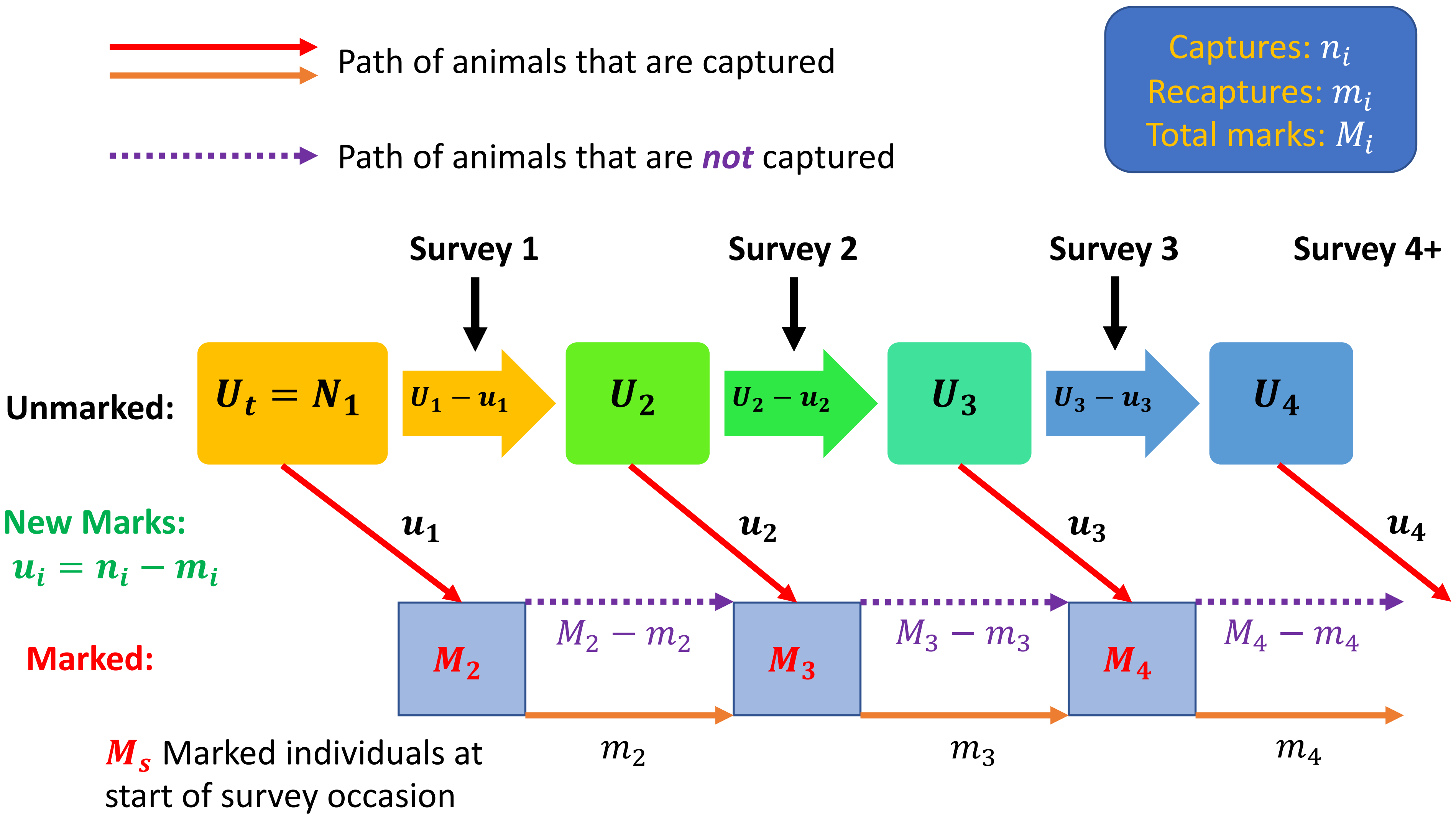
# FISH 621
# Estimation of Fish Abundance:
# 8: Jolly-Seber Model for Open Populations

Dr. Curry Cunningham: cjcunningham@alaska.edu

# Schnabel Experimental Design



# Example of Mean Petersen and Schnabel

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

- Data
  - $s = 10$ sampling periods take place, in each of which …
    - Number of captures recorded: $n_i$
    - Number of marked individuals are recorded: $m_i$
    - All unmarked individuals $u_i = n_i - m_i$ are marked
    - All captures are released back into the population $N$

| Period ($i$) | Captures ($n_i$) | Recaptures ($m_i$) | New Marks ($u_i$) | Total Marks ($M_i$) | $n_i M_i$ |
|---|---|---|---|---|---|
| 1 | 20 | 0 | 20 | 0 | 0 |
| 2 | 20 | 4 | 16 | 20 | 400 |
| 3 | 20 | 3 | 17 | 36 | 720 |
| 4 | 20 | 2 | 18 | 53 | 1,060 |
| 5 | 20 | 4 | 16 | 71 | 1,420 |
| 6 | 20 | 3 | 17 | 87 | 1,740 |
| 7 | 20 | 3 | 17 | 104 | 2,080 |
| 8 | 20 | 5 | 15 | 121 | 2,420 |
| 9 | 20 | 4 | 16 | 136 | 2,720 |
| 10 | 20 | 3 | 17 | 152 | 3,040 |
| **Total** | | **31** | | | **15,600** |

