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CHANGES IN THE ABUNDANCE OF SILVEREYES IN A CENTRAL VICTORIAN VINEYARD DURING THE GRAPE RIPENING PERIOD

THOMAS C. BURTON

Division of Biological and Chemical Science, La Trobe University, Bendigo, P.O. Box 199, Bendigo, Victoria 3550

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Population parameters of Silvereyes in Chateau Leamon, a vineyard in central Victoria, were estimated on the basis of capture-recapture methods employed during the grape ripening seasons 1988–1993, using the Jolly-Seber model, the Peterson model and a model of Seber. In the context of low survival rates, results from the Jolly-Seber model were erratic, and as short seasons yielded few data, the Jolly-Seber model was too wasteful. Populations generally rose during a season, despite the loss of many Silvereyes from the population, indicating that birds moved into the vineyard during the season. Annual survival rates were very low (mean 25% p.a.). The Tasmanian subspecies typically arrived between late March and early April, and formed up to 26% of the total Silvereye population. Few Silvereyes banded in the vineyard were recovered elsewhere.

INTRODUCTION

The Silvereye Zosterops lateralis is one of several bird species known to cause damage to soft fruits (Rooke 1984). Between 1988 and 1993, as part of a larger study of bird damage to grapes in the Central Victorian region, I studied the

population dynamics of the Silvereye in one vineyard, Chateau Leamon, at Big Hill near Bendigo, using a trapping-retrapping method.

The subspecies of Silvereye that predominates and breeds in Central Victoria is Zosterops l. halmaturina (Simpson and Day 1989). However,

Z. l. lateralis, a larger bird with darker flanks, visits the region in autumn, migrating from Tasmania. The timing of entry of Z. l. lateralis and its frequency in the population were unknown.

As grapes ripened it was expected that the numbers of grape-eating birds would rise. To lessen bird damage, growers employ a number of strategies to deter birds from entering or staying in the vineyard. At Chateau Leamon, the methods used were a gas gun (1988–1990) reinforced by shooting (1988–89). Thus the population of Silvereyes was expected to be dynamic, exhibiting immigration, death and possibly emigration and birth (early in the ripening period).

The aims of this study were to determine (a) whether migratory birds of the Tasmanian subspecies arrived in time and abundance to contribute to grape damage; (b) whether the Silvereye populations rose during the grape ripening periods; (c) the persistence of Silvereyes in the vineyard during grape ripening periods; (d) the annual survival of the local subspecies; and (e) where Silvereyes went after the grapes were harvested.

Dettmann (1995) drew the attention of Australian ornithologists to the Jolly-Seber model for estimating population parameters. This model is a powerful tool for dealing with open populations, i.e. ones which are undergoing changes. As I was unfamiliar with this model, I had structured my trapping sessions to obtain data that would allow estimates of population by use of Bailey's modification of the Peterson model (Begon 1979), and estimates of survival from week to week on a model of Seber (1973, in Tanner 1978). Application of these methods as well as the Jolly-Seber model allowed me to compare the utility of these models in a study such as this one.

METHODS

Study site

Chateau Leamon is 10 km south of Bendigo (36°50′49″S, 144°13′46″E). The 4.2 ha vineyard incorporates a winery, a house currently occupied and a derelict house surrounded by mature fruit trees, including quinces, plums and pomegranates. The varieties of grapes grown are riesling, shiraz, semillon, cabernet franc and cabernet sauvignon.

Dates of harvest varied from year to year: 1989, 12 May; 1990, 25 April; 1991, 3 April; 1992, 5 April; and 1993, 14 April.

The western edge of the irregularly shaped vineyard fronts onto the four-laned Calder Highway, and the eastern half of the vineyard is bordered by land cleared for grazing and land planted to young vines. On the northern margin close to the highway, a neighbour has a garden planted partly to native shrubs and trees, notably grevilleas and eucalypts. Close to the highway on the southern margin, the vineyard abuts a grey box/red ironbark forest, part of the catchment of the Sandhurst Reservoir.

Field methods

Silvereyes were trapped in mist-nets placed between rows of vines, at points on the boundary where birds had been observed to enter or leave the vineyard, and between fruit trees. Positions of nets were varied during and between sampling sessions, in order to maximize catching rates and to minimize learning of net positions. All Silvereyes were banded with numbered metal alloy rings and with a site-specific combination of coloured bands (orange/orange on right leg). The subspecies of all birds were determined from the colour of the flank which I confirmed by examination of specimens in the National Museum of Victoria and the South Australian Museum: drab "buff" (Simpson and Day 1989) in Z. l. halmaturina, and "rufous" (Simpson and Day 1989) in *Z. l. lateralis*.

