Capture-Recapture Analyses of the Frog
*Leiopelma pakeka* on Motuara Island

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SUMMARY

This Research Report provides details of the MARK analysis appraising the
translocation of the frog *Leiopelma pakeka* from Maud Island to Motuara
Island in the Marlborough Sounds.

1 Introduction

Data from a capture-recapture study of the frog *Leiopelma pakeka* on Motuara Island are analysed using the mark-recapture analysis package MARK, found at

http://www.cnr.colostate.edu/~gwhite/mark/mark.htm
On 5 May 1997, 300 marked adult frogs from Maud Island were released on Motuara Island in Grid 1 (100 m²). Recaptures were recorded in 6 more samples (July and October 1997, January, March, July and October 1998). Because of few recaptures and assumed dispersal, another area, Grid 2 (surrounding Grid 1, approximately 100 m²) was added. Both grids were searched for a further 4 sessions, in August 1999, 2000, 2001 and 2002 respectively.

There are 342 individual frogs in the data set: the original 300 plus 42 new recruits. Of the original 300, 155 have been recaptured at least once.

The first analysis (Section 2) uses MARK for a recaptures-only multistrata model. This gives information about survival rates and capture probabilities over time and on the two grids, as well as probabilities of movement between the grids. The next analysis (Section 3) finds abundance estimates, derived from the MARK analysis.

2 Multistrata Models and Parameter Estimation

We used the MARK package to do a recaptures-only model with allowance for movement between grids (“Multistrata Recaptures Only” in MARK). This approach conditions on first capture (or release), and models survival rates ($\phi$), capture probabilities ($p$) and probability ($\psi$) of movement between strata (grids).

We firstly tried some basic models, and followed these with more specialised models taking account of release and initial dispersal.

2.1 Basic Multistrata Models

Multistrata models were introduced and developed by Nichols and Kendall (1995) and Kendall and Nichols (2002). A description of the use of multistrata models in MARK is found in the “MARKBOOK” Chapter 9: There and Back: Multistrata Models, available at

http://canuck.dnr.cornell.edu/misc/cmr/mark/docs/book/
The multistrata models allow for three types of parameter:

- **Survival rate** $\phi$, where $\phi_j$ is the probability that an animal alive at sample $j$ will survive until sample $j + 1$. Failure to “survive” means either death or emigration out of the study area. If the interval between the samples is $a$ years (e.g. $a = 0.5$ for a 6-month interval), the annual survival rate during the interval from sample $j$ to $j + 1$ is $\phi_j^a$.

- **Capture rate** $p$, where $p_j$ is the probability that an animal alive and in the sampled area at sample $j$ will be captured at $j$.

- **Transition rate** between strata (grids), $\psi$, where $\psi_j^{AB}$ is the probability an animal alive in stratum $A$ at sample $j$ will move to Stratum $B$ and be alive there at sample $j + 1$. We have two strata, $A = \text{Grid 1}$ and $B = \text{Grid 2}$. If the interval between the samples is $a$ years, the annual transition rate from $A$ to $B$ during the interval from sample $j$ to $j + 1$ is $(\psi_j^{AB})^a$.

Each of these parameters may depend on any or all of:

- Time ($t$) - i.e. variation from one session (trip) to the next
- Group ($g$) - whether part of the initial release ("R") or a new frog ("N")
- Stratum ($s$) or grid - the location of the frog at trip $j$.

**Notation**

Following Lebreton et al. (1992) we let $\phi_{tsgs}$ indicate a model in which survival depends on time (trip), group and stratum (grid), where the * indicates interactive effects. Simpler models may have the survival parameter(s) denoted by $\phi_{tsg}, \phi_{ts}, \phi_{gs}, \phi_t, \phi_g$ or $\phi_s$, while a $\phi$ with no subscript indicates that $\phi$ is constant over all times, groups and strata. Similar notation may be used for $p$ and $\psi$, so that, for example, the model

$$\{\phi_t, p_{tsg}, \psi_s\}$$
would have annual survival varying over time, capture probabilities varying by
time and by type of frog (whether released or a new recruit), and probabilities
for annual movement between strata being different in the two directions
(Grid 1 to 2, or 2 to 1) but constant over time and type of frog.

MARK model-fitting results

The capture-recapture package MARK was used to fit a full model or global
model

\[
\{ \phi_{tgs}, p_{tgs}, \psi_{tgs} \}
\]

