INTEGRATED POPULATION MODEL SELECTION

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Collaborators

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OUTLINE

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 ρ;
- recovery probability, λ;
- measurement error variance σ^2;

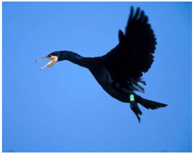
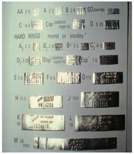
STATE-SPACE MODEL

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

$$\begin{pmatrix} N_{1,t} \\ N_{2,t} \\ \vdots \\ N_{A-1,t} \\ N_{A+,t} \end{pmatrix} = \begin{pmatrix} 0 & \rho\phi_1 & \cdots & \rho\phi_1 & \rho\phi_1 \\ \phi_2 & 0 & 0 & 0 & 0 \\ & & \vdots & & \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & \phi_{A+} & \phi_{A+} \end{pmatrix} \begin{pmatrix} N_{1,t-1} \\ N_{1,t-1} \\ \vdots \\ N_{A-1,t-1} \\ N_{A+,t-1} \end{pmatrix} + \begin{pmatrix} \epsilon_{1,t} \\ \epsilon_{1,t} \\ \vdots \\ \epsilon_{a-1,t} \\ \epsilon_{A,t} \end{pmatrix} \quad (1)$$

$$y_t = \begin{pmatrix} 0 & 1 & \cdots & 1 \end{pmatrix} \times \begin{pmatrix} N_{1,t} & N_{2,t} & \cdots & N_{A+,t} \end{pmatrix} + \eta_t \quad (2)$$

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).

Ring-recovery model

- 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:

	2	3	$\cdots$	T
R_1	$(1-\phi_1)\lambda$	$\phi_1(1-\phi_2)\lambda$	$\cdots$	$\prod_{a=1}^{A-1}\phi_a\phi_A^{T-A}(1-\phi_A)\lambda$
R_2		$(1-\phi_1)\lambda$	$\cdots$	$\prod_{a=1}^{A-1}\phi_a\phi_A^{T-A-1}(1-\phi_A)\lambda$
$\vdots$				$\vdots$
R_{T-1}				$(1-\phi_1)\lambda$

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:

$$\begin{pmatrix} N_{1,t} \\ N_{A,t} \end{pmatrix} = \begin{pmatrix} 0 & \rho\phi_1 \\ \phi_A & \phi_A \end{pmatrix} \begin{pmatrix} N_{1,t-1} \\ N_{A,t-1} \end{pmatrix} + \begin{pmatrix} \epsilon_{1,t} \\ \epsilon_{A,t} \end{pmatrix} \tag{3}$$

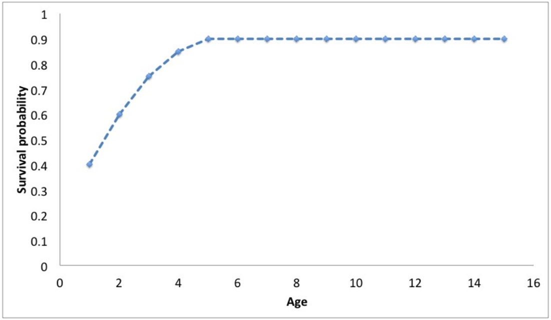
$$\begin{pmatrix} N_{1,t} \\ N_{2,t} \\ N_{A,t} \end{pmatrix} = \begin{pmatrix} 0 & \rho\phi_1 & \rho\phi_1 \\ \phi_A & 0 & 0 \\ 0 & \phi_A & \phi_A \end{pmatrix} \begin{pmatrix} N_{1,t-1} \\ N_{2,t-1} \\ N_{A,t-1} \end{pmatrix} + \begin{pmatrix} \epsilon_{1,t} \\ \epsilon_{2,t} \\ \epsilon_{A,t} \end{pmatrix} \tag{4}$$

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: $\phi(1, 2+)$ vs $\phi(1, 2, 3+)$;
  - Step 2: $\phi(1, 2, 3+)$ vs $\phi(1, 2, 3, 4+)$ 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

		Number of adult age classes						
		1	2	**3**	4	5	6	7
min AIC	RR	0	40	**74**	16	4	9	7
	Int	0	0	**62**	38	19	18	13
parsimony AIC	RR	0	56	**85**	3	2	3	1
	Int	0	30	**91**	11	5	8	5
LRT	RR	0	63	**84**	3	0	0	0
	Int	0	36	**105**	9	0	0	0

- Minimum AIC performs better for demographic data alone than integrated data;

Results

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

		Number of adult age classes						
		1	2	**3**	4	5	6	7
min AIC	RR	0	40	**74**	16	4	9	7
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LRT	RR	0	63	**84**	3	0	0	0
	Int	0	36	**105**	9	0	0	0

- 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

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

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

Results

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

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LRT	RR	0	63	**84**	3	0	0	0
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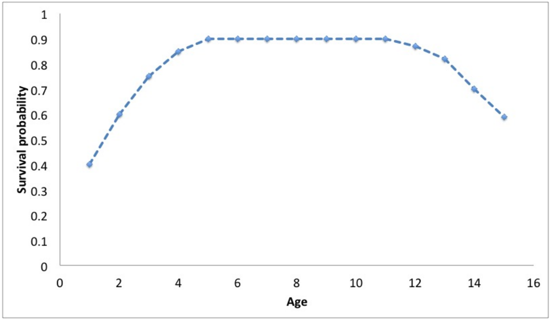
- LRT approach performs the best for integrated models.

