Metapopulation Dynamics of a Disease System

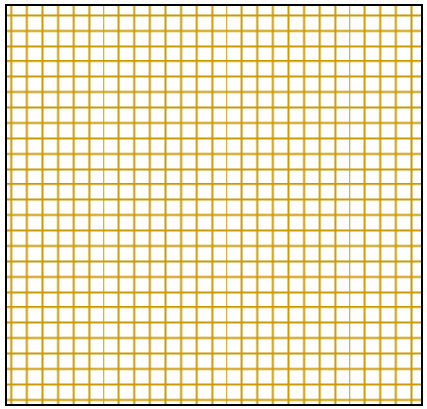
Colleen Webb
Department of Biology
Colorado State University

Roadmap

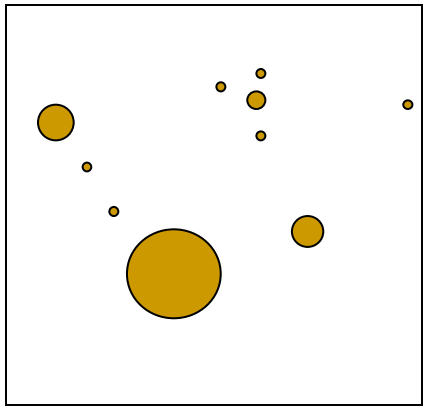
- What are metapopulations?
- Metapopulation modeling
- Hypothesis testing in a metapopulation framework
- Prairie dogs and plague: an application of metapopulation models to a disease system
  - with Dylan George, Mike Antolin, and Lisa Savage

How do we model space?

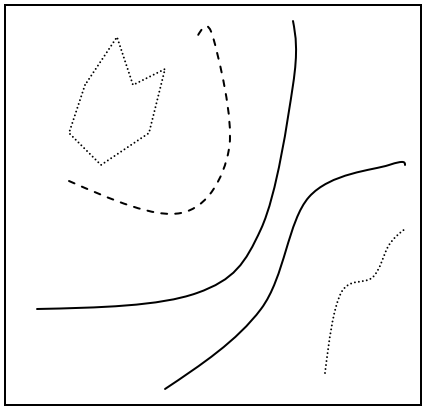
Continuous space



Metapopulations

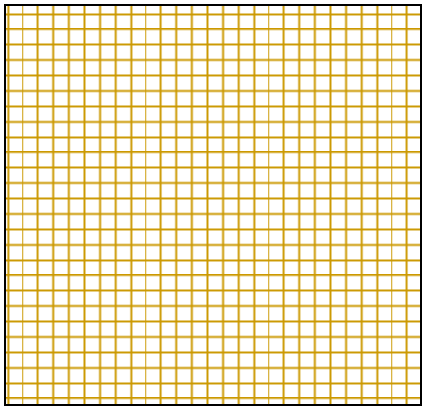


Landscape Ecology



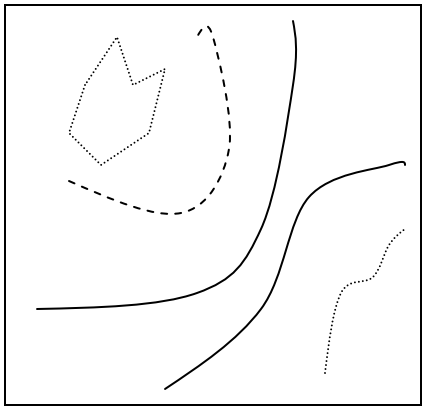
After Hanskii and Gaggiotti 2004

Continuous Space



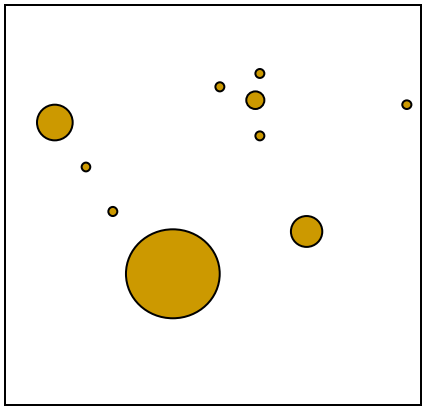
- Frequently assumes environment is homogeneous
- Models spatially restricted interactions or migration
- Lattice based models
  - Interacting particle systems
  - Cellular automata
  - Coupled-map lattices
  - Individual based simulations
- Often highly theoretical

