



## CAPTURE-RECAPTURE MODELS IN ECOLOGY: MULTI-STATE DEVELOPMENTS

RACHEL MCCREA  
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# COLLABORATORS

- ▶ Hannah Worthington
- ▶ Ming Zhou
- ▶ Eleni Matechou
- ▶ Diana Cole
- ▶ Ruth King
- ▶ Richard Griffiths

# OUTLINE

## INTRODUCTION

## MULTISTATE REMOVAL MODELS

- Background

- New model

- Parameter redundancy

- Parameter redundancy

## MULTISTATE INTEGRATED STOPOVER MODELS

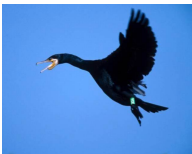
- Background

- New model

- Results

## DISCUSSION

# INDIVIDUAL MARKING



## Capture-recapture data

- ▶ 1 0 0 1 0
- ▶ 1 1 0 1 1
- ▶ 0 0 1 0 1
- ▶ . . .

# CLOSED POPULATION MODEL, $M_t$

- ▶  $p_t$ : probability an individual is captured at occasion  $t$ .

- ▶ Capture-recapture data and probabilities

- ▶ 1 0 0 1 0  $p_1(1 - p_2)(1 - p_3)p_4(1 - p_5)$

- ▶ 1 1 0 1 1  $p_1p_2(1 - p_3)p_4p_5$

- ▶ 0 0 1 0 1  $(1 - p_1)(1 - p_2)p_3(1 - p_4)p_5$

- ▶ ...

# CLOSED POPULATION MODEL

- ▶ Some individuals will not be captured at all during the study;
- ▶ The encounter history for these individuals is given by

$$\text{▶ } 0 \ 0 \ 0 \ 0 \ 0 \quad (1 - p_1)(1 - p_2)(1 - p_3)(1 - p_4)(1 - p_5)$$

- ▶ It is the number of individuals who are never captured that we need to estimate.

The likelihood has the form:

$$L \propto \frac{N!}{(N - D!)} \prod_{i=1}^D \Pr(h_i) \times \Pr(h_0)^{N-D} \quad (1)$$

- ▶  $h_i$ : observed encounter history for individual  $i$ ;
- ▶  $h_i$ : observed encounter history of never encountered;
- ▶  $N$ : population size;
- ▶  $D$ : number of observed individuals.

## CLOSED POPULATION MODEL, $M_b$

- ▶  $p$ : probability of initial capture;
- ▶  $c$ : probability of subsequent capture.

- ▶ Capture-recapture data and probabilities

- ▶ 1 0 0 1 0

$$p(1-c)(1-c)c(1-c)$$

- ▶ 1 1 0 1 1

$$pc(1-c)cc$$

- ▶ 0 0 1 0 1

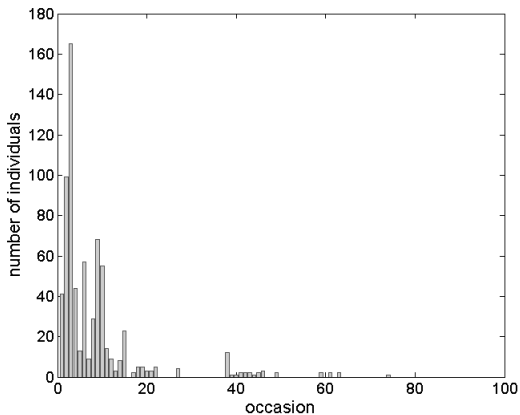
$$(1-p)(1-p)p(1-c)c$$

- ▶ ...



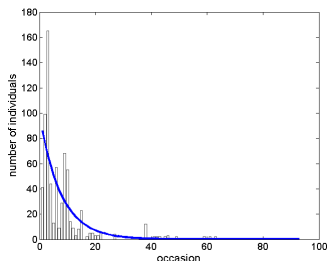
# REMOVAL DATA

$n_t$ : size of sample removed at sample  $t$ .



