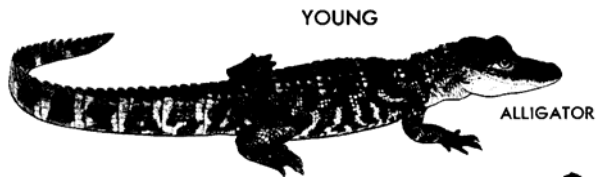


Begin Capture-Recapture Material

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CAPTURE-RECAPTURE MODELS: OVERVIEW

INTRODUCTION

CLOSED POPULATION MODELS

Two Samples Case (Lincoln-Petersen)

General Case

OPEN POPULATION MODELS

Survival- Cormack-Jolly- Seber Model

Popn Size and Recruitment- Full Jolly-Seber Model

Multi-State Models

COMBINATION CLOSED AND OPEN POPN MODELS

1. INTRODUCTION

- History of capture-recapture goes back to Laplace (1786) who used it to estimate the population size of France.
- Explosion of work since the 1950s. Applications first to fish and wildlife populations, but now there are many other examples such as the census undercount problem.
- Primary sources are my 1990 Wildlife monograph and the appropriate sections in Williams et al.(2002)
- My knowledge of this area has been profoundly influenced by Jim Nichols, Ken Burnham, Jean-Dominique Lebreton, Steve Buckland, Neil Arnason, John Skalski, and Cavell Brownie.

INTRODUCTION (continued)

In addition, older workers like Richard Cormack, George Seber, George Jolly, and Douglas Robson, my graduate advisor at Cornell, were also crucial and I thank them for insights and intelligence.

I want to mention that there are many related areas of study like tag-return models, removal and catch-effort models, selective removal models and methods for radio-tagged animals. We will also discuss these.

MARKING METHODS

There are so many we can't list them all:

- Leg bands (birds, mammals)
- Neck collars (geese)
- Nasal tags (ducks)
- Fin tags (fish)
- Fin clips (fish)
- Natural marks photo id (whales)
- Natural marks genetic id (bears)
- Toe clippings (mammals)
- Radio tags (all)
- Radio isotope tags (otters)

RECAPTURE METHODS

Classic Recaptures- traps, nets etc used for all captures

Example: Small mammal traps

Example: Birds captured and recaptured in mist nets

Resighting- After first captures all subsequent “captures” are by resighting.

Example: Geese with visible neck collars

Example: Tagged Raccoons “caught” by a camera trap.

Example: Naturally marked tigers “caught” by camera trap

2. THE LINCOLN-PETERSEN MODEL

2.1 Estimation of population size

2.2 Model assumptions

2.3 Examples

CAPTURE-RECAPTURE MODELS

LINCOLN-PETERSEN MODEL

N - Population size

n_1 - No. of marked animals in the population

n_2 - Sample size

m_2 - No. of marked animals in the sample

Sample

Population

$$(m_2/n_2) \approx (n_1/N)$$

$$\hat{N} = n_1 n_2 / m_2$$

CAPTURE-RECAPTURE MODELS

LINCOLN-PETERSEN MODEL

$$\hat{N} = n_1 n_2 / m_2$$

Unsatisfactory in small samples!

What happens if no marked animals in second sample?

A modification has been developed.

CHAPMAN'S MODIFICATION TO REDUCE BIAS

$$\frac{m_2 + 1}{n_2 + 1} = \frac{n_1 + 1}{N + 1}$$

$$\hat{N}_c = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

This estimator is **approximately** unbiased. (Some negative bias)

Unbiased: If you repeated the study many times and took the average \bar{N} , it would be equal to N .

Variances and St Errors are given in the text

PETERSEN MODEL ASSUMPTIONS

1. Closure
2. Equal Catchability
3. Zero Mark Loss (Marking is definitive)

THE CLOSURE ASSUMPTION

The population is closed to:

additions: births, immigrants

and to

deletions: deaths, emigrants

THE EQUAL CATCHABILITY ASSUMPTION

Two General Alternatives that will be explored in depth later.

1. Heterogeneity

Animals may vary in capture probability due to age, sex, social status, or many other factors.

