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Multistate models for ecological data

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- Eleni Matechou

Outline

Multistate capture-recapture models

Multistate closed population models

Multistate stopover models

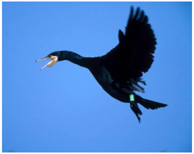
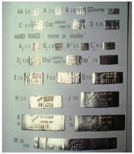
Multistate removal models

Discussion

Section 1

Multistate capture-recapture models

Individual marking

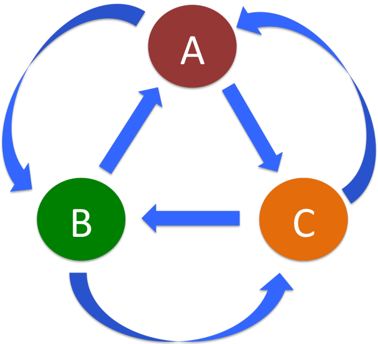



Capture-recapture data

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

SITE OR STATE-SPECIFIC INFORMATION

- A 0 0 B 0
- A C 0 C C
- 0 0 B 0 C
- ...



MULTISTATE CAPTURE-RECAPTURE MODEL

Parameters of the model:

- $\phi_t(r)$: probability an animal alive at time t in state r, survives until time $t+1$;
- $\psi_t(r)$: probability an animal alive in state r at time t moves to state s by time $t+1$;
- $p_{t+1}(s)$: probability an animal alive in state s at time $t+1$ is recaptured.

Model can be fitted using method of maximum-likelihood.

Application

- Mountain chicken frog, *Leptodactylus fallax*;
- Found on only Montserrat and Dominica in the Eastern Caribbean.

- Susceptible to Chytridiomycosis;
- *The worst infectious disease ever recorded among vertebrates in terms of the number of species impacted, and its propensity to drive them to extinction (Gascon et al. 2007).*

TREATMENT GROUPS

Itraconazole treatment (n=80)

Washed in 500ml 0.01% itraconazole bath for 5 minutes in a disposable food grade plastic bag.

Stream water control (n=42)

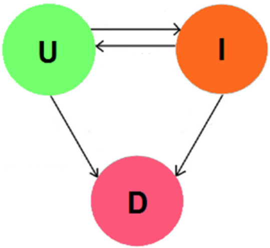
Washed in 500ml stream water bath for 5 minutes to replicate stresses of treatment.

Non-bath control (n=106)

Handled for 5 minutes to replicate stresses of capture but no treatment regime.

