# Capture-recapture models in ecology: multi-state developments

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German Statistical Week

Hamburg, September 2015

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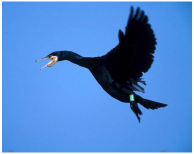
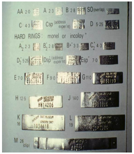
- Eleni Matechou
- Diana Cole
- Ruth King
- Richard Griffiths

# Outline

# 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
  - `0 0 0 0 0` $\qquad (1-p_1)(1-p_2)(1-p_3)(1-p_4)(1-p_5)$
- It is the number of individuals who are never captured that we need to estimate.

The likelihood has the form:

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

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

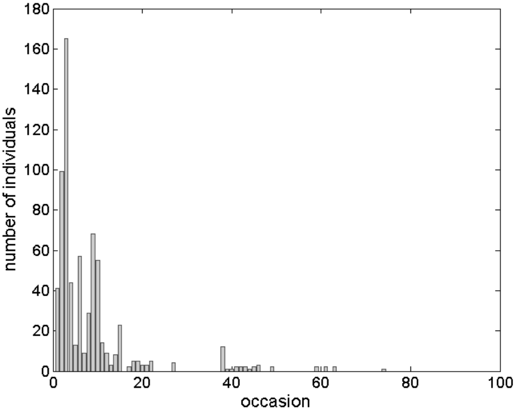
# CLOSED POPULATION MODEL, $M_b$

- $p$: 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` $(1-p)(1-p)p(1-c)c$
  - ...

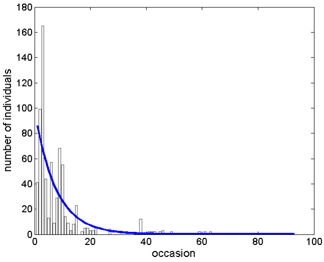
# REMOVAL DATA

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



# LINK TO MODEL $M_b$

- Basic geometric model
  Pr(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 $c = 0$.



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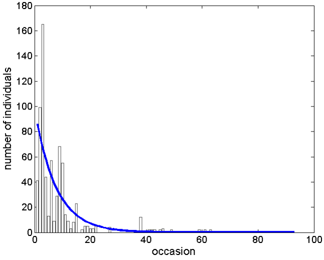
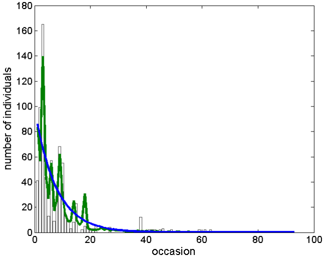
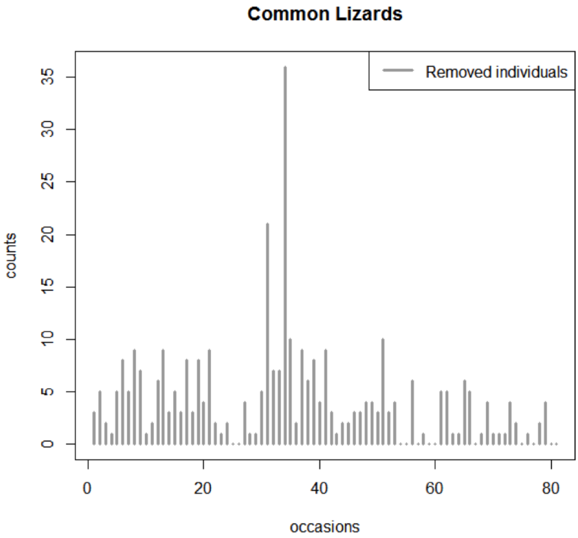
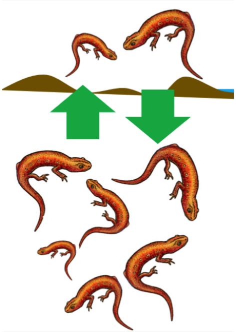


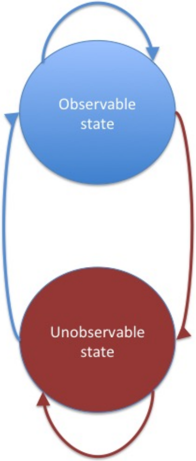
# WHY DO DATA EXHIBIT UNEXPECTED PEAKS?



