Barn swallow post-fledging survival: Using Stan to fit a hierarchical ecological model

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Introduction

Population dynamics

- Youngs
- Reproduction
- Juvenile survival
- Adult survival
- Immigration
- Emigration

Population
Questions

Does family matter?

Which time period determines post-fledging survival?

<table>
<thead>
<tr>
<th>pre-fledging</th>
<th>post-fledging</th>
</tr>
</thead>
<tbody>
<tr>
<td>genetic parents</td>
<td>parental care</td>
</tr>
<tr>
<td>food</td>
<td>food</td>
</tr>
<tr>
<td>weather</td>
<td>weather</td>
</tr>
<tr>
<td></td>
<td>predation</td>
</tr>
</tbody>
</table>
Barn swallow

world-wide distribution
long-distance migrant
populations overall slightly but constantly decreasing
Methods

Measurement of post-fledging survival using telemetry

daily searches
21 days after fledging
Methods

Non-experimental broods

Cross-foster experiment

Nest family

Fledgling family

Brood 1

Brood 2

4 years
116 individuals
26 families

3 years
206 individuals
46 families (nest and fledgling families)
Questions

Non-experimental broods

Cross-foster experiment

Nest family

Brood 1

Brood 2

Fledging family

Between-family variance? Family effect?

Comparison of nest and fledgling family effects
Methods

Estimating daily survival probability using a Cormack-Jolly-Seber model

\[
\begin{align*}
\text{day} & \quad 1 & 2 & 3 & 4 & 5 & \cdots \\
\text{state} & \quad 1 & \phi & 1 & 1 & 0 & 0 \\
\text{observation} & \quad 1 & 0 & 1 & 0 & 0 \\
\end{align*}
\]

\( \phi \): apparent survival
\( \rho \): detection probability

\[
\begin{align*}
z_{it} & \sim \text{Bernoulli}(z_{it-1}\phi_{it}) \\
y_{it} & \sim \text{Bernoulli}(z_{it}\rho_{it})
\end{align*}
\]

Cormack (1964)
Jolly (1965)
Seber (1965)
Lebreton et al. (1992)
Methods

Effect of including a family random effect for survival probability

Likelihood
\[ z_{it} \sim \text{Bernoulli}(z_{it-1}\phi_{it}) \]
\[ y_{it} \sim \text{Bernoulli}(z_{it}\rho_{it}) \]

Linear predictors
\[ \text{logit}(\phi_{it}) = \beta_{\text{timeclass}[i]} + d_{\text{family}[i]} \]
\[ \text{logit}(\rho_{it}) = \alpha_{\text{year}[i]} + \gamma_{\text{year}[i]} \text{age}_i + q_{\text{family}} \]

Random effects
\[ d_{\text{family}} \sim \text{Norm}(0, \sigma_d) \]
\[ q_{\text{family}} \sim \text{Norm}(0, \sigma_q) \]

Prior distributions
\[ \alpha_{\text{year}}, \gamma_{\text{year}}, \beta_t \sim \text{Norm}(0, 5) \]
\[ \sigma_d, \sigma_q \sim \text{Student-t}(1, 0, 1)[0,) \]

Data
116 individuals of 26 families, non-experimental broods
Methods

Comparing effect of nest and fledgling family on survival

Likelihood
\[ z_{it} \sim \text{Bernoulli}(z_{it-1}\phi_{it}) \]
\[ y_{it} \sim \text{Bernoulli}(z_{it}\rho_{it}) \]

Linear predictors
\[ \text{logit}(\phi_{it}) = \beta_{\text{timeclass}[t]} + d_{\text{nest-family}[i]} + e_{\text{fledgling-family}[i]} \]
\[ \text{logit}(\rho_{it}) = \alpha_{\text{year}[i]} + \gamma_{\text{year}[i]}\text{age}_t + q_{\text{fledgling-family}[i]} \]

Random effects
\[ d_{\text{nest-family}} \sim \text{Norm}(0, \sigma_d) \]
\[ e_{\text{fledgling-family}} \sim \text{Norm}(0, \sigma_e) \]
\[ q_{\text{fledgling-family}} \sim \text{Norm}(0, \sigma_q) \]

Prior distributions
\[ \alpha_{\text{year}}, \gamma_{\text{year}}, \beta_t \sim \text{Norm}(0, 5) \]
\[ \sigma_d, \sigma_e, \sigma_q \sim \text{Student-t}(1,0,1)[0,) \]

Data
206 individuals of 46 families, cross-fostered broods
## Methods

<table>
<thead>
<tr>
<th>Model size</th>
<th>non-experimental broods</th>
<th>cross-fostered broods</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>without</td>
<td>with</td>
</tr>
<tr>
<td><strong>Parameters</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_{\text{time class}}$</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>$\alpha_{\text{year}}$</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>$\gamma_{\text{year}}$</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>$\sigma_d, \sigma_q$</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>$d_{\text{family}}$</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>$q_{\text{family}}$</td>
<td>26</td>
<td>26</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>42</td>
<td>69</td>
</tr>
<tr>
<td><strong>Data</strong></td>
<td>$116 \times 21 = 2436$</td>
<td>$206 \times 21 = 4326$</td>
</tr>
</tbody>
</table>

