Lecture 19

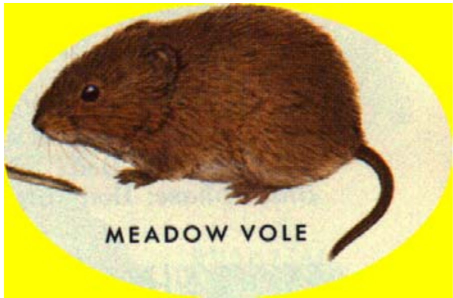
GENERAL JOLLY-SEBER MODEL

Brief Contrast of Survival Methods

Review CJS And Extensions

Open Cr Models For Estimating Popn

Size and Recruitment Related Parameters



OPEN CAPTURE- RECAPTURE MODEL

JOLLY-SEBER MODEL

FIRST CAPTURES(18)

Recruitment Models

Traditional JS

Super Population

Temporal Symmetry

RECAPTURES (17)

Cormack-Jolly-Seber

Restrictions

Generalisations

Multi-State Models

OPEN CAPTURE- RECAPTURE MODEL

JOLLY-SEBER MODEL

CORMACK-JOLLY-SEBER COMPONENT(17)

(Survival and Capture)

Restrictions

Parsimony

Generalisations

Multiple Groups
Covariates

Multi-State Models

Transitions, Survival,
Movement

Review CJS and Extensions

- Concepts of CJS
- Contrast to Telemetry and Tag-Return estimates of survival
- Multi-State Models

Cormack-Jolly-Seber Models Concepts

- Estimates Apparent Survival

$$\varphi = SF$$

$$S - Survival$$

$$F - Fidelity\,(1 - Emigration)$$

- Uses the conditional recapture likelihood as that is where the information on survival is in the capture history data.
- I showed you how to consider multiple groups and other aspects of analyses in MARK. The principle of parsimony and use of AIC was a central concept.One could also consider multiple ages as well.
- Tag induced mortality and Tag loss is confounded with true mortality.
- Heterogenity of capture probability is not a big problem-robustness.
- Any other key concepts you can think of?

Contrast CJS, Tag-Return, Telemetry Survival Estimates

What if you were designing a survival study in the field? How would you decide which one to use? Adv and Disadv of each one?

CJS Adv and Disadv-

Tag-Return Adv and Disadv-

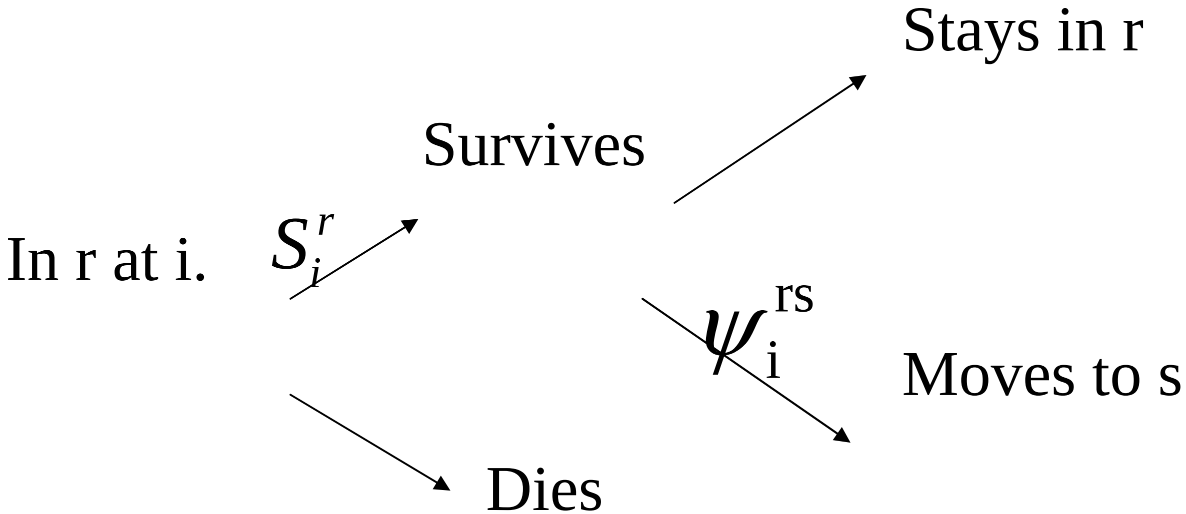
Telemetry Adv and Disadv-

Multi-State-Generalisation

SURVIVAL AND MOVEMENT

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = S_i^r \psi_{\mathrm{i}}^{\mathrm{rs}}$$

