Lecture 11 – Multi-state models

Resources

Hestbeck, J.B., J.D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523-533.

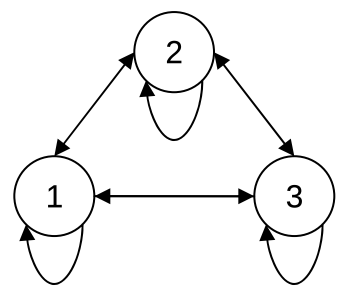
Nichols, J.D., J.E. Hines, K.H. Pollock, R.L. Hinz, and W.A. Link. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. Ecology 75:2052-2065.

Williams et al. Chapter 17.3-17.5

LeBreton, J.-D., T. Almera, and R. Pradel. 1999. Competing events mixtures of information and multistratum recapture models. Bird Study 46(Suppl.) S39-S46.

Overview

1. Further generalization of the original CJS model.
2. Similar in many respects to the age-structured open model – survival was transition to the next time period or age
3. Also similar in many respects to time variable covariates – survival in condition or state at time t equals transition to the next condition
4. Multi-state or multi-strata models



   a. Individuals classified into discrete states that could represent locations, ages, size classes, etc.
   b. Models permit stochastic transitions or movements among states
   c. Contrast with deterministic transitions among ages
   d. Description of the population requires sampling all states (e.g., locations)
   e. Estimate capture and survival probabilities of individuals in different states
   f. Additionally, estimate a suite of transition probabilities
   g. First developed by Arnason (1972, 1973) using moment estimators
   h. MLEs first developed by Hestbeck *et al.* (1991) for multiple locations
   i. Nichols et al. (1992) developed for a multiple phenotypic states (sizes)
   j. Brownie et al. (1993) and Schwartz et al. (1993) developed more generalized approaches
   k. Recently, Lebreton et al. suggested that multi-state models formed a unifiying approach for all mark-recapture models
   l. Biological questions:
      1) Estimates of stage- (or age-) specific survival rates for use in population models
      2) Survival rates of breeding and nonbreeding states for examining costs of reproduction and fitness tradeoffs.
      3) Ecologists and managers have become more aware that animal distributions do not necessarily reflect habitat quality without measures of fitness-related

parameters such as survival and reproduction. Multi-strata models can be used to examine habitat quality as well as movement rates among habitats.

5. Markovian models
   a. State is stochastically determined as a function of state at some previous time – Markov process.
      a. Typically consider only the first order Markov process – state at $t+1$ is a function of state at t.
      b. Memory model – 2nd order Markov process – state at $t+1$ is a function of state at t and $t-1$. Theoretically, could be generalized to consider movement as a function of state at any prior time – not considered here.
6. Data structure
   a. Capture histories that indicate state at each occasion.
      a. Use letters or numbers instead of 1s (MARK uses either). 0s indicate failure to capture or observe on that occasion.
      b. Example:

         Capture history: N00BNB indicates individual observed in state N at occasion 1, not seen on occasions 2 and 3, observed in state 4 on occasion 4, observed in N on occasion 5, and finally in B on occasion 6.
      c. Summary statistics:

         Releases on occasion i

         $$\mathrm{R}_i = \begin{bmatrix} \mathrm{R}_i^1 \\ \mathrm{R}_i^2 \\ \mathrm{R}_i^3 \end{bmatrix}$$ for i = 1:K-1, and

         Recaptures of animals m_{ij}^{rs} released in state r at time i and recaptured in state s at time j.

         $$m_{ij} = \begin{bmatrix} m_{ij}^{11} & m_{ij}^{12} & m_{ij}^{13} \\ m_{ij}^{21} & m_{ij}^{22} & m_{ij}^{23} \\ m_{ij}^{31} & m_{ij}^{32} & m_{ij}^{33} \end{bmatrix}$$, for i = 1:K-1, and $j = i + 1{:}K$,
      d. Can be reduced to a modified m-array.

         Ms-array example: Williams et al. (2002 p456)

TABLE 17.17 Multistate m_{ij}^{rs}-Array Representation for Data Resulting from a Four-Period Capture–Recapture Study on a Population with Three States[a]

