

**ESTIMATION OF ANIMAL ABUNDANCE
FOCUSING ON CAPTURE-RECAPTURE
METHODS**

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Lecture 18

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WHY ASSESS POPULATIONS?

- Animal populations are under threat from exploding human populations, development, and pollution. Some populations may also be subject to excessive fishing (tuna) or hunting (elephants).
- Need information to form basis of sound objective natural resource management based on scientific methods (often little science, politics, and emotion dominate).

OVERVIEW OF METHODS OF ASSESSING POPULATIONS

Direct methods of monitoring

Census Method

Count all animals in the population
(in usually unrealistic practice)

Sampling Methods

Count animals in sampling units (or areas)

Absolute Abundance

Estimate popn size by adjusting for 'unseen' animals and only part of area being sampled

Relative Abundance

Use incomplete count as an 'index' of popn size

CENSUS

Usually it is impossible to count all the members of a wildlife population for practical reasons.

- Exceptions are small, localized populations of highly visible and valuable endangered species.
- Examples are the California Condor (now extinct* in the wild) and the Puerto Rican Parrot (popn size in wild is only around 35 birds)

*recent releases

ABSOLUTE ABUNDANCE ESTIMATION

Not all area sampled and not all animals 'seen'

$$\hat{N} = C / \alpha \hat{\beta}$$

C = count of animals seen

α = fraction of area sampled

$\hat{\beta}$ = estimate of the fraction of animals seen or caught

Note: there are many ways to estimate β . For example, capture-recapture, line transects etc.

ABSOLUTE ABUNDANCE ESTIMATION

Example: Aerial survey of caribou in Alaska.

C = count of caribou seen = 551

α = fraction of area sampled = 0.1

$\hat{\beta}$ = estimate of the fraction of animals seen or caught = 0.5

Note: there are many ways to estimate β . For example, two independent observers in the plane. We will discuss details of this later in lecture.

$$\begin{aligned}\hat{N} &= C / \alpha \hat{\beta} \\ &= 551 / (0.1 \times 0.5) \\ &= 551 \times 10 \times 2 \\ &= 11020\end{aligned}$$

ABSOLUTE ABUNDANCE ESTIMATION

CAPTURE METHODS

- Capture-Recapture
- Removal and Catch-Effort
- Change-in-Ratio or Selective Removal

COUNT METHODS

- Line Transects
- Variable Circular Plots
- Double Sampling (e.g., ground, aerial)
- Counts from multiple observers with mapping

All can be viewed as methods to estimate β in

$$\hat{N} = C / \alpha \hat{\beta}$$

SYNOPSIS



Photo by Ken Felsman

INTRODUCTION

THE TWO-SAMPLE LINCOLN-PETERSEN MODEL

GENERALISATIONS

CLOSED MODELS

OPEN MODELS

THE ROBUST DESIGN

MARKING METHODS

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

Examples:

- Leg bands (**birds, mammals**)
- Neck collars (**geese**)
- Nasal tags (**ducks**)
- Fin tags (**fish**)
- DNA tags (**many**)
- Natural marks (**whales**)
- Toe clippings (**mammals**)
- Radio tags (**many**)



Why Are We Concerned About Salamander Populations?

?



Photo by Ken Felsman

- World-wide amphibian declines
- Indicator species of forest health
- Need for more extensive monitoring programs (DAPTF, ARMI, NAAMP...)
- **How to estimate abundance and diversity of amphibian systems?**

Elastomer marking by injecting different colours under the skin on different parts of the body to give unique combinations



(One of my Ph D students Larissa Bailey marked over 6,000 salamanders in 3 yr study in the Great Smokey Mountains National Park)

THE LINCOLN-PETERSEN MODEL

Estimation of population size

Model assumptions

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

$$\frac{\underline{m}_2 + 1}{n_2 + 1} = \frac{\underline{n}_1 + 1}{N + 1}$$

$$\hat{N}_c = \frac{(\underline{n}_1 + 1)(\underline{n}_2 + 1)}{(m_2 + 1)} - 1$$

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

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 from:
births, immigrants

and to deletions from:
deaths, emigrants

THE EQUAL CATCHABILITY ASSUMPTION

Two General Alternatives

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” or “Trap happy”

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 WILDLIFE MONOGRAPH, p. 11)

$n_1 = 87$ (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.

