Integrated Population Model Selection

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OUTLINE

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  Results

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CONCLUSIONS
INTEGRATED POPULATION MODEL

\[ L_G(\Theta|d_1, d_2, \ldots, d_K) = L_1(\theta_1|d_1) \times L_2(\theta_2|d_2) \times \ldots \times L_K(\theta_K|d_K) \]

where

\[ \Theta = \theta_1 \cup \theta_2 \cup \ldots \cup \theta_K \]
INTEGRATED POPULATION MODEL

- Advantages
  - unites capture-recapture and time-series methodology;
  - provides a simultaneous description of all the data;
  - increased precision of parameter estimates;
  - coherent estimation of parameters otherwise not estimable from individual component analyses alone (new methods to diagnose estimable parameters are given in Cole and McCrea, 2015).

- Wide number of applications
  - eg. lapwings, grey herons, cormorants, greater snow geese, soay sheep;
  - A review of applications is given in Schaub and Abadi (2011).
INTEGRATED POPULATION MODEL

This talk focuses on combining census (or abundance indices) and demographic data such as ring-recovery data.

- state-space models can be used to describe census data, and if Gaussian assumptions are made the Kalman filter can be used to form the likelihood function (Besbeas et al, 2002; Brooks et al, 2004);
- large range of models for capture-recapture data and they are generally of product-multinomial form (McCrea and Morgan, 2014).
PARAMETERS OF THE INTEGRATED MODEL

- annual survival probabilities, \( \{\phi_a\} \), which vary with age up to age \( A > 1 \), and then remain constant with increasing age;
- productivity \( \rho \);
- recovery probability, \( \lambda \);
- measurement error variance \( \sigma^2 \).
STATE-SPACE MODEL

State-space models are based on two equations, the transition equation (1) and the observation equation (2).

\[
\begin{bmatrix}
N_{1,t} \\
N_{2,t} \\
\vdots \\
N_{A-1,t} \\
N_{A+,t}
\end{bmatrix} =
\begin{bmatrix}
0 & \rho \phi_1 & \cdots & \rho \phi_1 & \rho \phi_1 \\
\phi_2 & 0 & 0 & 0 & 0 \\
0 & 0 & \ddots & 0 & 0 \\
0 & 0 & \cdots & \phi_{A+} & \phi_{A+}
\end{bmatrix}
\begin{bmatrix}
N_{1,t-1} \\
N_{1,t-1} \\
\vdots \\
N_{A-1,t-1} \\
N_{A+,t-1}
\end{bmatrix} +
\begin{bmatrix}
\epsilon_{1,t} \\
\epsilon_{1,t} \\
\vdots \\
\epsilon_{a-1,t} \\
\epsilon_{A,t}
\end{bmatrix}
\] (1)

\[
y_t = \begin{bmatrix}
0 & 1 & \cdots & 1
\end{bmatrix} \times \begin{bmatrix}
N_{1,t} \\
N_{2,t} \\
\vdots \\
N_{A+,t}
\end{bmatrix} + \eta_t
\] (2)
RING-RECOVERY DATA

- Cohorts of individuals are marked and released back into the population;
- When individuals die, they may be recovered dead or their rings/marks may be recovered;
- Data can be summarised by the statistics:
  - $R_i$: number of marked individuals released at occasion $t_i$;
  - $d_{ij}$: number of individuals released at occasion $t_i$ and recovered dead in the time interval $(t_{j-1}, t_j)$. 
For individuals marked as young, with age-dependent survival up to age $A$, and $T(>A)$ recovery occasions, the probabilities corresponding to the observed data are:

<table>
<thead>
<tr>
<th></th>
<th>2</th>
<th>3</th>
<th>\ldots</th>
<th>$T$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_1$</td>
<td>$(1 - \phi_1)\lambda$</td>
<td>$\phi_1(1 - \phi_2)\lambda$</td>
<td>\ldots</td>
<td>$\prod_{a=1}^{A-1} \phi_a \phi_A^{T-A}(1 - \phi_A)\lambda$</td>
</tr>
<tr>
<td>$R_2$</td>
<td>$(1 - \phi_1)\lambda$</td>
<td>\ldots</td>
<td>$\prod_{a=1}^{A-1} \phi_a \phi_A^{T-A-1}(1 - \phi_A)\lambda$</td>
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<tr>
<td>$R_{T-1}$</td>
<td>$(1 - \phi_1)\lambda$</td>
<td>\ldots</td>
<td>\ldots</td>
<td>$(1 - \phi_1)\lambda$</td>
</tr>
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</table>
SELECTING THE AGE-STRUCTURE FOR AN IPM