If movement is at end of interval



MULTI-STATE MODELS

- Used SURVIV, MSSURVIV and MARK on two examples to illustrate this methodology.

•Microtus Mass Class Model

Nichols et al. (1992) Ecology

•Canada Geese going to three different wintering grounds,

Mark-resight Hestbeck et al.(1991) Ecology

Fish Movement between locations

Schwartz et al Biometrics 1993

Roseate Tern breeding colonies

Spendelow et al (1995) Ecology

•Whale Size States

Fujiwara and Caswell Ecology 2002

•Butterflies in patches

Hanski Ecology 2001and other papers

EXAMPLE

Some of many Possible Capture Histories

Five Periods and Two States A and B

0 means not detected in either state

AA0AA

ABA0A

A0BA0

A0000

BBA00

BAA00

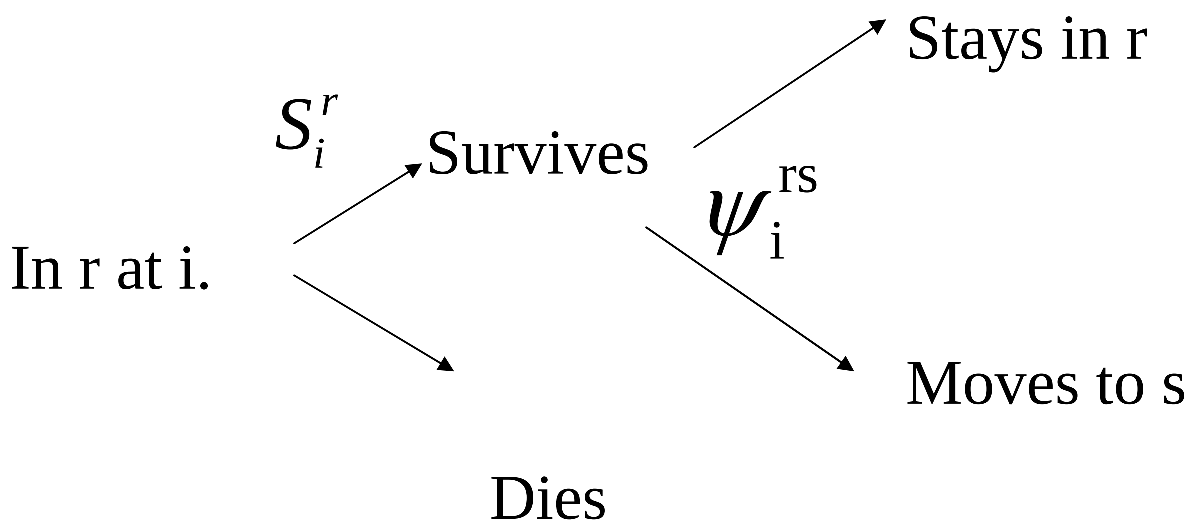
000BA

0A0B0

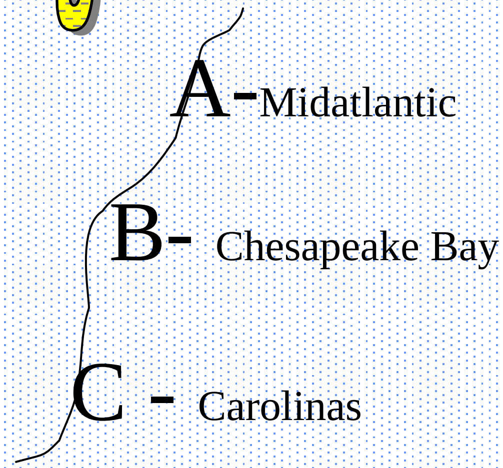
SEPARATION OF SURVIVAL AND MOVEMENT

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = S_i^r \psi_{\mathrm{i}}^{\mathrm{rs}}$$

