Direct Inference About λ

Population Modeling
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Definition

λ_i = finite rate of population increase

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

Clear that information is contained in open-model capture-recapture data, as JS model permits inference about N_i

Inference About λ_t Using JS

- Both N_i and λ_i can be estimated, but only as derived parameters
- Would be nice to directly model λ_i

"The Theory of Everything": Life of S. J. Hawking

- Last scene: sequence of clips moving progressively backwards through time (age 72 back to Hawking as young Ph.D. student)
- Mirrored idea that theory of universe could be deduced by considering current expansion, then reversing time order to consider compactness and eventual origin

Reverse-time Capture-recapture Dylan (1964, 1965, 1982)

"The present now will later be past,
The order is rapidly fading,
And the first one now will later be last,
For the times they are a-changin."

"But I was so much older then,
I'm younger than that now."

"Time is running backwards,
And so is the bride."

Reverse-time Capture-recapture C.H.N. Jackson (1936, 1939)

- Studied tsetse flies in Tanganyika territory
- Recognized temporal symmetry of CR data
- "Negative method" of abundance estimation
  - Proportions of recaptures at *t* originally marked in successive previous occasions
- Help from Ronald Fisher

Reverse-time Capture-recapture Pollock, Solomon and Robson (1974)

...a backward process with recruitment and no mortality is statistically equivalent to a forward process with mortality and no recruitment.

Reverse-time Modeling: Parameters

γ_i= seniority parameter; probability that an animal in the sampled population at period *i* was also in the sampled population at *i*-1

p_i= capture probability at period *i*

Notation of Pradel (1996)

Reverse-time Modeling

$$P(0101 | \text{Last caught at } 4) = \gamma_4 (1 - p_3) \gamma_3 p_2 (1 - \gamma_2 p_1)$$

γ_i = probability that an animal in population at *i* is a survivor from the previous period

1- γ_i = probability that an animal in population at *i* is a new recruit

Pradel's Model

$$\begin{array}{lcccccc} & \multicolumn{6}{c}{\phi_1 \quad \phi_2 \quad \phi_3 \quad \phi_4 \quad \phi_5} \\ \text{Capture history:} & 1 & 1 & 0 & 0 & 1 & 1 \end{array}$$

$$\begin{array}{lcccccc} & \multicolumn{6}{c}{\gamma_2 \quad \gamma_3 \quad \gamma_4 \quad \gamma_5 \quad \gamma_6} \\ \text{Capture history:} & 1 & 1 & 0 & 0 & 1 & 1 \end{array}$$

λ_i = ?

Pradel's Full Likelihood: Temporal Symmetry Model

2 ways to write expected number of animals alive in 2 successive sample periods:

$$N_i \phi_i = N_{i+1} \gamma_{i+1}$$

$$\text{so } \lambda_i = \frac{N_{i+1}}{N_i} = \frac{\phi_i}{\gamma_{i+1}}$$

Pradel's Full Likelihood

Simultaneous forward- and reverse-time modeling

$$P(x_{0101} | N_1) = N_1 \lambda_1 (1 - \gamma_2 p_1) p_2 \phi_2 (1 - p_3) \phi_3 p_4$$

$$\text{where } \lambda_1 = \frac{\varphi_1}{\gamma_2}$$

Pradel's Full Likelihood: 3 Parameterizations

- Full likelihoods include φ_i , p_i and:

- γ_i = seniority parameter
- λ_i = population growth rate
- f_i = recruitment rate (recruits at i+1 per animal at i)

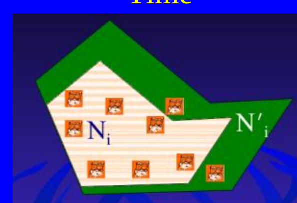
J-S Assumptions

- All animals have same ϕ, p
- Marks are neither lost or overlooked, and are recorded correctly
- Sampling periods are instantaneous
- All emigration from the sampled area is permanent
- The fate of each animal with respect to capture and survival probability is independent

Assumption Violations: λ Modeling

- Expansion of the study area over time
- Permanent trap response in capture probability
- Heterogeneous capture probabilities
- Combined effects of trap response and heterogeneity

Expansion of the Study Area over Time



Bias of λ_i

$$Bias(\hat{\lambda}_i) = E(\hat{\lambda}_i) - \lambda_i \approx \frac{N_{i+1}+N'_{i+1}}{N_i} - \frac{N_{i+1}}{N_i} = \frac{N'_{i+1}}{N_i}$$

$$Rbias(\hat{\lambda}_i) = \frac{E(\hat{\lambda}_i)-\lambda_i}{\lambda_i} = \frac{N'_{i+1}}{N_{i+1}}$$