			Period of first recapture j (state of recaptures)								
			2			3			4		
Release period i	State of release r	Number released	(1	2	3)	(1	2	3)	(1	2	3)
1	1	R_1^1	m_{12}^{11}	m_{12}^{12}	m_{12}^{13}	m_{13}^{11}	m_{13}^{12}	m_{13}^{13}	m_{14}^{11}	m_{14}^{12}	m_{14}^{13}
1	2	R_1^2	m_{12}^{21}	m_{12}^{22}	m_{12}^{23}	m_{13}^{21}	m_{13}^{22}	m_{13}^{23}	m_{14}^{21}	m_{14}^{22}	m_{14}^{23}
1	3	R_1^3	m_{12}^{31}	m_{12}^{32}	m_{12}^{33}	m_{13}^{31}	m_{13}^{32}	m_{13}^{33}	m_{14}^{31}	m_{14}^{32}	m_{14}^{33}
2	1	R_2^1				m_{23}^{11}	m_{23}^{12}	m_{23}^{13}	m_{24}^{11}	m_{24}^{12}	m_{24}^{13}
2	2	R_2^2				m_{23}^{21}	m_{23}^{22}	m_{23}^{23}	m_{24}^{21}	m_{24}^{22}	m_{24}^{23}
2	3	R_2^3				m_{23}^{31}	m_{23}^{32}	m_{23}^{33}	m_{24}^{31}	m_{24}^{32}	m_{24}^{33}
3	1	R_3^1							m_{34}^{11}	m_{34}^{12}	m_{34}^{13}
3	2	R_3^2							m_{34}^{21}	m_{34}^{22}	m_{34}^{23}
3	3	R_3^3							m_{34}^{31}	m_{34}^{32}	m_{34}^{33}

[a] R_i^r denotes the number of animals in state r that are released at time i; m_{ij}^{rs} denotes the number of members of R_i^r that are next captured at time j and found to be in state s at that time.

matrix representation:

TABLE 17.18 Matrix Representation of the Multistate m_{ij}^{rs}-Array Data Summary in Table 17.17[a]

		Recapture period j		
Release period i	Number released	2	3	4
1	$\underline{R}_1$	$\underline{m}_{12}$	$\underline{m}_{13}$	$\underline{m}_{14}$
2	$\underline{R}_2$		$\underline{m}_{23}$	$\underline{m}_{24}$
3	$\underline{R}_3$			$\underline{m}_{34}$

[a] $\underline{R}_i$ and $\underline{m}_{ij}$ are the release and recapture matrices, respectively.

7. Model structure

Parameters similar to those from the CJS model only now state specific:

φ_i^{rs} - probability of survival in s at i +1, given alive in r at i. Note that this incorporates probability of survival in s from i to i+1 and transition from state r to s.

p_i^r - probability of recapture (encounter) in r at i.

Example for 2 states N and B

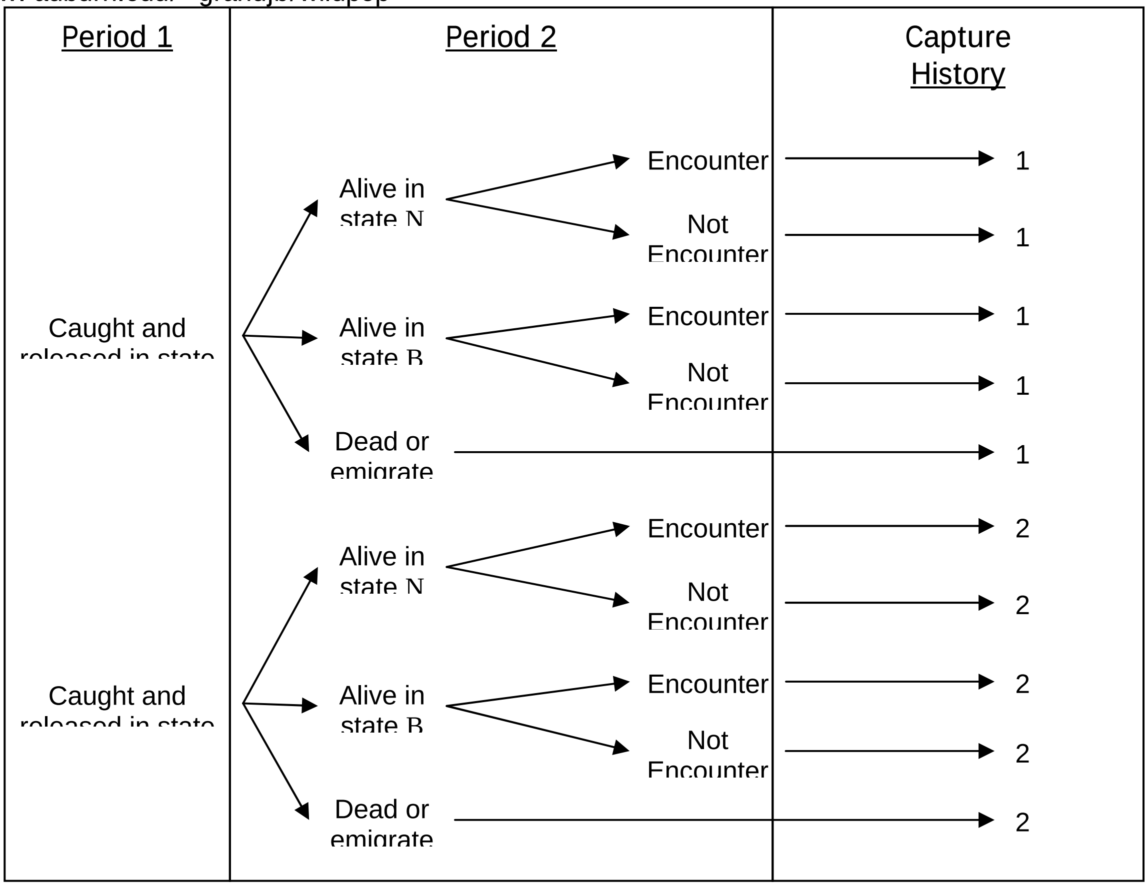
$$\Pr(\text{NN0B0| release in N at 1}) = \varphi_1^{\text{NN}} p_2^{\text{N}} \left[\varphi_2^{\text{NN}} \left(1 - p_3^{\text{N}}\right) \varphi_2^{\text{NB}} p_4^{\text{B}} + \varphi_2^{\text{NB}} \left(1 - p_3^{\text{B}}\right) \varphi_3^{\text{BB}} p_4^{\text{B}} \right]$$
$$\times \left(1 - \varphi_4^{\text{BB}} p_5^{\text{B}} - \varphi_4^{\text{BN}} p_5^{\text{N}}\right)$$