# AN UNDERGROUND CITY?

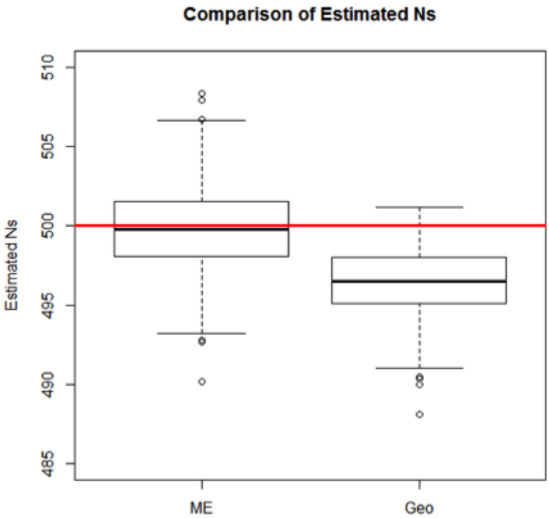


# MULTISTATE REMOVAL MODEL




- 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



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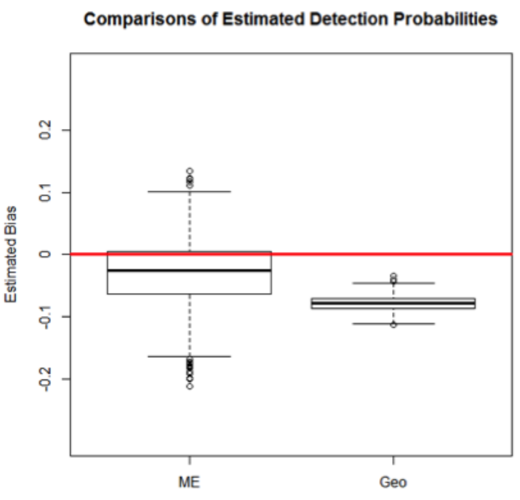

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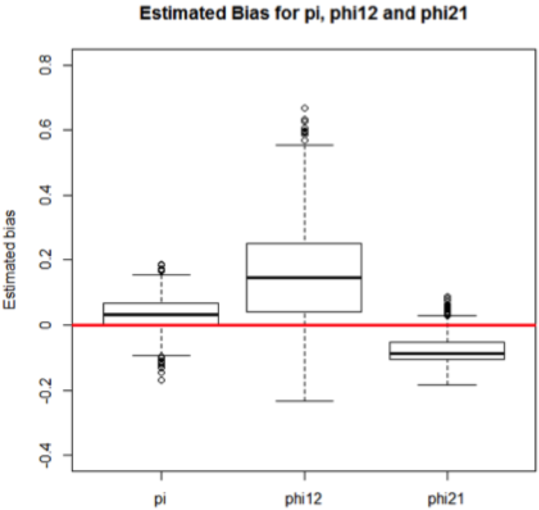


# PARAMETER REDUNDANCY

- 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 $\text{rank}(D) = \dim(\theta)$, all parameters are estimable;
- If $\text{rank}(D) < \dim(\theta)$ 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:

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

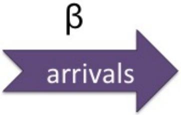
# STOPOVER MODEL

- 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



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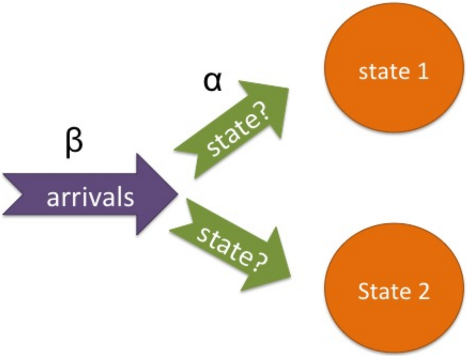

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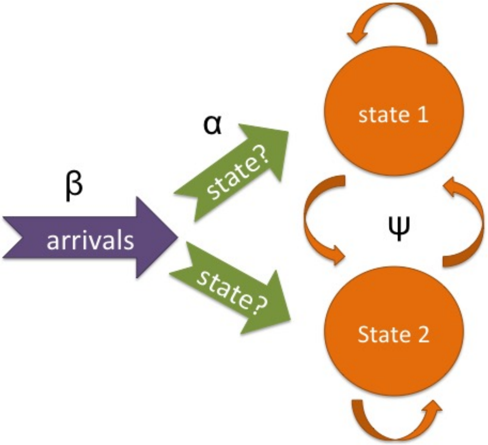
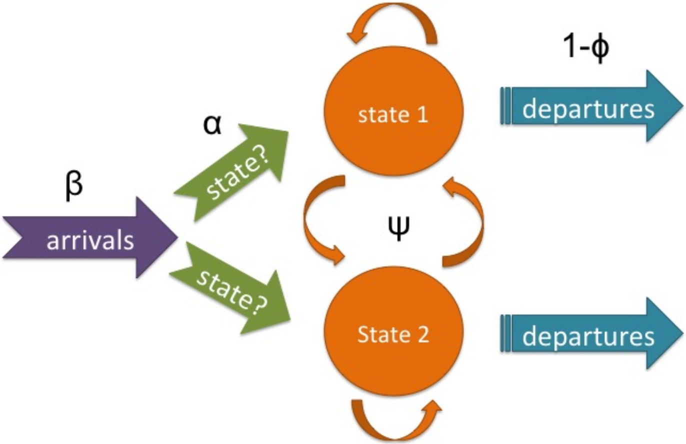
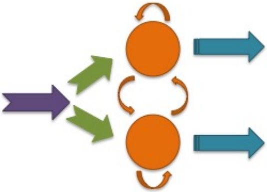
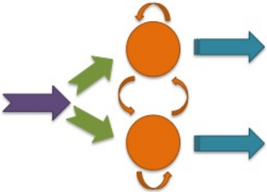


