ANZIAM J. 52 (CTAC2010) pp.C206–C221, 2011

Modelling banding effect and tag loss for Little Penguins *Eudyptula minor*

L. A. Sidhu[1] E. A. Catchpole[2] P. Dann[3]

(Received 29 January 2011; revised 21 May 2011)

Abstract

We present a framework for using Matlab to analyse mark-recapture data arising from studies that use more than one type of tag to mark animals for later identification. We consider life history data collected for groups of single and double tagged animals. We include tag loss probabilities in the likelihood function, which removes a common source of bias in the estimation of survival rates. We show how the formation of appropriate summary statistics, and use of vectorisation, vastly improves speed in computing the likelihood function. We illustrate our methods by analysing seven years of mark-recapture data for 2483 Little Penguins *Eudyptula minor* on Phillip Island in south-eastern Australia.

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http://anziamj.austms.org.au/ojs/index.php/ANZIAMJ/article/view/3941 gives this article, Published June 6, 2011. ISSN 1446-8735.

1 Introduction

Individually numbered metal flipper bands have been used to mark Phillip Island penguins since 1968 [19], leading to numerous studies of these birds [19, 20, 21, 10, 11, 24]. Recent research on Little Penguins and several other penguin species found that banding has a negative effect [1, 9, 14, 12]. For Little Penguins, the adult survival rate is less for banded birds than for unbanded, transpondered birds [12]; for Adélie Penguins, banded birds have lower survival rates than unbanded birds until their first moult after banding [1], and use more energy when swimming [9]. For King Penguins, survival rates of banded chicks are lower than unbanded, transpondered chicks [14], and, significantly, banded and non-banded birds are affected differently by climate [22].

Many studies assume that tags are permanently retained by the animals [23, p. 196], but this can negatively bias the survival estimates [28, 4, 8]. Studies involving double tagged animals, which were pioneered by Beverton and Holt [3], allow the estimation of tag loss [2, 27, 15, 25], the effect of tag loss on the survival estimates [26], and the effect of the tags on survival [13, 18].

This paper illustrates the use of Matlab to study the effect of banding on the survival of Little Penguins. We derive novel expressions and give Matlab code for the likelihood. These are based on summary statistics, which minimise computation within the likelihood function, and which are in vectorisable form. Our use of two types of tag, bands and transponders, with some birds double tagged, allows us to estimate effects of banding and transpondering on survival rates, and the loss rates of both types.

2 Methods

2.1 The data

We analyse seven years of mark-recapture data for three groups of birds: one flipper banded group (the B group), one unbanded group that were injected with passive induction transponders (T group), and one group that were marked with both devices (BT group). All birds were marked as adults of unknown age, with approximately equal numbers in each group. Initial marking was carried out over four breeding seasons from January 1995 to January 1998, while the recaptures extended over a further three seasons, until January 2001. Dann et al. [12] report further details.

Selected fields of the records for three birds, each initially marked with a band and transponder, appear in Table 1. Bird 1 was marked in the first season of the study, and was seen again, still retaining both the band and the transponder, in the third and fifth seasons, and not seen again thereafter ('vanished'). Bird 2 was marked in the second season, then not seen again until the fifth season, by which time it had lost its transponder. This bird was seen again, still with its band, in the sixth and seventh seasons, so is known to have been alive at the end of the study. Bird 3 was marked in the third season, seen again, with transponder only retained, in the fourth and

Table 1: Some fields from the mark-recapture records for three birds.

BIRD	DATE	BAND	TRANSP	BD	WT	SX
	1995-01-10	85212	1D27AD2	122	1010	2
1	1997-02-11	85212	1D27AD2	0	0	2
	1998-10-27	85212	1D27AD2	0	900	2
	1995-11-29	91572	09697C3	142	1140	1
2	1999-01-13	91572	0	0	1150	1
	1999-11-24	91572	0	0	1220	1
	2001-01-03	91572	0	0	1250	1
	1996-11-20	91914	0F57111	125	1490	2
3	1997-12-16	0	0F57111	0	1150	2
	1998-01-15	0	0F57111	0	1150	2
	1999-01-06	0	0F57111	0	1190	2

BAND	Band number if fitted, 0 otherwise
TRANSP	Transponder number if fitted, 0 otherwise
BD	Bill depth measurement (on initial capture), 0 otherwise
WT	Weight: 0 = unknown
SX	Sex: 0 = unknown, 1 = male, 2 = female

fifth seasons, and not seen subsequently.