$\Pr(\text{NN0B0| release in N at 1}) =$

surviving and remaining in N during 1-2 and seen at 2 in N,

surviving and remaining in N from 2-3 and not seen in N at 3 and surviving in N and moving to B in 3-4 and seen in B at 4, or

surviving in N and moving to B during 2-3 and not seen in B at 3 and surviving and remaining in B in 3-4 and being seen in B at 4.



Note that φ_i^{rs} includes remaining in the study population, and survival in r from i-1 to i, and movement between r and s. For many questions of interest it is necessary to decompose these into separate rates of survival (S_i^r) and movement (ψ_i^{rs}):

$$\varphi_i^{rs} = S_i^r \psi_i^{rs} .$$

It's also important to note that movement is conditional upon survival and the movement probabilities (rates) must sum to one.

$$\sum \psi_i^{rs} = 1$$

8. Model assumptions

The first two assumptions of the CJS model are modified as follows:

1) Every marked animal present in state r immediately following sampling period i has the same probability of recapture, and
2) Every marked animal present in state r immediately following the sampling period i has the same probability of survivng until i +1 and moving to state s by period i +1.

Thus, homogeneity assumptions apply only within each state. In addition to the remaining CJS assumptions:

7) The state transition probabilities reflect a first-order Markov process, i.e., state at time i +1 is dependent only on the state at time i.

9. Estimation

Estimation is by MLE with one of the transition rates estimated by one minus the sum of the remaining transition probabilities. The default in MARK is for the probability of remaining in r to be estimated as one minus the sum of the other transitions. However, the user can choose which rate is estimated by this difference and it's useful to pick rates that are small for estimation and large rates to be determined by the difference method.

10. Alternative modeling
    a. Alternative models can be cast similar to the other models we've discussed by imposing constraints on parameters.
    b. Survival and transition can be modeled using time specific or individual covariates
    c. Multiple groups are possible
    d. Age models – two ways
        1) As with the CJS open models by constraining parameters
        2) Define each age as a separate state and only estimate the parameters that correspond to the age transitions by fixing all other transitions = 0.

Lebreton et al. (1999) have illustrated that many of the specialized models for age-specific parameters or multiple data types (e.g., live and dead, resighting and recovery) can be developed in the framework of multi-state models. Recently, innovative models have been developed for the situation when initial state is unknown and for the misclassification of state.

11. Model selection, estimator robustness, and model assumptions

Model selection – as with other MLE approaches use AIC and LRTs.

GOF – program U-care provides a generalized approach to estimating GOF and c-hat for multistate and robust design.

12. Memory models
13. Reverse time
14. Mark-recapture with auxiliary data
    a. Barker's model
    b. Burnham's model
15. Robust design

Stochastic variation and simulation

Resources:

Caswell, H. 2001. Matrix population models. 2nd ed. Sinauer Associates, Inc. Sunderland, Mass.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and P. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph No. 5. Bethesda, MD, USA. 437pp.

Variance components

It is important to understand the sources of variation when developing models for simulations from parameter estimates. Generally there are two sources that are considered—process (environmental) variation and sampling variation.

1. Sampling variance ($\mathrm{var}\left(\hat{\theta}|\theta\right)$) – a measure of precision and repeatability. Sampling variation occurs because only partial information is available about the population. If the sampling scheme is unbiased, the composition of the sample is a result of a random selection. The

observer has some control over this parameter estimate through the study design (e.g., sample size, stratification, selection of covariates).