**Schnabel**

$$N' = \frac{\sum n_i M_i}{\sum m_i}$$

$$N' = \frac{15600}{31} \approx 503$$

# 3. Schumacher-Eschmeyer Regression Method

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

- Let $y_i = m_i/n_i$ and assume $y_i$ has a binomial distribution
  - With expected value: $\tilde{p}_i = M_i/N$
    - And variance: $\sigma_i^2 = \tilde{p}_i(1-\tilde{p}_i)/n_i$
- A standard linear ***regression-through-the-origin*** model can be written
  - $y_i = \beta M_i + e_i$ , where…
    - $\beta = 1/N$
    - $e_i \sim Normal\left(0, \sigma_i^2\right)$
- Because variance is not constant (across $i = 2, \ldots, s$)
  - Weighted least squares should be used, leading to
    - $\tilde{\beta} = \frac{1}{\tilde{N}} = \frac{\sum_{i=2}^{s} w_i y_i M_i}{\sum_{i=2}^{s} w_i M_i^2}$, with $w_i \propto \frac{1}{\sigma_i^2}$
- Since $N$ is unknown and $\tilde{p}_i(1-\tilde{p}_i)$ varies little
  - For $\tilde{p}_i$ between 0.2 and 0.8
    - Choosing $w_i$ to be sample size (i.e. $w_i = n_i$) often works well
  - $\tilde{\beta} = \frac{1}{\tilde{N}} = \frac{\sum_{i=2}^{s} n_i y_i M_i}{\sum_{i=2}^{s} n_i M_i^2} = \frac{\sum_{i=2}^{s} m_i M_i}{\sum_{i=2}^{s} n_i M_i^2}$

# 3. Schumacher-Eschmeyer Regression Method

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

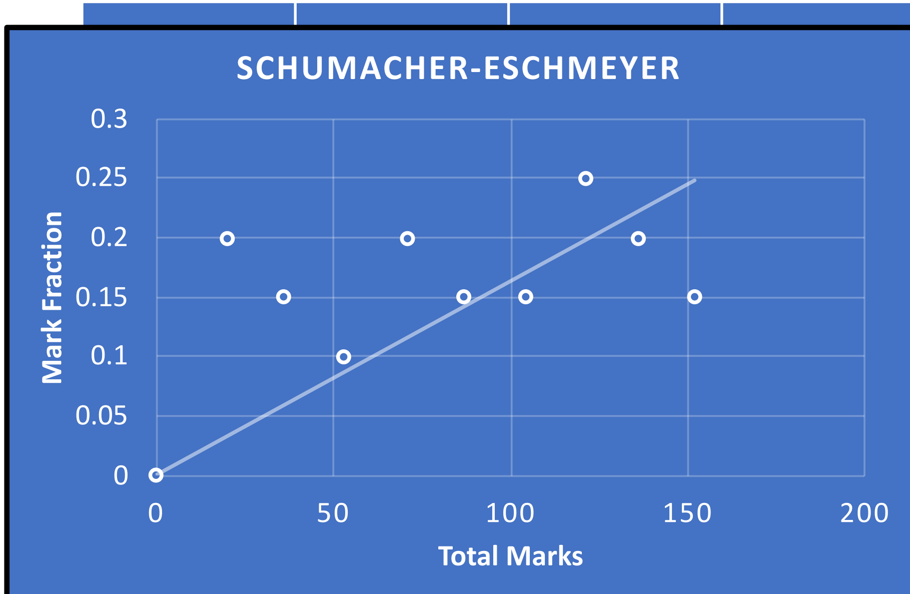
- Regression through the origin
  - $y_i = \beta M_i + e_i$ , where…
    - $y_i = m_i / n_i$
    - $\beta = 1/N$
    - $e_i \sim Normal(0, \sigma_i^2)$
  - $\tilde{\beta} = \frac{1}{\tilde{N}} = \frac{\sum_{i=2}^{s} m_i M_i}{\sum_{i=2}^{s} n_i M_i^2}$, therefore $\tilde{N} = \frac{1}{B}$

| Period ($i$) | Captures ($n_i$) | Recaptures ($m_i$) | New Marks ($u_i$) | Total Marks ($M_i$) | Mark Fraction ($m_i/\mathrm{n_i}$) |
|---|---|---|---|---|---|
| 1 | 20 | 0 | 20 | 0 | 0.00 |
| 2 | 20 | 4 | 16 | 20 | 0.20 |
| 3 | 20 | 3 | 17 | 36 | 0.15 |
| 4 | 20 | 2 | 18 | 53 | 0.10 |
| 5 | 20 | 4 | 16 | 71 | 0.20 |
| 6 | 20 | 3 | 17 | 87 | 0.15 |
| 7 | 20 | 3 | 17 | 104 | 0.15 |
| 8 | 20 | 5 | 15 | 121 | 0.25 |
| 9 | 20 | 4 | 16 | 136 | 0.20 |
| 10 | 20 | 3 | 17 | 152 | 0.15 |