Landscape Ecology



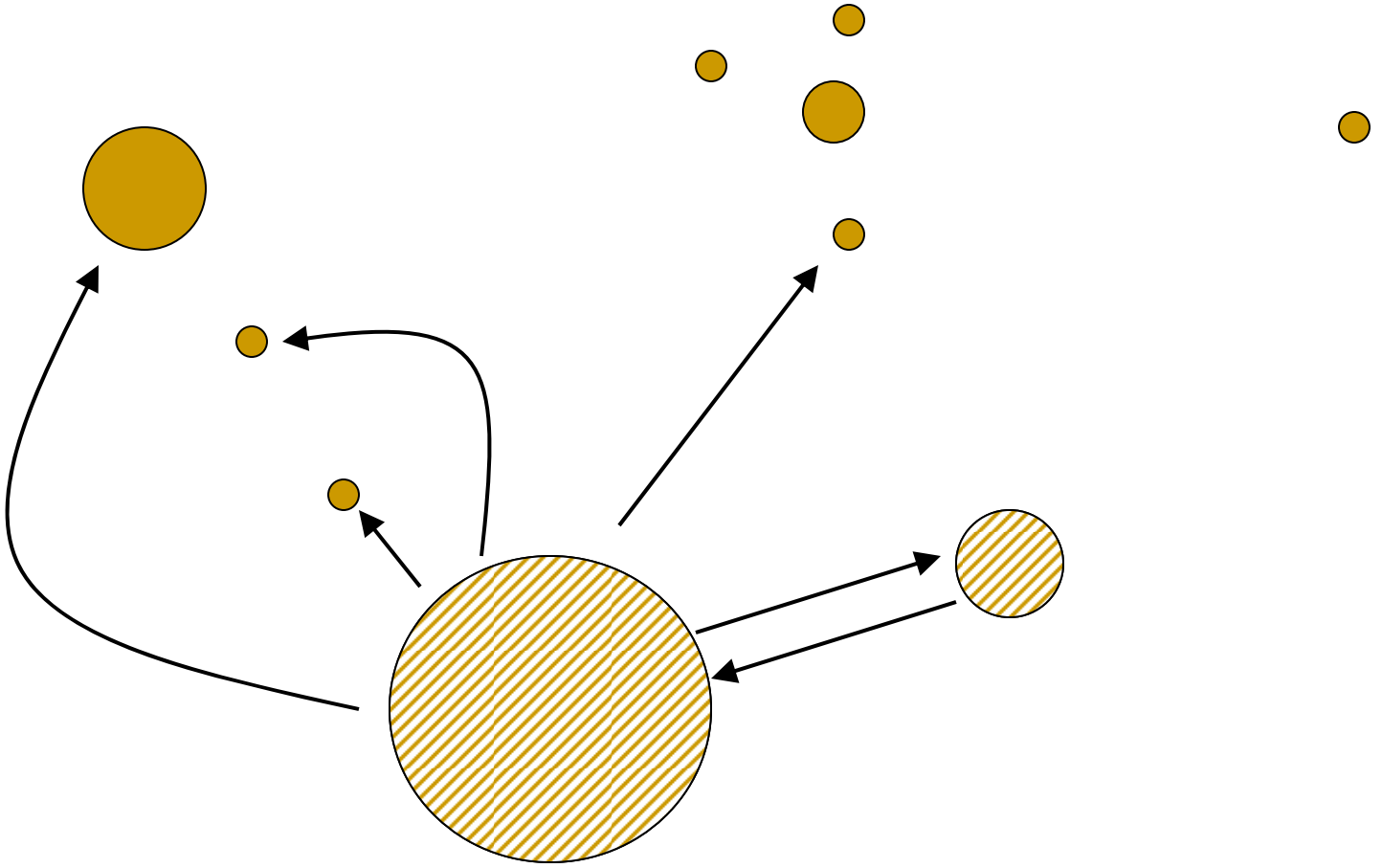
- Detailed description of real landscape
- Models individual movement in complex environment
- Connectivity at landscape level
- Network and simulation models

Metapopulations



- Assumes heterogeneous environment and discrete patches
- Models “state” of patch
- Connectivity at patch level
- Network and simulation models

Classical Metapopulations



Stochastic Patch Occupancy Models (SPOM)

- Stochastic (i.e., not deterministic)
- Heterogeneous
  - Patches differ in probability of extinction, colonization, becoming infected, recovering, etc.
  - Differences in probabilities depend on landscape structure
    - Patch size
    - Patch quality
    - Patch isolation