# Multistate stopover model

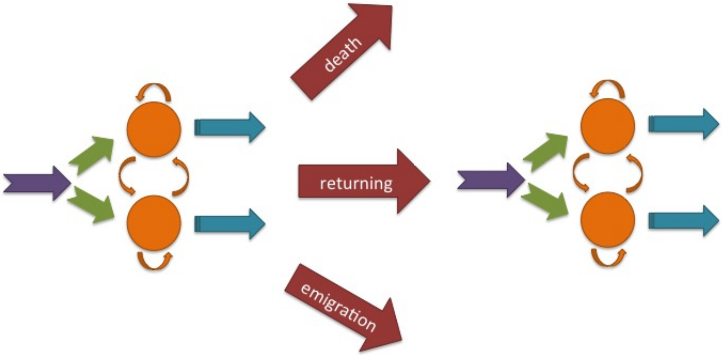


# INTEGRATING OVER MULTIPLE YEARS





# Integrating over multiple years



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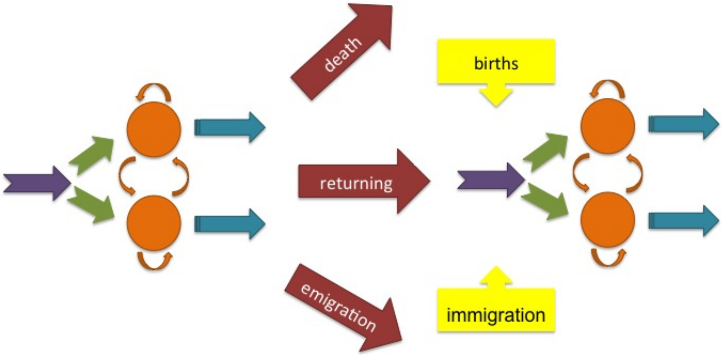
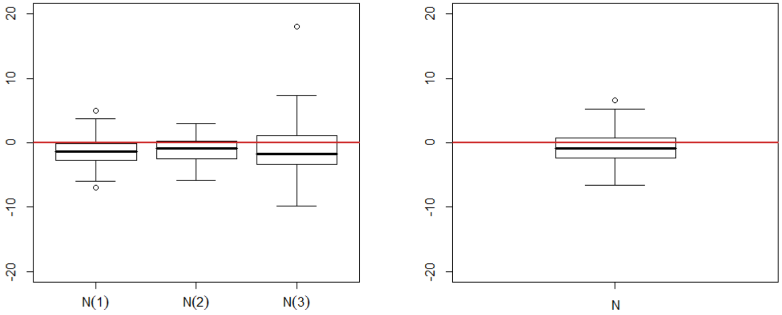


# Simulation results



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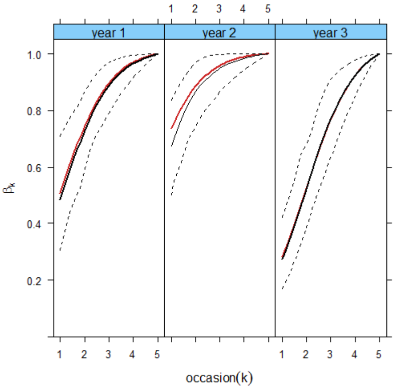


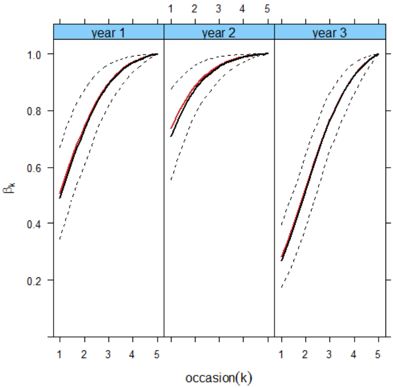

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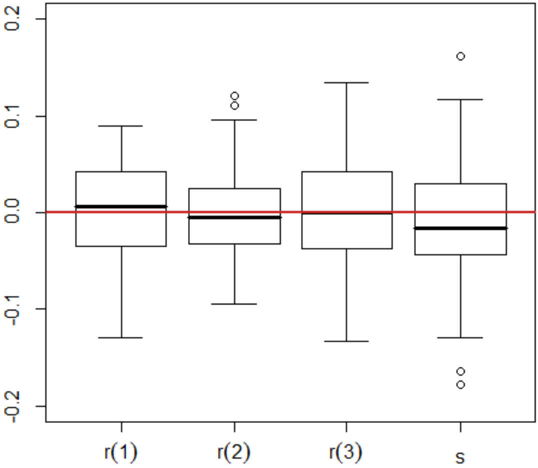

# ADVANTAGES

- 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.

# REFERENCES


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