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

# 3. Schumacher-Eschmeyer Regression Method

- Regression through the origin
  - $y_i = \beta M_i + e_i$ , where…
    - $y_i = m_i / n_i$
    - $\beta = 1/N$
    - $e_i \sim Normal(0, \sigma_i^2)$
  - $\tilde{\beta} = \frac{1}{\tilde{N}} = \frac{\sum_{i=2}^{S} m_i M_i}{\sum_{i=2}^{S} n_i M_i^2}$, therefore $\tilde{N} = \frac{1}{B}$




| | Total Marks ($M_i$) | Mark Fraction ($m_i/n_i$) |
|---|---|---|
| 0 | 0 | 0.00 |
| 6 | 20 | 0.20 |
| 7 | 36 | 0.15 |
| 8 | 53 | 0.10 |
| 6 | 71 | 0.20 |
| 7 | 87 | 0.15 |
| 7 | 104 | 0.15 |
| 5 | 121 | 0.25 |
| 6 | 136 | 0.20 |
| 7 | 152 | 0.15 |

# 3. Schumacher-Eschmeyer Regression Method

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

- Regression through the origin
  - $y_i = \beta M_i + e_i$ , where…
    - $y_i = m_i / n_i$
    - $\beta = 1/N$
    - $e_i \sim Normal(0, \sigma_i^2)$
  - $\tilde{\beta} = \frac{1}{\tilde{N}} = \frac{\sum_{i=2}^{s} m_i M_i}{\sum_{i=2}^{s} n_i M_i^2}$, therefore $\tilde{N} = \frac{1}{B}$

| Period ($i$) | Captures ($n_i$) | Recaptures ($m_i$) | New Marks ($u_i$) | Total Marks ($M_i$) | $n_i M_i$ | $n_i M_i^2$ |
|---|---|---|---|---|---|---|
| 1 | 20 | 0 | 20 | 0 | 0 | 0 |
| 2 | 20 | 4 | 16 | 20 | 400 | 8,000 |
| 3 | 20 | 3 | 17 | 36 | 720 | 25,920 |
| 4 | 20 | 2 | 18 | 53 | 1,060 | 56,180 |
| 5 | 20 | 4 | 16 | 71 | 1,420 | 100,820 |
| 6 | 20 | 3 | 17 | 87 | 1,740 | 151,380 |
| 7 | 20 | 3 | 17 | 104 | 2,080 | 216,320 |
| 8 | 20 | 5 | 15 | 121 | 2,420 | 292,820 |
| 9 | 20 | 4 | 16 | 136 | 2,720 | 369,920 |
| 10 | 20 | 3 | 17 | 152 | 3,040 | 462,080 |
| **Total** | | **31** | | | **15,600** | **1,683,440** |

$$\tilde{\beta} = \frac{\sum_{i=2}^{s} m_i M_i}{\sum_{i=2}^{s} n_i M_i^2}$$

$$\tilde{\beta} = \frac{15{,}600}{1{,}683{,}440}$$

$$\tilde{\beta} = 0.009267$$

$$\tilde{N} = \frac{1}{\tilde{\beta}} = 107.9$$

# 3. Schumacher-Eschmeyer Regression Method

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

- Regression through the origin
  - $y_i = \beta M_i + e_i$ , where…
    - $y_i = m_i / n_i$
    - $\beta = 1/N$
    - $e_i \sim Normal(0, \sigma_i^2)$
  - $\tilde{\beta} = \frac{1}{\tilde{N}} = \frac{\sum_{i=2}^{s} m_i M_i}{\sum_{i=2}^{s} n_i M_i^2}$, therefore $\tilde{N} = \frac{1}{B}$

WRONG!!!

| Period ($i$) | Captures ($n_i$) | Recaptures ($m_i$) | New Marks ($u_i$) | Total Marks ($M_i$) | $n_i M_i$ | $n_i M_i^2$ |
|---|---|---|---|---|---|---|
| 1 | 20 | 0 | 20 | 0 | 0 | 0 |
| 2 | 20 | 4 | 16 | 20 | 400 | 8,000 |
| 3 | 20 | 3 | 17 | 36 | 720 | 25,920 |
| 4 | 20 | 2 | 18 | 53 | 1,060 | 56,180 |
| 5 | 20 | 4 | 16 | 71 | 1,420 | 100,820 |
| 6 | 20 | 3 | 17 | 87 | 1,740 | 151,380 |
| 7 | 20 | 3 | 17 | 104 | 2,080 | 216,320 |
| 8 | 20 | 5 | 15 | 121 | 2,420 | 292,820 |
| 9 | 20 | 4 | 16 | 136 | 2,720 | 369,920 |
| 10 | 20 | 3 | 17 | 152 | 3,040 | 462,080 |
| **Total** | | **31** | | | **15,600** | **1,683,440** |

$$\tilde{\beta} = \frac{\sum_{i=2}^{s} m_i M_i}{\sum_{i=2}^{s} n_i M_i^2}$$

$$\tilde{\beta} = \frac{15{,}600}{1{,}683{,}440}$$

$$\tilde{\beta} = 0.009267$$

$$\tilde{N} = \frac{1}{\tilde{\beta}} = 107.9$$

# 3. Schumacher-Eschmeyer Regression Method

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

- Regression through the origin
  - $y_i = \beta M_i + e_i$ , where…
    - $y_i = m_i / n_i$
    - $\beta = 1/N$
    - $e_i \sim Normal(0, \sigma_i^2)$
  - $\tilde{\beta} = \frac{1}{\tilde{N}} = \frac{\sum_{i=2}^{s} m_i M_i}{\sum_{i=2}^{s} n_i M_i^2}$, therefore $\tilde{N} = \frac{1}{B}$