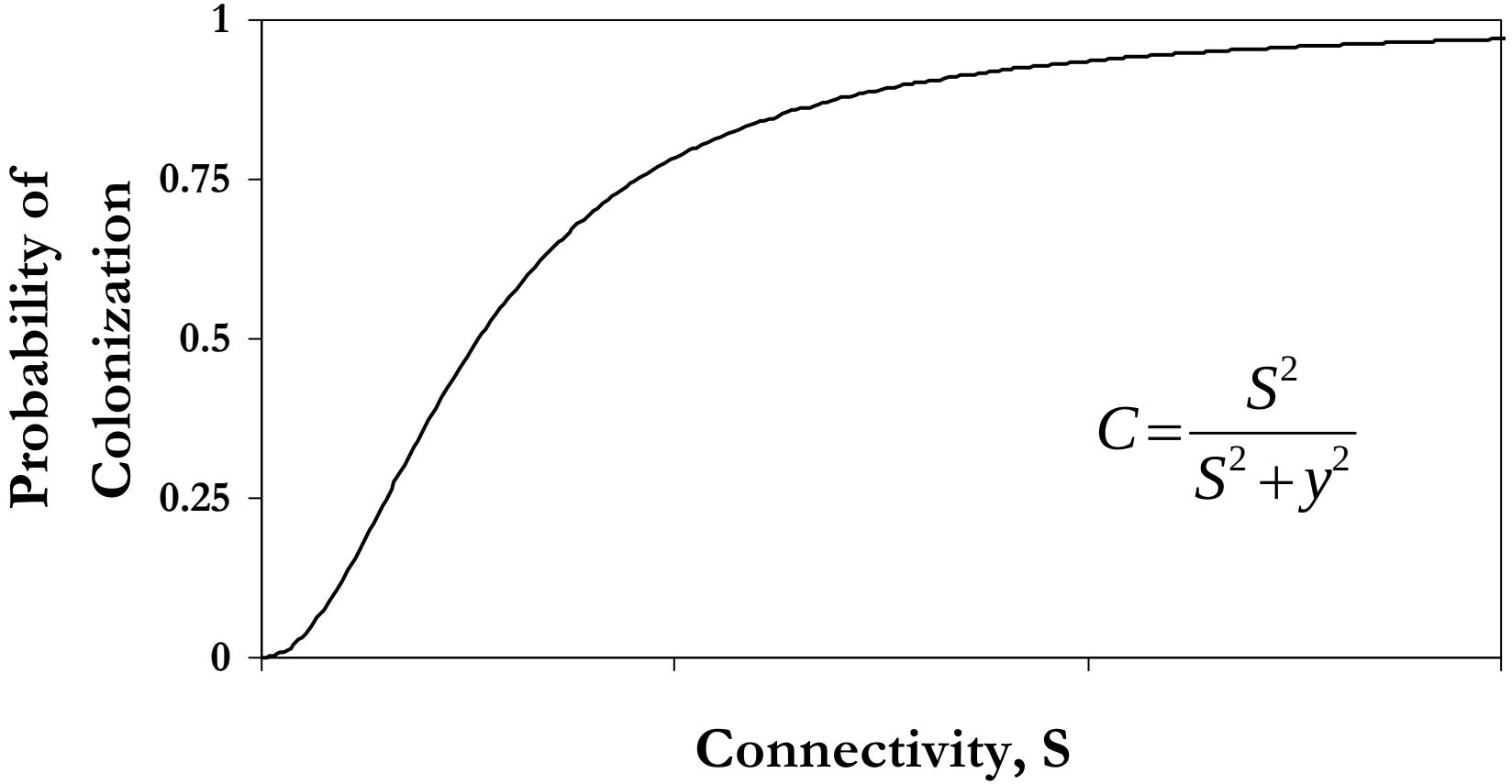
SPOM Basics

- Construct functions that describe probability of colonization and probability of extinction
- Parameterize probability functions
  - Use MLE to estimate parameters of probability functions from subset of data
- Simulate model
  - From a starting description of the states of the patches project the probability functions forward in time to make predictions about the system
- Validate model
  - Validate model predictions using remaining data and Goodness-of-fit tests

