

# Lecture 17

## **JOLLY-SEBER OPEN MODEL**

**Survival and Capture Probability Estimation (Ch 17)**

**Population Size and Recruitment Estimation (Ch 18)**

Read- Wildlife Monograph Ch 4- The old fashioned approach but I think you will find it useful. Part of the class today will follow this material

Note- Reading 17.1 and 17.3 then later 18.1to18.3,

# Open Population Models

(More than two samples necessary)

Additions: Births or Immigrants (not separable)

Deletions: Deaths or Emigrants (not separable)

These models allow estimation of “apparent survival rates” and “recruitment” as well as population sizes.

# FULL JOLLY-SEBER MODEL PARAMETERS AND UNOBSERVED RANDOM VARIABLES

\*Population Sizes

$$N_1, N_2, \dots, N_{k-1}, N_k$$

Survival Rates

$$\phi_1, \phi_2, \dots, \phi_{k-2}, \phi_{k-1}$$

Capture Probabilities

$$p_1, p_2, \dots, p_{k-1}, p_k$$

Recruitment Numbers

$$B_1, B_2, \dots, B_{k-2}, B_{k-1}$$

\*Marked Population Sizes

$$M_1, M_2, \dots, M_{k-1}, M_k$$

# PARAMETER ESTIMATION

- Can obtain MLE's numerically using a program like JOLLY or MARK. Allows parameter constraints, goodness-of-fit tests to be easily computed.
- First I shall present explicit M.L. estimators with their intuition to motivate the model better. This is the old fashioned approach. I will not expect you to calculate estimators this way.
- To start with we shall express estimators in terms of the marked population sizes. Later we shall show how to estimate these quantities.

Table 4.1. Notation for the Jolly-Seber model described in detail in Chapter 4 of this monograph.

## PARAMETERS

$M_i$  = the number of marked animals in the population at the time the  $i$ th sample is taken ( $i = 1, \dots, k$ ;  $M_1 \equiv 0$ ).

$N_i$  = the total number of animals in the population at the time the  $i$ th sample is taken ( $i = 1, \dots, k$ ).

$B_i$  = the total number of new animals entering the population between the  $i$ th and  $(i + 1)$ th sample and still in the population at the time  $(i + 1)$ th sample is taken ( $i = 1, \dots, k - 1$ ).

$\phi_i$  = the survival probability for all animals between the  $i$ th and  $(i + 1)$ th sample ( $i = 1, \dots, k - 1$ ).

$p_i$  = the capture probability for all animals in the  $i$ th sample ( $i = 1, \dots, k$ ).

## STATISTICS

$m_i$  = the number of marked animals captured in the  $i$ th sample ( $i = 1, \dots, k$ ).

$u_i$  = the number of unmarked animals captured in the  $i$ th sample ( $i = 1, \dots, k$ ).

$n_i$  =  $m_i + u_i$ , the total number of animals captured in the  $i$ th sample ( $i = 1, \dots, k$ ).

$R_i$  = the number of the  $n_i$  that are released after the  $i$ th sample ( $i = 1, \dots, k - 1$ ). This may not be all of the  $n_i$  due to losses on capture as discussed in the text.

$r_i$  = the number of the  $R_i$  animals released at  $i$  that are captured again ( $i = 1, \dots, k - 1$ ).

$z_i$  = the number of animals captured before  $i$ , not captured at  $i$ , and captured again later ( $i = 2, \dots, k - 1$ ).

# JOLLY-SEBER MODEL

This model makes the following assumptions:

1. Every animal present in the population at the time of  $i^{\text{th}}$  sample ( $i = 1, 2, \dots, k$ ) has the same probability of capture ( $p_i$ ).
2. Every marked animal present in the population immediately after the  $i^{\text{th}}$  sample has the same probability of survival ( $\phi_i$ ) until the  $(i + 1)^{\text{th}}$  sampling time ( $i = 1, 2, \dots, k-1$ ).
3. Marks are not lost or overlooked.
4. All samples are instantaneous and each release is made immediately after the sample.
5. All emigration is permanent.
6. Fates of animals are independent

# Parameter Estimation

## Jolly-Seber Model

- First will cover intuitive approach. This is an open population version of  $M(t)$ .
- Later I will break up into components for more formal inference

# Estimation of Capture Probability

An estimate is obviously the fraction of animals captured at time  $i$ , so that

$$\hat{p}_i = m_i / \hat{M}_i [= n_i / \hat{N}_i] \quad (4.4)$$

**Note:** Only  $p_2, p_3, \dots, p_{k-1}$  are estimable.

$p_1$  and  $p_k$  are not estimable.