*future plans: capture-recapture data of size $20'000 \times 60 = 1'200'000$*
Methods

Fitting the model: Results for iteration 4000-8000 (~10 min)

**BUGS (M-H)**

10 lowest n_eff-values

4 – 97

**Stan (HMC)**

1050- 4676
Methods

Implementation in Stan (by Bob Carpenter and Daniel Lee)

```stan
// log likelihood
for (i in 1:I) {
  if (last[i]>0) {
    for (t in 1:last[i]) {
      if(t>1) increment_log_prob(log(phi[i, t-1]));
      if (y[i,t] == 1) increment_log_prob(log(p[i,t]));
      else increment_log_prob(log1m(p[i,t]));
    }
  }
  increment_log_prob(log(chi[i,last[i]+1]));
}
//y[i,t]
// 1101110100000...
// 1111011100000...
//prob. surviving t days
//prob. being captured
//prob. not being captured
//prob. not being captured
//between t+1 and end
//of study
```
Methods

Implementation in Stan (by Bob Carpenter and Daniel Lee)

//chi[i,k]: prob. that individual i is not resighted
between day t and the end of the study given it is alive at day t-1

transformed parameters{
...

chi[i,T+1] <- 1.0;
t <- T;
while (t > 1) {
  chi[i,t] <- (1 - phi[i,t-1]) + phi[i,t-1] * (1 - p[i,t]) * chi[i,t+1];
t <- t - 1;
}
chi[i,1] <- (1 - p[i,1]) * chi[i,2];
...
}

chi[i,k]: prob. that individual i is not resighted between day t and the end of the study given it is alive at day t-1
Methods

Implementation in Stan (by ecologists)

//logit-link function, linear predictor including random effects

transformed parameters{
  ...
  phi[i,t] <- inv_logit(b[timeclass[t]] + sigmaphi*fameffphi[family[i]]);
  ...
}

model{
  ...
  sigmaphi ~ student_t(1,0,1); // restricted to positive values
  for(g in 1:nfam){
    fameffphi[g]~normal(0, 1);
  }
  ...
}
Results & Discussion

Detection probability (p)

Non-experimental broods

- Day after fledging

Cross-fostered broods

- Nest- and fledgling family effects on $\phi$

no random effect on $\phi$

family effect on $\phi$

-> large between-family variance in detection probability ($\sigma_q = 0.82-0.85$)

-> inclusion of family random effect on $\phi$ has no influence on estimated detection probability
Results & Discussion

**Effect of including a family random effect for survival probability $\phi$**

fitted to 26 non-experimental broods (116 individuals)

$\rightarrow$ large between-family variance in survival ($\sigma_d = 1.50$)

*with family random effect*

*without family random effect*
Results & Discussion

Effect of including a family random effect for survival probability

Daily survival probability

Day after fledging

survival of a (hypothetical!) average family
average survival of all individuals that reached a specific age
Effect of including a family random effect for survival probability

Proportion that survived the first 3 weeks

\[ \text{Day after fledging} \]

Proportion alive

- Without family random effect: survivor curve of the population
- With family random effect: survivor curve of an average family

-> important for modeling population dynamics!
Results & Discussion

Effect of including a family random effect for survival probability

Proportion that survived the first 3 weeks

-> important for modeling population dynamics!

without family random effect: survivor curve of the population

with family random effect: survivor curve of an average family
Results & Discussion

Comparing effects of nest and fledgling family on survival

Nest family

Brood 1

Brood 2

Fledgling family

$\sigma_{\text{nest-family}} = 0.37 \ (95\% \text{ CrI: } 0.02, 0.80)$

$\sigma_{\text{fledgling-family}} = 0.31 \ (0.02, 0.70)$

$P(\sigma_{\text{nest-family}} > \sigma_{\text{fledgling-family}}) = 0.58$
Comparing effects of nest and fledgling family on survival

Nest family

- Brood 1
- Brood 2

2 weeks incubation
3 weeks nestlings

Fledgling family

- Fledging
- 3 weeks becoming independent
  (parental care 6-14 days)

Genetics, predation, ??...

Temperature
Grüebl et al. 2010

Food
Møller 2001

Parental care
Grüebl & Naef-Daenzer 2010

Predation
Naef-Daenzer et al. 2001

Weather, food, ??...

Results & Discussion
Comparing effects of nest and fledgling family on survival

- Nest family
  - Nestling period
    - ~70% survival

- Fledgling family
  - Fledging period
    - ~40% survival
Summary & Conclusions

• Stan is very useful for fitting hierarchical mark-recapture models

• Strong differences in survival between families

• Including a grouping structure of individuals changes the meaning of the survival estimates -> important for population modeling!

• The study stresses the importance of good breeding conditions for the Barn swallow population
Thanks

Thank you!

Stan core team for sharing Stan!

Photos: Martina Laida
Marc Tschudin
Ruedi Wüst

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