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USE OF THE JOLLY-SEBER MODEL TO DETECT VARIATION IN SURVIVAL, POPULATION SIZE AND RECRUITMENT OF BRIDLED HONEYEATERS AT PALUMA, QUEENSLAND

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Attention is drawn to deficiencies in some methods of estimating survival, including 'known to be alive' or 'calendar of captures' methods. The Jolly-Seber model is recommended for estimation of survival, population size and recruitment from capture-recapture data.

The Jolly-Seber model is described and used to analyse banding data collected from 184 Bridled Honeyeaters at Paluma, Queensland between 1982 and 1987. The average population size was 191 (±90) but population varied markedly with season. A large influx of birds was detected in the April/June quarter in 1984 and 1986 when populations were estimated at 750 and 322 birds respectively. The local population in non-influx seasons averaged 80 birds. Annual survival (interpreted as proportion of birds remaining in the population) averaged 0.751 (±0.256) overall with an expectation of further life of 3 years 6 months but survival also varied seasonally. In 1982–84 when most data were available annual survival averaged 0.672 during the period July–March (expectation of further life of 2 years 4 months) but dropped to 0.077 during the April–June influx period (expectation of further life of 4 months). Recruitment to the local population averaged 12 birds per quarter throughout the year but received a boost of several hundred birds during the April–June quarter in some years.

INTRODUCTION

Estimates of survival are available for comparatively few species of Australian birds and some of the estimation methods used are known to yield biased estimates of survival rates (Brownie *et al.* 1985). Rowley and Russell (1991) have summarized the methods and the resulting survival estimates for 35 Australian species. Yom Tov *et al.* (1992) introduced a new method to analyse a further 35 species, including 22 not included in Rowley and Russell's summary but their method underestimates survival.

It is appropriate to use life table methods to estimate survival when we are reasonably certain of the fate of all animals in our sample. The problems arise in the capture-recapture situation when we do not know the fate of missing animals.

Good methods are now available for estimating survival rates in open populations from capture-recapture data (Seber 1982; Pollock *et al.* 1990). Based on the Jolly-Seber model (Jolly 1965; Seber 1965), these methods also provide for the estimation of population size and recruitment.

Nevertheless several inappropriate methods are still being used to estimate average annual survival from capture-recapture studies. These suffer from a number of shortcomings, and problems arising from their use are worse if we wish to compare estimates from different places or species or estimates derived from different methods of analysis.

Nicholls and Woinarski (1988) have described three methods of estimating survival which are based on the number of birds known to be alive (KTBA). Unfortunately all three suffer from problems. Method 1 is a modification of Lack's (1954) method. Lack's method underestimates survival by an unknown but potentially large amount. Method 1 can be positively or negatively biased. Methods 2 and 3 provide overestimates of survival (again to an unknown degree). The latter methods (cited in Seber 1982, Pp. 252–253) were adapted from life-tables where the fate of all individuals is known and are no longer appropriate when this is not true. All these methods assume that survival is constant over the period of interest, which will rarely be the case.

Nichols and Pollock (1983) and Seber (1982, 1986) drew attention to the serious biases in such methods and recommended that they be dropped. Nichols and Pollock showed that the KTBA approach assumes that survival rates are equal to capture rates (i.e. all birds in the area of interest will be captured on every occasion) and this assumption is rarely true for capture-recapture data. KTBA methods are shown to estimate complicated functions of survival rates and probabilities of capture. The Jolly-Seber method was demonstrated to be superior to the KTBA estimates and Nichols (1986) showed that KTBA estimates were especially inappropriate for use in comparative studies.

The Jolly-Seber model, derived independently by Jolly (1965) and Seber (1965), has been found to be a useful model for populations in which there is death, permanent migration and recruitment. These are often referred to as *open* populations. A population which remains unchanged during the period of investigation (i.e. the effects of mortality, recruitment and migration are negligible) is called a *closed* population. In populations where migration is present, recruitment includes both birth and immigration, and mortality includes both death and permanent emigration.