If movement is at end of interval



Wintering Geese



Estimation of survival and movement probs

A → A	A → B	A → C
B → A	B → B	B → C
C → A	C → B	C → C

WINTERING CANADA GEESE

SURVIVAL PROBS SHOWN HERE (S^r)

Location	Estimate(SE)
A	0.58 (0.015)
B	0.66 (0.016)
C	0.49 (0.019)

WINTERING CANADA GEESE

MOVEMENT PROBS ONLY SHOWN HERE* (ψ^{rs})

Transition	Estimate(SE)
A A	0.71(0.016)
A B	0.29(0.016)
A C	0.00(0.001)
B A	0.10(0.006)
B B	0.89(0.007)
B C	0.02(0.002)
C A	0.07(0.010)
C B	0.37(0.024)
C C	0.56(0.025)

*Probability of movement given survived and they assumed the animals moved at the end of interval.They add to 1 in each set.

RETURN TO OPEN CAPTURE- RECAPTURE MODELS FOR ESTIMATING ABUNDANCE AND RECRUITMENT

There are three components of the Full Likelihood for the Jolly-Seber Model.

$L = L_1$(First Captures)*L_2(Losses on Capture)*L_3(Recaptures)

L_1(First Captures) - allows estimation of population sizes and recruitment parameters (and also includes survival and capture probabilities).

L_2(Losses on Capture) - important that we allow for this but these parameters are not of biological interest.

L_3(Recaptures) - this is the CJS likelihood and this component is where we estimate survival and capture probabilities

OPEN CAPTURE- RECAPTURE MODEL

JOLLY-SEBER MODEL

- FIRST CAPTURES(18)
  - Recruitment Models
  - Traditional JS
  - Super Population
  - Temporal Symmetry
- RECAPTURES (17)
  - Cormack-Jolly-Seber
  - Restrictions
  - Generalisations
  - Multi-State Models

OPEN CAPTURE- RECAPTURE MODELS FOR ESTIMATING ABUNDANCE AND RECRUITMENT

L_1(First Captures) - allows estimation of population sizes and recruitment parameters (and also includes survival and capture probabilities).

There are three different but related approaches for handling this likelihood component.

OPEN CAPTURE- RECAPTURE MODEL

JOLLY-SEBER MODEL

RECRUITMENT MODELS(18)

Traditional JS

Super Population

Temporal Symmetry

OPEN CAPTURE- RECAPTURE MODELS FOR ESTIMATING ABUNDANCE AND RECRUITMENT

- Original Jolly-Seber Intuitive Approach based on Moment estimators for N and B parameters. See 18.2.
- "Super Population" Approach. See 18.3.
- "Temporal Symmetry" Approach. See 18.4.

Jolly-Seber Intuitive Approach to Estimation.

Goes back to Jolly(1965) and Seber(1965)

Population Size Estimation

$$\hat{N}_i = n_i/\hat{p}_i$$

$$i = 2,..k-1$$

Birth Numbers Estimation

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i(\hat{N}_i - n_i + R_i)$$

$$i = 2,..,k-2$$

Table 4.4. Jolly-Seber estimates and approximate standard errors[a] for a gray squirrel population at Alice Holt Forest Research Station, Surrey, England, November 1972–September 1974.

