On Valuing Patches: Estimating Relative Contributions to Metapopulation Growth

Population Modeling
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USGS

Outline

- Brief history
- Patch contributions: a framework
- Reverse-time capture-recapture modeling
- Example: banner-tailed kangaroo rats
- Summary

Key Citations & Acknowledgements

- Conceptual framework
  - Runge, J.P., M.C. Runge, and J.D. Nichols. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. Amer. Natur. 167:925-938.
- Capture-recapture modeling
  - Nichols, J.D., J.E. Hines, J.-D. Lebreton, and R. Pradel. 2000. Estimation of contributions to population growth: a reverse-time capture-recapture approach. Ecology 81:3362-3376.
- K-rat metapopulation
  - Sanderlin, J.S., P.M. Waser, J.E. Hines, and J.D. Nichols. 2011. On valuing patches: estimating contributions to population growth with reverse-time capture-recapture modeling. Proc. Royal Soc. London (2012)

Metapopulation Concept

- Trace back to Levins (1969, 1970)
- System of local populations that interact via dispersal
- Intermediate position along continuum with endpoints:
  - Completely isolated local populations
  - Single interactive population

Source-Sink Concept

- Pulliam (1988)
  - Related concepts: Lidicker (1975), Hansson (1977), Holt (1984), Schmida and Ellner (1984)
- Observation: some local populations contribute more to metapopulation than others
- Sources (common ideas)
  - Within-patch survival and reproduction produce $\lambda > 1$
  - Self-sufficient: do not require immigration

Source-Sink Concept

- Fair amount of confusion
- Example:
  - A sink is a local population "maintained solely by immigration" (Holt 1984)
  - Consider many N. American passerines
    - Few birds produced on study areas ever return as young breeders; most disperse elsewhere
    - Local study area populations are thus maintained by immigration
    - But adult survival and reproductive output are high
    - Are such local populations sinks?

Contributions of Local Populations

- Simple idea: consider the contribution of a local population to the entire metapopulation system (Runge et al. 2006)
- Contribution metric should include recruits to both the focal local population and the other local populations in system
- Can rank different local populations by their contributions to the metapopulation system

Contributions of Local Populations: Computation

- Asymptotic contributions
  - Multi-population analog of Fisher's reproductive value (Willekens and Rogers 1978)
  - Reflects relative contribution of a local population to metapopulation size in the distant future
  - What is relative probability that a randomly selected animal in metapopulation in distant future is a descendant from a specific local population at time *t* in the past

Contributions of Local Populations: Computation

- Time-specific contributions (2 approaches to inference):
  - Demog. parameter estimates for focal patch:
    - patch-specific survival (young and adults),
    - patch-specific reproduction,
    - patch-specific dispersal-recruitment (young and adults of focal patch) with respect to all system patches
  - Reverse-time CR
    - patch-specific abundance
    - patch-specific contribution parameters

Multistate Reverse-time Modeling

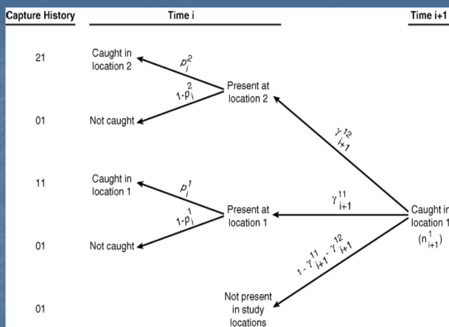
- Situation: capture-recapture sampling at multiple locations
- Question: what is the relative contribution to population growth at a site of surviving animals from the same location vs. migrants from the other site(s)

Multistate Reverse-time Modeling: Data

- Capture history data, e.g.,
  - 1 0 2 1 0
  - 0 = no capture
  - 1 = capture at location 1
  - 2 = capture at location 2
- n^r_t = number of adults captured in location *r* at time *t*

Multistate Reverse-time Modeling: Parameters

- $\gamma^{rs(l)}_t$ = probability that an adult in local pop *r* at time *t* was an animal of age *l* (0=juvenile, 1=adult) in local pop *s* at time *t*-1
- $p^{r(l)}_t$ = probability that an animal of age *l* in local pop *r* at time *t* is captured