The original Jolly-Seber model distinguished between the probability of an animal surviving and its probability of being caught. It allows both quantities to vary between sampling periods and it has since been extended in a number of directions. It can include tags recovered from dead animals (Buckland 1980) and the case where different cohorts have different catchabilities (Buckland 1982; Buckland, Rowley and Williams 1983). It can allow for survival varying with age class (Pollock 1981) and for tag loss and trap shyness. These and other refinements are mentioned by Seber (1986) and Nicholls (1992).

Although used widely by mammalogists and by overseas ornithologists the Jolly-Seber method has been largely ignored by Australian ornithologists. Given its advantages over other methods of estimating survival it has been thought worthwhile to describe the method and give an example of its use with Australian data.

In this paper the Jolly-Seber method is used to estimate survival, population size and recruitment from capture-recapture data covering the period 1982 to 1987 for a population of Bridled Honeyeaters at Paluma, Queensland. Estimates are then compared between years and between seasons.

METHODS

Study Site

The study site was located 5 km west of Paluma (19°0'S, 146°9'E) and about 80 km north-west of Townsville in Queensland. The Paluma Range rises to 1 050 m above sea level and rainfall supports an area of tropical rainforest. Wet sclerophyll forest dominated by Flooded Gum *(Eucalyptus grandis)* occurs on the rainforest margin. Within the wet sclerophyll forest the understorey consists of rainforest plants or wet sclerophyll species.

The climate is tropical, with high rainfall, high humidity and warm to hot temperatures. Mean annual rainfall for Paluma is 2 665 mm with most rain falling between January and March.

Birds were trapped in mist nets which were opened for a minimum of 6 hours from 6.30 a.m. on each occasion. Banding was carried out once a month from June 1982 to December 1984, then sporadically thereafter up to May 1987.

The data analysed consist of the capture histories of 184 Bridled Honeyeaters caught at the study site between June 1982 and May 1987. It was not possible to detect whether birds were juvenile or adult, and only 14 of the birds could be sexed (9 females, 5 males) so that age and sex have been ignored in the analysis.

Data were initially consolidated into annual totals based on calendar years. This time span is appropriate for birds of the wet tropics where breeding, although it can occur in all months, is frequently initiated by the onset of the wet season in midsummer. To allow calculation of seasonal effects the data were also analysed as quarterly totals for January–March, April–June, July–September and October–December for the years 1982 to 1986.

Statistical Analysis

Estimates of the parameters were obtained using the Jolly-Seber method described below which follows Seber (1982). All measures of variation are standard errors which were calculated from the formula given by Pollock *et al.* (1990), using the program JOLLY (Brownie *et al.* 1985; Pollock *et al.* 1990).

It is assumed that at the first time of banding there is a population of N_1 birds (of a particular species or group) present in the area of interest. At the second point in time the number of birds present will be N_2. Between the two times we assume that B_1 birds have been recruited to the population, by birth or immigration, and that L_1 birds have been lost through death or emigration. We shall call the proportion of birds lost the mortality rate (d_1), although this will include losses through emigration as well as death. The number L_1 of birds lost between the two times is equal to d_1N_1. If we call the survival S_1, then mortality $(d_1) = 1 - S_1$. We can now say that the number of birds present at time 2 is equal to the number present at time 1, plus birds recruited to the population through birth or immigration, minus birds lost from the population through death or emigration,

i.e. $N_2 = N_1 + B_1 - (1 - S_1)N_1$

This can be generalized so that, for each pair of consecutive times, say time i and time $i + 1$,

$N_{i+1} = N_i + B_i - (1 - S_i)N_i$.

The objective is to estimate population size (N_i), recruitment (B_i) and survival (S_i), and their corresponding standard errors, for each time period.

We assume:

(1) every bird in the population has the same probability of being caught in a given sample, provided it is alive and in the population at that time;
(2) every bird in the population has the same probability of surviving from one sampling period to the next;
(3) every bird captured in the population has the same probability of being returned to the population;
(4) birds do not lose bands and all bands are correctly reported on recovery;
(5) sampling time is small in relation to total time;
(6) losses to the population from emigration or death are permanent.

