Capture-recapture Models for Open Populations: Multip;le States

Population Modeling
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Multistate Models: History

- First developed by Arnason (1972, 1973) and almost completely ignored
- Developed independently by Hestbeck et al. (1991)
- Modern development:
  - Brownie et al. (1993), Schwarz et al. (1993)
  - Reviews by Lebreton et al. (2002, 2009)

Multistate Models: Data Structure

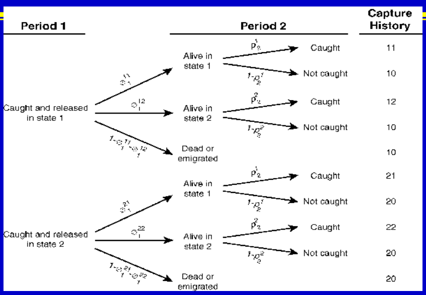
- Open capture-recapture study
- At each capture, animals are categorized by "state"
  - Location (Hestbeck et al. 1991)
  - Size class (Nichols et al. 1992)
  - Breeding state (Nichols et al. 1994)
  - Disease state (Jennelle et al. 2007)
- State of an animal <u>may</u> change from 1 period to the next

Multistate Models: Capture History Data

- Capture history: no longer adequate to use just 1's and 0's
- 0 still denotes no capture
- Assign a positive number or letter to each state
  - e.g., with 3 states: 1, 2, 3
- Example: 3-site system
  - Possible histories: 10310, 00201

Multistate Models: Notation

- ϕ_i^{rs} = probability that animal in state *r* at sample period *i* is alive in state *s* at sample period *i*+1
- p_i^r = probability that animal in state *r* at sample period *i* is captured



Multistate Models: Capture History Expectations

- P(011020 | released in state 1 at period 2) =

$$\phi_2^{11} p_3^1[\phi_3^{11}(1-p_4^1)\phi_4^{12}+\phi_3^{12}(1-p_4^2)\phi_4^{22}]p_5^2$$
$$(1-\phi_5^{21}p_6^1-\phi_5^{22}p_6^2)$$

Multistate Models: Decomposition of ϕ_i^{rs}

- Sometimes reasonable and desirable to decompose ϕ_i^{rs} into survival and transition/movement components:

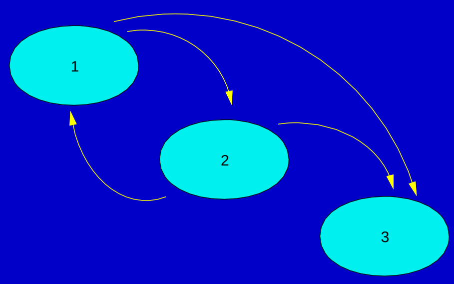
$$\phi_i^{rs} = S_i^r \psi_i^{rs}$$

- S_i^r = probability that animal in state *r* at period *i* survives until period *i*+1
- ψ_i^{rs} = probability that animal in state *r* at period *i* and alive at period *i*+1, is in state *s* at *i*+1

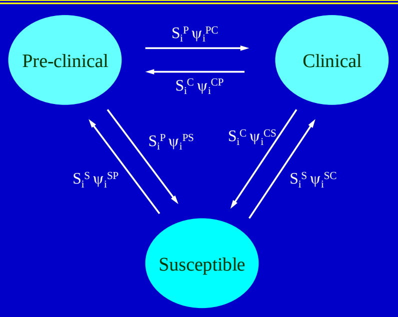
Parameter Estimation

- Multinomial likelihood, conditional on new releases in each sample period
- Data: numbers of new releases at each state in each period and number of animals with each capture history
- Model: probability structure for each capture history
- Maximum likelihood (e.g., programs MARK, MSURGE, ESURGE)

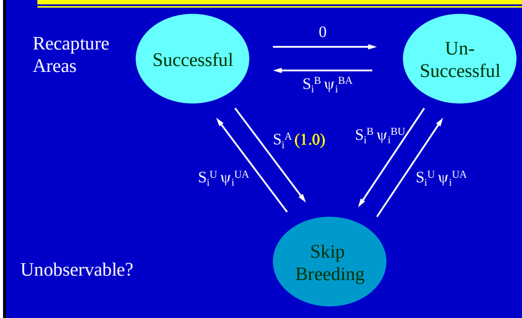
Migration Stopover (e.g., Bechet et al. 2003, Greater Snow Geese)



