Heterogeneity and population dynamics

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Population dynamics in the wild

**Ecology**: Impact of global change

**Evolution**: How to adapt when facing changing environments

**Management**: Propose and evaluate strategies
Population dynamics in the wild

- Investigating process in natural populations
- Long-term individual monitoring datasets
- Methodological issues when moving from lab to natural conditions
  - Issue 1: detectability < 1
  - Issue 2: individual heterogeneity (IH)
Issue of detectability < 1

- How to reliably estimate demographic parameters in the wild?

- Individuals may be seen or not

- If they’re not... Are they breeding? Are they on the study site? Are they dead?

- Individually mark and monitor individuals: capture-recapture (CR) data
Why bother with detection < 1?

Bias in survival and rate of senescence

Capture-recapture approach

Naïve approach detection = 1
Why bother with detection < 1?

Bias in shape of selection

Capture-recapture approach

Naïve approach detection = 1

Survival

Body mass
Issue of individual heterogeneity (IH)

- Standard CR models assume homogeneity

- Inter-individual variation in demographic parameters = individual heterogeneity (IH)

- From a statistical point of view, IH can cause bias in parameter estimates

- From a biological point of view, IH is of interest – individual quality
Accounting for individual heterogeneity

- CR models do not cope that well with IH
- If you’re a biologist, rely on empirical measures (mass, gender, age, experience, etc.)
  - How to incorporate this information?
- If you’re a statistician, intrinsic property of individuals
  - How to filter out the signal from noisy observations?
Capture-recapture models

- Intro: CR data and state-space models

- How to account for individual variation?
  - Random-effect models
  - Non-parametric Bayesian approach

- Perspectives
Common marking methods

- Ear tags for mammals / leg bands for birds
- Passive integrated transponder (PIT) tags
photo-identification

Lynx

Whales
DNA identification

Bears

Orang-utans

Wolves

Bats
An encounter history: \( h_i = (1 \ 0 \ 1) \)

\[
\begin{array}{ccc}
\phi & \phi \\
\_ & \_ & \\
1 & 0 & 1 \\
\uparrow & \uparrow & \\
1-p & p & \\
\end{array}
\]

\[
\Pr(h_i) = \phi (1-p) \phi p
\]

- Survival probability \( \phi \)
- Detection probability \( p \)
Modelling CR data

- A probabilistic framework developed in the 60s
  \[ \Pr(h_i) = \phi (1 - p) \phi p \]

- Central role of likelihood (frequentist / bayesian)
  \[ L = \prod_i \Pr(h_i) \]

- How to deal with IH in survival and/or detection?
State-space modelling of CR data

Dynamic process model

Hidden states

Survival

\[ X_{i,t-1}] \]

\[ \phi_{i,t} \]

State equation

\[ X_{i,t} \mid X_{i,t-1} \sim \text{Bernoulli}(\phi_{i,t} X_{i,t-1}) \]

Observation

Observations

detection

\[ Y_{i,t-1} \]

\[ Y_{i,t} \]

\[ p_{i,t} \]

Observation equation

\[ Y_{i,t} \mid X_{i,t} \sim \text{Bernoulli}(p_{i,t} X_{i,t}) \]
Case study in conservation biology

- Wolf is recolonizing France
- Problematic interactions with human activities
- Population dynamics as a tool for management and conservation
Results on wolves (1995-2003)
Sources of heterogeneity in wolves

- Wide area and genetic CR data
- Social species
Random effect CR model

- On logit scale, detection probability is:
  \[ \text{logit}(p_i) = \mu + \varepsilon_i \]

- With random effect
  \[ \varepsilon_i \sim N(0, \sigma^2) \]

- Uniform prior on SD \( \sigma \) of the random effect
Results on wolves (1995-2003)

SD random effect

Mean detection
Results on wolves (1995-2003)
Results on wolves (1995-2003)

WITHOUT heterogeneity

WITH heterogeneity
Non-parametric Bayesian approach

- $F(x) = \int N(x|\theta, \sigma^2) Q(d\theta)$ where $Q(d\theta)$ is a discrete mixing distribution

- Dirichlet process as prior on $Q(d\theta)$

- On the logit scale: $\logit(p_i) = \mu + \epsilon_i$

- With $\epsilon_i \sim N(\theta_h, \sigma^2)$ with probability $\pi_h$

- $\pi_h$ defined by stick-breaking prior
Results on wolves (1995-2003)

nb of clusters

0 50 150 250

1 2 3 4 5
Results on wolves (1995-2003)
Results on wolves (1995-2003)
Wolf survival

homogeneity

random effect

mixture of normals
Conclusions

- CR methodology is catching up with ‘p=1’ world
- IH needs to be accounted for
- State-space models: IH as well as $p < 1$
- If possible, biological view – measure IH on the field
## Perspectives

- **Model selection?**

<table>
<thead>
<tr>
<th>Model</th>
<th>Dev</th>
<th>DIC</th>
<th>pD</th>
</tr>
</thead>
<tbody>
<tr>
<td>homogeneous</td>
<td>174.9</td>
<td>273.6</td>
<td>98.5</td>
</tr>
<tr>
<td>(single) normal random effect</td>
<td>126.1</td>
<td>228.8</td>
<td>101.1</td>
</tr>
<tr>
<td>mixture of normal distributions</td>
<td>124.3</td>
<td>227.9</td>
<td>103.8</td>
</tr>
</tbody>
</table>

- **Computational burden?**

- **User-friendly implementation?**
References

**Dirichlet process**

**Capture-recapture models**