Permanent Trap Response in Capture Probability

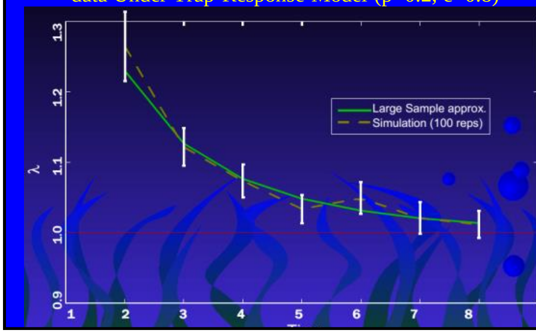
occasion i

occasion i+1

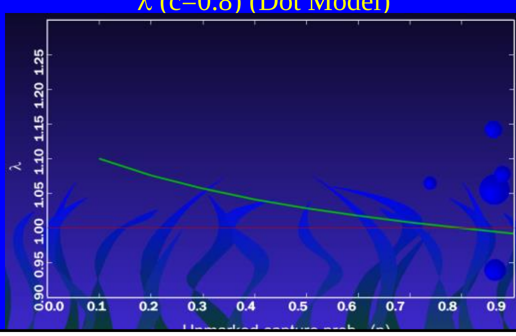
Approximation

- Large Sample approximations
  - 100,000 or 200,000 animals in population
  - 10 sampling periods
  - Population size constant over time (λ=1)
  - Survival (ϕ) =0.85
  - Capture prob. for unmarked animals (p) = 0.2
  - Capture prob. for marked animals (c) = 0.8
- Small Sample simulations
  - 100 animals in population
  - 100 iterations
- MARK models (ϕ_t, p., λ.), (ϕ_t, p., λ_t), (ϕ_t, p_t, λ_t)

Comparison of Large Sample Approx. vs Simulated data Under Trap-Response Model (p=0.2, c=0.8)



Effect of Trap Response on Estimate of λ (c=0.8) (Dot Model)



Heterogeneous Capture Probabilties

- Different individuals have different capture probabilities
- No temporal variation or trap response

Computer Simulation

- Large-sample approximations
  - Heterogeneity modeled as 2-group distribution
  - 100,000 animals with capture prob. = p^1 = 0.9
  - 100,000 animals with capture prob. = p^2 = 0.1,0.2,…0.9
- Small-sample simulations
  - 50 animals with capture prob. = p^1
  - 50 animals with capture prob. = p^2
- # births = # deaths [E(λ) = 1]
- MARK models (ϕ_t, p., λ.) and (ϕ_t, p_t, λ_t)

Simulated data (p_1 =0.1, p_2 =0.9) (Full Model)

Bias and Modeling Considerations

- Trap response more important than heterogeneity
- Temporal trend in λ_i in both cases
- Initial estimates of population growth (usually λ_2) exhibit substantially greater bias than subsequent estimates

Recommendations

- Keep study area expansion negligible or incorporate into modeling
- Omit from our model set models that incorporate temporal trends in λ_i
- Use the appropriate estimator
- Devote substantial thought to the design and analysis of studies aimed at estimation of λ_i

Pradel's Full Likelihood: Potential Uses

- Direct estimation of λ and its temporal variance
- This λ should correspond well to observed population changes because:
  - It does not rely on asymptotics (e.g., temporal constancy of vital rates, stable age distribution)
  - It incorporates movement as well as birth and death
- Can model λ as a function of covariates and specific vital rates (proper way to do "key factor analysis")

Superpopulation Approach to Inference About λ

- Schwarz-Arnason (1996) based on Crosbie-Manly (1985)
- Basic idea: use new captures to draw inference about recruitment to population
- Superpopulation, N^* = total number of individuals alive during at least 1 sampling occasion during the study, $i = 1, \ldots K$

Superpopulation Approach to Inference About λ

- Define an entry probability, β_i = Pr (member of N^* first entered the sampled population between periods i and i+1)
- Then compute N_i recursively:

$$N_{i+1} = N_i \phi_i + N^* \beta_i$$

Superpopulation Approach to Inference About λ

- Recursive approach to computing N_i requires a starting point (e.g., an estimate of N_1)
- But can't estimate p_1 under JS model
- Requires a constraint:

$$p_1 = p_2, p_1 = 1$$

Other Potential Approaches to Inference About λ

- Use MCMC with basic JS approach
- Rewrite N_i as: $N_i = N_1 \prod_{j=1}^{i-1} \lambda_j$
- Estimate N_i as:

$$\hat{N}_i = n_i / \hat{p}_i$$

Summary

- Direct inference about λ possible using:
  - Temporal symmetry (Pradel 1996)
  - Superpopulation (Schwarz-Arnason 1996)
  - Various MCMC approaches
- If direct modeling not required, can estimate as derived parameter, e.g.,

$$\lambda_i = \phi_i / \gamma_{i+1} = f_i + \phi_i$$