# Population Size Estimation

$$m_i / n_i \approx M_i / N_i$$

Similar to the Lincoln-Petersen model solve the equation and obtain:

$$\begin{aligned}\hat{N}_i &= n_i \hat{M}_i / m_i \\ \hat{N}_i &= n_i / \hat{p}_i\end{aligned}\tag{4.1}$$

Note:  $\hat{M}_i$  will be estimated later.

Note: Only  $N_2, N_3, \dots, N_{k-1}$  are estimable. Not  $N_1$  nor  $N_k$ .

# SURVIVAL RATE ESTIMATION

$(M_i - m_i + R)$  is the number of marked animals alive in the population just after time  $i$ .

$M_{i+1}$  is the number of the above animals alive at time  $i + 1$ .

Therefore an intuitive estimator of survival is

$$\hat{\phi}_i = \hat{M}_{i+1} / (\hat{M}_i - m_i + R_i) \quad (4.2)$$

Note:  $\hat{M}_{i+1}$  and  $\hat{M}_i$  have to be estimated and that equation will be given later.

Note:  $\phi_1, \phi_2, \dots, \phi_{k-2}$  are estimable.

$\phi_{k-1}$  is not estimable.

# SURVIVAL RATE ESTIMATION

We really should refer to the parameter as apparent survival.

$$\varphi_i = S_i F_i$$

$\varphi_i$  – apparent survival

$S_i$  – true survival

$F_i$  – fidelity (prob did not emigrate)

Note- We cannot get true survival from capture-recapture data alone. Add telemetry to estimate F or assume that F=1 in particular applications.

# Estimation of Birth Numbers

An equation for estimation of birth numbers is

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i (\hat{N}_i - n_i + R_i) \quad (4.3)$$

The first term of the equation represents the total number of animals at time  $i + 1$  and the second term represents those animals at time  $i + 1$  that were present at time  $i$ .

# Estimation of Marked Population Size

(The derivation is given on the next page).

$$\hat{M}_i = m_i + (R_i Z_i / r_i) \quad (4.5)$$

Note:  $M_2, M_3, \dots, M_{k-1}$  are estimable.

The  $\hat{M}_i$  are crucial to the estimation of all the other parameters in this intuitive approach.

$M_1 = 0 \longrightarrow N_1$  is not estimable.

$M_k$  is not estimable.

$Z_i/(M_i - m_i)$  Proportion of marked animals not seen at  $\mathbf{i}$ , that are seen again.

$r_i/R_i$  Proportion of animals seen at  $\mathbf{i}$ , that are seen again.

$$Z_i/(M_i - m_i) \approx r_i/R_i$$

which gives

$$\hat{M}_i = m_i + (R_i Z_i / r_i)$$

**Note- I wont expect you to use these equations, I just want you to understand roughly why the method works.**

# FULL JOLLY-SEBER MODEL

Population Sizes  $N_1, \hat{N}_2, \dots, \hat{N}_{k-1}, N_k$

Survival Rates  $\hat{\phi}_1, \hat{\phi}_2, \dots, \hat{\phi}_{k-2}, \phi_{k-1}$

Capture Probabilities  $p_1, \hat{p}_2, \dots, \hat{p}_{k-1}, p_k$

Marked Population Size  $M_1, \hat{M}_2, \dots, \hat{M}_{k-1}, M_k$

Recruitment Numbers  $B_1, \hat{B}_2, \dots, \hat{B}_{k-2}, B_{k-1}$

# ASSUMPTIONS and MODEL ROBUSTNESS

- **Heterogeneity of capture probabilities**

- Serious negative bias of population size estimators

- Mild negative bias on survival estimators i.e., Survival estimators robust to heterogeneity

