

# Random Effects Modelling with Capture-Recapture Data

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# Motivation

Why use capture-recapture?



Figure: Ringed Blackbird [7]

# The Cormack-Jolly-Seber Model

We will be using a standard model known as the Cormack-Jolly-Seber (CJS) model. For this we assume;

1. The population is only open to animals leaving,
2. All emigration during the study is permanent,
3. Sampling is instantaneous,
4. No marks are lost during the study.

# Cormack-Jolly-Seber Structure

The CJS model conditions on the first capture of an animal and includes parameters;

1.  $p_i$ , the probability of **recapture** in period  $i$ ,  $i = 2, \dots, K$
2.  $\phi_i$ , the probability of **apparent/local** survival between occasions  $i$  and  $i + 1$ ,  $i = 1, \dots, K - 1$

Occasion	1	2	3	4	5
Capture History	1	0	1	1	0

## Capture Histories to Probabilities

What is the probability of capture history  $\omega^* = \{1, 0, 1, 1, 0\}$ ?

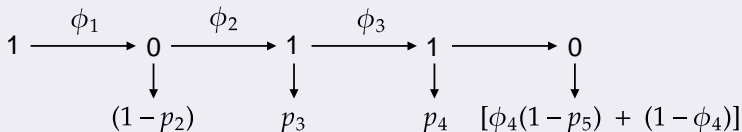


Figure: Order of Parameter Occurrence

Hence,

$$\mathbb{P}(\omega^*) = \phi_1(1 - p_2) \cdot \phi_2 p_3 \cdot \phi_3 p_4 \cdot (1 - \phi_4 p_5)$$

The final survival and capture probabilities are confounded.

# Likelihood Formation in MARK/RMark

The programme MARK formulates the likelihood as;

$$\mathcal{L}(\phi, \mathbf{p} \mid \text{Capture Histories}) = \prod_{\omega \in \Omega} [\mathbb{P}(\omega)]^{n_{\omega}}$$

where

- ▶  $\Omega$  is the set of possible capture histories,
- ▶  $n_{\omega}$  is the number of animals with capture history  $\omega$ ,
- ▶  $\mathbb{P}(\omega)$  is the probability of capture history  $\omega$ .

This is solved numerically by Newton-Rhapsom.

# Adding Covariates

We can model parameters as a function of environmental or individual covariates;

$$\log\left(\frac{\phi_i}{1 - \phi_i}\right) = \mathbf{x}_i^T \boldsymbol{\beta}$$

This can be substituted into the likelihood for numerical optimisation.

# Random Effects

Suppose variations over time are due only to natural variance. i.e.

$$\log\left(\frac{\phi_i}{1 - \phi_i}\right) = \beta_0 + \epsilon_i$$

where:

- ▶  $\beta_0$  is an unknown mean,
- ▶  $\epsilon_i \sim N(0, \sigma^2)$  with  $\sigma^2$  known as the process or environmental variance.

This random effect motivates a switch to Bayesian inference.



# Random Effects Illustration

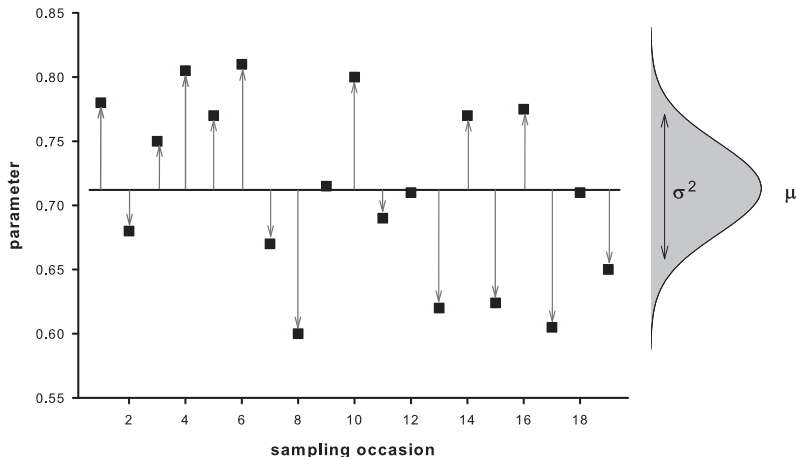


Figure: Process Variance of a Parameter from [1][p893]

## Random Effects Simulation

We simulated capture-recapture data with a population size  $N = 300$ , capture occasions  $K = 10$ , a constant recapture rate  $p = 0.5$  and survival rates such that;

$$\log\left(\frac{\phi_i}{1 - \phi_i}\right) = 1.4 + \epsilon_i$$

where;