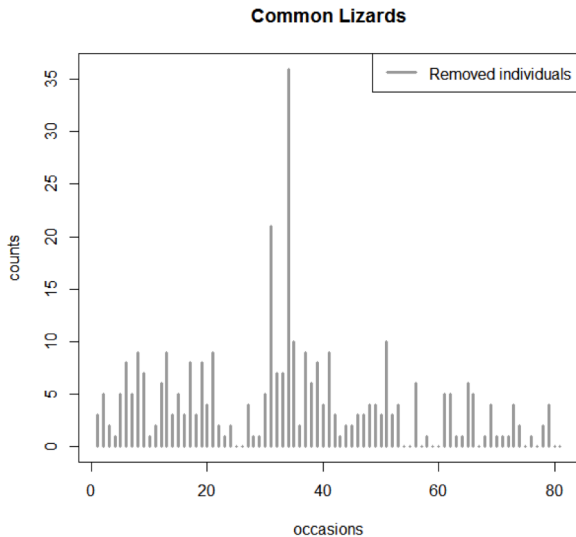
## LINK TO MODEL $M_b$

- ▶ Basic geometric model  
 $\Pr(\text{individual is removed at occasion } t) = (1 - p)^{t-1}p$
- ▶ Same model as used for time to conception for human couples;
- ▶ Equivalent to estimating  $p$  in  $M_b$ , and assuming  $c = 0$ .

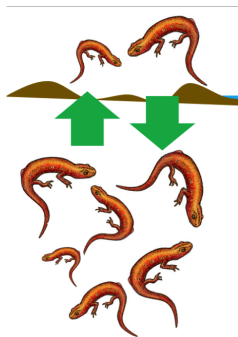




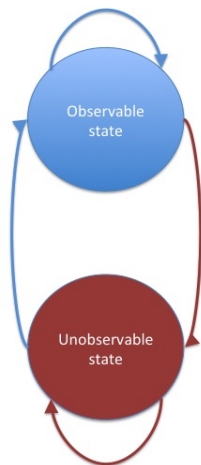
# WHY DO DATA EXHIBIT UNEXPECTED PEAKS?



# AN UNDERGROUND CITY?

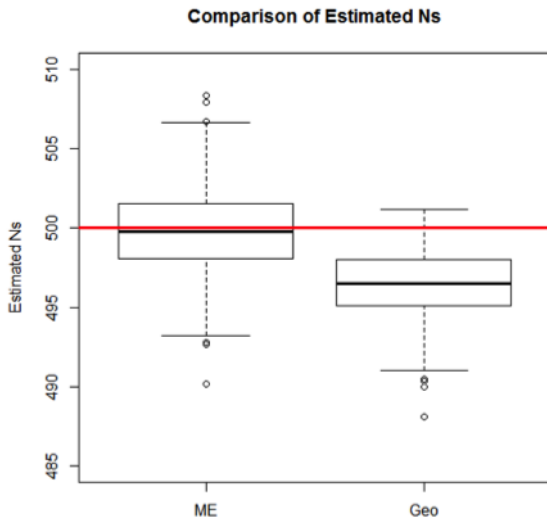


# MULTISTATE REMOVAL MODEL

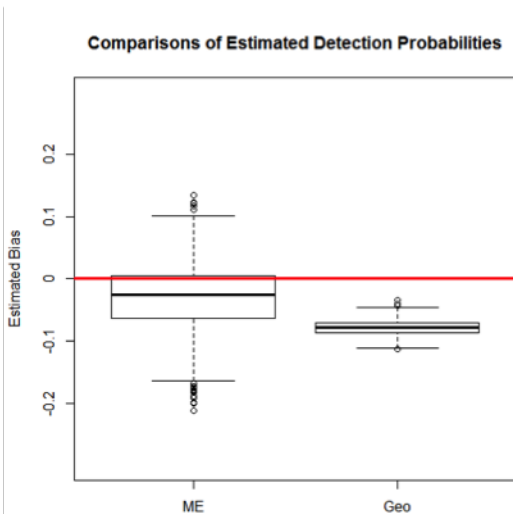


- ▶ Develop a two-state model, with one unobservable state with capture probability of 0;
- ▶ Naturally fits into a multievent framework, which is an HMM.