in which time, group and stratum all affect each type of parameter. This
was followed by various reduced models which are special cases of the
full model with reduced numbers of parameters, as shown in models 7-11 in
Table 1.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>#Par</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2574.414</td>
<td>0.000</td>
<td>17</td>
<td>754.778</td>
</tr>
<tr>
<td>2</td>
<td>2576.341</td>
<td>1.927</td>
<td>18</td>
<td>754.594</td>
</tr>
<tr>
<td>3</td>
<td>2578.956</td>
<td>4.542</td>
<td>15</td>
<td>763.521</td>
</tr>
<tr>
<td>4</td>
<td>2581.003</td>
<td>6.589</td>
<td>16</td>
<td>763.470</td>
</tr>
<tr>
<td>5</td>
<td>2591.440</td>
<td>17.026</td>
<td>14</td>
<td>778.096</td>
</tr>
<tr>
<td>6</td>
<td>2592.731</td>
<td>18.317</td>
<td>15</td>
<td>777.296</td>
</tr>
<tr>
<td>7</td>
<td>2604.026</td>
<td>29.612</td>
<td>30</td>
<td>756.448</td>
</tr>
<tr>
<td>8</td>
<td>2604.071</td>
<td>29.657</td>
<td>21</td>
<td>775.955</td>
</tr>
<tr>
<td>9</td>
<td>2620.521</td>
<td>46.107</td>
<td>47</td>
<td>734.670</td>
</tr>
<tr>
<td>10</td>
<td>3505.906</td>
<td>931.492</td>
<td>46</td>
<td>1622.362</td>
</tr>
<tr>
<td>11</td>
<td>3517.921</td>
<td>943.507</td>
<td>59</td>
<td>1603.789</td>
</tr>
</tbody>
</table>

AIC_c, the Akaike Information Criterion adjusted for small samples, is a mea-
sure of lack of fit of the model to the data; models with a lower AIC_c are
preferred (Burnham and Anderson, 1998). From the full model (AIC_c =
3517.921), an AIC_c reduction of 12.015 was achieved by removing all group
(released versus new) effects (model \{ \phi_{tgs}, p_{tgs}, \psi_{tgs} \}, AIC_c = 3505.906).
This may indicate that there is no difference of survival, capture and movement rates between the new recruits and the released frogs, or possibly that the number of new recruits is still too low to be able to provide evidence of a difference.

After this, a very large reduction in AIC came from simplifying $p_{t+s}$ to $p_t$. Other simplifications led to two competing “best” models of this type with minimum $\text{AIC}_c = 2604.026, 2604.071$ respectively. These were the models

$$\{\phi_{t+s}, p_t, \psi_{s}\}, \text{ and } \{\phi_{t}, p_t, \psi_{s}\},$$

indicating survival and capture probability dependent on time only, and movement probability on stratum only (so that the annual probability of moving from Grid 1 to Grid 2 is different from the probability of moving from Grid 2 to Grid 1). There is possibly some evidence for survival varying by stratum (grid) as well.

The AIC criterion indicated that no further model simplification of a standard type (e.g. constant annual survival) was appropriate. These simpler models are not shown in the table.

### 2.2 Models Allowing for Initial Release

Typically newly released animals will have a short initial phase, possibly with a high “mortality” rate (dispersal or death), during which they disperse and seek suitable territories to occupy. Starting with model $\{\phi_{t}, p_t, \psi_{s}\}$ from the previous section, we modelled this initial process in two ways.

1. We set $\phi$ to one value for the first interval after release, and thereafter to a constant annual value; this was labelled $\phi_{t2}$ because $\phi$ varies over time but takes only two different values.

2. We give $\phi$ three different survival rates, one for the interval just after release, the second for the next interval, and the third for all subsequent survival rates (to allow for a somewhat longer initial dispersal phase). This has label $\phi_{t3}$.

These models (numbers 5 and 6 in Table 1) showed good reduction of $\text{AIC}_c$, with $\{\phi_{t2}, p_t, \psi_{s}\}$ having a marginally lower $\text{AIC}_c$ than $\{\phi_{t3}, p_t, \psi_{s}\}$. After
this simplification of $\phi$ in the effect of time, we tried re-including $g$, $s$ or $g \times s$ effects in $\phi$. This gave the four best models at the top of Table 1.

Overall the best model is

$$\{\phi_{12gs}, p_t, \psi_s\}$$

showing there are annual survival rate differences between grids and between different frog groups (released or new). In each combination of grid by frog type, annual survival rate is constant through time, except that the newly released frogs on Grid 1 have one survival rate in the first interval of two months immediately post-release, with constant annual survival rate thereafter. Our best model retained trip-to-trip variation in capture rates (unsurprisingly, as weather affects availability on the surface for capture), and a difference between annual migration rates in the two directions, Grid 1 to 2 or Grid 2 to 1.

The chosen model has the estimated annual survival rates shown in Table 2.

<table>
<thead>
<tr>
<th>Group</th>
<th>Stratum</th>
<th>Interval</th>
<th>$\hat{\phi}$</th>
<th>s.e.$(\hat{\phi})$</th>
<th>95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Released</td>
<td>Grid 1</td>
<td>Just after release</td>
<td>0.066</td>
<td>0.022</td>
<td>(0.034,0.123)</td>
</tr>
<tr>
<td>Released</td>
<td>Grid 1</td>
<td>After Trip 2</td>
<td>0.812</td>
<td>0.039</td>
<td>(0.725,0.877)</td>
</tr>
<tr>
<td>Released</td>
<td>Grid 2</td>
<td>After Trip 2</td>
<td>0.988</td>
<td>0.029</td>
<td>(0.441,1.000)</td>
</tr>
<tr>
<td>New</td>
<td>Grid 1</td>
<td>After Trip 2</td>
<td>0.581</td>
<td>0.140</td>
<td>(0.310,0.812)</td>
</tr>
<tr>
<td>New</td>
<td>Grid 2</td>
<td>After Trip 2</td>
<td>0.633</td>
<td>0.170</td>
<td>(0.292,0.878)</td>
</tr>
</tbody>
</table>