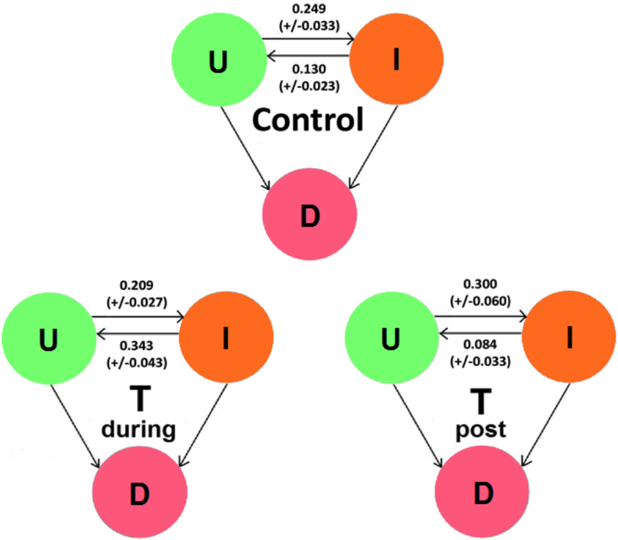
SWABBED PRE TREATMENT

Multistate model

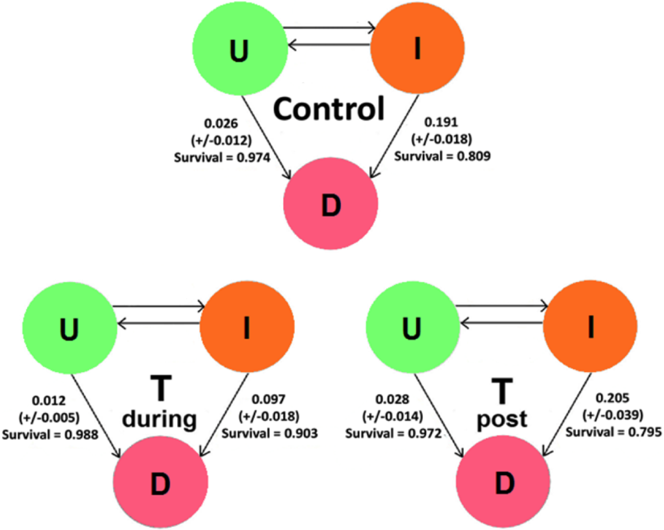


- Model selection, the top models have:
  - Group effect on survival and transition probabilities (estimated separately pre- and post-treatment);
  - No difference in survival or transmission between two control groups;
  - Group (and time) difference in recapture probability.

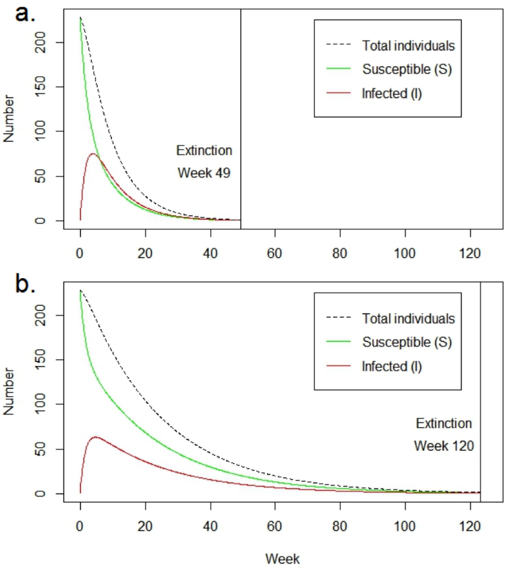
Transition probabilities



SURVIVAL PROBABILITIES



Population dynamics



Section 2

Multistate closed population models

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` $p_1 p_2 (1-p_3) p_4 p_5$
  - `0 0 1 0 1` $(1-p_1)(1-p_2)p_3(1-p_4)p_5$
  - ...

Closed population model, M_t

- 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` $(1-p_1)(1-p_2)(1-p_3)(1-p_4)(1-p_5)$
- 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_0: observed encounter history of never encountered;
- N: population size;
- D: number of observed individuals.

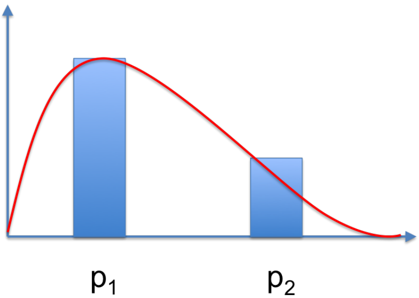
CLOSED POPULATION MODEL, M_b

- 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` $(1-p)(1-p)p(1-c)c$
  - $\ldots$

Closed population model, M_h

- Not all animals have the same capture probability
- Can be modelled in a number of ways:
  - Finite mixture models
  - Continuous models



KNOWN DISCRETE INFORMATION

- Suppose that:
  - capture probabilities are known to differ between individuals in different states;
  - individuals can move between these known states.

- The model is structurally equivalent to a closed version of the multistate capture-recapture model presented in Section 1;
- Now we also estimate population size, N.