# SIMULATION RESULTS



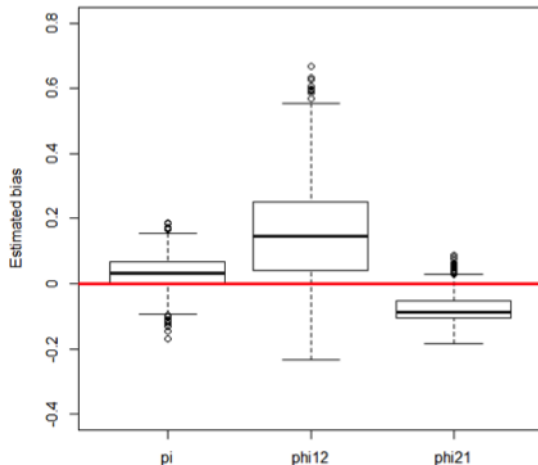
# SIMULATION RESULTS





# SIMULATION RESULTS

**Estimated Bias for  $\pi$ ,  $\phi_{12}$  and  $\phi_{21}$**



# PARAMETER REDUNDANCY

- ▶ A model is parameter redundant if you cannot estimate all of the parameters;
- ▶ Parameter redundancy is diagnosed by forming a derivative matrix  $D = \partial\kappa/\partial\theta$  where  $\kappa$  denotes an exhaustive summary for a model that provides a unique representation of the model and  $\theta$  denotes the parameters;
- ▶ If  $\text{rank}(D) = \text{dim}(\theta)$ , all parameters are estimable;
- ▶ If  $\text{rank}(D) < \text{dim}(\theta)$  the model is parameter redundant.

# PARAMETER REDUNDANCY

- ▶ Model  $\pi, p, \psi_{12}, \psi_{21}$  is parameter redundant;
- ▶ The estimable parameters are:  $\pi p, p\psi_{21}$  and  $p(\psi_{12} - 1) - \psi_{12} - \psi_{21}$ .
- ▶ If  $p$  is modelled using a temporal covariate, the model is full rank.

# JOLLY-SEBER MODEL

- ▶ The studied population might not be closed, but still want to be able to estimate population size;
- ▶ Parameters for the Jolly-Seber model:
  - ▶  $N$ : population size;
  - ▶  $\beta_t$ : proportion of individuals first available for capture at occasion  $t+1$ ;
  - ▶  $p_t$ : probability an individual is captured at occasion  $t$ ;
  - ▶  $\phi_t$ : probability an individual present in the study area at occasion  $t$  remains in the study area until occasion  $t+1$ .

# JOLLY-SEBER MODEL

- ▶ When forming the probability of an observed encounter history we need to sum over possible entry and departure times.
  - ▶ Suppose individual  $i$  is first captured at occasion  $f_i$  and last captured at occasion  $l_i$ ;
  - ▶  $x_{ij} = 1$  if individual  $i$  is captured at occasion  $j$ ,  $x_{ij} = 0$  otherwise.

$$\Pr(h_i) = \sum_{b=1}^{f_i} \sum_{d=l_i}^T \beta_{b-1} \left( \prod_{j=b}^{d-1} \phi_j \right) (1 - \phi_d) \left\{ \prod_{j=b}^d p_j^{x_{ij}} (1 - p_j)^{1-x_{ij}} \right\}$$

# JOLLY-SEBER MODEL

Corresponding probability of an individual not captured during the study:

$$\Pr(h_0) = \sum_{b=1}^T \sum_{d=1}^T \beta_{b-1} \left( \prod_{j=b}^{d-1} \phi_j \right) (1 - \phi_d) \left\{ \prod_{j=b}^d (1 - p_j) \right\}$$

The likelihood, once again, has the same form:

$$L \propto \frac{N!}{(N-D)!} \prod_{i=1}^D \Pr(h_i) \times \Pr(h_0)^{N-D} \quad (1)$$

# STOPOVER MODEL

- ▶ Generalised version of the Jolly-Seber model (Pledger et al, 2009)
- ▶ Parameters are defined to be age-dependent, where **age** corresponds to the time spent in study area:
  - ▶  $N$ : population size;
  - ▶  $\beta_t$ : proportion of individuals first available for capture at occasion  $t+1$ ;
  - ▶  $p_t(a)$ : probability an individual which entered the study  $a$  occasions previously is captured at occasion  $t$ ;
  - ▶  $\phi_t(a)$ : probability an individual present in the study area at occasion  $t$ , which entered the study  $a$  occasions previously, remains in the study area until occasion  $t+1$ .
- ▶ Can naturally be expressed in an HMM framework.