- **Trap Response of Capture probabilities**

- Trap Happy**

- Negative bias on population size estimators

- Little effect on survival estimators

- Trap Shy**

- Positive bias on population size estimators

- Little effect on survival estimators

# ASSUMPTIONS and MODEL ROBUSTNESS

- Heterogeneity of survival probabilities

Complex but if survival rates vary over animals in a consistent way from sample to sample there is often a positive bias in survival rates

Interactions between heterogeneity of capture and survival probabilities can cause positive or negative biases in survival rates

# Assumptions (continued)

- **Mark Induced Mortality**

- Positive bias on population size estimators especially when capture probability is small

- Severe negative bias on survival estimators

- **Tag Loss**

- Positive bias on population size estimators especially when capture probability is small

- Severe negative bias on survival estimators

- **Emigration**

- Confounded (not separable from) mortality. We should call survival apparent survival.

- Temporary emigration causes problems that will be discussed later

# EXAMPLE

## Gray squirrel study in an English oak forest

- Two-year study with monthly sampling
- Baited traps with corn
- Toe clipping used for marking
- Natural boundaries suggest that survival and recruitment estimators are not confounded with migration processes.
  
- Data Table 4.3, Estimators Table 4.4. Old approach—now we would use MARK so we can fit a variety of sub models but it still illustrates the key points
- High capture probabilities except for August 1973 to December 1973. Therefore the precision of estimators is generally very good.

Table 4.3. Capture–recapture statistics for a gray squirrel population at Alice Holt Forest Research Station, Surrey, England, November 1972–September 1974.

| Period | Date         | $n_i^a$ | $m_i$ | $R_i$ | $r_i$ | $z_i$ |
|--------|--------------|---------|-------|-------|-------|-------|
| 1      | Nov 1972     | 46      |       | 46    | 43    |       |
| 2      | Dec 1972     | 46      | 42    | 46    | 44    | 1     |
| 3      | Jan 1973     | 48      | 42    | 48    | 48    | 3     |
| 4      | Feb 1973     | 46      | 42    | 46    | 45    | 9     |
| 5      | Mar 1973     | 51      | 46    | 50    | 46    | 8     |
| 6      | Apr 1973     | 37      | 37    | 37    | 35    | 17    |
| 7      | May 1973     | 41      | 41    | 41    | 40    | 11    |
| 8      | May–Jun 1973 | 42      | 39    | 42    | 37    | 12    |
| 9      | Jun 1973     | 47      | 43    | 47    | 40    | 6     |
| 10     | Jul 1973     | 31      | 26    | 31    | 26    | 20    |
| 11     | Aug 1973     | 8       | 7     | 8     | 8     | 39    |
| 12     | Sep 1973     | 2       | 2     | 2     | 2     | 45    |
| 13     | Oct 1973     | 1       | 0     | 1     | 1     | 47    |
| 14     | Nov 1973     | 4       | 3     | 4     | 3     | 45    |
| 15     | Dec 1973     | 9       | 8     | 9     | 8     | 40    |
| 16     | Jan 1974     | 19      | 17    | 18    | 17    | 31    |
| 17     | Feb 1974     | 19      | 14    | 19    | 18    | 34    |
| 18     | Mar 1974     | 27      | 20    | 27    | 24    | 32    |
| 19     | Apr 1974     | 36      | 36    | 36    | 32    | 20    |
| 20     | May 1974     | 45      | 34    | 44    | 33    | 18    |
| 21     | Jul 1974     | 74      | 46    | 73    | 15    | 5     |
| 22     | Aug 1974     | 22      | 20    | 22    | 2     | 0     |
| 23     | Sep 1974     | 3       | 2     | 2     |       |       |

<sup>a</sup> Notation is explained in Table 4.1.