2.2 The likelihood

The data are summarized by 'penguin year', where penguin year t_j extends from 1 July in calendar year t_j to 30 June in calendar year t_{j+1}, so that birds encountered alive in the same breeding season are grouped together. The annual tag histories for the three birds of Table 1 appear in Table 2.

For convenience, instead of saying that a bird was recaptured at some stage during the penguin year t_j, we say the bird was recaptured 'at t_j', and think of t_j as the nominal census date during the jth breeding season. Similarly we

Table 2: Annual tag histories for the three birds of Table 1. The first digit in each entry is an indicator variable for the presence of a band, and the second for a transponder. For example '10' means that a bird was seen at some stage in that year with a band but no transponder, and '00' means that the bird was not seen in that year.

	Penguin Year						
Bird	1994	1995	1996	1997	1998	1999	2000
1	11	00	11	00	11	00	00
2	00	11	00	00	10	10	10
3	00	00	11	01	01	00	00

think of the survival and tag retention probabilities as extending from one census date to the next.

For penguin i over the period t_j to t_{j+1}, let $\phi_{i,j}$ be the survival probability, and $\rho_{B,i,j}$ and $\rho_{T,i,j}$ be the respective probabilities of retaining its band or transponder. Let $p_{i,j}$ be the probability (conditional on surviving and retaining a tag) it is recaptured at t_{j+1}.

The likelihood contributions, subsequent to marking, for the three birds from Tables 1 and 2 are as follows. For clarity, the i subscripts referring to the bird are omitted.

$$\begin{aligned}
&1.\quad L = \rho_{B,1}\cdots\rho_{B,4}\rho_{T,1}\cdots\rho_{T,4}\times\phi_1\phi_2\phi_3\phi_4\times(1-p_1)p_2(1-p_3)p_4\times\chi_{BT,5}\\
&2.\quad L = \rho_{B,2}\cdots\rho_{B,6}(1-\rho_{T,2}\rho_{T,3}\rho_{T,4})\times\phi_2\cdots\phi_6\times(1-p_2)(1-p_3)p_4p_5p_6\\
&3.\quad L = (1-\rho_{B,3})\rho_{T,3}\rho_{T,4}\times\phi_3\phi_4\times p_3p_4\times\chi_{T,5}
\end{aligned} \qquad (1)$$

where χ_B, χ_T and χ_{BT} are the 'vanishing probabilities',

$$\chi_{B,i,j} = \Pr(\text{not seen after } t_j \mid \text{seen alive with B and not T at } t_j),$$

with $\chi_{T,i,j}$ and $\chi_{BT,i,j}$ defined similarly, with 'B and not T' replaced by 'T and not B' and 'B and T' respectively. These are calculated recursively, starting with $\chi_{B,i,k} = \chi_{T,i,k} = \chi_{BT,i,k} = 1$, where k is the number of occasions (in our case $k = 7$), via the equations

$$\chi_{B,i,j} = (1 - \rho_{B,i,j}) + \rho_{B,i,j}(1 - \phi_{i,j}) + \rho_{B,i,j}\phi_{i,j}(1 - p_{i,j})\chi_{B,i,j+1},$$