**Correct!!!**

| Period ($i$) | Captures ($n_i$) | Recaptures ($m_i$) | New Marks ($u_i$) | Total Marks ($M_i$) | $m_i M_i$ | $n_i M_i^2$ |
|---|---|---|---|---|---|---|
| 1 | 20 | 0 | 20 | 0 | 0 | 0 |
| 2 | 20 | 4 | 16 | 20 | 80 | 8,000 |
| 3 | 20 | 3 | 17 | 36 | 108 | 25,920 |
| 4 | 20 | 2 | 18 | 53 | 106 | 56,180 |
| 5 | 20 | 4 | 16 | 71 | 284 | 100,820 |
| 6 | 20 | 3 | 17 | 87 | 261 | 151,380 |
| 7 | 20 | 3 | 17 | 104 | 312 | 216,320 |
| 8 | 20 | 5 | 15 | 121 | 605 | 292,820 |
| 9 | 20 | 4 | 16 | 136 | 544 | 369,920 |
| 10 | 20 | 3 | 17 | 152 | 456 | 462,080 |
| Total | | 31 | | | 2,756 | 1,683,440 |

$$\tilde{\beta} = \frac{\sum_{i=2}^{s} m_i M_i}{\sum_{i=2}^{s} n_i M_i^2}$$

$$\tilde{\beta} = \frac{2,756}{1,683,440}$$

$$\tilde{\beta} = 0.001637$$

$$\tilde{N} = \frac{1}{\tilde{\beta}} = 610.8$$

# Jolly-Seber Background

- References
  - Seber (1982), Chapter 5
    - General and concise description of Jolly-Seber methods
  - Brownie et al. (1986)
    - Presented modifications of the Jolly-Seber model for capture-recapture data, which assume constant survival and/or capture rates.
    - Where appropriate, because of the reduced number of parameters, these models lead to more efficient estimators than the Jolly-Seber model.
  - Hightower and Gilbert (1984)
  - Arnason and Mills (1981)
  - Arnason et al. (1982)

# Jolly-Seber Background

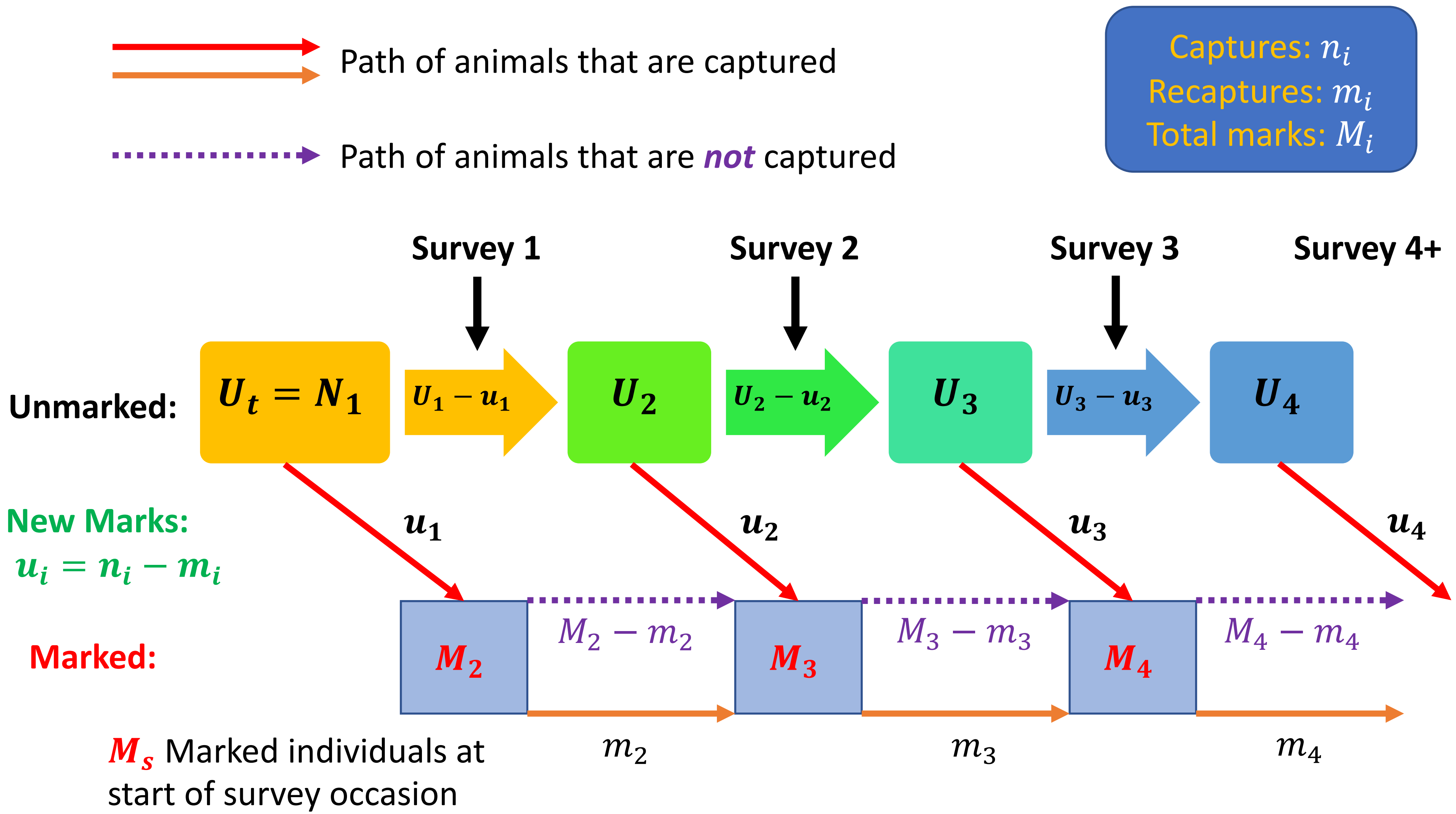
- Methodology extends the Schnabel experimental design
  - To ***open*** populations that have
    - Mortality, recruitment, immigration, and/or permanent emigration
- The Schnabel experimental design is ***followed***, except
  - Some individuals ***need not*** be returned to the population after capture
  - Animals must receive a recognizable mark or tag
    - That allows the occasion of capture to be determined (individual ID will work)
- Complications of sampling ***without*** replacement
  - Will be ignored for now
    - So likelihoods are based on binomial or multinomial distributions