Closed population model, M_h^R

Parameters of the model:

- $\phi_t(r)$: probability an animal alive at time t in state r, survives until time $t+1$;
- $\psi_t(r,s)$: probability an animal alive in state r at time t moves to state s by time $t+1$;
- $p_{t+1}(s)$: probability an animal alive in state s at time $t+1$ is recaptured;

Closed population model, M_h^R

Parameters of the model:

- $\phi_t(r)$: probability an animal alive at time t in state r, survives until time $t+1$;
- $\psi_t(r,s)$: probability an animal alive in state r at time t moves to state s by time $t+1$;
- $p_{t+1}(s)$: probability an animal alive in state s at time $t+1$ is recaptured;
- $\alpha(r)$: probability an animal is in state r at occasion 1.

CLOSED POPULATION MODEL, M_h^R

- If the state of an individual is uncertain, then the model becomes a closed version of the multievent model (Pradel, 2005);
- In the limiting case where no states are observed upon recapture and there are no transitions between states, the model reduces to the finite mixture model, M_h;
- Model M_h^R can be efficiently fitted using a *hidden Markov model* framework.

Application

- Great crested newt, *Tristurus cristatus*, field study site
- Data from 2010 and 2013 breeding seasons
- States: new and old ponds

Results

2010			
Parameter	MLE	SE	95% CI
N	33.95	1.44	(33.05, 51.23)
$p(1)$	0.82	0.083	(0.60, 0.93)
$p(2)$	0.33	0.045	(0.25, 0.43)
$\psi(1,2)$	0.31	0.076	(0.18, 0.47)
$\psi(2,1)$	0.034	0.019	(0.011, 0.10)
$\alpha(1)$	0.48	0.094	(0.31, 0.66)
2013			
Parameter	MLE	SE	95% CI
N	45.96	1.85	(44.31, 56.50)
$p(1)$	0.36	0.061	(0.25, 0.48)
$p(2)$	0.41	0.048	(0.32, 0.50)
$\psi(1,2)$	0.053	0.035	(0.014, 0.18)
$\psi(2,1)$	0.075	0.033	(0.031, 0.17)
$\alpha(1)$	0.33	0.087	(0.19, 0.52)

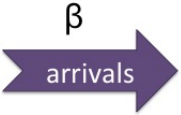
Section 3

Multistate stopover models

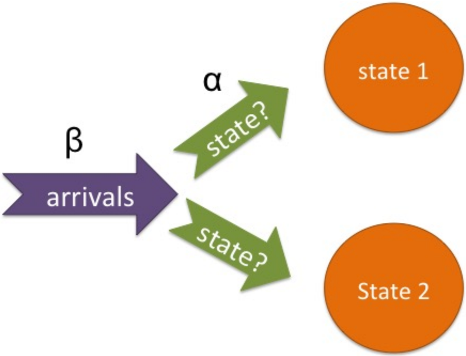
Multistate stopover model

- The studied population might not be closed, but still want to be able to estimate population size