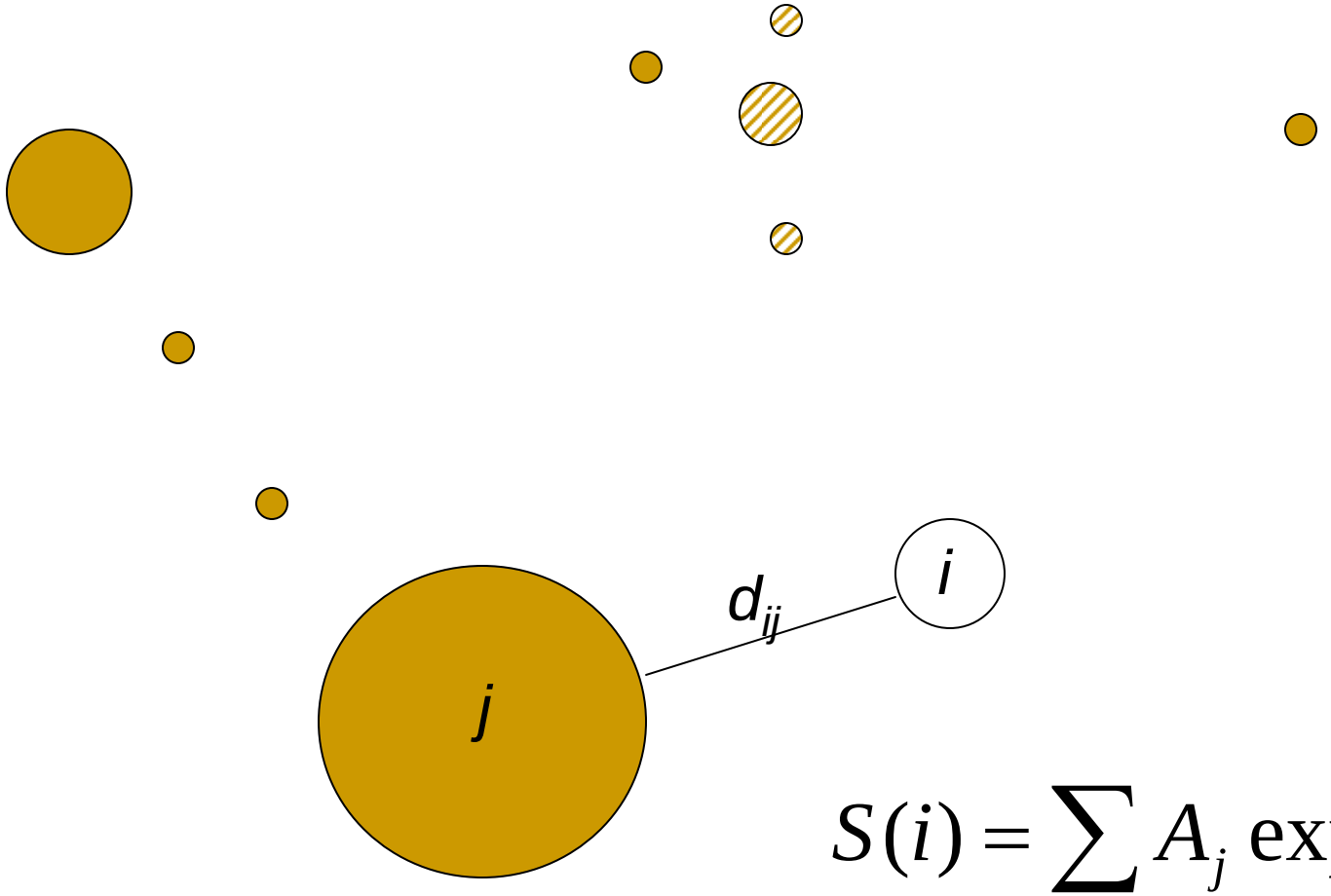
Constructing Probability Functions and Hypothesis Testing

- Differences in probabilities depend on landscape structure
- Hypotheses about how landscape structure impacts probabilities can be incorporated