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

# Jolly-Seber Notation

- We will use the same notation we saw for Schnabel estimation
  - With the addition of the following parameters, which will be treated as ***random variables***
    - $N_i$ = number in the population ***just prior*** to sampling at occasion $i$ at time $t_i$
    - $U_i = N_i - M_i$ =unmarked number in the population
    - $\phi_i$ = survival (or permanent emigration) from $t_i$ to $t_{i+1}$
    - $B_i$ = recruitment (or immigration) into the population from $t_i$ to $t_{i+1}$
    - $N_i(h)$ = members of $B_h$ (cohort) still alive and present at time $t_i$

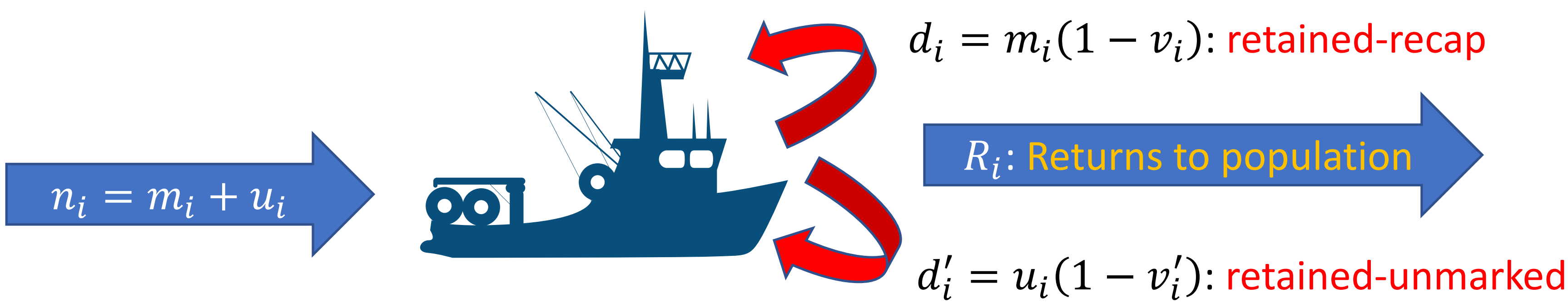
# Schnabel Experimental Design



Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

# Jolly-Seber Notation

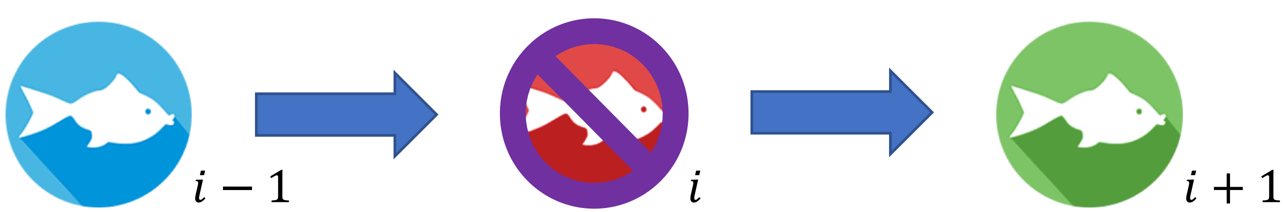
- Additional data variables and parameters
  - $n_i = m_i + u_i = R_i + d_i + d_i'$ is the number sampled, where…
    - $R_i$ = number ***returned to the population*** from number sampled $n_i$ (including $m_i$)
    - $d_i$ = number of $m_i$ (recaptures) ***not*** released
    - $d_i'$ = number of $u_i$ (unmarked) ***not*** released
    - $v_i$ = probability of a ***marked member*** being ***released***
    - $v_i'$ = probability of an ***unmarked*** member being ***released***
    - $\chi_i$ = probability of a release ***not*** being recaptured



Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

# Jolly-Seber Notation

- Additional data variables and parameters
  - $n_i = m_i + u_i = R_i + d_i + d_i'$ is the number sampled, where…
- Data
  - $m_{hi}$ = number caught in the $i$th sample
    - ***Last caught*** in sample $h$
  - $r_i$ = number of $R_i$ (releases) later ***captured***
  - $z_i$ = number caught ***before*** sample $i$
    - ***Not*** captured in sample $i$
    - And ***captured*** after $i$



Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

# Jolly-Seber Assumptions

- 1) There is a constant probability of capture
  - $p_i = 1 - q_i$ at sampling occasion $i$
    - i.e. no behavioral or heterogeneity effects
  - Therefore…
    - Expected ***total*** captures: $E(n_i) = N_i p_i$
    - Expected recaptures: $E(m_i) = M_i p_i$
    - Expected ***unmarked*** captures: $E(u_i) = U_i p_i$
- 2) To estimate abundance and survival
  - The constant survival $\phi_i$ for each time period
    - Applies to ***marked*** members $M_i$
  - To estimate recruitment
    - Necessary to assume it applies to ***unmarked*** members as well $U_i$

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$

# Jolly-Seber Assumptions

- 3) Each animal in the marked $M_i$ or unmarked $U_i$ group
  - Has the same probability of being returned to the population
    - Tag bounty ???? But, what about the free hats!
- 4) Other Schnabel assumptions apply:
  - Samples are instantaneous
  - No tag loss (but see below) or non-reporting
- 5) Some releases occur at each period
  - Otherwise some parameters are not estimable!