Period	Date	$\tilde{N}_i$[b]	$\widehat{SE}$	$\tilde{\phi}_i$	$\widehat{SE}$	$\tilde{B}_i$	$\widehat{SE}$
1	Nov 1972			0.94	0.037		
2	Dec 1972	47.1	0.39	0.96	0.030	6.3	0.77
3	Jan 1973	51.3	0.70	1.00	0.004	4.5	1.27
4	Feb 1973	56.0	1.19	0.99	0.023	5.1	1.53
5	Mar 1973	60.5	1.51	0.94	0.041	0.0	1.06
6	Apr 1973	54.9	1.23	0.95	0.038	0.0	0.00
7	May 1973	52.3	0.60	1.00	0.030	3.9	1.22
8	May–Jun 1973	56.5	2.06	0.90	0.052	3.7	1.45
9	Jun 1973	54.6	1.57	0.92	0.067	8.7	3.30
10	Jul 1973	58.9	4.59	0.84	0.066	2.2	6.60
11	Aug 1973	51.8	5.99	1.00	0.000	0.0	5.99
12	Sep 1973						
13	Oct 1973						
14	Nov 1973						
15	Dec 1973	58.3	9.20	0.93	0.115	1.0	6.57
16	Jan 1974	55.3	4.30	0.98	0.068	13.1	8.25
17	Feb 1974	66.4	8.14	1.00	0.071	6.8	10.14
18	Mar 1974	74.5	7.91	0.93	0.067	0.0	6.28
19	Apr 1974	58.4	2.13	0.99	0.071	18.2	4.22
20	May 1974	76.0	6.12	1.00	0.168	33.9	8.86
21	Jul 1974	110.3	18.10	0.21	0.048	0.0	2.23
22	Aug 1974	21.9	0.00				
23	Sep 1974						

[a] $\widehat{SE}(\tilde{N}_i)$ and $\widehat{SE}(\tilde{B}_i)$ include only sampling variation or "error of estimation"; $\widehat{SE}(\tilde{\phi}_i)$ was obtained using the full variance estimator of Jolly (1965).

[b] Notation explained in Table 4.1.

Jolly-Seber Intuitive Approach

Population Size Estimation

$$\hat{N}_i = n_i / \hat{p}_i$$

$$i = 2,..k - 1$$

Population Change Estimation(λ) is also very important to ecologists

$$\hat{\lambda}_i = \hat{N}_{i+1} / \hat{N}_i$$

$$i = 2,...,k - 2$$

Note-These quantities estimable are for the full model if we assume survival or capture is constant over time we can estimate all the quantities ie at 1 and k-1 as well.

Jolly-Seber Intuitive Approach

Population Change(λ) Estimation.

$$\hat{\lambda}_i = \hat{N}_{i+1}/\hat{N}_i$$

eg for Squirrel Example

$$\hat{\lambda}_2 = \hat{N}_3 / \hat{N}_2 = 51.3/47.1 = 1.09$$

Could also do a regression of estimated population size with time and estimate an average lambda that way.

Problems- **SEs will be large, Cannot allow important restriction that recruitment rate is constant over time or perhaps other restrictions.**

Super Population Approach

Sources

Crosbie and Manly (1985)

Schwartz and Arnason (1996) Biometrics Paper

Program POPAN

Now can be accessed through MARK

Super Population Approach

Time Line of New Animals coming into the population

1 2 3…. (k-1) k

B_0 B_1 B_2 $B_{(k-1)}$

$N = B_0 + B_1 + B_2 + \ldots + B_{(k-1)}$ is the super population of all the animals that existed at some time during the study.

$$N = \sum_{i=0}^{k-1} B_i$$

with

$$B_0 = N_1$$

Super Population Approach

Likelihood Component 1

Recruitment Parameterisation (New)

$$\{N,\beta_0,\beta_1,\beta_2,\ldots,\beta_{(k-1)}\}$$

Note-the β's are entry probabilities and

$$\beta_0+\beta_1+\ldots+\beta_{(k-1)}=1$$

Likelihood Component 3 (CJS)