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

| Period | Date         | $\hat{N}_i^b$ | $\hat{S}\hat{E}$ | $\hat{\phi}_i$ | $\hat{S}\hat{E}$ | $\hat{B}_i$ | $\hat{S}\hat{E}$ |
|--------|--------------|---------------|------------------|----------------|------------------|-------------|------------------|
| 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     |               |                  |                |                  |             |                  |

<sup>a</sup>  $\hat{S}\hat{E}(\hat{N}_i)$  and  $\hat{S}\hat{E}(\hat{B}_i)$  include only sampling variation or “error of estimation”;  $\hat{S}\hat{E}(\hat{\phi}_i)$  was obtained using the full variance estimator of Jolly (1965).

<sup>b</sup> Notation explained in Table 4.1.

# Gray Squirrel (Example Conclusions)

**Population Sizes** - Slight negative bias possible due to heterogeneity and trap happy response.

**Survival Rates** - Should be very accurate and precise. Values are very close to one, except the last one. This may be due to losses of young animals, but it is difficult to tell because the study ends here.

**Recruitment Numbers** - There is only recruitment in April, and May of 1974. In 1973 there was no recruitment. It was a bad year for squirrels to reproduce (poor acorn crop).

# FULL JOLLY-SEBER MODEL

Population Sizes  $N_1, \hat{N}_2, \dots, \hat{N}_{k-1}, N_k$

Survival Rates  $\hat{\phi}_1, \hat{\phi}_2, \dots, \hat{\phi}_{k-2}, \phi_{k-1}$

Capture Probabilities  $p_1, \hat{p}_2, \dots, \hat{p}_{k-1}, p_k$

Marked Population Size  $M_1, \hat{M}_2, \dots, \hat{M}_{k-1}, M_k$

Recruitment Numbers  $B_1, \hat{B}_2, \dots, \hat{B}_{k-2}, B_{k-1}$

# MODEL RESTRICTIONS AND EXTENSIONS

The Full Jolly-Seber version of model has a very large number of parameters. Perhaps we could reduce the number of parameters?

## Principle of Parsimony

Have as small a number of parameters as realistically possible.

## Advantages

1. Simplicity
2. Reduce problems of non-estimability
3. Smaller SEs of remaining parameter estimates.
4. If too simple will induce bias, so Use AIC Criteria that we discussed earlier to strike the right balance.

# MODEL RESTRICTIONS

- Model A - Full Model

$$\phi_1, \phi_2, \dots, \phi_{k-1}$$

$$p_1, p_2, \dots, p_k$$

- Model B - Constant Survival

$$\phi_1 = \phi_2, \dots, = \phi_{k-1} = \phi$$

- Model C - Constant Capture

$$p_1 = p_2, \dots, = p_k = p$$

- Model D - Constant Survival, Constant Capture

$$\phi_1 = \phi_2, \dots, = \phi_{k-1} = \phi$$

$$p_1 = p_2, \dots, = p_k = p$$

# MODEL RESTRICTIONS AND EXTENSIONS

## PROGRAMS

- Program **JOLLY** allows one to restrict capture and survival probabilities to be equal.(Models A,B and D) We can illustrate with **Roseate Tern Data**. (See Ch 5.3.3 of Monograph if you like)
- Program **JOLLYAGE** allows one to include different age classes.We can illustrate with **Canada Goose Data**. (See Ch 6.7 of Monograph if you like)
- These can be run remotely from the Patuxent website similar to how I showed you for **CAPTURE**.
- Program **MARK** is a newer program and allows one to restrict capture and survival probabilities to be equal.(Models A,B, C and D and any other models you can think of). It can also handle the age dependence of the Canada goose example as well.

## Roseate Tern (Example). JOLLY

Briefly presented

- Adult terns captured and banded on nests on Falkland Island, Connecticut. Recaptures in subsequent years.
- Study covered 1978-1984.
- Summary data in Section 5.3.3. Of Monograph.
- We then fit

Jolly-Seber Model (A)

Constant Survival Model (B)

Constant Survival and Capture Model (D)

## Conclusions on **Roseate Tern** Data

- Model B is the best model based on various tests. Now if we used MARK would use AIC.
- We display the Model B output in Table 5.6 of Monograph

Table 5.6. Estimates and approximate standard errors under the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D), for roseate tern data collected by Spendelov (1982) on Falkner Island, Connecticut, from 1978 to 1984.