with a similar equation for $\chi_{T,i,j}$, and

$$\begin{aligned}\chi_{BT,i,j} = {}& (1 - \rho_{B,i,j})(1 - \rho_{T,i,j}) + (\rho_{B,i,j} + \rho_{T,i,j} - \rho_{B,i,j}\rho_{T,i,j})(1 - \phi_{i,j}) \\ & + \rho_{B,i,j}(1 - \rho_{T,i,j})\phi_{i,j}(1 - p_{i,j})\chi_{B,i,j+1} \\ & + (1 - \rho_{B,i,j})\rho_{T,i,j}\phi_{i,j}(1 - p_{i,j})\chi_{T,i,j+1} \\ & + \rho_{B,i,j}\rho_{T,i,j}\phi_{i,j}(1 - p_{i,j})\chi_{BT,i,j+1}\,,\end{aligned}$$

for $c_i \leqslant j \leqslant k - 1$, where c_i is the initial marking occasion for bird i.

The overall likelihood comprises the product of the likelihoods for each bird. Model fitting then proceeds by maximising the likelihood. This is quite computer intensive, and computational time was reduced in two ways: by avoiding manipulation of the data within the likelihood function, and by expressing the likelihood in vectorised form. Both of these were achieved by first constructing a set of indicator (0/1) matrices from the data.

2.3 Sufficient statistics

The matrices W_B, Z_B and V_B (the 'ones', 'zeros' and 'vanishing' matrices, respectively) are defined for bird i in group B as

$$W_{B,i,j} = \begin{cases} 1 & \text{if seen at } t_{j+1}, \\ 0 & \text{otherwise,} \end{cases}$$

$$Z_{B,i,j} = \begin{cases} 1 & \text{if not seen at } t_{j+1} \text{ but seen later,} \\ 0 & \text{otherwise,} \end{cases}$$

for $c_i \leqslant j \leqslant k-1$, and

$$V_{B,i,j} = \begin{cases} 1 & \text{if seen at } t_j \text{ and not seen again,} \\ 0 & \text{otherwise,} \end{cases}$$

for $c_i \leqslant j \leqslant k$. In a similar manner, W_T, Z_T, V_T, W_{BT} and Z_{BT} (but not V_{BT}) are defined for birds in groups T and BT respectively.

Additional matrices W_1, W_2, Z_1, Z_2, V_{10}, V_{01}, V_{11}, VO_B and VO_T are required for the double tagged BT birds. Unlike W_{BT} and Z_{BT}, which use all of the recapture data, W_1 and Z_1 are calculated using only information from the bands—that is, encounters with birds that have lost their bands are ignored. Similarly, W_2 and Z_2 use only the information gained from the transponders.

The 'vanishing' matrices for the BT birds are defined as follows:

$$V_{10,i,j} = \begin{cases} 1 & \text{if seen with B and not T at } t_j\text{, and not seen again,} \\ 0 & \text{otherwise,} \end{cases}$$

for $c_i \leqslant j \leqslant k$. Similarly for V_{01} and V_{11}, with 'B and not T' replaced by 'T and not B' and 'B and T' respectively. Finally, to define the VO matrices, let

$$\nu_{B,i} = \begin{cases} j & \text{if band is seen for the last time at } t_j \text{ and is known to be lost,} \\ 0 & \text{if band is not known to be lost,} \end{cases}$$

$$o_{B,i} = \begin{cases} j & \text{if the 'other' tag (the transponder) is seen at } t_j \text{ for the first} \\ & \quad \text{time since the band was lost,} \\ 0 & \text{if band is not known to be lost,} \end{cases}$$

with ν_T and o_T defined similarly. A band is 'known to be lost' if the bird is encountered later with its transponder only. Then

$$VO_{B,i,j} = \begin{cases} 1 & \text{if } \nu_{B,i} > 0 \text{ and } o_{B,i} > 0 \text{ and } \nu_{B,i} \leqslant j \leqslant o_{B,i} - 1\,, \\ 0 & \text{otherwise,} \end{cases}$$

for $c_i \leqslant j \leqslant k-1$. In other words, VO_B indicates those occasions (if any) from when the band vanishes up until, but not including, the occasion when the other tag is next seen. VO_T is defined similarly.

