Modelling bird populations in two regions of a small island using two-type discrete-time population-size-dependent branching processes

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Motivation

The black robin (*Petroica traversi*) is an endangered bird species inhabiting two distinct regions on Rangatira island: Top Bush (TB) - a exposed region with harsh conditions, and Woolshed Bush (WSB) - a lower, more fertile forest (Figure 3b). Such island populations are restricted by the number of suitable nesting spaces available in each region. A two-type population-size-dependent branching process is used to study the evolution of the female black robin population, with the goal of estimating the *carrying capacities* of TB and WSB, taking into account dispersal between the two sub-populations. A discrete-time model structure allows for the specification of the key events impacting population size: death, nesting, dispersal and giving birth.

Model structure

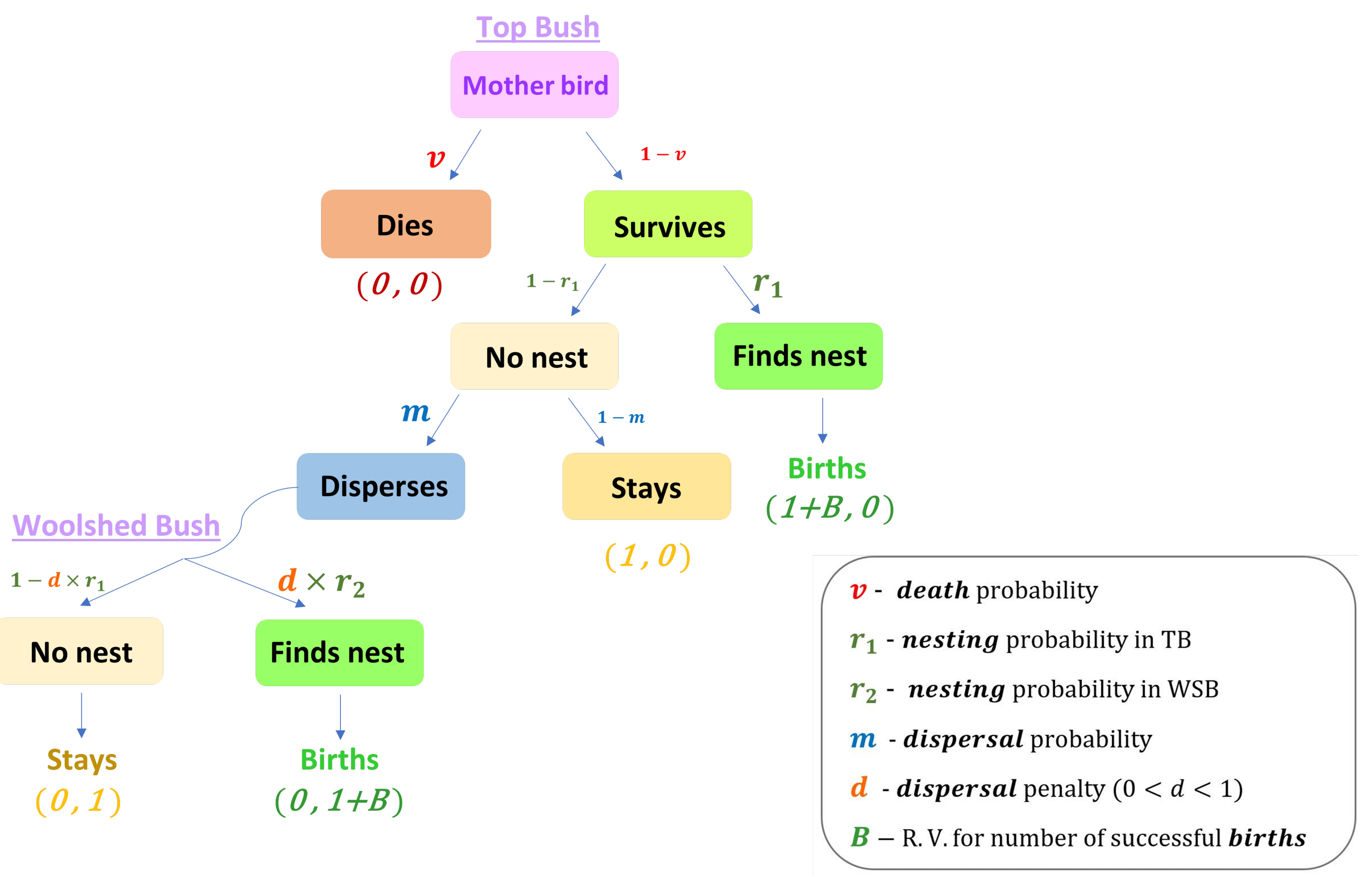


Figure 1. The sequence of 'decisions' and their probabilities describing the *offspring distribution*, O^{TB}, of a female bird from Top Bush - the number of birds (including itself) that it passes on to each region in the following year