| Model<br>and year                           | $\hat{\phi}_i$    | $\hat{SE}$ | $\hat{p}_i$       | $\hat{SE}$ | $\hat{M}_i$ | $\hat{SE}$ | $\hat{N}_i$ | $\hat{SE}$ | $\hat{B}_i$ | $\hat{SE}$ |
|---|-------------------|------------|-------------------|------------|-------------|------------|-------------|------------|-------------|------------|
| Model A—Jolly-Seber model                   |                   |            |                   |            |             |            |             |            |             |            |
| 1978  | 0.74              | 0.137      |                   |            |             |            |             |            |             |            |
| 1979  | 0.52              | 0.075      | 0.25              | 0.068      | 68          | 11.9       | 544         | 141.8      | 143         | 95.6       |
| 1980  | 0.90              | 0.114      | 0.23              | 0.049      | 101         | 11.3       | 426         | 82.7       | 200         | 84.8       |
| 1981  | 0.61              | 0.085      | 0.36              | 0.054      | 160         | 17.2       | 581         | 80.7       | 20          | 45.4       |
| 1982  | 0.55              | 0.102      | 0.37              | 0.056      | 192         | 23.2       | 372         | 51.3       | 26          | 23.6       |
| 1983  |                   |            | 0.34              | 0.064      | 143         | 21.7       | 230         | 38.7       |             |            |
| $\bar{x}$                                   | 0.66              | 0.033      | 0.31              | 0.026      |             |            |             |            |             |            |
| Model B—constant survival model             |                   |            |                   |            |             |            |             |            |             |            |
| 1979  |                   |            | 0.27              | 0.060      | 64          | 6.36       | 525         | 102.0      | 192         | 114.8      |
| 1980  |                   |            | 0.19              | 0.037      | 120         | 8.80       | 536         | 84.9       | 144         | 76.1       |
| 1981  | 0.67 <sup>a</sup> | 0.028      | 0.42              | 0.049      | 146         | 9.84       | 517         | 49.4       | 42          | 41.1       |
| 1982  |                   |            | 0.36              | 0.042      | 190         | 14.1       | 376         | 31.8       | 28          | 28.1       |
| 1983  |                   |            | 0.28              | 0.043      | 166         | 16.6       | 273         | 29.5       | 171         | 39.1       |
| 1984  |                   |            | 0.40              | 0.066      | 135         | 16.8       | 358         | 50.9       |             |            |
| Model D—constant survival and capture model |                   |            |                   |            |             |            |             |            |             |            |
| 1979  |                   |            |                   |            | 58          | 6.37       | 466         | 44.0       | 55          | 33.4       |
| 1980  |                   |            |                   |            | 111         | 9.02       | 360         | 33.2       | 383         | 43.5       |
| 1981  | 0.69 <sup>a</sup> | 0.023      | 0.31 <sup>a</sup> | 0.023      | 166         | 12.1       | 667         | 55.6       | -22         | 36.6       |
| 1982  |                   |            |                   |            | 203         | 15.1       | 420         | 35.3       | -6          | 22.9       |
| 1983  |                   |            |                   |            | 171         | 16.7       | 268         | 26.2       | 242         | 31.5       |
| 1984  |                   |            |                   |            | 175         | 22.7       | 462         | 45.7       |             |            |

<sup>a</sup> These estimates pertain to all years in the study because of the assumptions of constant survival and/or capture.

# OPEN CAPTURE- RECAPTURE MODELS FOR ESTIMATING DEMOGRAPHIC PARAMETERS

## Components of Data

**Recaptures** - this component is where we estimate survival and capture probabilities. You can see that from the intuitive estimators.

**First Captures and Recaptures**- allows estimation of population sizes and recruitment parameters (and also survival and capture probabilities). You also can see that from the intuitive estimators.

# OPEN CAPTURE- RECAPTURE MODELS FOR ESTIMATING DEMOGRAPHIC PARAMETERS

We do not discuss the likelihoods much in this class but---

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

$$L=L_1(\text{First Captures}) * L_2(\text{Losses on Capture}) * L_3(\text{Recaptures})$$

$L_1(\text{First Captures})$  - allows estimation of **population sizes** and **recruitment parameters** (and also includes survival and capture probabilities).