Statistical analysis

The Jolly-Seber model (Donnelly and Guyer et al. 1993; Dettmann 1995) was used to estimate population sizes. Estimates were made by hand, using formulae in Heyer et al. (1993). A second estimate of population was obtained from same-visit capture-recapture data. Birds were captured, banded and released until a sufficient number, typically about 30, had been released (r). A line was then drawn under the last entry, all nets were cleared and some nets moved. Silvereyes captured subsequent to this operation were counted in the second sample (n), of which a number (m) were birds that had been liberated in the first sampling period. The population (N) was estimated by Bailey's formula (Begon 1979):

$$N = \frac{r(n+1)}{m+1}$$

and the standard error was estimated by

SE =
$$\sqrt{\frac{r^2(n-1)(n-m)}{(m+1)^2(m+2)}}$$

Thus if 30 birds were liberated in the first sample and 39 captured in the second sample, of which 14 had been members of the first sample, the estimated population size is

$$N = \frac{30(39+1)}{14+1} = 80.0$$

and the standard error is

SE =
$$\sqrt{\frac{30^2(39-1)(39-14)}{(14+1)^2(14+2)}}$$
 = 15.4

Application of these formulae was based upon the assumption that no changes occurred in the population during the sample period, i.e. that any changes that occurred in the population did so between sample periods, and required that sample periods should be as short as possible.

The survival of birds between visits was estimated by two methods: the Jolly-Seber model, using formulae in Heyer et al. (1993), and the Seber model (Tanner 1978). This latter method requires two mark and release operations and a single recapture. During the first mark/release session, birds were banded and released (M_1) . Birds captured and released during the second mark/ release session are designated M_2 . The sample captured during the recapture session, which commences immediately after the end of the second mark/release session, typically includes birds recaptured from the first mark/release session (R_1) and birds recaptured from the second mark/release session (R_2) . Survival (S) over the period is estimated by comparing the proportion of birds recaptured from the first mark/release session (R_1/\dot{M}_1) with the proportion of birds recaptured from the second (R_2/M_2) .

$$S = \frac{R_1(M_2 + 1)}{(R_2 + 1) M_1}$$

and the variance σ^2 is given by

$$\sigma^2 = S^2 - \frac{R_1(R_1 - 1)(M_2 + 1)(M_2 + 2)}{M_1(M_1 - 1)(R_2 + 1)(R_2 + 2)}$$

Thus if 50 birds were handled in the first mark/release session (M_1) and 29 in the second (M_2) , 14 days after the first, and during the recapture session 10 birds (R_1) from the first mark/release session were caught, and 14 (R_2) from the second mark/release session, the survival rate over the 14 days would be

$$S = \frac{10(29+1)}{(14+1)50} = 0.40$$
 survival for the duration of two weeks

and the variance

$$\sigma^2 = 0.40 - \frac{10(10-1)(29+1)(29+2)}{50(50-1)(14+1)(14+2)} = 0.26$$

Annual survival was estimated by use of the Jolly-Seber model only, as data to allow use of the Seber model were not collected.

In 1989 I recorded the total length of net deployed. By multiplying the numbers of feet of net by the times in hours that the nets were deployed, I gained a measure of the effort I had expended, and I calculated a catch per unit effort by multiplying the number of birds caught by 1 000 and dividing by the effort (in foot-hours).

Movements out of vineyard

As well as attempting to find colour-banded Silvereyes within the region outside of the vineyard and alerting members of the Bendigo Field Naturalists Club, I placed press releases in local newspapers in other fruit growing regions (Goulburn Valley, Murray Valley, Sunraysia) and spoke on Mildura radio, requesting information of the colour-banded Silvereyes.

RESULTS

Populations

Population estimates calculated by Peterson model and Jolly-Seber model are presented in Table 1. In general estimated populations rose during grape ripening seasons. The estimates obtained using the Jolly-Seber model were higher than those obtained using the Peterson model. The values of z_i and m_i calculated from recapture data (see Dettmann 1995, for methods) frequently fell below 10. Standard errors were high relative to the population estimates. Estimates of survival by both methods usually fell below 1.0, i.e. marked birds tended to leave the population (Table 2). The estimates obtained from the Jolly-Seber

TABLE 1

Estimates of populations of Silvereyes at Chateau Leamon. Symbols — N_P , SE_P = estimated population and standard error — Peterson model; S_I and SE_I = estimated population and standard error — Jolly-Seber model; m_i , z_i calculated recapture data; C = catch per effort.