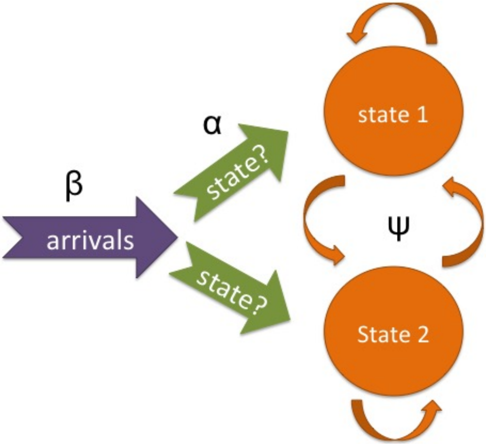
Multistate stopover model



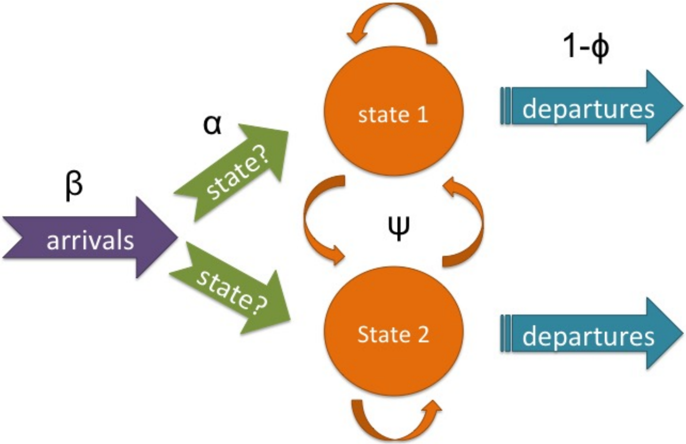
Multistate stopover model



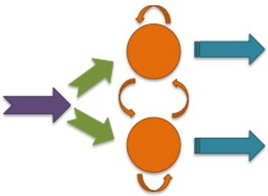
MULTISTATE STOPOVER MODEL

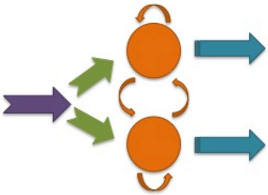


Multistate stopover model



INTEGRATING OVER MULTIPLE YEARS





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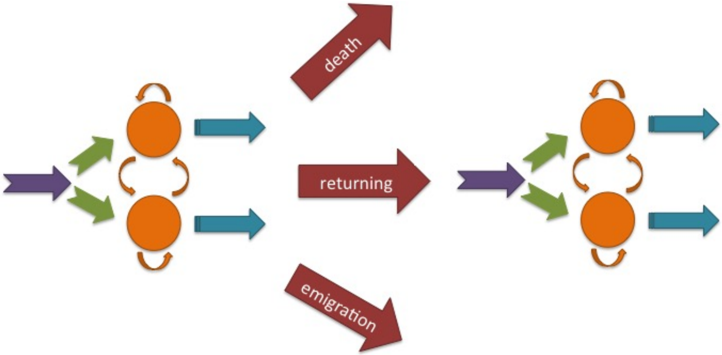

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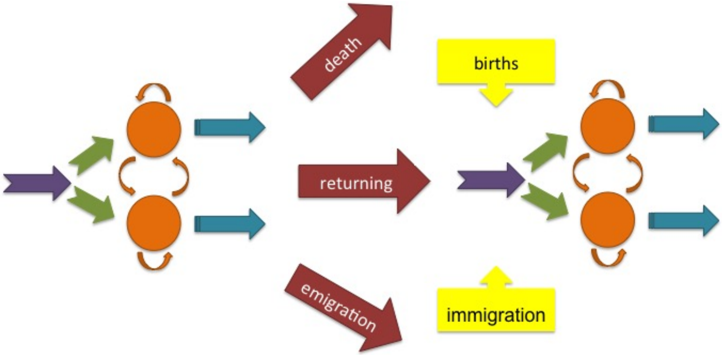


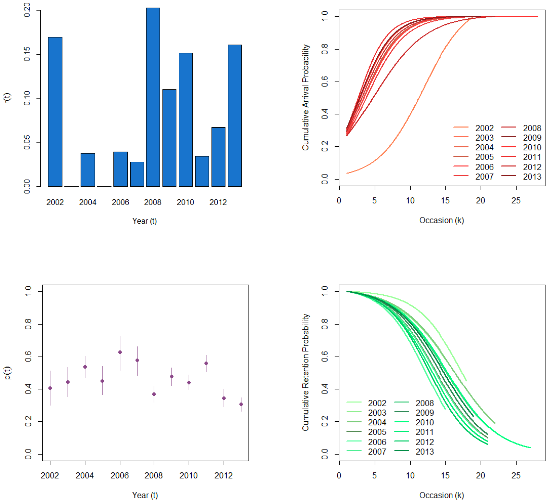
ADVANTAGES

- General framework, with other models forming a special case:
  - Robust design (closed and open);
  - Closed population models - including a multistate closed population model;
  - 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).