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

$L_3(\text{Recaptures})$  - this is the reduced Cormack-Jolly-Seber likelihood and this component is where we estimate **survival** and **capture** probabilities

# CORMACK-JOLLY SEBER MODEL

- \* Comprehensive Survival Modeling
- \* Extension to Stage Structured Models for survival within a stage and movement between stages.

# CORMACK-JOLLY-SEBER MODEL(Ch 17)

Survival Rates

$$\hat{\phi}_1, \hat{\phi}_2, \dots, \hat{\phi}_{k-2}, \phi_{k-1}$$

Capture Probabilities

$$p_1, \hat{p}_2, \dots, \hat{p}_{k-1}, p_k$$

WE JUST FOLLOW THE MARKED ANIMALS AND DON'T USE MARKED TO TOTAL RATIOS TO GET POPN SIZE OR BIRTH NUMBERS.

# Cormack-Jolly-Seber Model Motivation of Model Structure and Estimation

**We consider only recaptures and three sampling occasions**

**There are seven capture histories**

**1 1 1**

**1 1 0**

**1 0 1**

**1 0 0**

**0 1 1**

**0 1 0**

**0 0 1**

# Cormack-Jolly-Seber Model

## Motivation of Model Structure and Estimation

### Expected Values of Cells

|           |   |
|-----------|---|
| $X_{111}$ | $R_1 \varphi_1 p_2 \varphi_2 p_3$   |
| $X_{110}$ | $R_1 \varphi_1 p_2 (1 - \varphi_2 p_3)$   |
| $X_{101}$ | $R_1 \varphi_1 (1 - p_2) \varphi_2 p_3$   |
| $X_{100}$ | $R_1 [1 - \varphi_1 p_2 \varphi_2 p_3 - \varphi_1 p_2 (1 - \varphi_2 p_3) - \varphi_1 (1 - p_2) \varphi_2 p_3]$ |
| $X_{011}$ | $R_2 \varphi_2 p_3$   |
| $X_{010}$ | $R_2 (1 - \varphi_2 p_3)$   |
| $X_{001}$ | no chance for recaps yet  |

Note - We don't start the cell structure until after first capture and therefore don't have to consider new entries into the popn!

# **Cormack-Jolly-Seber Model**

## **Motivation of Model Structure and Estimation**

### **Intuitive Estimation**

**Can we separately estimate the components of**

**$\phi_2 p_3$ ?**

**No! Only the product of the two!**

# Cormack-Jolly-Seber Model

## Motivation of Model Structure and Estimation

$$X_{011} \cong R_2 \varphi_2 p_3$$

$$(\varphi_2 p_3)^{\hat{}} = X_{011} / R_2$$

# Cormack-Jolly-Seber Model

## Motivation of Model Structure and Estimation

### Expected Values of Cells

$$X_{111} \cong R_1 \varphi_1 p_2 \varphi_2 p_3$$

$$X_{101} \cong R_1 \varphi_1 (1 - p_2) \varphi_2 p_3$$

$$X_{111} + X_{101} \cong R_1 \varphi_1 \varphi_2 p_3$$

$$X_{111} / (X_{111} + X_{101}) \cong p_2$$

$$\hat{p}_2 = X_{111} / (X_{111} + X_{101})$$

# Cormack-Jolly-Seber Model

## Motivation of Model Structure and Estimation

### Expected Values of Cells

$$X_{111} \cong R_1 \varphi_1 p_2 \varphi_2 p_3$$

$$\hat{\varphi}_1 = X_{111} / R_1 \hat{p}_2 (\varphi_2 \hat{p}_3)$$

Therefore using previous results we can estimate the first survival rate.

MARK does it better (MLEs) (: -))!!