Model types and parameters

The population-size dependence of the branching process is described by the nesting probabilities r_1 and r_2. The Beverton-Holt (B-H) and Ricker models were considered.

x – female population of Top Bush
y – female population of Woolshed Bush

$Model$	$r_1(x)$	$r_2(y)$
$B-H:$	$\frac{c_1}{x+c_1}$	$\frac{c_2}{y+c_2}$
$Ricker:$	$2^{-\frac{x}{c_1}}$	$2^{-\frac{y}{c_2}}$

⋆ r_1 and r_2 decrease as the sub-populations grow

⋆ When $x = c_1$ or $y = c_2$, Pr(nesting) = $\frac{1}{2}$

	Parameters	Assumptions
Fixed	B	$Bin(n=5, p=0.1988)$
	v	0.32
	d	$\frac{1}{3}$.[4]
Free	m	$0 < m < 1$
	c_1	
	c_2	

- Only c_1 and c_2 differ between regions

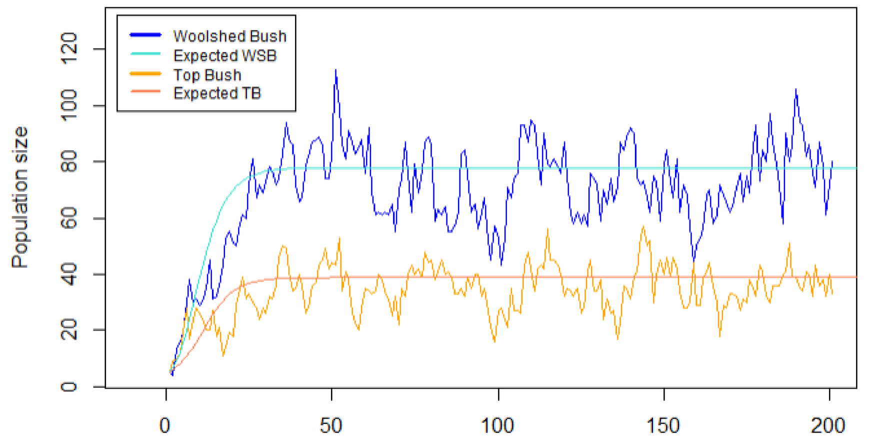
Equilibrium equations

For a set of parameter values, the carrying capacities of the sub-populations can be found by evaluating the population sizes for which the expected value from year to year remains stable.

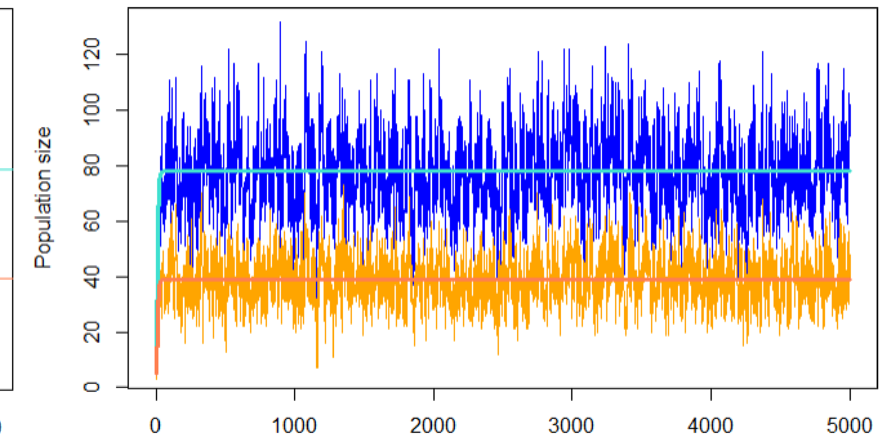
$$E(X_{n+1}|X_n = x, Y_n = y) = (1-v)\Big[\Big\{r_1(1+5p) + (1-r_1)(1-m)\Big\} + \Big\{(1-r_2)*m*(1+5pdr_1)\Big\}\Big] = x$$

$$E(Y_{n+1}|X_n = x, Y_n = y) = (1-v)\Big[\Big\{r_2(1+5p) + (1-r_2)(1-m)\Big\} + \Big\{(1-r_1)*m*(1+5pdr_2)\Big\}\Big] = y$$

Model simulation



(a) Population trajectories for WSB and TB over an initial 200 years.