Notation is summarized in Table 1. The values m_i, r_i, and z_i can be calculated from the tabulation of m_{ij}, i.e. the number caught in the ith sample next captured in the jth sample. The values m_i are the column totals, r_i are the row totals and z_i are the totals of the numbers in the rectangular block to the right of column i and above row i where $i = j$. Formulae for M_i, S_i, N_i, B_i and p_i are as follows:

Calculation of number of birds marked (M_i and M^*_i)

$$M_i = \frac{R_i + 1}{r_i + 1} \cdot z_i + m_i \; (i = 2, 3, \ldots, s - 1)$$

$$M^*_i = \frac{R_i}{r_i} \cdot z_i + m_i \; (i = 2, 3, \ldots, s - 1)$$

Calculation of survival (S_1 and S_i)

$$S_1 = \frac{M_2}{R_1}$$

$$S_i = \frac{M_{i+1}}{R_i + M^*_i - m_i} \quad (i = 2, 3, \ldots, s - 2)$$

Calculation of population size (N_i)

$$N_i = M_i \cdot \frac{n_i + 1}{m_i + 1} \; (i = 2, 3, \ldots, s - 1).$$

Calculation of recruitment (B_i)

$$B_i = N_{i+1} - S_i (N_i - n_i + R_i), \; (i = 2, 3, \ldots, s - 2)$$

Calculation of probability of capture (p_i).

$$p_i = \frac{m_i}{M_i} \; (i = 2, 3, \ldots, s - 1)$$

Examples of calculations are given in Table 4.

The expected life-span after capture, E_L, can be calculated from survival (S_i) using the formula

$$E_L = -1/\log_e (S_i).$$

TABLE 1

Summary of notation.

s	=	number of sampling periods,
p_i	=	probability of a bird being caught in the ith sample,
d_i	=	probability of a bird leaving the population between the ith and $(i+1)$th sample,
S_i	=	$1-d_i$ = probability of a bird surviving from the ith to the $(i+1)$th sample,
N_i	=	total number of birds in the population just before time i,
M_i	=	total number of banded birds in the population just before time i,
M^*_i	=	total number of banded birds in the population just before time i (ignoring possible bias for small numbers),
n_i	=	number of birds caught in the ith sample,
m_i	=	number of banded birds caught in the ith sample,
m_{ij}	=	number caught in the ith sample next captured in the jth,
R_i	=	number of banded birds released after the ith sample,
r_i	=	number of banded birds from the release of R_i birds which are later recaptured,
z_i	=	number of different birds caught before the ith sample which are not caught in the ith sample but are caught later,
B_i	=	number of new birds joining the population in the interval from time t_i to time t_{i+1} which are still alive and in the population at time t_{i+1},
L_i	=	number of birds leaving the population in the interval from time t_i to time t_{i+1},
E_L	=	expectation of life after capture
$\log_e (S_i)$	=	logarithm to base e of survival (S_i).

Known variables are: n_i, m_i, m_{ij}, R_i, r_i, z_i.
Unknown values are: p_i, S_i, N_i, M_i, B_i.
It is assumed: $m_1 = r_s = z_1 = z_s = M_1 = 0$ and $B_0 = N_1$.

Since survival has been defined in terms of birds remaining in the population, expected lifespan can be thought of as the expected time birds are present before they leave or die. For survival values greater than 0.1 the approximation $E_i = (2 - d)/2d$, where d is mortality, is sometimes used. However, for survival values below 0.1 the approximation no longer holds and the log formula is appropriate.

Estimates for annual and quarterly survival are not comparable. To transform the quarterly survival estimates to annual estimates it is necessary to take the log of S(quarterly), divide by 3, multiply by 12, and take the antilog.

RESULTS

Capture histories for individual birds can be represented by a series of zeros and ones, representing not captured or captured, respectively, in a particular period. Some typical capture histories are shown in Table 2. Bird 1 was captured in the first period and never seen again. Bird 2 was captured in the first period, retrapped in

TABLE 2

Capture histories for four hypothetical birds. 1 = captured, 0 = not captured.