# Jolly-Seber Model

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- New population = Survivors from old population + Recruitment
  - $N_{i+1} = \phi_i(N_i - n_i + R_i) + B_i = M_{i+1} + U_{i+1}$
- Expected ***unmarked*** population
  - $U_{i+1} = \phi_i(U_i - u_i) + B_i = U_i\phi_i q_i + B_i$
    - Constant ***non-capture*** probability: $q_i = 1 - p_i$
  - Unmarked population is made up of
    - Surviving unmarked members ***not*** caught

# Jolly-Seber Model

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- New population = Survivors from old population + Recruitment
  - $N_{i+1} = \phi_i(N_i - n_i + R_i) + B_i = M_{i+1} + U_{i+1}$
- Expected ***marked*** population
  - $M_{i+1} = \phi_i(M_i - m_i + R_i)$
  - $M_{i+1} \;= \phi_i M_i(q_i + p_i v_i) + \phi_i U_i(p_i v_i')$
    - $v_i$ = probability of a ***marked member*** being ***released***
    - $v_i'$ = probability of an ***unmarked*** member being ***released***
  - Surviving marked members
    - Those ***not*** caught ***and*** those caught ***and returned*** to the population after sample
    - And surviving
  - Previously ***unmarked*** members that are caught
    - And ***returned*** to the population as marked members

# Jolly-Seber Likelihood

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- The likelihood follows directly from the Schnabel experiment
  - With one major modification
    - In order to be considered for capture at occasion $i$, an animal must ***survive*** the ***prior*** period
- Therefore, the survival term $\phi_i$ must be added to
  - Capture and non-capture probabilities
    - In the binomial likelihood
- In addition, a captured animal must be ***re-released*** back into the population
  - With probability $v_i$ if already marked
    - And probability $v_i'$ if unmarked

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

# Jolly-Seber Cap History

- Example capture histories
  - (1 0 0 1 0)
    - $(p_1 v_1' \phi_1)(q_2 \phi_2)(q_3 \phi_3)(p_4 v_4 \phi_4)(q_5)$
  - (0 1 0 1 0)
    - $(q_1 \phi_1)(p_2 v_2' \phi_2)(q_3 \phi_3)(p_4 v_4 \phi_4)(q_5)$

# Jolly-Seber Likelihood

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- Seber and Brownie et al. show how do do this from capture histories
  - The net result being the likelihood component for marked recaputres
    - Can be expressed in terms of the sufficient statistics ($r_i$, $m_i$, $z_i$ )
  - $m_{hi}$ = number caught in the $i$th sample
    - ***Last caught*** in sample $h$
  - $r_i$ = number of $R_i$ (releases) later ***captured***
  - $z_i$ = number caught ***before*** sample $i$
    - ***Not*** captured in sample $i$
    - And ***captured*** after $i$

# Jolly-Seber Likelihood

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- Sufficient statistics ($r_i$, $m_i$, $z_i$ ) are calculated from
  - The recapture matrix ($m_{hi}$)
    - Shown below
- Which combined with information on the release process ($R_i$, $d_i$, $d_i'$)
    - $d_i$ = number of $m_i$ (recaptures) ***not*** released
    - $d_i'$ = number of $u_i$ (unmarked) ***not*** released
  - And the unmarked captures $u_i$
    - Produces the total likelihood
- The total likelihood $L$
  - Is the product of three different likelihood components
    - $L = L_1 L_2 L_3$

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

# Jolly-Seber Likelihood

- Likelihood component #1 ($L_1$)
  - Seber and Brownie et al. have slightly different forms of the likelihood
    - We'll consider the Brownie version:

$$L_1 = \prod_{i=1}^{s-1} \binom{R_i}{r_i} (1-\chi_i)^{r_i} \chi_i^{R_i - r_i} \prod_{i=2}^{s-1} \binom{m_i + z_i}{m_i} \left( \frac{p_i}{1 - q_i \chi_i} \right)^{m_i} \left( 1 - \frac{p_i}{1 - q_i \chi_i} \right)^{z_i}$$

  - The number of recaptures from release group $R_i$
    - Is binomially distributed
  - As is the number of recaptures from releases ***prior*** to period $i$
    - Divided into those caught at period $i$, and those caught after
  - This component gives estimates of the parameters $\phi_i$ and $p_i$
    - This could be obtained numerically, but there are closed-form solutions

# Jolly-Seber Likelihood

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- Likelihood component #2 ($L_2$)
  - The numbers ***not*** returned to the population are binomially distributed
    - $d_i \sim Binomial(m_i, 1 - v_i)$
    - $d_i' \sim Binomial(u_i, 1 - v_i')$
  - Multiplying these together gives the component $L_2$
    - Providing the estimators for the ***release probabilities*** (e.g. $\hat{v}_i = 1 - d_i/m_i$)
  - But otherwise have no connection to other estimates
    - i.e. nuisance parameters

# Jolly-Seber Likelihood

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- Likelihood component #3 ($L_3$)
  - The number of ***unmarked*** captures $u_i$ is binomially distributed
    - $L_3(u_i) \sim \prod_{i=1}^{s} Binomial(U_i, p_i)$
  - This provides estimators for the unmarked population at each time period
    - E.g. $\widehat{U}_i = u_i / \hat{p}_i$
  - With a connection to the first component ($L_1$)
    - Through the probabilities of capture
  - This necessarily assumes that capture probabilities apply equally to marked and unmarked members!