Inference

- Use maximum likelihood to estimate model parameters, $\hat{\gamma}_t^{rs(l)}$, $\hat{p}_t^{r(l)}$ based on capture-recapture data
- Use these parameter estimates to compute abundance and contributions as derived parameters

Abundance: Local and Metapopulation

- N_t^r = number of adults in local pop *r* at time *t*

$$\hat{N}_t^r = \frac{n_t^r}{\hat{p}_t^r}$$

- $\hat{N}_t^*$ = number of adults in metapopulation

$$\hat{N}_t^* = \sum_{r=1}^{R} \hat{N}_t^r$$

Contributions to Metapopulation Growth Rate

Metapopulation growth rate:

$$\lambda_t^* = \frac{N_{t+1}^*}{N_t^*} = \frac{\sum_{r=1}^{R} N_{t+1}^r}{\sum_{r=1}^{R} N_t^r}$$

Proportional contribution of local population *s* at time *t* to metapopulation growth rate, λ_t^* :

$$\hat{c}_t^s = \frac{\sum_{r=1}^{R} \hat{N}_{t+1}^r (\hat{\gamma}_{t+1}^{rs(1)} + \hat{\gamma}_{t+1}^{rs(0)})}{\sum_{r=1}^{R} \hat{N}_{t+1}^r}$$

Metapopulation Contributions from Extra-system Immigration

- Proportional contribution to local pop *r* from extra-system immigration:

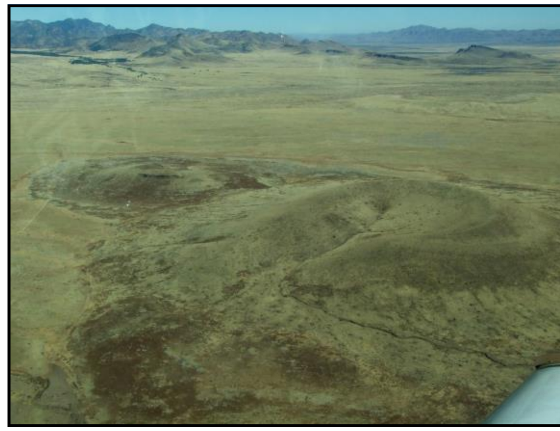
$$\hat{\gamma}_{t+1}^{r0} = 1 - \sum_{s=1}^{R} \left(\hat{\gamma}_{t+1}^{rs(1)} + \hat{\gamma}_{t+1}^{rs(0)}\right)$$

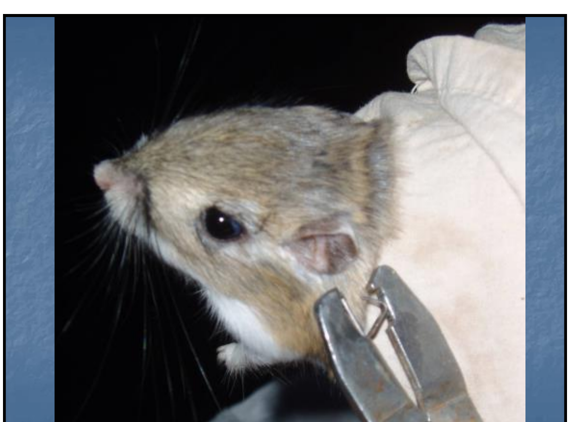
- Proportional contribution to metapopulation growth from extra-system immigration:

$$\hat{c}_t^0 = 1 - \sum_{s=1}^{R} \hat{c}_t^s = \frac{\sum_{r=1}^{R} \hat{N}_{t+1}^r \left(\sum_{s=1}^{R} (\hat{\gamma}_{t+1}^{rs(1)} + \hat{\gamma}_{t+1}^{rs(0)})\right)}{\sum_{r=1}^{R} \hat{N}_{t+1}^r}$$