(b) Populations oscillate about the carrying capacities for a long time.

Figure 2. Simulation of the Beverton-Holt model with $c_1 = 20, c_2 = 80, m = 0.3$. The resulting carrying capacities are $K_1 = 38.8, K_2 = 78.0$. Simulation algorithm adapted from [2]

Parameter estimation

Three methods of parameter estimation were explored:

1. **M.L.E. using a Central Limit Theorem approximation** for the sums of offspring distributions, $\sum_{j=1}^{x} \boldsymbol{O}_j^{TB}$ and $\sum_{k=1}^{y} \boldsymbol{O}_k^{WSB}$, as a Bivariate normal distribution.
   - $\boldsymbol{O}_i^{TB}$ and $\boldsymbol{O}_i^{WSB}$ are each bivariate random variables whose components represent the number of bird i's *offspring* that end up in TB and WSB, respectively.
   - The likelihood is formed by calculating the transition probabilities from populations (x_i, y_i) to (x_{i+1}, y_{i+1}):

$$P_{(x_i,y_i)\to(x_{i+1},y_{i+1})} := P\big((X_{n+1}, Y_{n+1}) = (x_{i+1}, y_{i+1})|(X_n, Y_n) = (x_i, y_i)\big) = P\big(\textstyle\sum_{j=1}^{x_i} \boldsymbol{O}_j^{TB} + \sum_{k=1}^{y_i} \boldsymbol{O}_k^{WSB} = (x_{i+1}, y_{i+1})\big)$$

2. **M.L.E. using the Probability Generating Function** of the total offspring distribution:

$$G(s_1, s_2) = [G_{TB}(s_1, s_2)]^x * [G_{WSB}(s_1, s_2)]^y$$

$$G_{TB}(s_1, s_2) = v + (1-v)(r_1(1-p+ps_1)^5 s_1 + (1-r_1)[(1-m)s_1 + m\{dr_2(1-p+ps_2)^5 s_2 + (1-dr_2)s_2\}])$$

⋆ G_{WSB} has a symmetrical form to G_{TB}

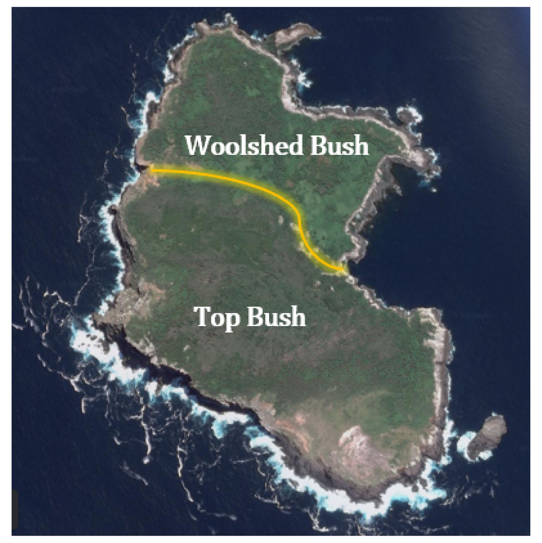
   - The transition probabilities can be extracted using the multidimensional inversion formula described in [1]

3. **Least Squares Estimation**, through minimising the sum of squares of model's expected deviations from the data, conditional on the populations of the preceding year:

$$SS := \sum_{i=0}^{n-1} \Big[(x_{i+1} - E(X_{i+1}|x_i, y_i))^2 + (y_{i+1} - E(Y_{i+1}|x_i, y_i))^2\Big]$$

- The Least Squares approach proved the most practical for computation.
- The C.L.T. approximation can be inaccurate for small populations
- The P.G.F. inversion is computationally demanding for large population sizes.