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

PERHAPS FIRST RECORDED USE OF THE
LINCOLN-PETERSEN MODEL!

PETERSEN EXAMPLE 3.

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

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.

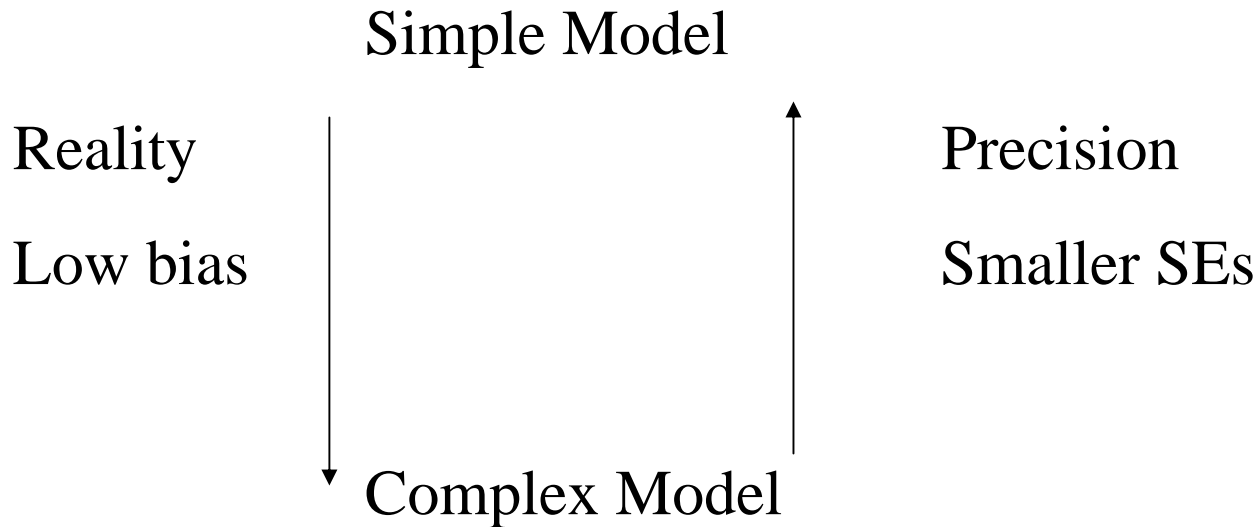
Note- We can handle these issues by better models if we add some additional samples (see later in lecture)

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

Statistical Modelling Approach

- Capture-recapture sampling leads to statistical models and hence is a complex form of model based sampling.
- One key concept is the likelihood and maximum likelihood estimation (We will derive some simple ones).
- Another key concept is that there is often a large number of possible models and so model selection using the AIC criteria is used. (I just mention this in case you are interested).

MODEL SELECTION



Key Points

Principle of parsimony.

Trading off Reality vs Precision

MODEL SELECTION

Akaike Information Criteria

- Reduce parameters to achieve parsimony and higher precision of estimates.
- Need enough parameters to be realistic model.
- We need a way of trading off reality (more parameters) vs precision (less parameters)!

MODEL SELECTION

Akaike Information Criteria

Use Model selection criteria which is to:

$$\text{Minimize } AIC = -2 \log L + 2(\# \text{ pars})$$

First term

-2 log L-note L is Likelihood function evaluated at the MLE values

Second Term

Penalty for over parameterization so we add a term of twice the no of parameters.