Standard Colonization Function

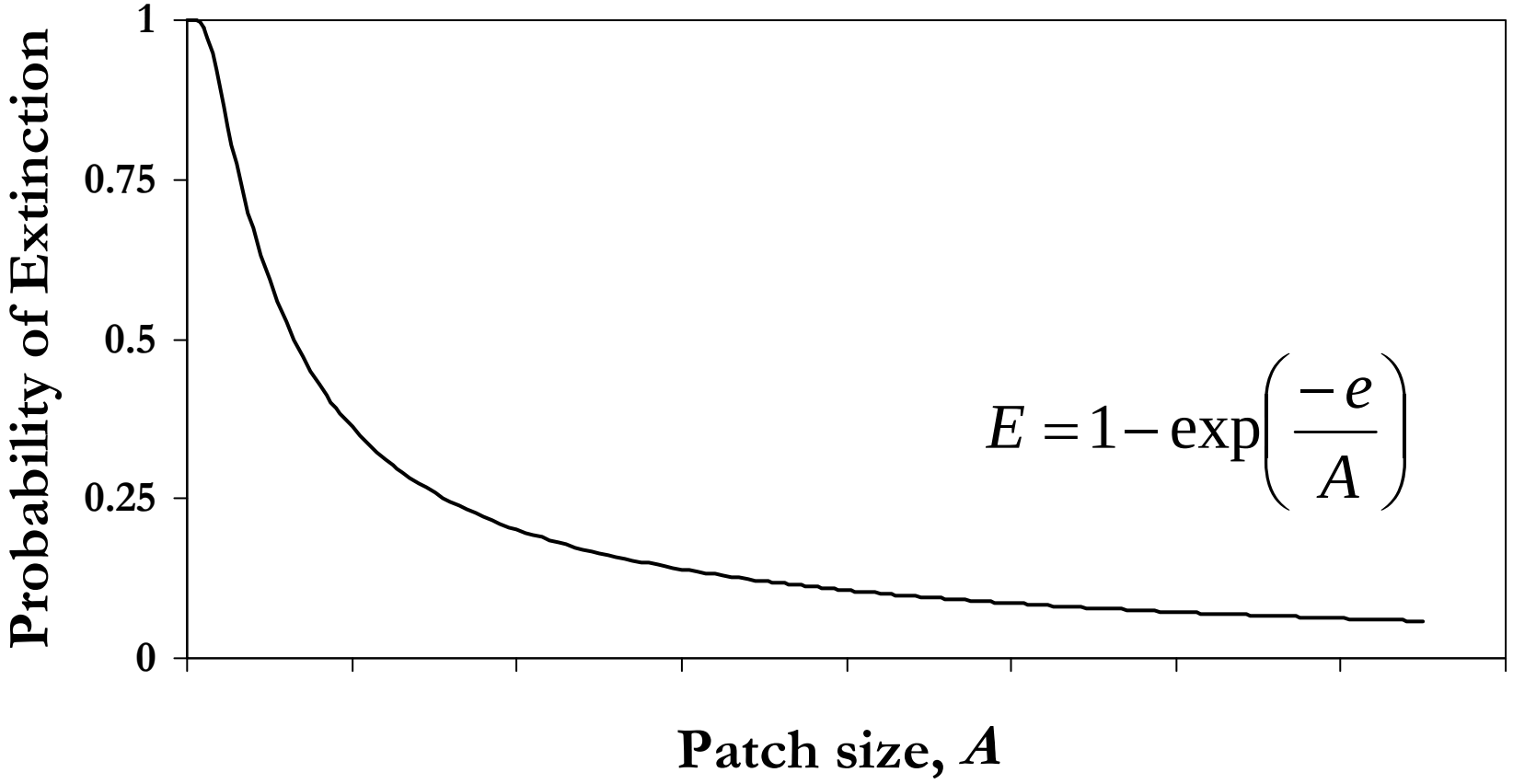


Connectivity



$$S(i) = \sum_j A_j \exp(-\alpha d_{ij}) p_j$$

Standard Extinction Function



Parameterization - Data Needs

- Size and location of patches
- Occupancy or state data through time

Time

Patch	1	2	3	4
1	0	0	0	1
2	1	---	1	0
3	1	1	0	1
4	1	1	---	0
5	0	0	1	1

Parameterize Probability Functions

- Construct likelihood function
- In one year, we want to know the probability of observing the states of patches given the states of patches in the previous year
  - $P[O(t+1)\,|\,O(t)]$
- This involves probability functions
  - Colonization occurs when O(i,t)=0 and O(i,t+1)=1

Model Simulation

- Plug estimated parameters into probability functions
- Project metapopulation occupancy from initial occupancy matrix using parameterized probability functions

Metapopulation Dynamics of Prairie Dogs and Plague: Implications for Persistence

Dylan George, Colleen Webb, Mike Antolin, and Lisa Savage

Department of Biology

Colorado State University

Plague in Black-tailed Prairie Dogs

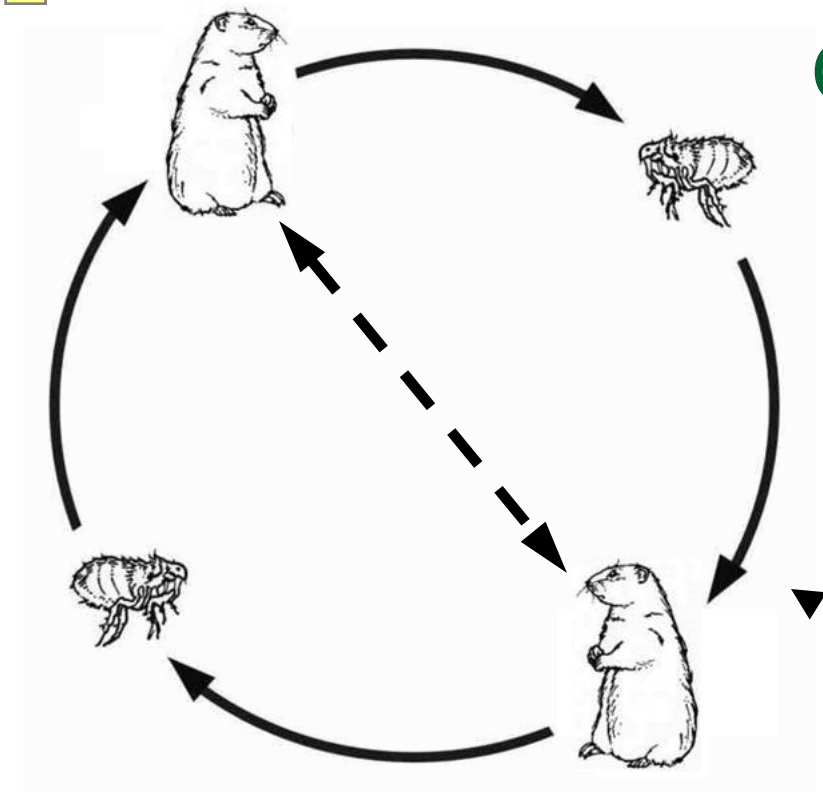
- Colonial species
  - Form discrete towns on landscape
- Highly susceptible to *Yersinia pestis*
- ~ 100% mortality results in town extinction
- *Y. pestis* vectored by fleas

Photo by L. Savage

How does plague persist?