Example: Banner-tailed Kangaroo Rat Metapopulation

- Studied by P. Waser
- 8 local populations (Cochise County, Arizona)
- Capture-recapture sampling in late July-early August, 1994-2000
- Robust design with 3 days trapping
- Ear tagged individuals
- Age as juvenile (born same year, 0) and adult (1)





Hypotheses and Predictions

- Hypothesis:
  - Animal age influences the contributions of one local population to another
- Prediction:
  - Relative contributions from other local populations should be greater for young animals than adults
- Rationale:
  - Previous CR study (forward-time analysis) indicated greater dispersal rates for young animals

Hypotheses and Predictions

- Hypothesis:
  - Distance between 2 local populations influences the contributions of one local population to the other
- Prediction:
  - Relative contributions to a focal population from other local populations should be greater for local populations that are nearby
- Rationale:
  - Previous CR study indicated greater dispersal rates between local populations that are separated by shorter distances

Hypotheses and Predictions

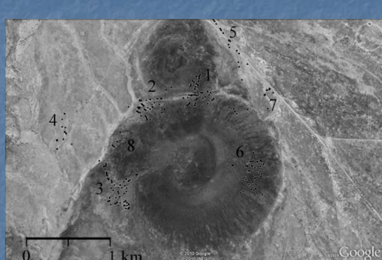
- Hypothesis:
  - Do not expect large variation among local populations in per capita contributions to metapopulation growth
- Prediction:
  - Contributions of local populations should depend primarily on their population sizes
- Rationale:
  - Previous studies have not provided evidence of large differences in survival and/or reproductive rates among local populations

Hypotheses and Predictions

- Hypothesis:
  - Location of a local population is relevant to its contributions to system
- Prediction:
  - Central local populations will contribute more to system than peripheral local populations
- Rationale:
  - More likely for emigrants from central local populations to immigrate to local populations within the system
  - Some peripheral populations near roads (mortality source)

Hypotheses and Predictions

- Hypothesis:
  - Location of a local population is relevant to where its contributions come from
- Prediction:
  - Central local populations will receive smaller contributions from outside system than peripheral local populations
- Rationale:
  - Simple location argument: closest local populations in all directions are within system for central populations but not necessarily for peripheral



Hypotheses and Predictions

- Hypothesis:
  - System-wide population size/density is relevant to contributions
- Prediction (?):
  - Contributions from within-system and extra-system dispersal will be reduced when density is high
  - Self-contributions will be greater when density is high
- Rationale:
  - Success of potential immigrant recruits will be lower when local population size is large (density-dependent immigrant recruitment probability)

Model Set: Sources of Variation Considered

- Contribution probabilities
  - Central vs. peripheral (denote as C)
  - Years of high (1994-1998) vs. low (1999-2000) density (N)
  - Animal age (juvenile, adult) (A)
  - Distance between each pair of local populations (D)
- Capture probabilities
  - Animal age (A)
  - Year (T)
- Most general model

  γ^{rr} (A*C*N) , γ^{rs} (A+C+N+D) , p^{r} (A*T)

Model Fit and Selection

- Goodness of fit assessed by parametric bootstrap
- Estimates of model parameters ($\hat{\gamma}_t^{rs(l)}, \hat{p}_t^{r(l)}$) computed using model-averaging
- Estimates of derived parameters ($\hat{N}_t^r, \hat{c}_t^r$) based on model-averaged parameter estimates

Results: Model Selection

Model	$\Delta QAIC_c$	Weight
γ^{rr} (A) γ^{rs} (D+A)	0.00	0.36
γ^{rr} (A*C) γ^{rs} (D+A)	0.69	0.26
γ^{rr} (A*N) γ^{rs} (D+A)	1.38	0.18
γ^{rr} (A*C) γ^{rs} (D+A+C)	2.13	0.12
γ^{rr} (A*N) γ^{rs} (D+A+N)	3.58	0.06
γ^{rr} (A*C*N) γ^{rs} (D+A+C)	7.54	<0.01

Results: Abundance Estimates for Entire System

- High-density years, 1994-1998:

  $\hat{N}^{*}_{94-98} = 116$

- Low-density years, 1999-2000:

  $\hat{N}^{*}_{99-00} = 72$

Results: Estimated Contributions

- Estimates of age-specific contributions of every local population to itself and every other local population for high-density and low-density years, $\gamma_t^{rs(l)}$
- Estimates of contributions of extra-system immigrants to every local population for high-density and low-density years, γ_t^{r0}

Origin	Focal[1, 2]							
Juv	1	2	3	4	5	6	7	8
1	0.323 (0.066)	0.001 (0.001)	0.000 (0.000)	0.000 (0.000)	<0.001**	0.000 (0.000)	0.007 (0.006)	0.000 (0.000)
2	0.001 (0.001)	0.323 (0.066)	0.000 (0.000)	<0.001*	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.002 (0.002)
3	0.000 (0.000)	0.000 (0.000)	0.306 (0.060)	0.002 (0.002)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.002 (0.002)
4	0.000 (0.000)	<0.001*	0.002 (0.002)	0.306 (0.060)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	<0.001**
5	<0.001**	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.306 (0.060)	<0.001**	0.007 (0.006)	0.000 (0.000)
6	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	<0.001**	0.306 (0.060)	0.007 (0.006)	0.000 (0.000)
7	0.004 (0.004)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.007 (0.006)	0.007 (0.006)	0.306 (0.060)	0.000 (0.000)
8	0.000 (0.000)	0.001 (0.001)	0.002 (0.002)	<0.001**	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.306 (0.060)

Results: Contributions as Function of Distance & Age

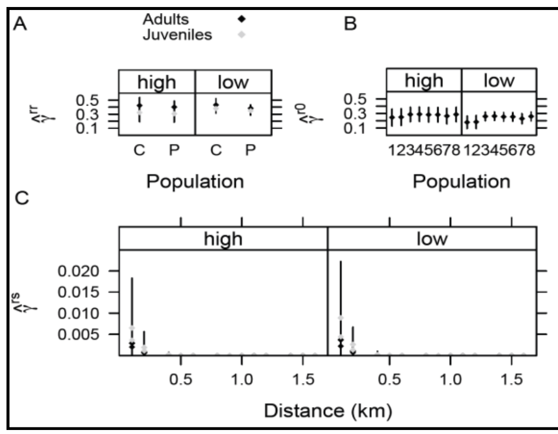
- The relative contribution of local population s to local population r, $\gamma^{rs(l)}$, is a decreasing function of distance between r and s
- Self-contributions are greater for adults than juveniles, $\hat{\gamma}^{rr(1)} > \hat{\gamma}^{rr(0)}$
- Contributions to other local populations are greater for juveniles than adults, $\hat{\gamma}^{rs(0)} > \hat{\gamma}^{rs(1)}$

Results: Contributions as Function of Centrality

- Summed model weights for centrality: 0.40
- For each density level and age,
  - Self-contributions greater for central populations, $\hat{\gamma}^{rr(l)}(Cen) > \hat{\gamma}^{rr(l)}(Per)$
  - Contributions from extra-system immigration greater for peripheral pops, $\hat{\gamma}^{r0}(Cen) < \hat{\gamma}^{r0}(Per)$

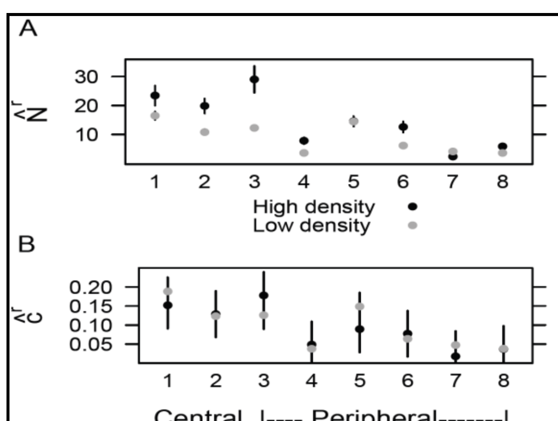
Results: Contributions as Function of System Density

