

Stat 534: formulae referenced in lecture, week 8:
Open population models and extensions

Age-based models

- 1st yr survival often different from “adult” survival
- can separate age and time effects if mark and age individuals in multiple years
- can use age-based models to evaluate senescence at older ages
 - birds and many mammals: often banded as nestlings / new borns, before they leave the nest / den.
- Biggest conceptual issue: age \neq year of life.
Age 0 individuals = 1st year of life
- likelihood is just a bookkeeping exercise
- Notation used in McCrea and Morgan:
 - $p_j(a)$ “probability that an individual alive and in its a^{th} year of life at time t_j is captured at that time”
 - $\phi_j(a)$ “apparent probability that an individual in its a^{th} year of life at occasion t_j survives until time t_{j+1} ”
- CJS-like likelihood depends on # releases for each age and time and # age-specific recaptures at each time
- McCrea and Morgan, p. 74, gives the expression for the log likelihood - not illuminating
- RMark code is at Mike Conroy’s (U Georgia) site:
<https://sites.google.com/site/cmrsoftware/lecture-lab-schedule/5--covariates-age-and-cohort-structure/known-age-releases-each-occasion>

Pradel reverse time estimators

- see hand-written notes
- Notation

- γ_{i+1} : “seniority” parameter
- fraction of population at time $i + 1$ also alive at time i
- # Births between i and $i + 1 = N_{i+1}(1 - \gamma_{i+1})$
- Pradel gives a direct estimate of birth rate
 - Included in the likelihood
 - Not a derived parameter
- CJS estimates survival of marked individuals
- Pradel estimates birth rate for individuals that are or will be marked

Pradel temporal symmetry model: estimate pop growth rate

- Combine CJS (forward time) and Pradel (reverse time)
- \Rightarrow direct estimate population growth rate

$$\frac{N_{i+1}}{N_i} = \lambda_i = \frac{\phi_i}{\gamma_i}$$

- Explanation/derivation in hand-written notes

Mark-recovery data:

- Individuals recaptured when dead
- Very common for harvested species
- Don’t have to worry about trailing 0’s in the capture history
- Other big difference: know when death occurs
- Notation:
 - ϕ : apparent survival, 1 - (death + emigration)
 - S : true survival: death only
- Capture probability becomes reporting probability

- Assess with reward bands, commonly worth \$100.
Assume $p_i = 1.0$ for a bird with a reward band
- Two parameterizations, Brownie and Seber, see handwritten notes
- Brownie $f = \text{Seber } r(1 - s)$

POPAN = “superpopulation” models

- Explicit model for births
- Two founding papers: Crosby-Manly (1985) and Schwartz-Arneson (1996)
- N is now the size of the superpopulation
 - All individuals ever born into the population during the study period
 - Not the # alive individuals at time i
- # unmarked at time $i = B_i +$ (# born earlier, not seen until i)
- One set of parameters is “Pent” = Probability that an individual in the superpopulation enters the population at time i
 - Connected to births: $B_i = NP[\text{enter live population at time } i]$
 - Sum Pent = 1, because everyone enters the live population at some time
 - Requires a multinomial probability
- “Stop over” models, Pledger 2009
 - birth = arrive at a migratory rest area
 - death = depart - may depend on time since birth = “age”
 - $N =$ # using the migratory area

Robust Design

- Motivation (Pollock 1981, 82)
 - Models make assumptions, almost never met exactly.

