common point of reference in capture-recapture. It consists of the following assumptions:

- Encounter probability, p , constant for all sample occasions and all individuals
- Then, encounter observations are Bernoulli random variables (just coin flips) and the individual frequencies are binomial:

$$y[i,k] \sim \text{Bernoulli}(p) \text{ for all } i=1,2,\dots,N \text{ and } k=1,2,\dots,K$$

-- same as --

$$y[i] \sim \text{Binomial}(K, p) \text{ for all } i=1,2,\dots,N$$

ANALYSIS OF MODEL M0

- Looks like binomial GLM, logistic regression, etc..
- Key technical issue: unlike a typical GLM, N , the size of some ideal data set, is unknown
- 3 things we have to talk about:
 - “conditional likelihood”
 - “full likelihood”
 - “data augmentation”

The binomial model and the likelihood

- Under model M0 assumptions, encounter frequencies are binomial:

$$y_i \sim \text{Binomial}(K, p) \text{ for all } i=1,2,\dots,N$$

- **But N is not known**, we only observe y_i IF $y_i > 0$. i.e., the observed data have a “**zero-truncated binomial**” distribution

$$f(y) = \text{Bin}(y; K, p) / (1 - (1-p)^K)$$

- **This is the basis of the “conditional likelihood” for estimating parameters of closed population models.**
- This is called the “**conditional likelihood**” because it is “conditional on capture”, i.e., conditional on $y > 0$, or “conditional on n ”

Conditional likelihood in R

```
lik0.cond<-function(parms) {  
  p<-  plogis(parms[1])  
  pcap<- 1-(1-p)^K  
  part1<- sum(log(dbinom(y, K, p) / pcap))  
  -1*(part1)  
}
```

The full likelihood

- But n is also part of the observable data. What is the distribution of n ?

$$n \sim \text{Bin}(N, 1-(1-p)^K)$$

- So the “joint likelihood” or “full likelihood” is the product of the previous bit (the conditional likelihood) and this bit for n :

$$\begin{aligned} \text{Full likelihood} &= [\text{conditional likelihood}] * \text{Bin}(N, 1-(1-p)^K) \\ &= \text{binomial likelihood with combinatorial term} \end{aligned}$$

This is called the “full likelihood” “joint likelihood” “unconditional likelihood” **because it has N in it.**

The full likelihood as an R function

```
lik0<-function (parms) {  
  p<-  plogis (parms [1])  
  n0<-  exp (parms [2])  
  N <-nind + n0  
  part1<- sum (log (dbinom (y, K, p)))  
  part2<-lgamma (N+1) -  
          lgamma (n0+1) + n0*log (dbinom (0, K, p))  
  -1* (part1 + part2)  
}
```

In R, $\text{lgamma}(N+1) = \log(\text{factorial}(N))$

Simulate some data and obtain the MLE

R work session

Fort Drum bear data

Hair snare study

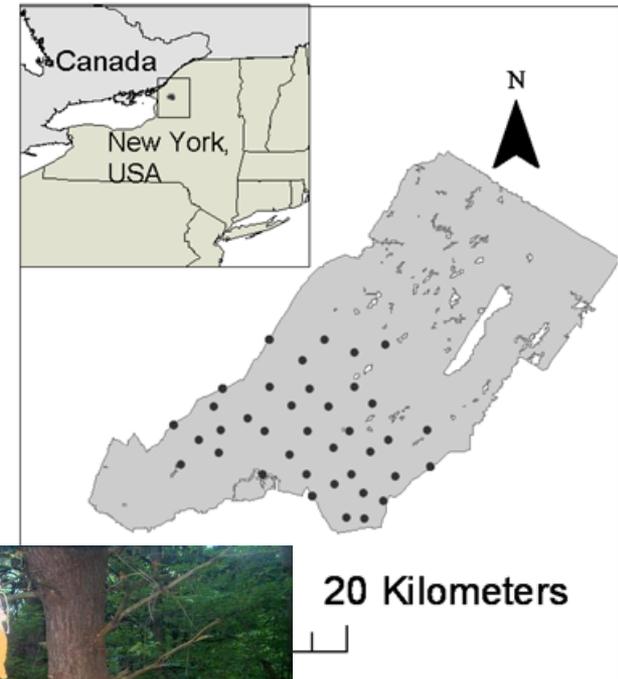
J = 38 hair snares

K = 8 weeks of sampling

n = 47 individuals captured

Load the data:

```
library(scrbook)  
data(beardata)
```



Fort Drum bear data

```
> library(scrbook)
> data(beardata)

> str(beardata)
List of 4
 $ trapmat      : 'data.frame':      38 obs. of  2 variables:
  ..$ V1: num [1:38] 448 439 439 442 442 ...
  ..$ V2: num [1:38] 4886 4881 4879 4884 4881 ...
 $ bearArray: num [1:47, 1:38, 1:8] 0 0 0 0 0 0 0 0 0 0 ...
 $ flat       : num [1:151, 1:4] 1 1 1 1 1 1 1 1 1 1 ...
  ..- attr(*, "dimnames")=List of 2
  .. ..$ : NULL
  .. ..$ : chr [1:4] "Session" "ID" "Occasion" "trapID"
 $ sex       : num [1:47] 1 1 2 1 1 1 1 2 1 2 ...
```

BASIC DATA FORMATTING

- In practice we have too much data for ordinary capture-recapture models
 - Individuals can be captured at > 1 trap during a sample occasion
- Therefore we have to summarize the data (i.e., throw some of it out)
- A typical encounter data file (EDF) has 3 pieces of information
 - Individual captured
 - Trap of capture
 - Occasion of capture

BASIC DATA FORMATTING

- A typical encounter data file (EDF) has 3 pieces of information
 - Individual captured
 - Trap of capture
 - Occasion of capture
- It is convenient to organize this into a 3-dimensional array:
individuals x traps x occasions
- In order to fit ordinary CR models we need to reduce this to a 2-dimensional matrix: **individuals x occasions**
- Lets do this for the Fort Drum bear data

THIS IS REALLY IMPORTANT!