Survival Parameterisation (Earlier)

$$\{\phi_1,\phi_2,\ldots,\phi_{(k-1)}\}$$

Capture Parameterisation(Earlier)

$$\{p_1,p_2,\ldots,p_k\}$$

Super Population Approach

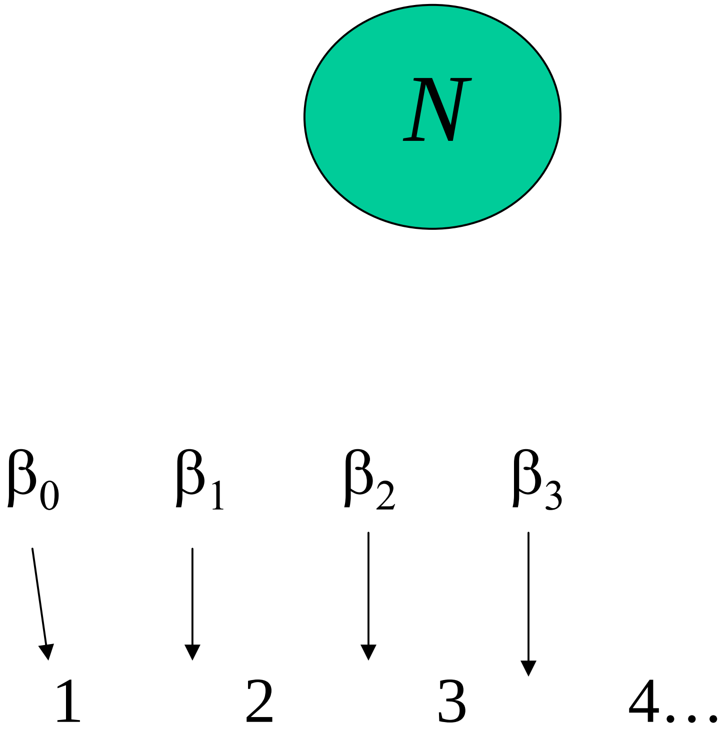
Recruitment Parameterisation

$\{N, \beta_0, \beta_1, \beta_2, \ldots, \beta_{(k-1)}\}$

β's are entry probabilities (new animals coming in) and they have to sum to 1.

$$\sum_{0}^{k-1} \beta_i = 1$$

Schematic of Recruitment Process in Super Popn Models



All animals that ever came into popn.

βs are the period entry probabilities. Note that the first one is different than the others. We define it as probability that animals that were there before study started and survived to period 1.

Super Population Approach

Recruitment Parameterisation

$$\{N, \beta_0, \beta_1, \beta_2, \ldots, \beta_{(k-1)}\}$$

Recall that the super population size is

$$N = B_0 + B_1 + B_2 + \ldots + B_{(k-1)}$$

β's are entry probabilities (new animals coming in) and they have to sum to 1.

$$\sum_{0}^{k-1} \beta_i = 1$$

Super Population Approach

Recruitment Parameterisation

$$\{N, \beta_0, \beta_1, \beta_2, \ldots, \beta_{(k-1)}\}$$

The program allows us to put restrictions on the β's such as

$$\beta_1 = \beta_2 = \ldots = \beta_{(k-1)} = \beta$$

but don't include β_0 in the constraint!!

Detection History Probability Examples to Motivate What We Are Doing Here

- Aim to show how the recruitment entry probabilities come into the first capture probabilities. Quite complex.
- Aim to show how the apparent survival and capture probabilities are all that come into the recapture probabilities. Much simpler expressions
- I will show these on the blackboard. Later if I have time I may put them into a ppt slide.

Super Population Approach

Recruitment Parameterisation

$\{N, \beta_0, \beta_1, \beta_2, \ldots, \beta_{(k-1)}\}$

Conversion to Recruitment Numbers and Population Sizes

$$\hat{B}_i = N\hat{\beta}_i$$

$$\hat{N}_1 = \hat{B}_0$$

$$\hat{N}_{i+1} = \hat{B}_i + \hat{\varphi}_i(\hat{N}_i - n_i + R_i)$$

Note how there is a term for the new recruits (first) while there is also a term for animals present the previous time that survived (second).

Super Population Approach

Example Table 18.3 on Meadow Vole Data with 6 monthly periods.p 511 in Text.