2. Trap response

Animals may vary in capture probability according to their previous capture history:

“Trap shy” and “Trap happy”

THE EQUAL CATCHABILITY ASSUMPTION

Discuss Bias in these Cases. (Direction, Magnitude).

1. Heterogeneity?

2. Trap response

Trap Happy?

Trap Shy?

THE NO-MARK LOSS ASSUMPTION

1. Loss of marks will cause serious overestimation of population size.
2. Can estimate and adjust for mark loss if use a double marking scheme.

We need to assume that the two tags are lost independently.

PETERSEN MODEL EXAMPLE 1.

(RABBITS FROM MONOGRAPH, Text p. 296)

$n_1 = 87$ (marked with paint)

$n_2 = 14$ (second sample by resighting)

$m_2 = 7$ (marked in second sample)

$$\hat{N}_c = \frac{88 \times 15}{8} - 1 = 164$$

95 % *CI*

$$164 \pm 1.96 \times SE(\hat{N})$$

$$164 \pm 1.96 \times 35.82$$

$$164 \pm 70$$

$$94 - 234$$

Second sample was too small to achieve good precision.!

PETERSEN EXAMPLE 2.

(QUAIL)

p. 11 of Wildlife Monograph

1. January: $n_1 = 148$ marked from live trapping (corn bait)

2. February: Controlled hunt

$n_2 = 82$ shot

$m_2 = 39$ shot were marked

$\hat{N}_c = 308$ $SE(\hat{N}_c) = 29.7$

95% *CI*

$308 \pm 1.96 \times 29.7$

308 ± 58

250 – 366

Note: Again two distinct sampling methods used.

PETERSEN EXAMPLE 3.

POPULATION SIZE OF FRANCE (Laplace 1783)

n_1 = number of births recorded in one year for France

n_2 = number of people in certain parishes

m_2 = number of births in those same parishes

FIRST RECORDED USE OF THE LINCOLN-PETERSEN MODEL!

PETERSEN EXAMPLE 4. CENSUS UNDERCOUNT ADJUSTMENT

One stratum - Black males

n_1 = number found by census

n_2 = number found in Post Enumeration Survey Sample (PES)

m_2 = number in PES that were also found in census

Overall – There are many stratum estimates which have to be added together

CAPTURE-RECAPTURE MODELS

LINCOLN-PETERSEN MODEL

Design Issues (14.1.4)

Precision- Adequate capture probabilities to estimate standard errors that are small.

Minimise Model Bias- Satisfy Assumptions

1. **Closure**- Short studies, no mortality, no recruitment, no immigration or emigration.

2. **Equal Catchability**

Heterogeneity- Hard to avoid unless one can use different methods of capture in each sample. Problem is if some animals high or low capture probs in both samples

Trap Response- Using two different methods again good. Baited traps raise plus and minus issues.

Note- We can handle these issues better if we add some additional samples(see later in lecture)

3. **No Tag Loss** – Obviously avoid, Use double tagging if a problem.

CLOSED vs. OPEN

- I shall concentrate on situations where each animal *uniquely* marked so that a *detailed capture history* of each animal form the basis of the data modeled.
- I shall define a *closed population* as one that is constant i.e., there are no *additions* due to *recruitment* or *immigration* and there are no *deletions* due to *mortality* or *emigration*.
- I shall define an *open population* as one that allows the above process of *additions* or *deletions*. Often in open population models it will not be possible to separate *recruitment* from *immigration*, or *mortality* from *emigration*, but there are some exceptions.

CAPTURE-RECAPTURE MODELS

TWO SAMPLES

CLOSED POPULATION

Lincoln-Petersen (14)

SEVERAL SAMPLES > 2

CLOSED
POPULATION
MODELS (14)

OPEN
POPULATION
MODELS (17-18)

COMBINATION
CLOSED +
OPEN (19)

JOLLY-SEBER MODEL

SURVIVAL
MODELING (17.1,2)

STAGE
MODELING (17.3)

POPULATION SIZE AND
CHANGE (18)

2. CLOSED POPULATION MODELS (14.2)

- 1 Introduction
- 2 M_0 : The Equal Catchability Model
- 3 M_b : Trap Response Model
4. M_h : The Heterogeneity Model
5. M_{bh} : The Heterogeneity and Trap Response Model
- 6 M_t : The Time Model (Schnabel)
- 7 Other Time Dependent Models
- 8 Model Selection (CAPTURE, Then AIC)
- 9 Example

Hypothetical example to illustrate that capture history information can be summarized by a series of zeros and ones for each animal.