Application

- Return to the Great crested newt data
- Able to incorporate all data:
  - weekly captures in breeding season;
  - data from 2002-2014;
  - pond-specific information from 2010 onwards.

Provisional results



Section 4

Multistate removal models

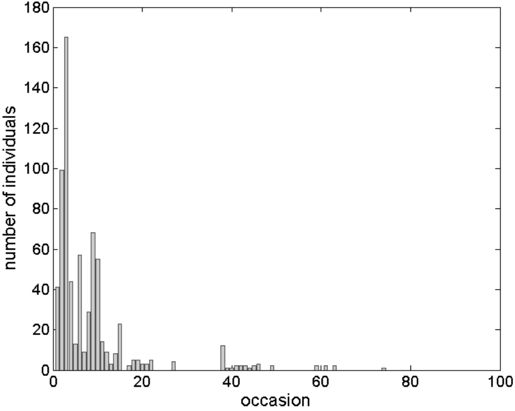
Closed population model, M_b

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

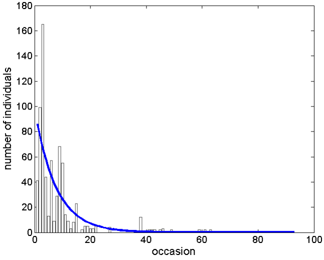
Removal data

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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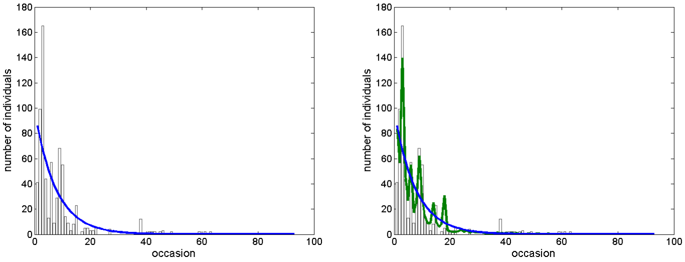
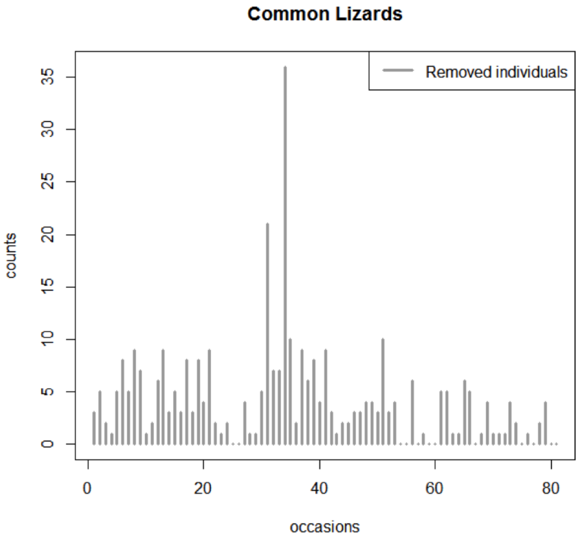
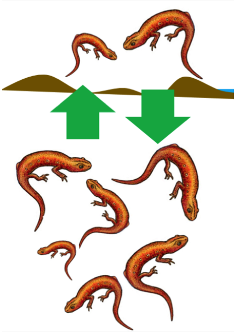


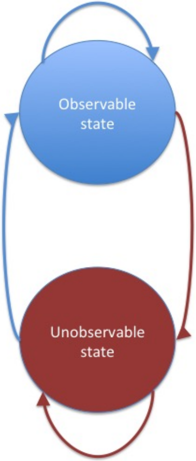
Why do data exhibit unexpected peaks?



AN UNDERGROUND CITY?