Bird	Capture period 1	2	3	4	5
1	1	0	0	0	0
2	1	1	0	0	0
3	1	1	1	0	1
4	0	1	0	0	0

period 2 but not caught again. Bird 3 was caught in periods 1, 2, 3 and 5. Bird 4 was caught in period 2 but not recaptured.

As many birds may have the same capture history, such information can be compressed by introducing a weighting variable, or count, beside each type of capture history to indicate how many birds are represented with that history. The full set of annual capture histories for the Bridled Honeyeaters is given in Table 3.

TABLE 3

Capture-histories for Bridled Honeyeaters at Paluma. 1 = captured, 0 = not captured.

Capture period 1	2	3	4	5	6	Number of birds
1	1	1	1	0	0	2
1	1	1	0	0	1	1
1	1	1	0	0	0	3
1	1	0	1	1	0	1
1	1	0	0	0	1	2
1	1	0	0	0	0	6
1	0	1	1	0	0	2
1	0	1	0	0	0	2
1	0	0	0	0	1	1
1	0	0	0	0	0	23
0	1	1	1	1	0	1
0	1	1	1	0	0	1
0	1	1	0	0	1	1
0	1	1	0	0	0	6
0	1	0	0	1	0	1
0	1	0	0	0	1	1
0	1	0	0	0	0	27
0	0	1	1	0	1	1
0	0	1	1	0	0	4
0	0	1	0	1	1	1
0	0	1	0	1	0	1
0	0	1	0	0	1	1
0	0	1	0	0	0	53
0	0	0	1	1	0	1
0	0	0	1	0	0	15
0	0	0	0	1	0	16
0	0	0	0	0	1	10

The number of birds caught in each year can be calculated from the total of the weights in rows with a 1 in the appropriate year column. The complete set of yearly totals for captures are given in Table 4.

The capture histories are also needed to tabulate the pairs of successive captures, m_{ij}. For instance the number of birds that were caught in year 1, next in year 2, is 15. These are the birds that contribute to the capture combination (1,2). Birds with the capture history 1 1 1 0 1 contribute towards 3 separate cells, namely the (1,2), (2,3) and (3,5) combinations. The full tabulation of 'this and the next' captures on an annual basis, designated m_{ij}, is shown in the body of Table 4.

TABLE 4

Tabulation of m_{ij}, the number caught in the *i*th sample next caught in the *j*th sample of Bridled Honeyeaters at Paluma.

j:	1	2	3	4	5	6	
n_j:	43	53	80	28	22	19	
R_j:	43	53	80	28	22	19	
i							r_i
1		15	4	0	0	1	20
2			15	1	1	3	20
3				11	2	3	16
4					3	1	4
5						1	1
m_j:		15	19	12	6	9	
z_j:		5	6	10	8		

$r_1 = 15 + 4 + 1 = 20$, $r_2 = 15 + 1 + 1 + 3 = 20$.

$r_3 = 11 + 2 + 3 = 16$.

$m_2 = 15$, $m_3 = 4 + 15 = 19$.

$z_1 = 0$, $z_2 = 4 + 1 = 5$, $z_3 = 1 + 1 + 1 + 3 = 6$.

$$M_2 = \frac{53 + 1}{20 + 1} .5 + 15 = 27.86$$

$$M^*_2 = \frac{53}{20} .5 + 15 = 28.25$$

$$N_2 = 27.86. \quad \frac{53 + 1}{15 + 1} = 94.03$$

$$S_2 = \frac{47.59}{28.25 - 15 + 53} = 0.718$$

$$B_2 = 192.73 - 0.718\,(94.02 - 53 + 53) = 125.20$$

$$P_2 = \frac{15}{27.86} = 0.5384$$

TABLE 5

Annual population estimates and standard errors of estimates for the Bridled Honeyeater population at Paluma from 1982 to 1986.