►  $\epsilon_i \sim N(0, 0.5)$

We used MCMC to make posterior draws having used the uninformative priors from [5];

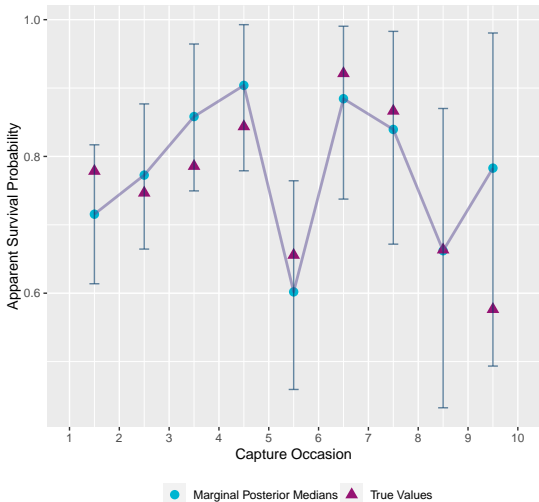
1.  $\beta_0 \sim \text{Un}(-5, 5)$
2.  $\sigma \sim \text{Un}(0, 3)$
3.  $\text{logit}(p) \sim N(0, 10^3)$

# MCMC Results

After 5000 burn in, a thinning rate of 5 applied to 100,000 posterior draws using WinBUGS, we have posterior estimates;

- ▶  $\hat{\beta}_0 = 1.402 (0.68, 2.6)$ ,
- ▶  $\hat{\sigma}^2 = 0.867 (0.068, 5.94)$ ,
- ▶  $\hat{p} = 0.467 (0.42, 0.51)$

# Apparent Survival Results



## Multiple Random Effects

Multiple random effects used by [3] for multiple colonies of Puffins in the North Atlantic. Extended by [5] to describe **multiple species** of birds on the Isle of May.



Figure: Puffins on the Isle of May

## Isle of May Birds

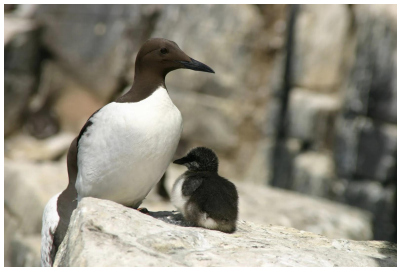


Figure: Two Guillemots [7]



Figure: Two Razorbills [7]

## Multi-Species Model

We set up likelihoods for each species using the CJS model and proceed to fit the model;

$$\log \left( \frac{\phi_{i,s}}{1 - \phi_{i,s}} \right) = f_s(\mathbf{x}_{i,s}^T) + \delta_i + \epsilon_{i,s}$$

where

- ▶  $\delta_i \sim N(0, \sigma_\delta^2)$ , constant across all species,
- ▶  $\epsilon_{i,s} \sim N(0, \sigma_s^2)$  exclusive to each species.
- ▶  $f_s(\mathbf{x}_{i,s}^T)$  is a unique covariate link function for each species.

# Measuring Synchrony

For each species, we define the **Intra-class correlation coefficient**;

$$ICC_s = \frac{\hat{\sigma}_\delta^2}{\hat{\sigma}_\delta^2 + \hat{\sigma}_s^2}$$

- ▶ Quantifies the environmental variance shared between species,
- ▶ High synchrony  $\Rightarrow ICC_s \rightarrow 1$ ,
- ▶ Low synchrony  $\Rightarrow ICC_s \rightarrow 0$



## What generates Synchrony?

We can fit a model for each species with and without covariates. This gives;

- ▶  $\hat{\sigma}_s^2(\text{res})$  the residual species variance from the covariate model
- ▶  $\hat{\sigma}_s^2(\text{total})$  the species variance from the intercept only model

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For each species we define;

$$C_s = 1 - \frac{\hat{\sigma}_s^2(\text{res})}{\hat{\sigma}_s^2(\text{total})}$$

- ▶ Covariates cause synchrony  $\Rightarrow C_s \rightarrow 1$
- ▶ Covariates do not synchrony  $\Rightarrow C_s \rightarrow 0$

## Isle of May results

The results of the study on Isle of May birds were;

- ▶ Puffins:  $ICC_1 = 0.894 (0.304, 0.999)$ , and  $C_{\text{puffins}} = 0.81$
- ▶ Guillemots:  $ICC_2 = 0.787 (0.350, 0.996)$ , and  $C_{\text{guillemots}} = 0.425$
- ▶ Razorbills:  $ICC_3 = 0.785 (0.205, 0.998)$ , and  $C_{\text{razorbills}} = 0.595$

This indicates common random effects can describe a large amount of variation between species.