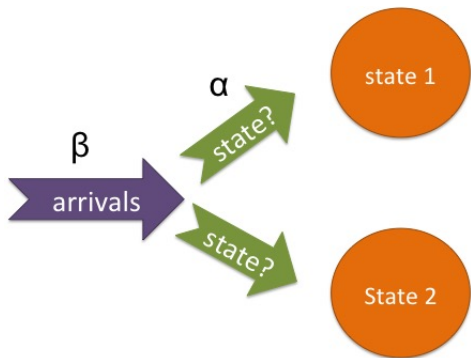
# MULTISTATE STOPOVER MODEL

- ▶ Individuals may be captured in different states;
- ▶ Multistate extensions exist for many capture-recapture models;
- ▶ Demonstrate that its possible to build transitions and state-dependence into the basic stopover model;
- ▶ HMM provides a useful, efficient framework for this.

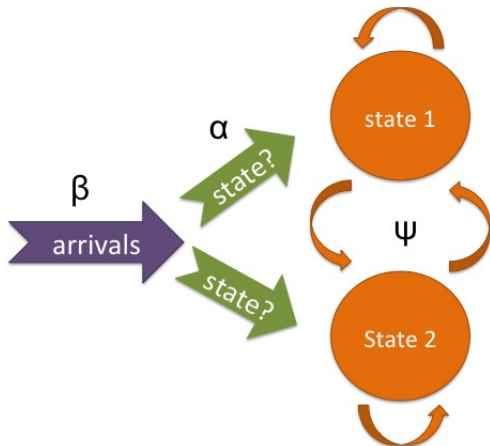




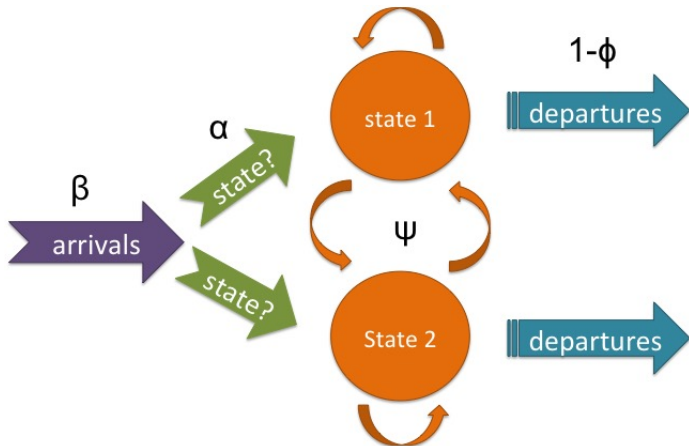
# MULTISTATE STOPOVER MODEL



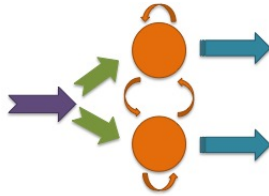
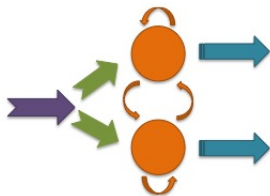
# MULTISTATE STOPOVER MODEL