Year	*i*	Number banded M_i	Survival S_i	Population size N_i	Recruitment B_i	Probability of capture P_i	SE (survival) $se[S_i]$
1982	1	0.00	0.648	—	—	—	0.140
1983	2	27.86	0.718	94.02	125.20	0.539	0.204
1984	3	47.59	0.636	192.73	33.51	0.399	0.310
1985	4	70.00	1.000	156.15	168.85	0.171	0.100
1986	5	98.00	—	322.00	—	0.061	—
Mean		60.86	0.751	191.23	108.18	0.293	0.259

TABLE 6

Seasonal population estimates for the Bridled Honeyeater population at Paluma for 3-month periods from 1982 to 1985.

Season	*i*	Number banded M_i	Survival S_i	Population size N_i	Recruitment B_i	Probability of capture P_i	SE (survival) $se[S_i]$
Apr.–June 1982	1	0.00	0.456	—	—	—	0.177
July–Sept. 1982	2	8.67	0.664	57.78	2.92	0.231	0.150
Oct.–Dec. 1982	3	17.20	1.000	41.28	35.56	0.233	0.359
Jan.–Mar. 1983	4	32.00	0.919	89.60	14.01	0.125	0.294
Apr.–June 1983	5	39.25	0.656	96.34	36.02	0.255	0.256
July–Sept. 1983	6	37.20	0.841	99.20	0.00	0.054	0.308
Oct.–Dec. 1983	7	38.27	0.877	63.79	20.43	0.287	0.316
Jan.–Mar. 1984	8	41.67	1.000	76.39	592.49	0.120	0.899
Apr.–June 1984	9	102.90	0.231	749.70	0.00	0.058	0.080
July–Sept. 1984	10	35.87	1.000	49.33	18.83	0.195	0.398
Oct.–Dec. 1984	11	51.33	0.680	82.13	0.00	0.273	—
Oct.–Dec. 1985	12	43.00	1.000	69.30	241.15	0.081	1.000
Oct.–Dec. 1986	13	63.00	0.167	322.00	0.00	0.061	—
Mean		48.62	—	137.15	58.55	0.142	—

Population variables estimated on an annual basis are summarized in Table 5. Seasonal population variables for the years 1982 to 1985 are given in Table 6.

Survival and expected life-span

A summary of survival estimates and expected life spans, all on an annual basis, is given in Table 7.

The overall average survival rate of Bridled Honeyeaters at Paluma was 0.751 (± 0.256) and survival increased somewhat over the four years (Table 5). The average life span was 3 years 6 months. However survival varied markedly between seasons. Calculated in annual terms, survival was lowest in the April–June quarter, with survival rates of 0.0433 in 1982, 0.1850 in 1983 and 0.0028 in 1984, with corresponding life expectancies of 4, 7 and 2 months respectively. Survival was higher in other seasons, up to 1.0 in the December 1982, and March and September 1984 quarters, but it varied from year to year.

Over the period 1982–84 for which most data was available, the mean survival rate for the March-June quarter was 0.077, with a corresponding life expectancy of 4 months. The mean survival for the other nine months was 0.671 with a corresponding life expectancy of 2 years 5 months. These survival figures are all expressed on an annual basis.

TABLE 7

Annual survival rate and expected life-span (years) of Bridled Honeyeaters for seasons during 1982–1985.

Period	Annual survival rate	Expected life-span (years)
Apr.–June 1982	0.0433	0.32
July–Sept. 1982	0.1943	0.61
Oct.–Dec. 1982	1.0000	—
1982	0.6478	2.30
Jan.–Mar. 1983	0.7130	2.96
Apr.–June 1983	0.1850	0.59
July–Sept. 1983	0.5007	1.45
Oct.–Dec. 1983	0.5921	1.91
1983	0.7183	3.00
Jan.–Mar. 1984	1.0000	—
Apr.–June 1984	0.0028	0.17
July–Sept. 1984	1.0000	—
Oct.–Dec. 1984	0.2136	0.65
1984	0.6364	2.21
Jan.–Dec. 1985	1.0000	—
1985	1.0000	—

Population size

The average population size of Bridled Honeyeaters during the study was 191 (± 90) birds, but population tended to increase as the study progressed, from 94 in 1983 to 322 in 1986. However, there were large increases in population in June of 1984 and 1986 where sizes were 750 and 322 respectively. The local population in non-influx seasons averaged 80 birds.