(a) Adult black robin. Photo: Dr Melanie Massaro



(b) Rangatira island. Source: @2022 Google

Figure 3

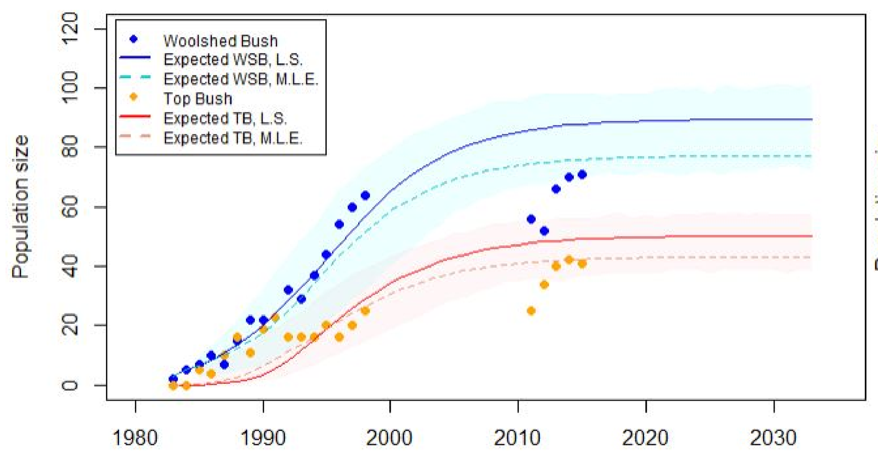
Estimates for black robin data

Parameter estimates

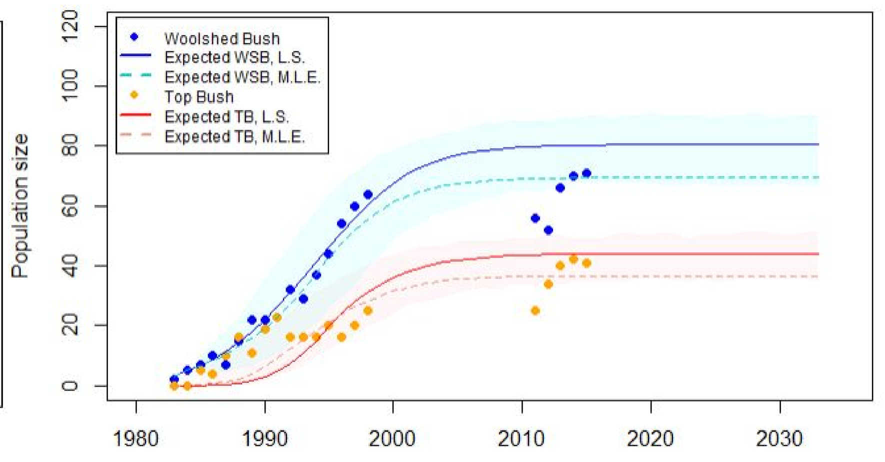
The Least Squares (L.S.) and C.L.T. approximation (M.L.E.) methods were implemented:

Model $Method$	c_1	c_2	m	K_1	K_2
B-H $L.S.$	27.1	89.7	0.358	50.3	89.6
Ricker $L.S.$	29.7	80.7	0.304	44.1	80.5
B-H $M.L.E.$	15.9	75.9	0.824	43.3	77.2
Ricker $M.L.E.$	18.4	70.1	0.811	36.7	69.5

- For the L.S. method, 60% prediction intervals were calculated by simulating 1000 trajectories using the estimated values for c_1, c_2 and m.



(a) **B-H model**, using L.S. and M.L.E.. Carrying capacities are $K_1 = 43.3$ and 50.3, $K_2 = 77.2$ and 89.6



(b) **Ricker model**, using L.S. and M.L.E.. Carrying capacities are $K_1 = 36.7$ and 44.1, $K_2 = 69.5$ and 80.5

Figure 4. Estimated trajectories of the populations in Top Bush and Woolshed Bush fitted to observed population numbers of female black robins. Data for 1983-1998 from [3]; data for 2011-2015 is unpublished

- Different triples of model parameters c_1, c_2 and m can produce identical estimates for the carrying capacities. As a result, the model may be poor at distinguishing between optimal triples of parameters for small datasets.
- Based on simulations, the Ricker model has the greater variance and Mean Square Error

Further extensions

- Estimate m separately and fit a model of two parameters c_1 and c_2
- Explore a population-size-dependent death rate $v(x, y)$
- Allow other parameters/the birth distribution to differ between the two regions e.g. v, B
- Expand m into breeding dispersal m_b and natal dispersal m_n, based on [3,4]
- Develop m into an 'informed' dispersal probability to model the information birds may have about which region has nesting space available.

References

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[2] Hautphenne, S. and Patch, B. (2021). Birth-and-death Processes in Python: The BirDePy Package.

[3] Kennedy, E. (2009). Extinction vulnerability in two small, chronically inbred populations of Chatham Island black robin Petroica traversi.

[4] Paris, D., Nicholls, A.O., Hall, A., Harvey, A., and Massaro, M. (2016). Female-biased dispersal in a spatially restricted endemic island bird. *Behav. Ecol. Sociobiol.*, 70:2061–2069.

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