As non-survival includes both death and dispersal off the study area, this table indicates a brief period from May to July 1997 of high mortality and/or dispersal, followed by a constant, high survival rate. There is not yet much data on new frogs, so the confidence intervals for their survival rates are much wider. However, their survival rates so far look lower - perhaps an indication of juvenile dispersal to find new territories outside the grids. There is not yet enough data from Grid 2 to confirm if survival rates are lower than on Grid 1; however, if it is lower, it could indicate continuing dispersal further outwards, as Grid 2 surrounds Grid 1.
The movement parameters, \( \psi \), support the view that non-survival includes a large dispersal component. There is no evidence that movement between grids varies over time, but it does differ by direction, with estimated annual probability of movement from Grid 1 to Grid 2 clearly exceeding that in the opposite direction (Table 3).

Table 3: Estimated Annual Movement Rates

<table>
<thead>
<tr>
<th>Direction</th>
<th>( \hat{\phi} )</th>
<th>s.e.(( \hat{\phi} ))</th>
<th>95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grid 1 to Grid 2</td>
<td>0.177</td>
<td>0.018</td>
<td>(0.144,0.215)</td>
</tr>
<tr>
<td>Grid 2 to Grid 1</td>
<td>0.062</td>
<td>0.015</td>
<td>(0.038,0.100)</td>
</tr>
</tbody>
</table>

3 Abundance Estimates

Estimates of abundance \( N_j \) at the time of trip \( j \) (\( j = 2, 3, \ldots, 11 \)) may be found from the capture probability estimates, provided we assume random sampling. If \( n_j \) is the number caught, and the probability of capture is \( p_j \), then the binomial distribution gives

\[ \hat{\phi} = \frac{n_j}{N_j}. \]

We use \( \hat{\phi}_j \) from the capture-recapture analysis, and estimate \( N_j \) using

\[ \hat{N}_j = \frac{n_j}{\hat{\phi}_j} \]

A delta theorem (Seber, 1973) provides an approximate standard error for \( \hat{N}_j \), the population size at sample \( j \):

\[ s.e. \left( \hat{N}_j \right) = \frac{n_j}{\hat{\phi}_j^2} \times s.e. \left( \hat{\phi}_j \right). \]

A 95\% confidence interval for \( N_j \) is

\[ \left( \frac{n_j}{U}, \frac{n_j}{L} \right), \]

where \( L \) and \( U \) are the lower and upper limits respectively of the 95\% confidence interval for \( p_j \). Using the chosen model, we obtain the estimates for abundance, their standard errors and confidence intervals given in Table 4. These estimates are also shown as a graph in Figure 1.
Table 4: Estimated Abundances

<table>
<thead>
<tr>
<th>Trip</th>
<th>$\hat{N}_j$</th>
<th>s.e.($\hat{N}_j$)</th>
<th>95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>179</td>
<td>22.4</td>
<td>(142,231)</td>
</tr>
<tr>
<td>3</td>
<td>172</td>
<td>22.2</td>
<td>(135,224)</td>
</tr>
<tr>
<td>4</td>
<td>160</td>
<td>29.9</td>
<td>(113,234)</td>
</tr>
<tr>
<td>5</td>
<td>162</td>
<td>27.6</td>
<td>(118,229)</td>
</tr>
<tr>
<td>6</td>
<td>160</td>
<td>21.3</td>
<td>(125,210)</td>
</tr>
<tr>
<td>7</td>
<td>150</td>
<td>35.8</td>
<td>(95,242)</td>
</tr>
<tr>
<td>8</td>
<td>156</td>
<td>23.2</td>
<td>(119,212)</td>
</tr>
<tr>
<td>9</td>
<td>168</td>
<td>21.7</td>
<td>(133,220)</td>
</tr>
<tr>
<td>10</td>
<td>149</td>
<td>18.1</td>
<td>(120,193)</td>
</tr>
<tr>
<td>11</td>
<td>150</td>
<td>18.5</td>
<td>(121,197)</td>
</tr>
</tbody>
</table>

Figure 1: $N$ estimates with 95% confidence intervals
4 Discussion

All the evidence from this population is pointing to an initial dispersal phase after translocation, followed by a high constant annual survival rate after settlement. There is evidence of outward dispersal off the grids.

Good numbers of new recruits are appearing, and their lower apparent survival rate in these early stages is to be expected if they have an early phase of dispersal off the grid.

Figure 1 illustrates the levelling out of the estimates, where the losses of the frogs originally released are now being offset by the new recruits. We note that the Jolly-Seber type of estimation has a decrease in the last 1-3 $N_j$ estimates, caused by a lack of opportunity for recaptures at the end of the sampling, whether or not the population size is decreasing (Pollock et al. 1990). The very slight decrease in the last two $N$ estimates could well be due to this cause, and the estimates will increase after more recaptures of the new recruits are obtained.

In summary, this appears to be a most successful translocation.

5 References