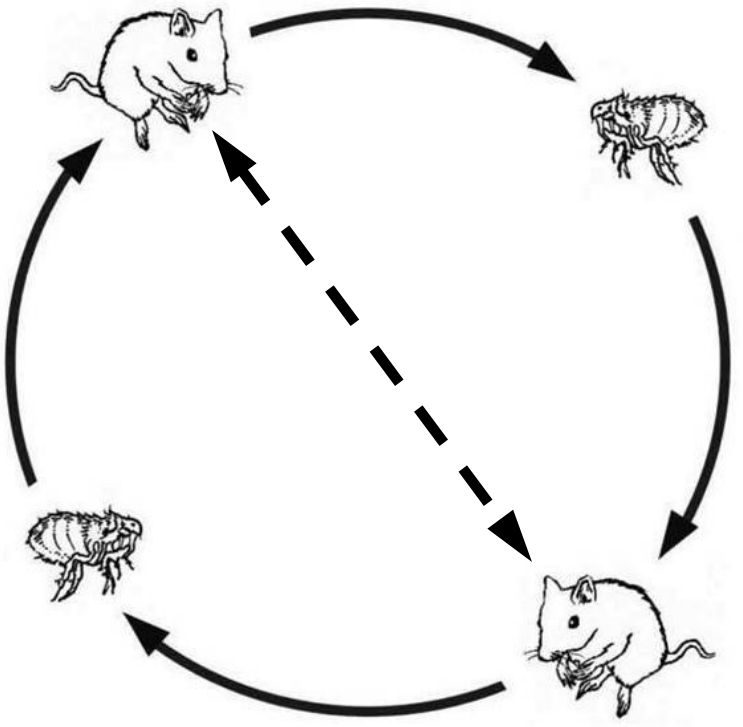
- Classic view of interacting enzootic – epizootic cycles
- Reintroduced from elsewhere
- Maintained by spatial structure of host and its fleas

Classical View



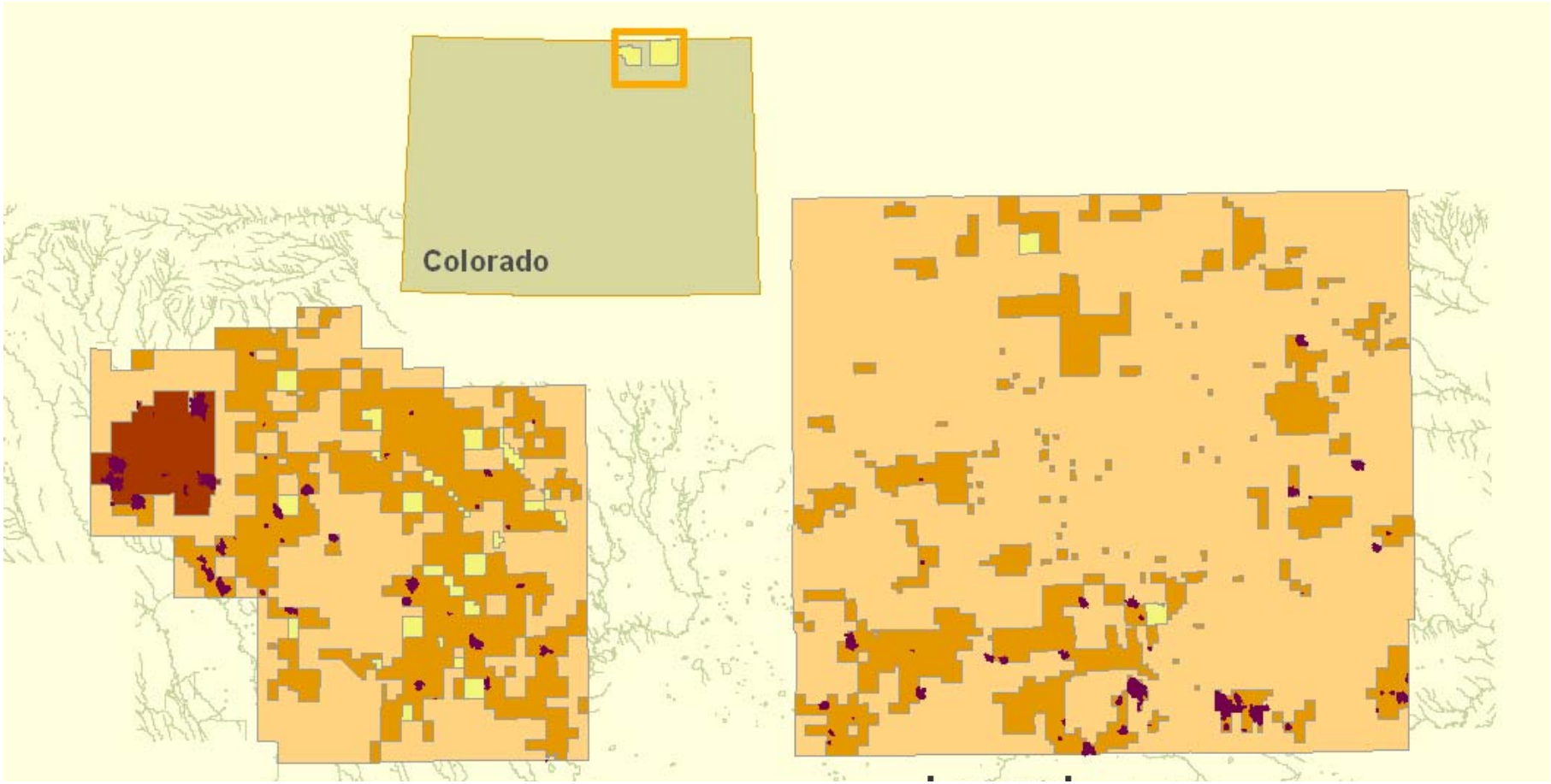
Epizootic Cycle
(amplifying)