	Capture		Period		
Animal	1	2	3	4	5
1	1	1	0	0	0
2	1	0	0	0	0
3	1	0	0	1	0
4	0	1	1	1	1

1. INTRODUCTION

- Remember that a closed population means that the population size stays constant during the whole study.
- Key older references are Otis et al. (1978) and White et al. (1982).
- There are eight models considered based on varying capture probabilities due to:
 - Heterogeneity
 - Trap Response
 - Time
 - and combinations of them.
- There is a program CAPTURE which can estimate parameters and carry out model selection. CAPTURE can be accessed through MARK. There are also additional newer procedures in MARK.

Table 3.1. Capture-recapture models for closed populations that allow for unequal capture probabilities. Monograph with minor changes.

<i>Model*</i>	<i>Source of variation in capture probability</i>	Heterogeneity	Trap response	Time	Estimator availability
M_o					yes
M_h	X ^a				yes
M_b			X		yes
M_{bh}	X		X		yes
M_t				X	yes
M_{th}	X			X	yes
M_{tb}			X	X	yes
M_{tbh}	X		X	X	no

*This set of 8 models comes from Otis et al. (1978).

^aXs denote the sources of variation in capture probability incorporated in the models.

2. M_0 : THE EQUAL CATCHABILITY MODEL

- * The simplest model but usually unrealistic
- * There are two parameters in this model
 - N - the population size
 - P - the probability of capture, which is constant over all animals over all periods.
- * M.L. Estimators found iteratively using the programs **CAPTURE** or **MARK**.
- * Estimators can be highly biased if heterogeneity or trap response is occurring. Variation in capture probabilities, due to time, are less troublesome.

3. M_b : TRAP RESPONSE MODEL

- This model makes the following **assumptions**:
 1. Every unmarked animal in the population has the same probability of capture (**p**) for all samples.
 2. Every marked animal in the population has the same probability of recapture (**c**) for all samples after it has been captured once.
- There are **three parameters** in the model:
 - N** - the population size
 - p** - the probability of capture for unmarked
 - c** - the probability of capture for marked
- M.L. estimators found iteratively using programs **CAPTURE** or **MARK**.

The Trap Response Model and Removal

- Under Model M_b , animals do not contribute any information for population size estimation after first capture.
- They can be thought of as having been “removed” from the unmarked population.
- Thus this model is statistically equivalent to the removal model where animals are actually physically removed. We will return to this later on in the semester

4 M_h : THE HETEROGENEITY MODEL

- This model allows capture probabilities to vary by animal, due to heterogeneity, but there is no trap response or time variation.
- The parameters in the model are:
 - N - the population size
 - p_j - the capture probability of animal j for $j = 1, \dots, N$
 - p_j s are assumed to come from distribution $F(\mathbf{p})$, otherwise the model is overparameterized.
- Estimators include:
 - Burnham's Jackknife
 - Lee and Chao's Coverage Estimator
 - Norris nonparametric MLE (Mixture Model)
- Burnham's estimator is widely used, but it has a questionable theoretical basis. It is given by program **CAPTURE**.

5. M_{bh} : THE HETEROGENEITY AND TRAP RESPONSE MODEL

- This model allows capture probabilities to vary due to heterogeneity and trap response, but not time.
- The parameters in the model are:
 - N - the population size
 - p_j - the unmarked capture probability for the j th animal
 - c_j - the marked capture probability for the j th animal

The (p_j, c_j) are assumed to come from some bivariate distribution $G(p, c)$.

6. M_t : THE TIME MODEL

- This is the traditional **Schnabel model** that only allows for time variation in capture probabilities.
- The parameters in the model are:
 - N - the population size
 - p_1, p_2, \dots, p_k - the unmarked capture probability of all animals in each sample.
- Programs **CAPTURE** or **MARK** provides the MLEs of N and the p s.