Maximum Likelihood Estimation for a Particular Model

- I will just show the likelihood method for closed capture-recapture sampling with 2 occasions but the ideas easily extend.
- Will show $L(N,p)$ for the Lincoln Petersen model
- Then use $L(N)/L(N-1) = 1$ and partial derivatives with respect to N .
- Will then look at more general models where trap response occurs.

Detailed Work on Likelihoods

- Will Use the whiteboard for this.
- I will start with the standard model where N , p_1 and p_2 are parameters.
- Later I will briefly discuss the trap response model where the parameters are N , p_1 , p_2 and c_2 .
- However to be able to be able to obtain estimates we have to put a restriction that $p = p_1 = p_2$ and $c=c_2$.

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

SEVERAL SAMPLES > 2

CLOSED
POPULATION
MODELS

OPEN
POPULATION
MODELS

COMBINED
CLOSED&OPEN
MODELS

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

GENERAL CLOSED MODELS

- 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 MARK which can estimate parameters and carry out model selection.

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</i>	<i>in</i>	<i>capture probability</i>
	Heterogeneity	Trap response	Time
M_o			Estimator availability 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.

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.

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 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.

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**.

M_h : THE HETEROGENEITY MODEL

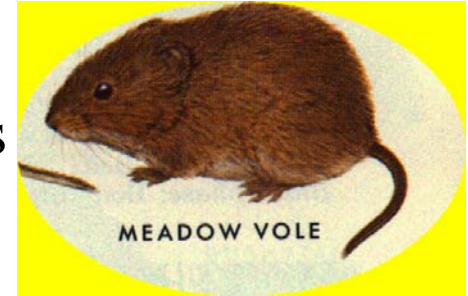
- This model allows capture probabilities to vary by animal, due to heterogeneity, but there is no trap response or time variation.
- The parameters in the model are:
 - N - the population size
 - p_j - the capture probability of animal j for $j = 1, \dots, N$
 - p_j s are assumed to come from distribution $F(\mathbf{p})$, 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**.

Combination Models

All the other models can also be
fitted using CAPTURE or
MARK.

EXAMPLE

- MD Meadow vole study by James Nichols
- Five sampling periods
- Traps prebaited with corn
- Will show Model M_h : The Heterogeneity Model output, because it was the chosen model using a model selection criteria. Heterogeneity models or trap response models are often needed in practice.



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

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, Scotland (Carrothers1973)

- Closed 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. Very complex
Model with several possible estimators

Chao 407 with standard error 27.42

Finite Mixture heterogeneity approach did not work here. Huge SE! Jackknife method also did not work well here. Heterogeneity models are complex to fit.

Model M(0) Null Model not to be used

MLE 368 with standard error 14.4896

Always underestimates when there is heterogeneity.



OPEN MODELS JOLLY-SEBER MODEL



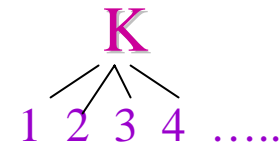
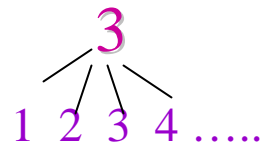
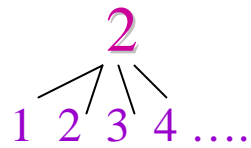
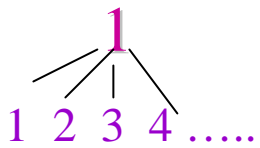
More Parameters Now

- Population Sizes
- Survival Rates
- Recruitment Rates
- Capture Probabilities

COMBINATION OF CLOSED AND OPEN MODELS

(“ROBUST DESIGN”)

PRIMARY PERIODS (e.g., months or years)



within (e.g., days)

ESTIMATION APPROACH

The population is open between the primary periods but closed between the secondary periods within a primary period. This allows more robust estimates of parameters than if we just had a series of primary periods with no secondary periods.