# Jolly-Seber Estimation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- The first task is to estimate the number of marks $M_i$ in the population prior to sampling
  - Because this is no longer known due to mortality
- The MLE derived from the likelihood equations can be explained intuitively
  - Break $M_i$ into two groups
    - $m_i$ = the number caught
    - $M_i - m_i$ = the number ***not*** caught
  - After sample $i$, there are two groups
    - $M_i - m_i$, of which $z_i$ are caught later
    - $R_i$, of which $r_i$ are caught later

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

# Jolly-Seber Estimation

- By equating the ***recapture*** proportions
  - The estimated number of marks is found
    - $\frac{z_i}{M_i - m_i} = \frac{r_i}{R_i} \Longrightarrow \frac{1}{\widehat{M}_i - m_i} = \frac{r_i}{R_i z_i} \Longrightarrow \widehat{M}_i = \frac{R_i z_i}{r_i} + m_i$
  - $r_i$ = number of $R_i$ (releases) later ***captured***
  - $z_i$ = number caught ***before*** sample $i$
    - ***Not*** captured in sample $i$
    - And ***captured*** after $i$
- Or the bias-corrected version
  - $M_i^* = \frac{R_i + 1}{r_i + 1} z_i + m_i$

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

# Jolly-Seber Estimation

- By equating the ***recapture*** proportions
  - The estimated number of marks is found
    - $\frac{z_i}{M_i - m_i} = \frac{r_i}{R_i} \Longrightarrow \frac{1}{\widehat{M}_i - m_i} = \frac{r_i}{R_i z_i} \Longrightarrow \widehat{M}_i = \frac{R_i z_i}{r_i} + m_i$
  - $r_i$ = number of $R_i$ (releases) later ***captured***
  - $z_i$ = number caught ***before*** sample $i$
    - ***Not*** captured in sample $i$
    - And ***captured*** after $i$
- Or the bias-corrected version
  - $M_i^* = \frac{R_i + 1}{r_i + 1} z_i + m_i$
- Note also that
  - $\frac{1}{\widehat{M}_i - m_i + R_i} = \frac{r_i}{R_i(z_i + r_i)}$

# Jolly-Seber Estimation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- The estimated probability of capture is then
  - $\hat{p}_i = \frac{m_i}{\widehat{M}_i}$
- From which the unmarked and total population can be estimated from
  - $\widehat{U}_i = \frac{u_i}{\hat{p}_i} = \frac{\widehat{M}_i u_i}{m_i}$
  - $\widehat{N}_i = \frac{n_i}{\hat{p}_i} = \frac{\widehat{M}_i n_i}{m_i}$
    - Our old friend the Petersen estimators!
- The bias-corrected estimators are:
  - $U_i^* = \frac{M_i^*(u_i+1)}{m_i+1}$
  - $N_i^* = M_i^* + U_i^* = \frac{M_i^*(n_i+2)}{m_i+1}$

# Jolly-Seber Estimation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- Survival is estimated from ***marked*** members alone
  - By taking the ratio of the estimated number marked prior to sample $i + 1$
    - And the estimated number marked just after sample $i$
  - $\phi_i^* = \frac{M_{i+1}^*}{\widehat{M}_i - m_i + R_i}$
  - First period: $i = 1$
    - $\phi_1^* = \frac{M_2^*}{R_1}$
- Note that $M_i^*$ is used in the numerator and $\widehat{M}_i$ is used in the denominator
  - To get the least biased estimator

# Jolly-Seber Estimation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- The proportion of marks in the population $\rho_i = M_i/N_i$
  - Is estimated by: $\rho_i = \frac{M_i}{N_i} = \frac{m_i}{n_i}$
- The estimated probability of not being caught after sample $i$ is
  - $\chi_i = 1 - r_i/R_i$
- Recruitment is estimated as
  - $B_i^* = U_{i+1}^* - \phi_i^*(U_i^* - u_i)$, or as
    - $B_i^* = U_{i+1}^* - U_i^* \phi_i^* \hat{q}_i$ (less biased)
  - Where $\hat{q}_i = 1 - \hat{p}_i$

# Jolly-Seber Estimation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- Estimates of abundance $N_i^*$ can be made for $i = 2, \ldots, s-1$
  - Estimates of survival $\phi_i^*$ for $i = 1, \ldots, s-2$
  - Estimates of capture probability $\hat{p}_i$ for $i = 2, \ldots, s-2$
  - Estimates of recruitment $B_i^*$ for $i = 2, \ldots, s-2$
- Note that $\phi_s$ and $B_s$ are undefined beyond the time period of consideration
- However, if there is ***no*** recruitment for the first period ($B_1 = 0$)
  - And all animals are ***released*** ($R_1 = n_1$)
  - Then a simple extrapolation is:
    - $N_1^* = N_2^* / \phi_1^*$