# Generalisations of the Cormack-Jolly-Seber Model using MARK

- Multiple age classes
- Multiple data sets
- Parameter constraints to achieve parsimony
- Model selection

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

There is penalty for over parameterization

# SURVIVAL AND CAPTURE PROBABILITY MODELING( Continued)

- Can allow for covariates so that if  $X_i$  is some covariate like weight or body condition

$$\text{logit}(\phi_i) = \alpha + \beta X_i$$

$$\text{logit}(\phi_i) = \ln(\phi_i / 1 - \phi_i)_i$$

logit is most common link function used.

It keeps survival rates between 0,1.

$$\log(\phi_i) = \alpha + \beta X_i \quad \text{would not!}$$

# SURVIVAL MODELING EUROPEAN DIPPER EXAMPLE

- Illustrated by European Dipper data taken from Lebreton et al. (1992) using SURGE. (MARK better now and I re analysed in that program). There are seven years with one recapture event per year. There were data for the two sexes separately but they were found to be similar so I combined them for ease of presentation
- Five models were compared using AIC (Akaike Information Criteria) and we show details of our analysis for those models.

## Dipper Combined Sex Analysis

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| Model             | AICc    | Delta<br>AICc | AICc<br>Weight | #Par |
|-------------------|---------|---------------|----------------|------|
| {Phi(f) p(.) PIM} | 666.160 | 0.00*         | 0.89445        | 3    |
| {Phi(.) p(.) PIM} | 670.866 | 4.71          | 0.08505        | 2    |
| {Phi(t) p(.) PIM} | 673.998 | 7.84          | 0.01776        | 7    |
| {Phi(.) p(t) PIM} | 678.748 | 12.59         | 0.00165        | 7    |
| {Phi(t) p(t) PIM} | 679.588 | 13.43         | 0.00109        | 11   |

**\*Best Model**

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# Model Details

- First we will look at the full CJS Model
- Next Look at the “Best Model” where survival differs between flood and nonflood years and where  $p$  is constant over years.

## Dipper Full CJS Model {Phi(t) p(t) PIM} Output

| Parameter | Estimate          | Standard Error   | Lower            | Upper            |
|-----------|-------------------|------------------|------------------|------------------|
| 1:Phi     | 0.7181818         | 0.1555470        | 0.3610409        | 0.9199575        |
| 2:Phi     | 0.4346708         | 0.0688290        | 0.3075047        | 0.5710588        |
| 3:Phi     | 0.4781705         | 0.0597091        | 0.3643839        | 0.5942685        |
| 4:Phi     | 0.6261177         | 0.0592656        | 0.5048461        | 0.7333741        |
| 5:Phi     | 0.5985335         | 0.0560517        | 0.4855434        | 0.7019412        |
| 6:Phi     | <b>*0.7284299</b> | <b>0.0000000</b> | <b>0.7284299</b> | <b>0.7284299</b> |
| 7:p       | 0.6962027         | 0.1657637        | 0.3302969        | 0.9141508        |
| 8:p       | 0.9230769         | 0.0728778        | 0.6161497        | 0.9889758        |
| 9:p       | 0.9130435         | 0.0581758        | 0.7140650        | 0.9778505        |
| 10:p      | 0.9007892         | 0.0538330        | 0.7360176        | 0.9672856        |
| 11:p      | 0.9324138         | 0.0458025        | 0.7684926        | 0.9828579        |
| 12:p      | <b>*0.7284328</b> | <b>0.0000000</b> | <b>0.7284328</b> | <b>0.7284328</b> |

\*\* Last phi and p and not separately estimable

# EUROPEAN DIPPER EXAMPLE

THREE PARAMETER “BEST” MODEL {Phi(f) p(.) PIM}

FLOOD SURVIVAL

$$\hat{\phi}_f = 0.469 \quad (0.043)$$

NONFLOOD SURVIVAL

$$\hat{\phi}_n = 0.607 \quad (0.031)$$

CAPTURE PROBABILITY

$$\hat{p} = 0.90 \quad (0.029)$$

A simple, but useful example of MARK'S utility in Model selection and estimation.

## EUROPEAN DIPPER EXAMPLE SUMMARY

- Very nice example which shows the value of the AIC procedure
- Very simple model is adequate –only 2 survival parameters estimated and 1 capture probability.
- Estimates are much more precise than for the full CJS model.