2.4 Computing the likelihood

The likelihoods for the three groups are

$$\begin{aligned}
L_B &= \prod_{i=1}^{n_B}\left[\prod_{j=c_i}^{k-1}\{\rho_{B,i,j}\phi_{i,j}\}^{W_{B,i,j}+Z_{B,i,j}} {p_{i,j}}^{W_{B,i,j}}(1-p_{i,j})^{Z_{B,i,j}} {\chi_{B,i,j}}^{V_{B,i,j}}\right], \\
L_T &= \prod_{i=1}^{n_T}\left[\prod_{j=c_i}^{k-1}\{\rho_{T,i,j}\phi_{i,j}\}^{W_{T,i,j}+Z_{T,i,j}} {p_{i,j}}^{W_{T,i,j}}(1-p_{i,j})^{Z_{T,i,j}} {\chi_{T,i,j}}^{V_{T,i,j}}\right], \\
L_{BT} &= \prod_{i=1}^{n_{BT}}\left[\left\{\prod_{j=c_i}^{k-1}\rho_{B,i,j}^{W_{1,i,j}+Z_{1,i,j}}\rho_{T,i,j}^{W_{2,i,j}+Z_{2,i,j}}\phi_{i,j}^{W_{BT,i,j}+Z_{BT,i,j}}\times\right.\right. \\
&\qquad\left. {p_{i,j}}^{W_{BT,i,j}}(1-p_{i,j})^{Z_{BT,i,j}} {\chi_{B,i,j}}^{V_{10,i,j}} {\chi_{T,i,j}}^{V_{01,i,j}} {\chi_{BT,i,j}}^{V_{11,i,j}}\right\}\times \\
&\qquad\left.\left(1-\prod_{j=c_i}^{k-1}\rho_{B,i,j}^{VO_{B,i,j}}\right)\left(1-\prod_{j=c_i}^{k-1}\rho_{T,i,j}^{VO_{T,i,j}}\right)\right],
\end{aligned} \tag{2}$$

where n_B, n_T and n_{BT} denote the numbers of birds in the three groups. The overall likelihood is the product of these three. The derivations of L_B and L_T are the same as by Catchpole et al. [6], except that subscript i refers to bird i rather than cohort i. The likelihood for the double tagged birds, L_{BT}, is verified in a similar way. If there are no double tagged birds, then only the first or second of these expressions is required.

The lower limit $j = c_i$ in the above expressions can be replaced by $j = 1$, if we define the (i, j)th entry of each of the summary matrices to be zero for $j < c_i$. These expressions are then in ideal form for vectorisation. For example, the MATLAB code for producing the negative log-likelihood, $\ell_B = -\log(L_B)$, is

```
ell_i =  sum((W_B.*(log(RHO_B)+log(PHI)+log(P)))')'...
      +  sum((Z_B.*(log(RHO_B)+log(PHI)+log(1-P)))')'...
      +  sum((V_B.*log(CHI))')';
ell_B = - sum(ell_i);
```

Here RHO_B, PHI, P and CHI are matrices formed from the parameters $\rho_{B,i,j}$, $\phi_{i,j}$, $p_{i,j}$ and $\chi_{B,i,j}$ respectively—or rather from the subsets of these corresponding to the B group of birds. These matrices consist of unknown parameters, which are varied in order to maximise the likelihood. For example, a model in which the survival probabilities vary with time, and depend on an individual covariate y (such as bill depth at initial marking) is

$$\phi_{i,j} = \operatorname{ilogit}(\alpha_j + \beta y_i)$$

where $\operatorname{ilogit}(x) = 1/(1 + \exp(-x))$ is the inverse logistic transform, and $\alpha = (\alpha_1, \ldots, \alpha_k)$ and β are unknown parameters. This is coded as

```
PHI = ilogit( ones(n_B,1)*alpha' + beta*y*ones(1,k) );
```

If the covariate contains missing values (for example, when the animal's sex is unknown) then ell_B will evaluate as NaN. Instead we use

```
ell_B = - sum(ell_i(~isnan(ell_i)));
```

which simply omits any animal with a missing covariate. This approach can be used for individual covariates that also vary over time, such as the animal's weight in Table 1. Other possible approaches in this case include imputation of missing covariate values [16] or a conditional probability approach [7].