- Summed weights for models including density: 0.25
- For both age classes:
  - Self-contributions from central pops greater for years of low density, $\hat{\gamma}^{rr(l)}(LowN) > \hat{\gamma}^{rr(l)}(HighN)$
- Contributions of extra-system immigrants to metapopulation
  - Greater for years of high density, $\hat{c}^0(HighN) > \hat{c}^0(LowN)$



Results: System Contributions as f(Local Population Size)

- Larger local populations made the larger contributions to metapopulation growth
- $c^r = f(N^r)$
- Range of estimates for $\hat{c}^r$: $[0.02, 0.19]$



Surprise (Problem?): Magnitude of Extra-system Contributions

- Estimated contributions of outside immigrants to metapopulation growth were large:
  - High density years: $\hat{c}^0 = 0.27$
  - Low density years: $\hat{c}^0 = 0.23$
- Surprising because:
  - within-system dispersal is small at larger distances
  - no substantial extra-system populations nearby

Surprise (Problem?): Magnitude of Extra-system Contributions

- Possible explanations:
  - Dispersal distances > 1km may be more common than indicated by within-system data
  - Our inference methods assume that all juveniles are available for capture during July-August sampling. Late-born young would appear to be extra-system immigrants.

Summary: Methodology

- Analysis revealed no conceptual flaws in contribution metrics for evaluating local populations
- Reverse-time CR provided:
  - Estimates of contributions of each local pop to other pops and to metapopulation
  - Inferences about sources of variation in these local population contributions

Summary: Ecology

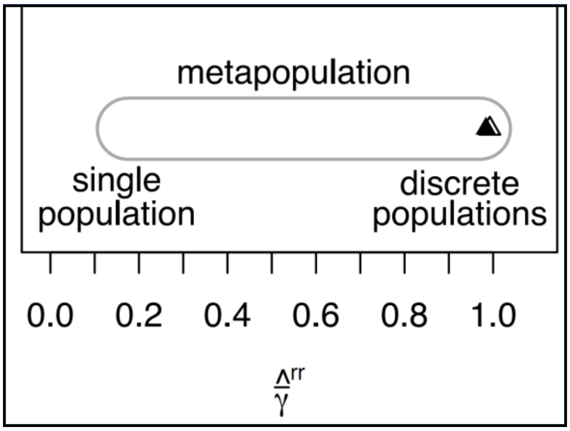
- Sources of variation in contributions of local populations to other local populations and to entire metapopulation:
  - Animal age
  - Distance between local populations
  - Local population size
  - Location (centrality) of local population
  - Overall size of metapopulation?

On Extra-system Immigration

- Seldom estimated well
- But when it is, estimates are always substantial, even in cases such as ours when we thought we were sampling entire metapopulation system
- Need new ideas about how to identify sources of extra-system immigration
  - Wen et al. (2011, 2013, 2014)

Classifying Metapopulations Based on γ^{rr}

- Continuum based on self-contributions of R local populations
- Discrete local populations
  - $\gamma^{rr} = 1$
- Single population
  - $\gamma^{rr} = \gamma^{rs} = 1/R$, or
  - $\gamma^{rs} = N^s / N^*$
- K-rat example: rescale all γ^{rs} assuming $\gamma^{r0} = 0$



Sources, Sinks and Contributions

- Estimated contributions to the metapopulation system varied substantially among local populations: $0.02 < \hat{c}^{r} < 0.19$
- Yet loss of any local pop would have resulted in reduced pop growth
- No local pop was a sink in sense of being totally irrelevant to metapopulation growth

On Contributing: Demographics versus Genetics

- Estimated demographic contributions of local pops to other local pops within system were very small:
  $\hat{\gamma}^{rs} < 0.02$
- These small demographic contributions were sufficient to seriously limit genetic differentiation among local pops: $0.01 < F_{st} < 0.03$
- Conclusion: numbers of animals required for demographic contributions among local pops are much greater than needed for genetic contributions