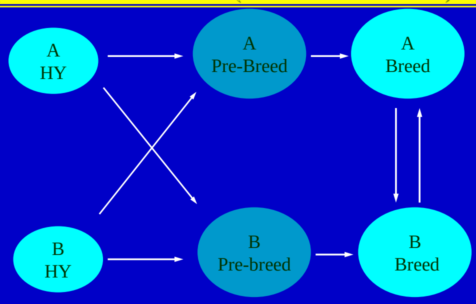
Disease States



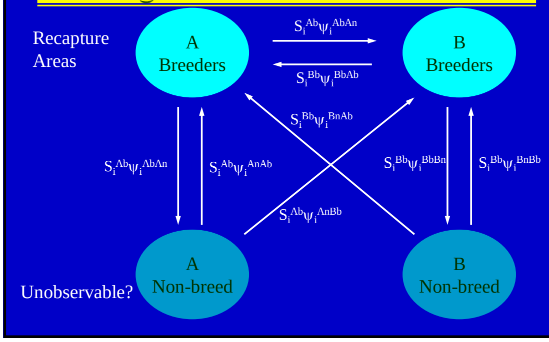
Albatross Breeding Studies – partial determinism



Multi-site age at first reproduction pre-breeders unobserv. (Lebreton et al. 2003)



States defined by location and breeding status



Multi-site model software

- MARK (G. White)
  - Can define which movement probability by subtraction
  - Multinomial logit transformation
  - Can include individual and group covariates (e.g., weight, age, climatological)
- MSURGE (Choquet et al.)
  - GOF test (UCARE)
  - Powerful model specification feature
- ESURGE (Choquet et al)
  - Uncertain state assignment

Multinomial logit transformation for 3 states

$$\psi_i^{BA} = \frac{e^{\beta_1}}{1 + e^{\beta_1} + e^{\beta_2}}$$

$$\psi_i^{BC} = \frac{e^{\beta_2}}{1 + e^{\beta_1} + e^{\beta_2}}$$

Multistate model assumptions

- Within state, age, sex, etc., all animals equally likely to survive, move to given location, be detected
- Marks do not affect survival or movement, are not lost, are recorded correctly
- Each bird acts independently with respect to survival, movement, detection
- Each state observable
- State is correctly assigned each time

Multistate models: why bother?

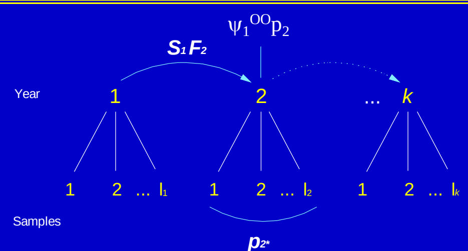
- Transitions and state-specific survival might be interesting biologically
- Reduces heterogeneity in survival or capture probability by partitioning animals

Unobservable States

What can we do about unobservable states?

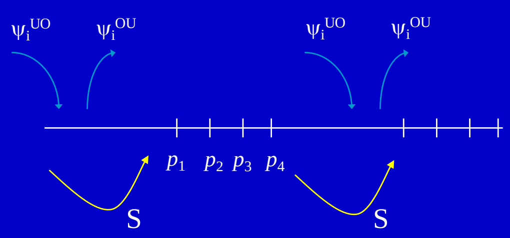
- Unobservable state: at least 1 area or group is inaccessible to sampling effort
- Combine capture/sighting with other sources of information
  - Telemetry
  - Universal band recoveries or sightings
  - Robust design
- Partial determinism with time constancy
- Shared parameters across groups with time constancy

Pollock's Robust Design: TE



Kendall and Nichols (1995), Kendall et al. (1997)

Closed Robust Design: TE



Design Issues: Unobservable States

- Exploit opportunity for robust design
- Include telemetry (preferably with p =1 and survival monitored)
- Create buffer zone around study area (search for marked animals)

Conclusions

- Existence of unobservable states should be minimized through design.
  - Robust design, telemetry, and other sources of information provide means to adjust for unobservable states.
- When design fixes not possible, certain model structures (constrained) permit inference

Mis-classified or Unknown States

How do we adjust for fact that calves are not seen each time with mother?

Assumption: breeding status is known for each sighted female

- *Problem*: Sometimes a calf is present but not sighted.
- *Implication*: Calf might be missed each time female is sighted and hence misclassified as non-breeder.
- *Solution*: adjust for misclassification (i.e., estimate calf detection probability).