- Integrated population model selection with regard to age-structure in survival (or other parameters) involves modelling across state-space model dimensions;
- An alternative approach to modelling age-variation in IPM is to form a maximal SSM, with specific age-structures obtained as special cases of this model.
TWO MODELLING APPROACHES

A two age-class state-space model could be defined by either of the following transition equations:

\[
\begin{pmatrix}
N_{1,t} \\
N_{A,t}
\end{pmatrix}
= \begin{pmatrix}
0 & \rho \phi_1 \\
\phi_A & \phi_A
\end{pmatrix}
\begin{pmatrix}
N_{1,t-1} \\
N_{A,t-1}
\end{pmatrix}
+ \begin{pmatrix}
\epsilon_{1,t} \\
\epsilon_{A,t}
\end{pmatrix}
\]  \quad (3)

\[
\begin{pmatrix}
N_{1,t} \\
N_{2,t} \\
N_{A,t}
\end{pmatrix}
= \begin{pmatrix}
0 & \rho \phi_1 & \rho \phi_1 \\
\phi_A & 0 & 0 \\
0 & \phi_A & \phi_A
\end{pmatrix}
\begin{pmatrix}
N_{1,t-1} \\
N_{2,t-1} \\
N_{A,t-1}
\end{pmatrix}
+ \begin{pmatrix}
\epsilon_{1,t} \\
\epsilon_{2,t} \\
\epsilon_{A,t}
\end{pmatrix}
\]  \quad (4)
MODEL SELECTION STRATEGIES

- Demographic data alone (eg. Besbeas et al, 2002);
- Demographic data alone used as starting point, then performing some model selection on integrated model (eg. McCrea et al, 2010);
- Integrated data.

Currently AIC is used for model selection of IPM.
AGE-DEPENDENT SURVIVAL PROBABILITIES

- Step-wise approach using likelihood-ratio tests (or score tests - eg. McCrea and Morgan, 2011)
  - Step 1: $\phi(1, 2+) \text{ vs } \phi(1, 2, 3+)$;
  - Step 2: $\phi(1, 2, 3+) \text{ vs } \phi(1, 2, 3, 4+) \text{ etc.}$
Simulation structure

- Simulation based on grey heron data, commonly used in the IPM literature;
- Simulated 20 years of ring-recovery data and 71 years of census data;
- Range of parameter values have been investigated, representative results presented here.
RESULTS

Table: 150 replications; number of times model is selected using the different approaches

<table>
<thead>
<tr>
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<th>Number of adult age classes</th>
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<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>min AIC</td>
<td>RR</td>
</tr>
<tr>
<td></td>
<td>Int</td>
</tr>
<tr>
<td>parsimony AIC</td>
<td>RR</td>
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<td>RR</td>
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- Minimum AIC performs better for demographic data alone than integrated data;
RESULTS

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- Minimum AIC often selects models with larger number of age classes; AIC known to have problems for state-space models alone - see Bengtsson and Cavanaugh (2006)
RESULTS

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Introducing parsimony argument into AIC reduces the number of models with very large number of age classes being selected;
RESULTS

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- LRT approach performs the best for integrated models.
**SENESCENCE**

*Senescence* is a decrease in reproductive output and/or survival with increasing age.

Step up augmented with step down
Figure: Ibex, *Capra ibex*
DATA DESCRIPTION

The data arise from a large monitoring study at the Gran Paradiso National Park in Italy.

- Multi-variate census data consisting of counts of adult males and adult females, yearlings and kids have been collected since 1956;
- Kid survival and productivity data from 2000.
STEP UP AUGMENTED WITH STEP DOWN

\[ \Phi(2+) \rightarrow \Phi(2,3+) \rightarrow \Phi(2,3,4+) \rightarrow \Phi(2:3,4,5+) \rightarrow \Phi(2:4,5+) \rightarrow \Phi(2:6,7:10,11+) \]
**Alternative Models**

- $\phi(2,\ldots,10,11+)$
- $\phi(2,6;7,10,11+)$
- $\phi(2;6,G[7+])$
- $\phi(2;6,7;10,G[11+])$
Optimal model selection for integrated population models has not previously been addressed;

Contrary to intuition adding information through integrated models can result in deterioration in model selection when AIC is used;

Simple corrections of AIC are impossible to find as they are model dependent and AIC variants such as AICc, BIC etc are not easily defined in IPM;

Step-wise approach using LRTs has been found to work well and is robust to irregular survival probability patterns, such as those in a population exhibiting senescence.
REFERENCES