Recruitment

Annual recruitment figures were misleading as recruitment varied markedly with season. Large influxes were measured following the March 1984 and December 1985 quarters, of 592 and 241 birds respectively. At other times recruitment averaged 12 birds per quarter.

Probability of capture

Probability of catching a bird in any one year decreased as the study progressed, from 0.54 (± 0.13) in 1983 to 0.06 (± 0.06) in 1986. On a quarterly basis, the probability of capture was correspondingly lower, averaging 0.14 per season.

DISCUSSION

Few estimates of survival or local population size are available for nomadic or migrant species in Australia and demographic estimates for tropical species are particularly sparse. The availability of the Paluma data set prompted this attempt to estimate some population parameters for Bridled Honeyeaters, a species which has not been widely studied to date.

The results of this study should be interpreted with caution as sample sizes were small and standard errors of estimates were correspondingly large. Seber (1982) recommends that m_i and z_i be greater than 10 for satisfactory estimates to be achieved and numbers were somewhat below this level for quarterly periods.

Nevertheless the results clearly demonstrate the presence of passage birds between March and June during the study. The survival rate drops in the April-June quarter of each year with birds remaining in the population for periods of 2 to 7 months. High recruitment levels between the March and June quarters led to population sizes of several hundred birds in the April-June quarter in 1984 and 1986.

These results suggest that there is a local population of between 50 and 100 Bridled Honeyeaters present in the study area throughout the year. The population is sometimes augmented by an influx of birds on passage during the April-June quarter.

It should be noted that overall averages of survival, population size and recruitment can mask possible variation. If there is reason to suspect seasonal or annual variation over the period of study, overall averages will be biased and can hide important variations in the variables under study.

Thus the average survival in non-influx months in 1982–84 was 0.672 with an average expected life span of 2 years 4 months, while the corresponding influx season (April-June) figures were 0.077 and 4 months respectively.

The Jolly-Seber approach has important advantages in this regard. It allows us to model variation from period to period. It also uses information from each pair of successive captures from every bird, regardless of when it was first caught, thus making maximum use of the information available. It further distinguishes between those marked animals caught at time *i* and those not caught at time *i* but caught later. This enables us to estimate the probability of capture, which in this case ranged from 0.539 in 1982 to 0.061 in 1986 as the rate of visits decreased. These values demonstrate how the assumption of complete captures, required by the KTBA methods, is violated in this case.

The Jolly-Seber method also allows us to calculate standard errors and confidence intervals so that we can use powerful statistical methods based on probability theory, assess the value of our estimates, and decide whether or not they remain constant or change over time or from place to place.

It is worth making several points about the model assumptions. First, assumptions 1, 2 and 6 are testable using goodness-of-fit tests (Pollock *et al.* 1985; Brownie *et al.* 1986). Second, it should be noted that some estimators are not sensitive to deviations from particular assumptions, whereas others are. For example differing capture probabilities (deviation from assumption 1) can lead to fairly large biases in estimates of population size but affect survival very little (Carothers 1973, 1979; Nichols and Pollock 1983). Permanent trap response (e.g. net shyness) likewise results in biased estimates of population size but produces no bias in survival estimates (Nichols *et al.* 1984). Finally, Jolly-Seber estimates perform better than KTBA estimators even when underlying assumptions are not met exactly. For instance, the commonly used estimator of survival as the proportion of birds seen in any one year after year *i* performs much worse than the Jolly-Seber survival estimator, even when capture probabilities differ (Nichols and Pollock 1983).

Seber (1982, 1986) and Nicholls (1992) have recommended that approaches based on 'minimum number known alive' or 'calendar of captures' methods be dropped and replaced by approaches based on models like Jolly-Seber.

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