# Benefits and Limitations

## Benefits:

- ▶ Detects links between populations,
- ▶ Describes expected variation and environmental effects,
- ▶ Combats parameter redundancy,
- ▶ Reduces parameter number

## Limitations:

- ▶ Requires data for multiple populations,
- ▶ Does not describe the synchrony source fully,
- ▶ Does not describe pairwise effects.

## Further Extensions

- ▶ Up to 4 random effects included in [2],
- ▶ Used for birth rates in an Integrated Population Model by [4],

There are further opportunities for;

- ▶ Different parameters and model types,
- ▶ Inclusion of predators or prey,
- ▶ Assessing synchrony over time

# Thank You!

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## References III



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## M-arrays

We can describe our CR-data using a series of sufficient statistics within an m-array. For example, given 5 sampling occasions;

Number Released	Number Recaptured				Never Recaptured
$R_1$	$m_{1,2}$	$m_{1,3}$	$m_{1,4}$	$m_{1,5}$	$m_{1,0}$
$R_2$		$m_{2,3}$	$m_{2,4}$	$m_{2,5}$	$m_{2,0}$
$R_3$			$m_{3,4}$	$m_{3,5}$	$m_{3,0}$
$R_4$				$m_{4,5}$	$m_{4,0}$

where;

- ▶  $R_i$  is the number captured in occasion  $i$  and subsequently released.
- ▶  $m_{i,j}$  is the number released from occasion  $i$  and first recaptured in period  $j$

Here,  $m_{i,0} = R_i - \sum_{j=i+1}^K m_{i,j}$

## M-array probabilities

For notation we use;

- ▶  $\phi_i$  - The probability of survival from period  $i$  to  $i + 1$
- ▶  $p_i$  - The probability of recapture in period  $i$  given the unit is alive

The probability of each  $m_{i,j}$  cell in the m-array is then defined as;

$$\nu_{ij} = \left\{ \prod_{k=i}^{j-1} \phi_k \prod_{k=i+1}^{j-1} (1 - p_k) \right\} p_j \quad \text{for } i < j$$

Similarly the probability of never being recaptured after first capture in  $i$  is;

$$\chi_i = 1 - \sum_{j=i+1}^T \nu_{ij}$$

## Multinomial distributions in M-arrays

To form a likelihood, we consider each row in the M-array as a multinomial distribution. For example;

$$\mathcal{L}_1(\phi, \mathbf{p} \mid R_1, \mathbf{m}_{1.}) = \binom{R_1}{m_{1,j}} \prod_{j=2}^5 \nu_{1j}^{m_{1,j}} \cdot \chi_1^{R_1 - \sum_{k=2}^5 m_{1,k}}$$

where we have the multinomial coefficient;

$$\binom{R_1}{m_{1,j}} = \frac{R_1!}{(m_{1,2})!(m_{1,3})!(m_{1,4})!(m_{1,5})!(R_1 - \sum_{j=2}^5 m_{1,j})!}$$

## Multinomial Likelihood

By combining the likelihoods of each row, we get the total likelihood;

$$\mathcal{L}(\phi, \mathbf{p} \mid \mathbf{R}_i, \mathbf{m}_{ij}) \propto \prod_{i=1}^{T-1} \prod_{j=i+1}^T \nu_{ij}^{m_{ij}} \cdot \chi_i^{R_i - \sum_{j=i+1}^T m_{ij}}$$

This gives us the full log-likelihood from which explicit MLEs may be found;

$$\log \mathcal{L}(\phi, \mathbf{p} \mid \mathbf{R}_i, \mathbf{m}_{ij}) = \sum_{i=1}^T \log(\mathcal{L}_i)$$

## Final Probability

- ▶ The least amount of data is in the final period,
- ▶  $\epsilon_9$  was the 6th percentile.

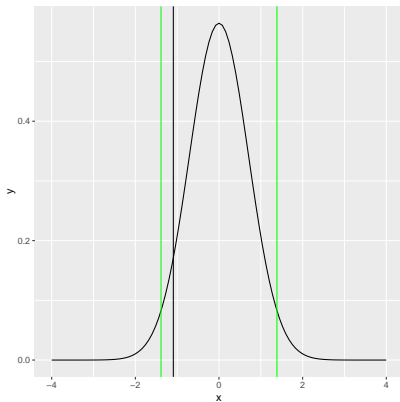


Figure: Central 95% of  $N(0,0.5)$  in Green

# Graph with MLEs