SENESCENCE

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



Current model selection approaches for diagnosing senescence are ad hoc - eg. Gaillard et al, (2004).

Step up augmented with step down

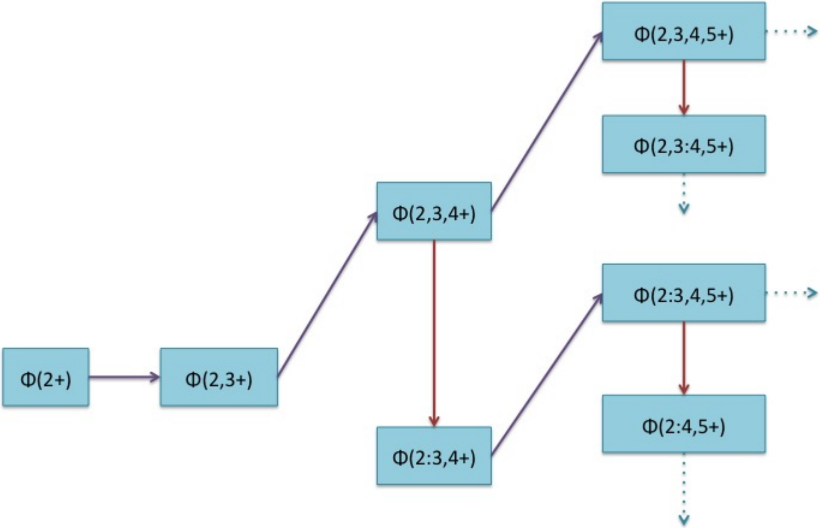


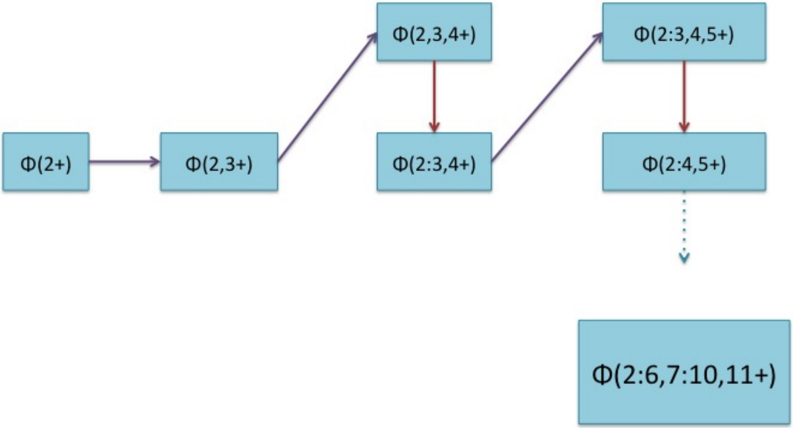
Figure: Ibex, *Capra ibex*

Data description

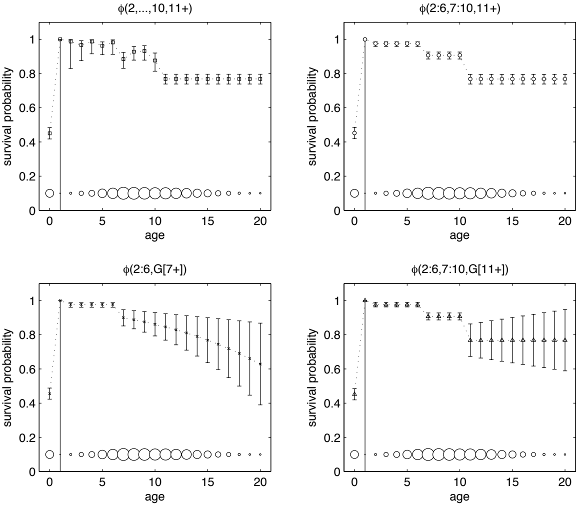
The data arise from a large monitoring study at the Gran Paradiso National Park in Italy.

- Multi-variate census data consisting of counts of adult males and adult females, yearlings and kids have been collected since 1956;
- Adult mark-recapture-recovery data from 1985.
- Kid survival and productivity data from 2000.

Step up augmented with step down



Alternative models



Conclusions

- 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.

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