Full Model $\{N, \phi_t, p_t, \beta_t\}$

$$\hat{B}_2 = 18, \hat{B}_3 = 21, \hat{B}_4 = 19 \quad SE's \approx 5$$

Notice How some of the quantities are not estimable here. Also notice how the entry number are quite similar which suggests use of a restricted version.

Super Population Model

- Minimal restrictions to estimate N and all the different par vectors - We need to constrain $p_1 = p_2$, $p_{k-1} = p_k$).

- Often we would use further restrictions. See example.

Super Population Approach

A Restricted Model {N, ϕ_t, p_t, β}with

equal entry probabilities. $\hat{B} = 24 \; SE = 1.31$

Notice how much smaller the SE is for the restricted model!

Text did not include the estimate of super population size (N) in the presentation which was annoying as I think it is a very important parameter in some cases.!

Value of the Super Population Size Parameter (N)

One can always use the super population approach to model recruitment and I recommend it as better than just using traditional Jolly-Seber

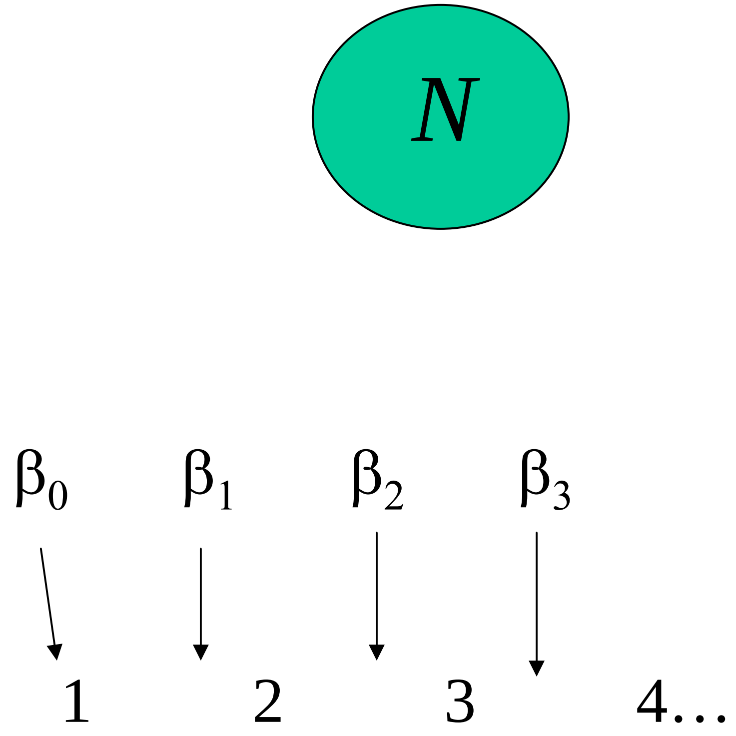
Also there are some cases where it is especially useful and the superpopulation estimate of N is of particular interest.

- Butterfly Populations
- Migratory Bird Stopover Studies
- Migratory Whale Stopover Studies

Butterfly Population Studies

- Consider a mark-recapture study on butterflies. In this case
- the N is all the butterflies that emerge in a particular flight period.
- The probability of emergence on particular days are our β_{ι}'s

Butterfly Population Studies



The βs are the daily emergence probabilities. Make Sure to start sampling before any emerge.

Migratory Bird Population Stopover Studies

Here a little different situation

N- Total number of birds of a species that stop at a certain stopover site at any time.

- Here the entry probabilities are the probs of arriving at a site

- Here the apparent survival probabilities are actually the period probabilities that they remain at the site conditional on them being there the period before. That is 1-the aparent survival probability is the probability they leave the area and move on.

Migratory Whale Population Stopover Studies

- Similar Conceptually to the Previous example on migratory bird mark-resight studies.

- We will discuss this in some detail in the next lecture.

Summary_Super Population Approach

- The big advantages of using this approach in POPAN is so that one can fit the restricted models for recruitment processes and also the super population size is itself of interest in some applications.

- One problem with the super population approach is that it does not allow one to directly parameterize in terms of popn change parameters(λ’s).

- This led researchers to consider the temporal symmetry approach considered briefly later in the semester.