2. Process variance (σ^2) – spatial or temporal deviance in population parameters due to environmental factors. These types of variation are not directly controlled by the observer, and are **characteristics of the population**.

For example, if the annual survival rate (θ) of beach mice at Bon Secour NWR was measured for 10 (n) years. The survival rate would most certainly vary among years due to differences in environmental conditions and this would be considered temporal (process) variation.

Another example, the fecundity (θ) of red-breasted sunfish is measured in a dozen (n) streams across south Alabama and Georgia to estimate spatial (process) variation in this population parameter.

The theoretical (total) variance is:

$$\mathrm{var}\left(\hat{\hat{\theta}}\right) = \frac{\sigma^2 + \mathrm{var}\left(\hat{\theta} \mid \theta\right)}{n}$$

and it's unbiased estimator is:

$$\hat{\mathrm{var}}\left(\hat{\hat{\theta}}\right) = \frac{\sum_{i=1}^{n}\left(\hat{\theta}_i - \hat{\hat{\theta}}\right)^2}{n(n-1)}.$$

In order to estimate the process variation we use a weighted procedure with weights equal to the reciprocal $\mathrm{var}\left(\hat{\hat{\theta}}\right)$:

$$w_i = \frac{1}{\sigma^2 + \mathrm{var}\left(\hat{\theta}_i \mid \theta\right)},$$

$$\hat{\hat{\theta}} = \frac{\sum_{i=1}^{n} w_i \hat{\theta}_i}{\sum_{i=1}^{n} w_i}$$

theoretical variance

$$\mathrm{var}\left(\hat{\hat{\theta}}\right) = \frac{1}{\sum_{i=1}^{n} w_i}$$

and the empirical estimate of the variance

$$\hat{\mathrm{var}}\left(\hat{\hat{\theta}}\right) = \frac{\sum_{i=1}^{n} w_i\left(\hat{\theta}_i - \hat{\hat{\theta}}\right)^2}{\left(\sum_{i=1}^{n} w_i\right)(n-1)}.$$

This ultimately leads to the following equation which can be solved for σ2:

$$\frac{1}{n-1}\sum_{i=1}^{n}\hat{w}\left(\hat{\theta}_I-\hat{\bar{\theta}}\right)^2=1$$

3. Example:

Estimates of clutch size and standard error are obtained from a population of nesting birds over ten-year period as follows:

Year	Mean clutch size ($\hat{\bar{y}}_i$)	$\hat{s}e(\hat{\bar{y}}_i)$
1	6.04	0.39
2	5.64	0.29
3	5.82	0.42
4	4.99	0.43
5	5.93	0.45
6	5.56	0.15
7	5.84	0.08
8	5.40	0.11
9	5.86	0.45
10	5.67	0.26
$\hat{\bar{y}}$	5.68	

The $\hat{s}e(\hat{y}_i)$ in this example include only sampling variation. Also, in this example $\hat{s}e(\hat{\bar{y}})$ is calculated using the empirical formula:

$$\hat{s}e(\hat{\bar{y}}_i)=\sqrt{\frac{\sum_{i=1}^{n}\left[\hat{y}_i-\hat{\bar{y}}\right]^2}{n(n-1)}}=0.096,$$

which includes both temporal variation and sampling variation. We can then iteratively solve for σ^2 to estimate the temporal variance in clutch size after controlling for sampling variance using the formulae:

$$w_i=\frac{1}{\sigma^2+\hat{\text{v}}\text{ar}(\hat{\bar{y}}_i)}$$

and

$$\frac{1}{n-1}\sum_{i=1}^{n}\hat{w}\left(\hat{\bar{y}}_i-\hat{\bar{y}}\right)^2=1.$$

Determi

				σ = **0.1049**		
Year	$(\hat{\bar{y}}_i)$	$\hat{s}e(\hat{\bar{y}}_i)$	$\left(\hat{\bar{y}}_i-\hat{\bar{y}}\right)^2$	w_i	$w_i\left(\hat{\bar{y}}_i-\hat{\bar{y}}\right)^2$	$w_i\hat{\bar{y}}_i$
1	6.04	0.39	0.133	6.227	0.826	37.614
2	5.64	0.29	0.001	10.509	0.011	59.314
3	5.82	0.42	0.020	5.336	0.106	31.039
4	4.99	0.43	0.468	5.208	2.438	26.000

5	5.93	0.45	0.064	4.735	0.301	28.071
6	5.56	0.15	0.013	30.113	0.404	167.438
7	5.84	0.08	0.026	54.886	1.448	320.458
8	5.40	0.11	0.075	44.051	3.301	237.981
9	5.86	0.45	0.036	4.673	0.166	27.408
10	5.67	0.26	0.000	12.740	0.000	72.277
	$\hat{\bar{y}}$ = 5.68		Sum	178.478	9.000	1007.598