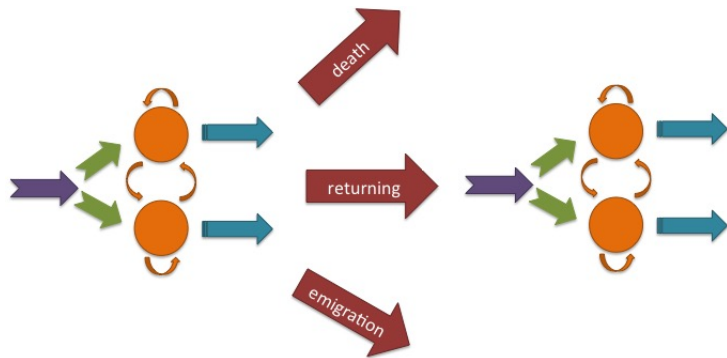
# MULTISTATE STOPOVER MODEL



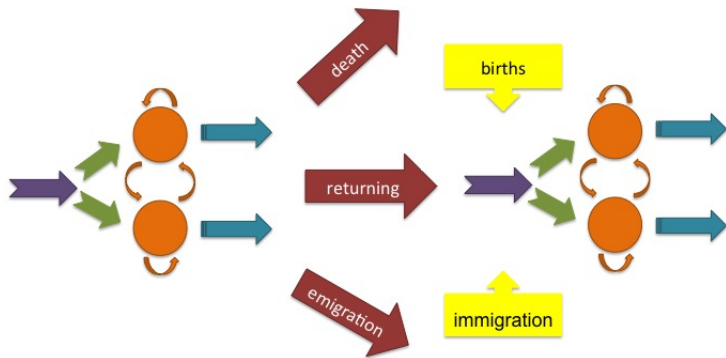
# INTEGRATING OVER MULTIPLE YEARS



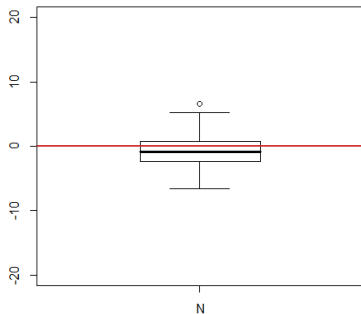
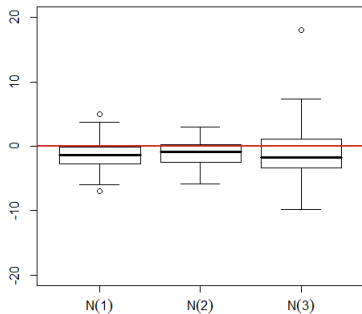
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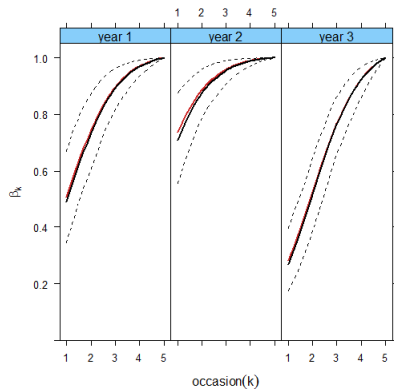
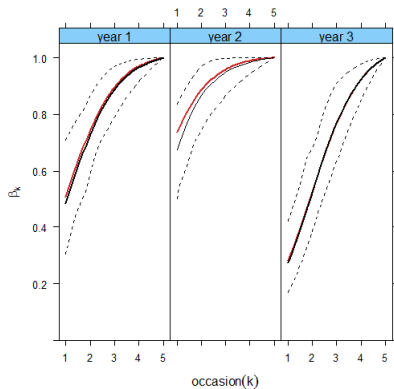


# SIMULATION RESULTS

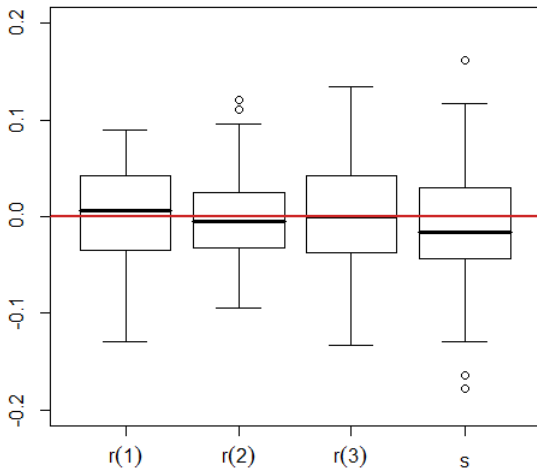




## SIMULATION RESULTS



## SIMULATION RESULTS



# ADVANTAGES

- ▶ General framework, with other models forming a special case;
  - ▶ Robust design (closed and open);
  - ▶ Closed population models - including a multistate closed population model (Worthington et al, 2015);
  - ▶ Stopover and Jolly-Seber models;
- ▶ Using all available data in a coherent model - compare Besbeas et al (2002);
- ▶ Natural generalisation of model selection methods for multistate models
  - ▶ Transdimensional simulated annealing (Brooks et al, 2003);
  - ▶ Step-wise procedures using score tests (McCrea and Morgan, 2011);

# DISCUSSION

- ▶ Removal modelling:
  - ▶ Developed a new model for individuals moving into unobservable states;
  - ▶ Matechou et al (2015) has relaxed the assumption of closure within removal models and these methods could be included in the multievent removal framework;
  - ▶ Further investigation of the poor performance of near-redundant models.
- ▶ Stopover modelling:
  - ▶ HMM framework has provided an efficient approach for dealing with complex capture-recapture data;
  - ▶ Integrating the analysis of multiple years of data has improved precision and accuracy of parameter estimates;
  - ▶ Assessment of goodness-of-fit is an active area of research.

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