Enzootic Cycle
(maintenance)



Reintroduction

Maintained by Spatial Structure of Host



Metapopulation model

- Can plague be maintained within prairie dogs (and their fleas) based on metapopulation structure?
- If so, how is this possible?
  - Can prairie dogs move plague around despite dying quickly?
  - Does something else move plague around and if so what?

Colonization

- Traditional colonization function based on connectivity

Extinction

- Extinctions due to plague – How does this depend on landscape features?
  - H1: Target size – Observed correlations between town area and probability of extinction
    - Traditional extinction function based on area
  - H2: Connectivity to recently plagued towns – Prairie dogs move plague around
    - Function like traditional colonization function, but colonization is by plague

Data

- Area and occupancy for 79 towns total
- 2 metapopulations: Eastern and Western
- 25 years of data
  - 20 years used for parameter estimation
  - 5 years reserved for validation

Hypothesis Testing

- Constructed two competing metapopulation models (Target size vs. Connectivity to plague sites)
- Estimated parameters for both using MLE
- Performed model selection using AIC

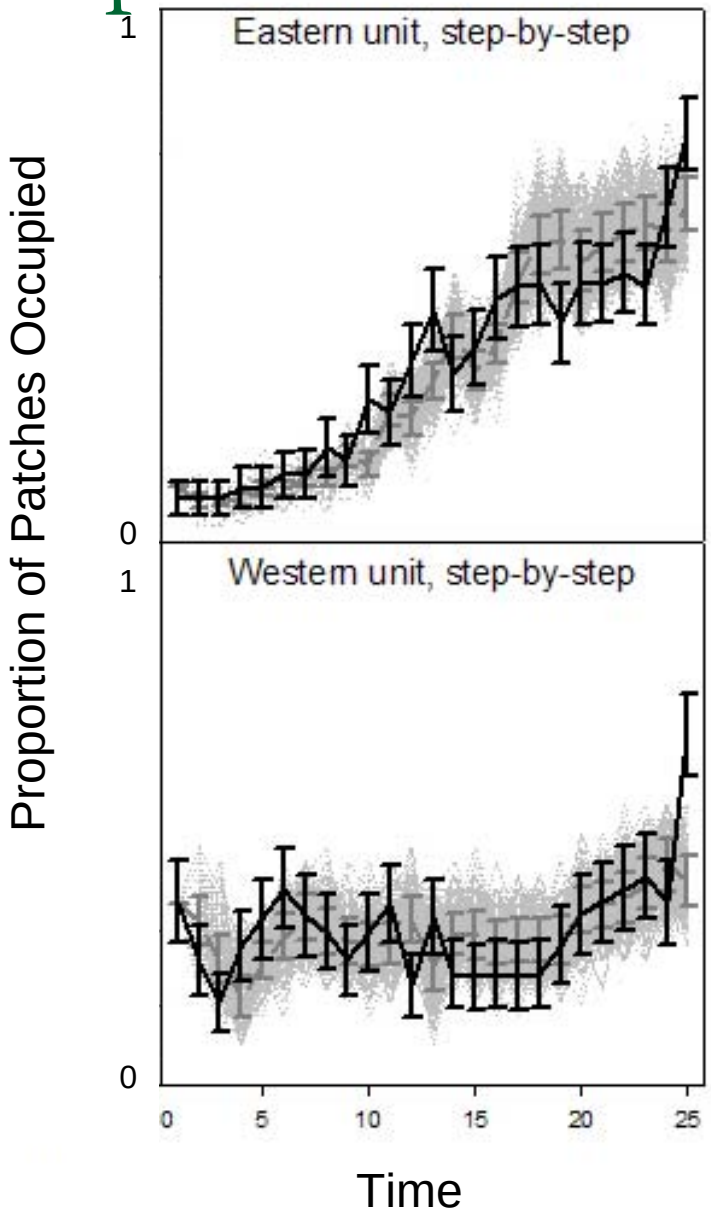
Model Validation, Simulation, and Prediction