# Jolly-Seber Implementation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- 1) Obtain the capture history raw data
  - Summarize in the matrix $m_{hi}$
    - For release group $h$ (row) the column $i$ gets
    - The number of marked recaptures that were next captured on occasion $i$

Recapture time $i$

| Release group $h$ | $m_{hi}$ | 1 | 2 | 3 | 4 | 5 | 6 | $r_h$ |
|---|---|---|---|---|---|---|---|---|
| | 1 | | 3 | 4 | 3 | 13 | 5 | 28 |
| | 2 | | | 2 | 4 | 4 | 7 | 17 |
| | 3 | | | | 7 | 23 | 7 | 37 |
| | 4 | | | | | 37 | 11 | 48 |
| | 5 | | | | | | 32 | 32 |
| | $m_i$ | | 3 | 6 | 14 | 77 | 62 | |

\# of releases, later recaptured

\# of total recaptures

# Jolly-Seber Implementation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- $c_{1i} = m_{1i}$ for release group 1
  - $c_{hi} = c_{h-1,i} + m_{hi}$ for other release groups

Recapture time $i$

| Release group $h$ | $m_{hi}$ | 1 | 2 | 3 | 4 | 5 | 6 | $r_h$ |
|---|---|---|---|---|---|---|---|---|
| | 1 | | 3 | 4 | 3 | 13 | 5 | 28 |
| | 2 | | | 2 | 4 | 4 | 7 | 17 |
| | 3 | | | | 7 | 23 | 7 | 37 |
| | 4 | | | | | 37 | 11 | 48 |
| | 5 | | | | | | 32 | 32 |
| | $m_i$ | | 3 | 6 | 14 | 77 | 62 | |

Recapture time $i$

| Release group $h$ | $c_{hi}$ | 1 | 2 | 3 | 4 | 5 | 6 | $z_{h+1}$ |
|---|---|---|---|---|---|---|---|---|
| | 1 | | 3 | 4 | 3 | 13 | 5 | 25 |
| | 2 | | | 6 | 7 | 17 | 12 | 36 |
| | 3 | | | | 14 | 40 | 19 | 59 |
| | 4 | | | | | 77 | 30 | 30 |
| | 5 | | | | | | 62 | |

# Jolly-Seber Implementation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- 3) Get $m_i$ by summing each column of $m$ matrix
  - $m_i = \sum_{h=1}^{i-1} m_{hi}$
    - Should be equal to first diagonal of $c_{hi}$

Recapture time $i$

| | $m_{hi}$ | 1 | 2 | 3 | 4 | 5 | 6 | $r_h$ |
|---|---|---|---|---|---|---|---|---|
| Release | 1 | | 3 | 4 | 3 | 13 | 5 | 28 |
| group | 2 | | | 2 | 4 | 4 | 7 | 17 |
| $h$ | 3 | | | | 7 | 23 | 7 | 37 |
| | 4 | | | | | 37 | 11 | 48 |
| | 5 | | | | | | 32 | 32 |
| | $m_i$ | | 3 | 6 | 14 | 77 | 62 | |

# of total recaptures

# Jolly-Seber Implementation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- 4) Get $r_h$ by summing each row of $m$ matrix
  - $r_h = \sum_{i=h+1}^{s} m_{hi}$

# of releases, later recaptured

Recapture time $i$

| Release group $h$ | $m_{hi}$ | 1 | 2 | 3 | 4 | 5 | 6 | $r_h$ |
|---|---|---|---|---|---|---|---|---|
| | 1 | | 3 | 4 | 3 | 13 | 5 | 28 |
| | 2 | | | 2 | 4 | 4 | 7 | 17 |
| | 3 | | | | 7 | 23 | 7 | 37 |
| | 4 | | | | | 37 | 11 | 48 |
| | 5 | | | | | | 32 | 32 |
| | $m_i$ | | 3 | 6 | 14 | 77 | 62 | |

# of total recaptures

# Jolly-Seber Implementation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- 5) Get $z_{h+1}$ by summing each row of $c_{hi}$ matrix
  - Minus the first element
    - $z_{h+1} = \sum_{i=h+2}^{s} c_{hi}$
    - $z_{h+1} - z_h = r_h - m_{h+1}$
    - Example: $h = 2$ 36-25=17-6

Recapture time $i$

| Release group $h$ | $c_{hi}$ | 1 | 2 | 3 | 4 | 5 | 6 | $z_{h+1}$ |
|---|---|---|---|---|---|---|---|---|
| | 1 | | 3 | 4 | 3 | 13 | 5 | 25 |
| | 2 | | | 6 | 7 | 17 | 12 | 36 |
| | 3 | | | | 14 | 40 | 19 | 59 |
| | 4 | | | | | 77 | 30 | 30 |
| | 5 | | | | | | 62 | |

# Jolly-Seber Implementation

Captures: $n_i$
Recaptures: $m_i$
Total marks: $M_i$
Returns: $R_i$
Recruitment: $B_i$
Survival: $\phi_i$

- 6) Get the data $n_i$ and $R_i$

| $i$ | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| $n_i$ | 1015 | 417 | 606 | 789 | 1906 | 1151 |
| $R_i$ | 1015 | 405 | 603 | 789 | 1880 | 0 |

- 7) Calculate all desired estimators using previous equations