These estimators are not robust to heterogeneity and trap response.

7. OTHER TIME DEPENDENT MODELS

- Model M_{tb} - now has estimator available in CAPTURE
- Model M_{th} - now has estimator available in CAPTURE
- Model M_{tbh} - is only a conceptual model and has no estimators of N available.

MODEL SELECTION

CAPTURE

- There is an old procedure in CAPTURE, which is quite complex, also it only works well if data are very good, i.e., high capture probabilities. The method is based on a whole series of tests which are summarised into one overall criteria between 0 and 1.

- Reduce the number of models to be chosen from if possible.

[Sometimes there may be biological reasons to eliminate some models, e.g, trap response. We will see this in the taxi cab example].

MARK

If one is using ML models in MARK then one can use AIC methods to chose among models

9. EXAMPLE

- Meadow vole study by James Nichols
- Five sampling periods
- Traps prebaited with corn
- Will show Model Selection Output
- Will show Model M_h : The Heterogeneity Model output, because it was the chosen model.

Precision of the estimator is quite good because of the high capture probabilities.

Table 3.3. Model selection procedure from program CAPTURE for the meadow vole data collected by J.D. Nichols at Patuxent Wildlife Research Center, Laurel, Maryland, in October 1981.

Model	M_0	M_h	M_b	M_{bh}	M_t	M_{th}	M_{tb}	M_{tbh}
Criteria	0.80	1.00*	0.38	0.59	0.00	0.32	0.52	0.98

This suggests one should use the M_h estimator although there is some evidence of trap response and time being present as well.

In the interests of simplicity and getting an estimate we need to use M_h estimator.

Table 3.4. Selected statistics and parameter estimated from program CAPTURE for meadow vole data collected at Patuxent Wildlife Research Center, Laurel, Maryland, in October 1981 by J.D. Nichols. Model M_h , the heterogeneity model, is used.

	Frequencies of capture ^a				
<i>i</i>	1	2	3	4	5
<i>F(i)</i>	29	15	15	16	27

Number of animals captured = 102^b

Average P-HAT = 0.44

Interpolated population estimate = 139, with Standard Error = 10.85

Approximate 95% Confidence Interval from 177 to 161

^a These are the numbers of animals caught from 1 to 5 times.

^bThis is the number of distinct animals captured at least once.

$p = 0.44$ is a very high probability

44% of animals were captured on each occasion

Taxi Cab Example from Edinburgh (Carrothers1973)

- Closed Population with a known population
N=420
- k=10 occasions on 10 days close together
- No trap response (:-)).
- Constant sampling effort so perhaps no time variation either.
- Heterogeneity likely.

Model selection criteria. Model selected has maximum value.

Model	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)
Criteria	0.91	1.00	0.45	0.61	0.00	0.51	0.39	0.6

Appropriate model probably is **M(h)**

Suggested estimator is **Jackknife** or **Chao** Estimator for M(h)

Model M(h) Suggested for use here

Jackknife 471 with standard error 36.32

Chao 407 with standard error 27.42

Finite Mixture approach did not work here. Huge SE!

Model M(0) Null Model not to be used

MLE 368 with standard error 14.4896

Always underestimates when there is heterogeneity.

M(t) very similar estimate to this one

MARK

- User friendly windows based program for capture-recapture, telemetry and band return models.
- Many options
- Can run CAPTURE and POPAN from MARK
- Uses AIC for model selection
- Allows multiple groups, age classes, multi-state extension, covariates
- Can download from their web site. Can also download an online book and other resources.

<http://welcome.warnercnr.colostate.edu/~gwhite/mark/mark.htm>

<http://www.phidot.org/software/mark/docs/book/>

Key References

Williams et al. (2002). Analysis and Management of Vertebrate Populations. Academic Press.

Amstrup et al. (2005). Handbook of Capture-Recapture Methods. Princeton University Press.

Pollock et al. (1990). Statistical Inference for Capture-Recapture Models. Wildlife Society Monograph. (pdf available). Old but still useful for the basics.