Striped Bass Case Study: Tag Return Models



Striped Bass

Morone saxatilis

Striped Bass Case Study: Tag Return Models

- Tags returned by anglers to the agency so somewhat similar to capture-recapture.
- We found Fishing and Natural mortality rates separately by age. We also had to estimate tag reporting rate.
- We also showed that recently that a disease outbreak of mycobacteriosis has caused the natural mortality rates to increase greatly.

Table 2. Parameter estimates with standard errors in parentheses from fitting the catch- and-release tag return models allowing age- and year-specific natural mortality and a selectivity model for fishing mortality to the Maryland striped bass data. Model (a) allows fishing mortality to vary by year ($F_y, F'_y, M_{Y_{91-98}}, M_{Y_{99-03}}, M_{A_{91-98}}, M_{A_{99-03}}, Sel_3, Sel_4, Sel_5$) and Model (b) allows fishing mortality to be constant before and after 1995, when fishing regulations were liberalized ($F_{91-94}, F_{95-03}, F'_y, M_{Y_{91-98}}, M_{Y_{99-03}}, M_{A_{91-98}}, M_{A_{99-03}}, Sel_3, Sel_4, Sel_5$). Reporting rates for both harvested and released fish were fixed at 0.43.

Parameter	(a)	(b)
F(91)	0.106 (0.014)	0.154 (0.007)
F(92)	0.163 (0.014)	0.154 (0.007)
F(93)	0.152 (0.011)	0.154 (0.007)
F(94)	0.162 (0.011)	0.154 (0.007)
F(95)	0.226 (0.013)	0.235 (0.007)
F(96)	0.190 (0.012)	0.235 (0.007)
F(97)	0.233 (0.015)	0.235 (0.007)
F(98)	0.244 (0.017)	0.235 (0.007)
F(99)	0.254 (0.019)	0.235 (0.007)
F(00)	0.260 (0.018)	0.235 (0.007)
F(01)	0.293 (0.022)	0.235 (0.007)
F(02)	0.230 (0.018)	0.235 (0.007)
F(03)	0.140 (0.022)	0.235 (0.007)
F'(91)	0.125 (0.016)	0.124 (0.016)
F'(92)	0.156 (0.013)	0.160 (0.014)
F'(93)	0.105 (0.009)	0.109 (0.009)
F'(94)	0.132 (0.010)	0.131 (0.010)
F'(95)	0.106 (0.009)	0.117 (0.009)
F'(96)	0.116 (0.009)	0.125 (0.010)
F'(97)	0.092 (0.009)	0.099 (0.009)
F'(98)	0.094 (0.010)	0.095 (0.010)
F'(99)	0.074 (0.010)	0.082 (0.010)
F'(00)	0.169 (0.014)	0.168 (0.014)
F'(01)	0.126 (0.013)	0.123 (0.012)
F'(02)	0.081 (0.009)	0.092 (0.009)
F'(03)	0.056 (0.012)	0.050 (0.011)
Sel3	0.663 (0.061)	0.627 (0.058)
Sel4	0.730 (0.044)	0.739 (0.044)
Sel5	0.967 (0.047)	1.000 (0.048)
MY_91-98	0.378 (0.021)	0.399 (0.021)
MY_99-03	0.836 (0.063)	0.858 (0.056)
MA_91-98	0.145 (0.009)	0.150 (0.009)
MA_99-03	0.673 (0.038)	0.645 (0.028)

Time Change 1999
M = 0.40 to 0.85 Younger
Fish (3-5)
M = 0.15 to 0.65 Adult Fish
(6+)

References for More Information

Pollock et al. (1990). Wildlife Monograph. I have the pdf and can send it to you if you are interested.

Thompson (2002). Sampling. Wiley. Chapter 18.

Williams, Nichols and Conroy. (2002). Analysis and Management of Animal Populations. Academic Press.

Jiang et al. (2007). Tag Return Models allowing for Harvest and Catch and Release: Evidence of Environmental and Management Impacts on Striped Bass Fishing and Natural Mortality Rates. NAJFM 27:387-396.