- `bearArray` = the encounter data, is a **3-d array**.....
 - Have to summarize over traps to fit **ordinary closed models**
 - Multiple captures in a sample occasion **have no meaning**

```
y <- beardata$bearArray
y <- apply(bearArray,c(1,3),sum)
y[y>1] <- 1 # multiple captures are redundant.
y.summed <- apply(y,1,sum)# total encounters out of K
```

- We model either the matrix `y` or the vector `y.summed`

Fort Drum bear data

R work session

Summary so far

Model M0

Its essence is a simple binomial model, just like logistic regression

- Conditional likelihood: “zero-truncated” binomial. Single parameter p .
- Full likelihood: binomial likelihood (has a term for n_0 “all zero” encounter histories)

Up next: Bayesian analysis

- We analyze the full likelihood using a method known as data augmentation. This creates a “zero-inflated” binomial model.

BAYESIAN ANALYSIS OF CLOSED CAPTURE-RECAPTURE MODELS

- If N is known, Model M_0 is just a logistic regression:

```
model {  
  
  p ~ dunif(0, 1)  
  
  for (i in 1:N) {  
    y[i] ~ dbin(p, K)  
  }  
  
}
```

But N is not known. Conceptually we could just put a prior on N , e.g., $N \sim \text{Dunif}(0, 1000)$, and analyze the model using standard methods of MCMC

However, the size of the data set, N , is a parameter of the model so as N is updated in the MCMC algorithm the size of the data set must change. **Can't do this in WinBUGS/JAGS.**

Bayesian analysis of closed population models

- Prior distributions:

- $N \sim \text{Dunif}(0, M)$, for M some big number
- $p \sim \text{unif}(0,1)$

Not amenable to a naïve implementation by MCMC (esp in BUGS/JAGS) because N , a parameter, the number of individual effects, is unknown. “variable dimension parameter space”

- Therefore:
 - RJMCMC/“Trans-dimensional” Gibbs sampling
 - **Data augmentation** <- easier, can be done in BUGS

DATA AUGMENTATION: HEURISTIC

- $N \sim \text{Dunif}(0, M)$ implies a “data set” with $M-n$ all-zero encounter histories. Some of the $y=0$ observations correspond to real individuals and some of them do not.
- Implementation: We add too many zeroes to the dataset – creating a zero-inflated version of the known- N dataset
- Model for the augmented data set is a zero-inflated binomial
- **THIS IS AN OCCUPANCY MODEL!**

HEURISTIC DEVELOPMENT

Occupancy data					
Site	-	occasion	-		
1	0	1	0	1	1
2	0	0	1	0	0
3	1	1	0	0	0
4	0	0	1	1	0
5	0	1	1	1	1
6	0	0	1	1	0
7	1	1	1	1	1
8	1	0	1	1	0
	0	0	0	0	0
	0	0	0	0	0
	0	0	0	0	0
	0	0	0	0	0
	0	0	0	0	0
M	0	0	0	0	0

Zeros are observed.
Allocate zeros to
"fixed" and
"sampling"

Model M0					
Ind.	-	occasion	-		
1	0	1	0	1	1
2	0	0	1	0	0
3	1	1	0	0	0
4	0	0	1	1	0
5	0	1	1	1	1
6	0	0	1	1	0
7	1	1	1	1	1
8	1	0	1	1	0

Zeros are NOT
observed. How many
"sampling" zeros are
there?

Model M0 + DA					
Ind.	-	occasion	-		
1	0	1	0	1	1
2	0	0	1	0	0
3	1	1	0	0	0
4	0	0	1	1	0
5	0	1	1	1	1
6	0	0	1	1	0
7	1	1	1	1	1
8	1	0	1	1	0
	0	0	0	0	0
	0	0	0	0	0
	0	0	0	0	0
	0	0	0	0	0
	0	0	0	0	0
M	0	0	0	0	0

Bound $N \leq M$ where
M is fixed.
Treat Model M0 as an
occupancy model.

DA AND OCCUPANCY MODELS

- DA makes capture-recapture models the same as occupancy models.
- The parameter ψ replaces population size N . They are related as follows: $N \sim \text{Binomial}(M, \psi)$

WHY CAN WE DO THIS?

- $N \sim \text{Unif}(0, M)$

- **Same as:**

- $N | \psi \sim \text{Bin}(M, \psi)$ $M = \text{fixed}$

- $\psi \sim \text{uniform}(0, 1)$

This 2-part prior implies: $N \sim \text{Uniform}(0, M)$, standard distribution theory result

- **Same as:**

- $z[i] \sim \text{Bern}(\psi)$ for $i=1, 2, \dots, M$ “data augmentation variables”

- $y[i] \sim \text{Bern}(p * z[i])$

- $\psi \sim \text{dunif}(0, 1)$ “data augmentation parameter”

- **The augmented data create a super-population of individuals available to be “recruited” by the MCMC algorithm.**

Fort Drum bear data

- Fit Model M0 in WinBUGS and JAGS using data augmentation

SUMMARY OF PART 1

- The essence of closed CR models is the binomial observation model for encounter frequencies
- Data augmentation is something you are probably unfamiliar with but it is really easy to analyze CR models using MCMC (esp. in BUGS).
- DA converts all capture-recapture models to “zero-inflated” models of one sort or another.
- We analyze all CR and SCR models using data augmentation. [even when we write our own code!]