Multi-state Model for Misclassification (Kendall et al. 2003)

CC $S_1^C \psi_1^{CC} p_2^{C\delta}$

CN $S_1^C[\psi_1^{CN} p_2^N + \psi_1^{CC} p_2^{C(1-\delta)}]$

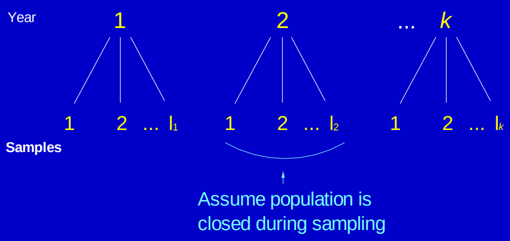
NC $[\pi_1 S_1^N \psi_1^{NC} + (1-\pi_1) S_1^C \psi_1^{CC}] p_2^{C\delta}$

- $p_i^{C\delta}$, $p_i^{C(1-\delta)}$ = probability female with first-year calf is seen in year *i* and her calf is seen or not seen, respectively.
- p_i^N = probability a non-breeder female is seen in year *i*.

How do we estimate detectability for the calf?

- Two sighting occasions per year (robust design).
  - Entire range of population is covered twice in a short period of time
    - ✓ so that if female is breeder calf will be there both times.
  - Each time individual is seen the date and presence/absence of first-year calf is noted.
  - Calf detection probability is estimated from sighting history of female and calf combined.

Pollock's Robust Design (multiple samples per year)



Within-season modeling (conditional on capture in a given year, Kendall et al. *2004*)

CC $\alpha \; p_1^C \delta_1 \; p_2^C \delta_2 \,/\, denom$

NN $[\alpha \; p_1^C (1-\delta_1) p_2^C (1-\delta_2) + (1-\alpha) p_1^N p_2^N] / denom$

$$denom = \alpha \, (p^{C\delta} + p^{C(1-\delta)}) + (1-\alpha) p^N$$

- α = P(adult female is a breeder).
- p_j^C= P(breeding female is seen in sample *j*).
- δ_j= P(calf is seen with female, if there).

Sighting probabilities for season & mixture parameter

$$p^{C\delta} = 1 - \prod_{j=1}^{2} (1 - p_j^C \delta_j)$$

$$p^{C(1-\delta)} = \prod_{j=1}^{2} (1 - p_j^C \delta_j) - \prod_{j=1}^{2} (1 - p_j^C)$$

$$p^N = 1 - \prod_{j=1}^{2} (1 - p_j^N)$$

$$\pi = (1-\alpha) p^N / [\alpha \; p^{C(1-\delta)} + (1-\alpha) p^N]$$

Comparison of Estimates Crystal River (program MSMisclass)

	Unadjusted MS		Adjusted MS	
Parameter	Estimate	s.e.	Estimate	s.e.
S^C	0.96	0.01	Same	
S^N	0.96	0.01	Same	
ψ_i^{NB}	0.31	0.04	**0.43**	0.06

Goodness of Fit: variance inflation factor= 1.9

Other estimates

Parameter	Estimate	s.e.
$\alpha_.$	0.30	0.032
$p_.$ (avg.)	0.41	0.043 (avg.)
$\delta_.^C$ *	0.73	0.06

* avg. P(adult female is seen but calf is not in given year) = 0.22

Other examples of mis-classified states

- Kittiwakes – some pre-breeders are squatters (Cam et al., 2002)
- Disease dynamics
  - Diseased animals show no clinical sign
  - Recovered animals show clinical signs
- Sex is mis-assigned

Unknown Sex

- Sex unknown when marked but perhaps determined later
- Approaches to adjusting estimation
  - Back-date all sexed individuals to initial capture occasion (***BIG MISTAKE!***)
  - Use multi-state with unknown sex
  - **Model unknowns as mixture of males and females**

Unknown Sex – sex assessed each time, but sometimes not determined

UMU $\eta_1(1-\delta_1^M)\phi_1^M p_2^M \delta_2^M \phi_2^M p_3^M (1-\delta_3^M)$

U0U $\eta_1(1-\delta_1^M)\phi_1^M (1-p_2^M)\phi_2^M p_3^M (1-\delta_3^M)$
$+ (1-\eta_1)(1-\delta_1^F)\phi_1^F (1-p_2^F)\phi_2^F p_3^F (1-\delta_3^F)$

- η_j = P(animal first seen in sample *j* is male).
- p_j^s = P(animal of sex *s* is seen in sample *j*).
- δ_j^s = P(sex is determined in sample *j*).

Comparison of Estimators

(Nichols et al. 2004)

	Estimators					
Param	Naive	s.e.	MS	s.e.	Mixt.	s.e.
S_i^M	0.86	0.009	0.79	0.012	0.80	0.010
S_i^F	0.78	0.012	0.69	0.014	0.70	0.015
S_i^U	0.67	0.012	0.76	0.009		

δ = 0.3, p = 0.5, u_i = 200 males, 300 females

State Uncertainty: General Solution

- Pradel (2005) Multievent modeling
- Program ESURGE (Choquet et al. 2009) to implement these models