3 Results

3.1 Survival probability

Since there is frequently a tagging effect on bird survival [17, 12], and the loss of a transponder would most likely occur immediately after marking, the survival probability and the probabilities of retaining the tags are likely to depend on time elapsed since marking [12].

We consider separate annual survival probabilities and probabilities of retaining the tags in the first year after marking and in all subsequent years, since there is no biological justification for considering more elaborate models.

Results, reported in detail by Dann et al. [12], suggest that (a) the survival rate of banded birds is worse than that of unbanded birds; (b) marking does cause trauma to the penguins, since the survival of the birds in their first year after marking is reduced, regardless of the type of tag used; and (c) the annual probability of losing a band is around 0.4%, while the probability of losing a transponder is 4% in the first year after tagging and 1% in subsequent years.

3.2 Computation

Rather than using our vectorised code, based on expressions such as (2), for the likelihood, it is fairly simple to write code that examines the tag history for each bird, such as those given in Table 2, and computes the contribution of that bird to the likelihood, as in (1). The speed gain of our approach—that is, using summary statistics and vectorisation—depends on the data. For the present study of 2483 birds and seven mark-recapture occasions, our approach gives a threefold speed increase.

Much more dramatic speed increases are possible when there are no double tagged animals and models do not involve individual covariates: for example covariates such as sea temperature, which are purely time dependent. We then define cohorts, by season of initial marking, and redefine the summary statistics appearing in L_B or L_T in (2), by summing over each cohort. For example [6], row c and column j of the 'ones' matrix W represents the number of animals from cohort c seen at t_{j+1}. In an unpublished case study of $54,484$ animals with 42 mark-recapture occasions, our summary statistic form of the likelihood executes over 100 times faster than the bird-by-bird approach.

4 Conclusions

We have shown how to use Matlab to study the effect of banding on survival incorporating tag loss, using mark-recapture data for any species. We give expressions for the likelihood for single and double tagged animals. These expressions, which use pre-computation of summary statistics to avoid any manipulation of the data within the likelihood code, are in ideal form for vectorisation. This leads to greatly improved execution times in Matlab. We then used Matlab to maximize the likelihood and to estimate the model parameters. We omitted details of Matlab functions which automate the modelling process, with each model specifiable by a few simple lines of code.

We illustrated our methods via a banding effects study for Little Penguins on Phillip Island, Victoria. As reported previously [12], banding has a negative effect on the survival of adult Little Penguins, with banded birds having an annual survival probability 6% lower than their unbanded counterparts. Indeed, the survival probability in the first year after marking is considerably lower than in subsequent years for both banded and unbanded birds, suggesting that marking results in trauma for the bird, regardless of the type of tag used. As expected, transponders are more likely to be lost than bands, and both devices are more likely to be lost in the first year after marking than in subsequent years.

The summary statistic form of the likelihood given in the three equations (2) is for mark-recapture studies, when only live animals are recaptured. In mark-recapture recovery studies [6] there are also recoveries of dead animals, and then (2) needs to be extended. Details are not given here, but are available from the home page of the second author [5].

Acknowledgements We are indebted to staff of the Phillip Island Nature Park, particularly Ros Jessop and Leanne Renwick, and to members of the Penguin Study Group and the Australian Bird and Bat Banding Scheme for providing the data upon which this study is based.

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Author addresses

1. **L. A. Sidhu**, School of Physical, Environmental and Mathematical Sciences, University of New South Wales at the Australian Defence Force Academy, Australia.
   `mailto:L.Sidhu@adfa.edu.au`

2. **E. A. Catchpole**, School of Physical, Environmental and Mathematical Sciences, University of New South Wales at the Australian Defence Force Academy, AUSTRALIA.

3. **P. Dann**, Research Group, Phillip Island Nature Park, Cowes, Phillip Island, AUSTRALIA.