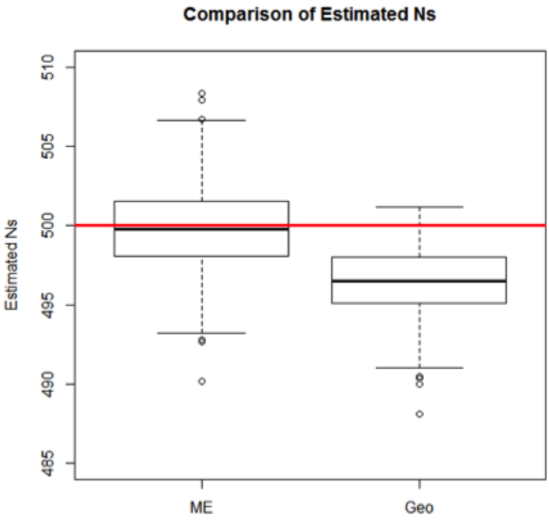


Multistate removal model

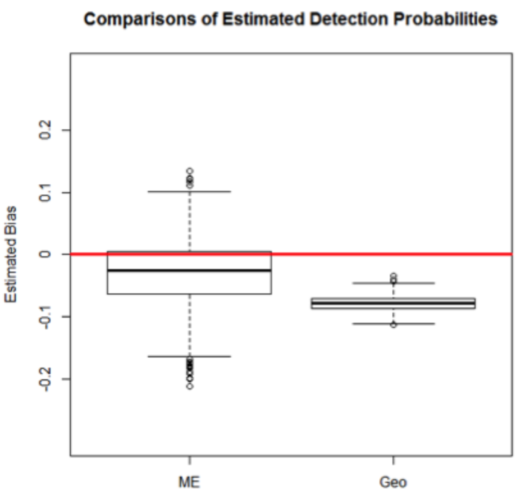


- Develop a two-state model, with one unobservable state with capture probability of 0;
- Naturally fits into a multievent framework, which is an HMM.

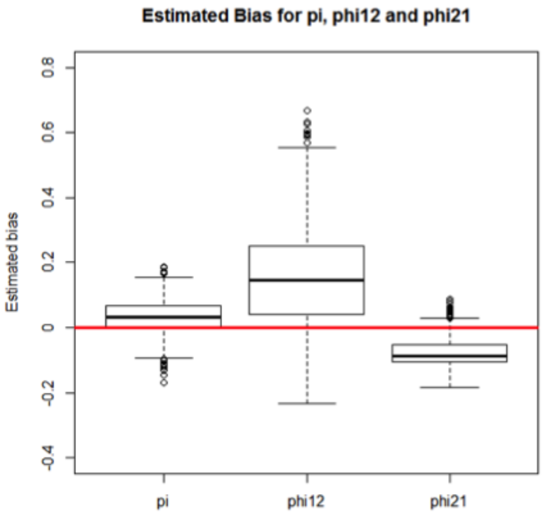
SIMULATION RESULTS



Simulation results



SIMULATION RESULTS



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 κ denotes an exhaustive summary for a model that provides a unique representation of the model and θ denotes the parameters;
- Model $\pi, p, \psi_{12}, \psi_{21}$ is parameter redundant;
- The estimable parameters are: πp, $p\psi_{21}$ and $p(\psi_{12} - 1) - \psi_{12} - \psi_{21}$;
- If p is modelled using a temporal covariate, the model is full rank.

DISCUSSION

- Multistate models are a powerful tool for understanding important ecological dynamics;
- Memory is an important feature which is often ignored due to the challenge in fitting these models;
- Many multistate models can be expressed conveniently in a hidden Markov model framework - forthcoming book! (King, McCrea and Langrock 2016/17);
- The use of semi-Markov models are a recent important advance in the capture-recapture literature (King and Langrock, 2015);
- The idea of relaxing the closure assumptions has been incorporated into the removal models (Matechou et al, 2015) and this could be considered in conjunction to the unobservable state models of this talk.

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