- How robust are estimates to violations of assumptions?
- estimates of survival probabilities are more robust than abundance estimates
- Two sampling levels
 - Primary, e.g. years, population open
 - Secondary, e.g. days or weeks, population closed
 $\Rightarrow N_i$
- survival:
 - open pop model on collapsed abundance (seen if seen in any 2nd period)
 - Can be done with CJS
 - Or full likelihood model (Kendall 1995)
- recruitment:
 - Combine abundance (closed) and survival (open)

Temporary emigration

- Animals leave area, but then return
- “on vacation” confounded with “not seen”
- Robust design provides two estimates of capture probability
 - From the closed pop model over the 2nd sampling intervals
 - From the open pop model over the primary sampling intervals
- Kendall’s approach: two emigration parameters
 - $\gamma'_j = \text{P}[\text{unavailable} \mid \text{not available at } j - 1]$
 “stayed away”
 - $\gamma''_j = \text{P}[\text{unavailable} \mid \text{available at } j - 1]$
 “was here but went away”
- Conditional on first capture (like CJS)

- So $P[101] = S_1 \left[\gamma_2''(1 - \gamma_3' + (1 - \gamma_2''(1 - p_2))(1 - \gamma_3'')) \right] S_2 p_3$
- And $P[110] = S_1 p_2 (1 - \gamma_2'') \left[S_2 (1 - \gamma_2'') (1 - p_3) + S_2 (\gamma_3'' + (1 - S_2)) \right]$

Multi-state / Multi-site models

- Examples:
 - 3 sites: individuals can move between them, know where caught each time
 - 2 states: breeding / not breeding, obs each capture time
 - 4 size groups: small, juvenile, breeding adult, large adult
- Big difficulty: only know site/state when captured, not when not detected
 - Age groups: if observe at 2nd and 4th year of life, know in 3rd in between
 - Size groups: if observe at juvenile in year 2 and breeding in year 4, don't know state in year 3
- Notation:
 - ϕ_i^r : apparent survival, animal in state r at year i , to year $i+1$
 - p_i^r : recapture probability, animal in state r at year i
 - $\Psi_i^{r,s}$: P [surviving animal from r at i to s at $i+1$]
 - * diagonal elements = P [stays in same state]
 - * Transitions between states assumed to be first order Markov process
 - * State at $i+1$ depends only on state at i , not earlier history

* Can extend to 2nd order Markov - many more transition parameters

- P[A0B]: Don't know time 2 state (A or B?)

$$P[A0B] = \phi_1^A p_3^B \left[\Psi_1^{AA} (1 - p_2^A) \phi_2^A \Psi_2^{AB} + \Psi_1^{AB} (1 - p_2^B) \phi_2^B \Psi_2^{BB} \right]$$

- Efficient way to calculate these probabilities
- Reminder about CJS m-array with 4 occasions

# released	next captured	never
R_1	$m_{12} \quad m_{13} \quad m_{14}$	$R_1 - (m_{12} + m_{13} + m_{14})$
R_2	$m_{23} \quad m_{24}$	$R_2 - (m_{23} + m_{24})$
R_3	m_{34}	$R_3 - m_{34}$

- Each entry is a scalar
- Multi-site/stage: Each entry is a matrix, classified by state at i and $i + 1$, e.g.:

$$M_{ij} = \begin{bmatrix} M_{ij}^{AA} & M_{ij}^{AB} \\ M_{ij}^{AB} & M_{ij}^{BB} \end{bmatrix}$$

- Parameters also organized as matrices. For 3 sites:

$$\Phi_i = \begin{bmatrix} \phi_i^1 & 0 & 0 \\ 0 & \phi_i^2 & 0 \\ 0 & 0 & \phi_i^3 \end{bmatrix}$$

$$\Psi_i = \begin{bmatrix} \Psi_i^{11} & \Psi_i^{12} & \Psi_i^{13} \\ \Psi_i^{21} & \Psi_i^{22} & \Psi_i^{23} \\ \Psi_i^{31} & \Psi_i^{32} & \Psi_i^{33} \end{bmatrix}$$

$$P_i = \begin{bmatrix} p_i^1 & 0 & 0 \\ 0 & p_i^2 & 0 \\ 0 & 0 & p_i^3 \end{bmatrix}$$

- Use matrix multiplication to account for all paths from i to j

$$M_{ij} = \prod_{k=i}^{j-2} [\Phi_k \Psi_k (I - P_{k+1})] \Phi_{j-1} \Psi_{j-1} P_j$$