- Target effects model selected using AIC
- Validated parameter estimates by comparison with empirical data
- Validated model structure and parameters using Step-by-Step Simulation
- Validated predictive ability using Full Simulation

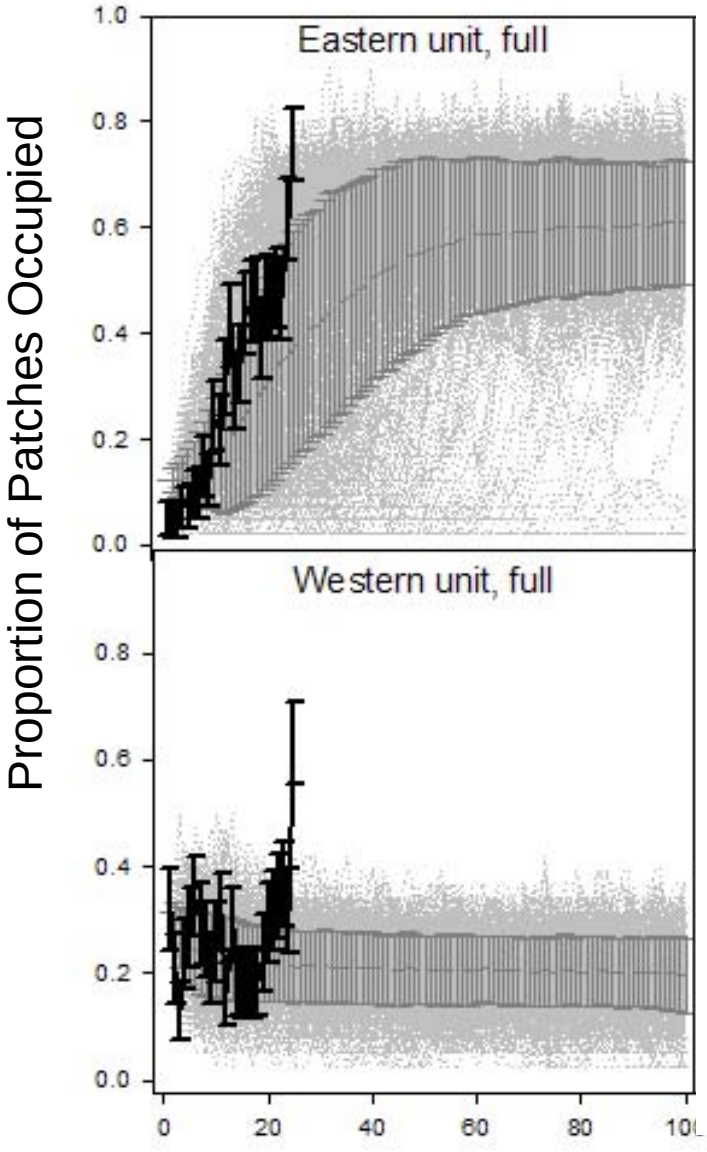
Parameter Estimates - Validation

Parameter	Western Metapop	Eastern Metapop	Validation Information
Avg. p- dog dispersal	591.71 m/yr	5.74 m/yr	7 km/mth maximum
Colonizing ability	1277.423	105.591	
Patch size threshold	0.497	0.586	(<1) Large patches susceptible
Extinction prob. at threshold	0.4454	1.214	

Step-by-Step Simulation - Validation



Full Simulation – Prediction Validation



Conclusions

- Prairie dog persistence with plague extinction provides support for the idea that virulent plague persists due to host metapopulation structure
- Selection of Target Effects model over Plague Connectivity model implies that agents other than prairie dogs move plague around the system
- These agents are likely alternative hosts for flea vectors, but need not be susceptible to plague

Acknowledgements

- U.S. National Science Foundation – Ecology of Infectious Diseases
- Shortgrass Steppe Long-term Ecology Research Site (LTER)
- RAPIDD Program
- NSF-IGERT at CSU (PRIMES)
- DoD SMART