	F	,		F	•		
Date	N _P	SE _P	N _J	SE _J	\mathbf{m}_i	\mathbf{z}_{i}	С
7/4/89	102.1	24.7	_	_	_		19
16/4/89	90.2	23.7	98	37	7	2	12
25/4/89	152.7	36.5	516	339	10	4	19
13/5/89	99.1	15.2	_	_	8	_	50
2/3/90	41.8	12.6	50	11	6	10	
29/3/90	63.1	18.0	66	13	13	5	
14/4/90	95.4	14.9	136	36	16	3	
21/4/90	128.3	34.6	_	_	18	_	
1/3/91	46.0	16.6	95	20	8	5	
8/3/91	62.0	13.5	184	27	15	10	
15/3/91	180.8	61.4	229	57	4	28	
31/3/91	156.7	27.8	_	_	48		
9/2/92	_		23	9	8	5	
28/2/92	72.5	19.8	208	82	6	7	
20/3/92	103.2	22.8	133	25	24	6	
3/4/92	102.0	43.5		_	20		
6/3/93	99.7	26.9				_	
26/3/93	56.0	10.5	81	26	12	3	
12/4/93	99.1	18.7	_	_	14		

model were more consistent (range 0.61–1.37) than those obtained by the Seber model (0.073–1.04). Recruitment levels using the Jolly-Seber model were high relative to population sizes in all periods except one (28/2/92–20/3/92).

Annual survival of Zosterops 1. halmaturina

The data and parameters of survival of Z. l. halmaturina estimated by use of the Jolly-Seber model are presented in Table 3. Values of m_i and z_i are low. Estimated populations vary widely between years, but estimates of annual survival are very consistent between years. Standard errors are very high in relation to estimates.

Arrival of Zosterops 1. lateralis

In all years except 1992, birds of the Tasmanian subspecies were first recorded in late March–early April (Table 4). *Z. l. lateralis* reached up to 26% of the total population of Silvereyes.

Recoveries

Single colour-banded Silvereyes were sighted at Strathfieldsaye (10 km ENE) and Flora Hill (9 km NNE). Single dead birds were recovered at Strathfieldsaye and at Harcourt (17 km S).

TABLE 2

Survival and recruitment parameters of Silvereyes at Chateau Leamon. Symbols — S_S , SD_S = survival and standard deviation — Seber model; S_J and SE_J = survival and standard error — Jolly-Seber model; B, SE_B = recruitment and standard error.

Period	Days	S_S	SD_S	S_J	SE_J	В	SE_B
7/4/89–16/4/89	9	0.19	0.11	_	_	_	_
16/4/89-25/4/89	9	0.28	0.17	1.37	0.61	382	275
25/4/89-13/5/89	18	0.073	0.065			_	_
2/3/90-29/3/90	27	1.04	0.45	0.81	0.26	26	19
29/3/90-14/4/90	16	0.30	0.15	0.82	0.22	86	33
14/4/90-21/4/90	7	0.16	0.10		_	_	
1/3/91-8/3/91	7	0.22	0.13	0.81	0.17	107	46
8/3/91-15/3/91	7	0.68	0.36	0.61	0.26	114	104
15/3/91-31/3/91	16	0.54	0.15			_	_
9/2/92-28/2/92	19	0.42	0.22	1.25	0.22	173	79
28/2/92-20/3/92	21	0.65	0.13	0.71	0.30	-15	58
20/3/92-3/4/92	13	0.78	0.60	_	_	_	_
6/3/93-26/3/93	20	0.23	0.11	_			_
26/3/93-12/4/93	17	0.18	0.13			_	_

TABLE 3

Annual survival parameters for Zosterops l. halmaturina at Chateau Leamon 1988–93. Symbols: i = number of year; $n_i = \text{birds captured in year } i$; $r_i = \text{banded birds released in year } i$; $m_i = \text{banded birds from previous years captured in year } i$; $z_i = \text{number of different birds caught before } i th sample, not caught in <math>i$ th sample, but caught in a later sample; $y_i = \text{number of birds banded in year } i$ and recaptured in subsequent years; $N_i = \text{estimated population just before year } i$; $S_i = \text{estimated probability of survival from year } i$ to year i+1; $LE_i = \text{estimated life expectancy based on estimated survival rate.}$

Year	i	\mathbf{n}_i	\mathbf{r}_{i}	m_i	\mathbf{z}_{i}	\mathbf{y}_i	N_i	\mathbf{S}_{i}	LE_i
1988	1	92	92	_	_	9	_	_	_
1989	2	189	189	5	4	8	3 167	0.26	0.85
1990	3	132	132	4	8	15	2 479	0.24	0.82
1991	4	156	155	22	1	5	381	0.24	0.82
1992	5	114	114	5	1	3	824		_
1993	6	114	_	4	_	_	_	_	

TABLE 4

Date of first record of Z. l. lateralis and the highest proportion of total Silvereye population attained by Z. l. lateralis.

Year	First Record	Number banded	Highest %				
1988	2 April	10	26.1				
1989	7 April	49	25.0				
1990	14 April	11	12.0				
1991	23 March	4	13.3				
1992	Not recorded before harvest						
1993	12 April	7	11.5				

DISCUSSION

Methods of estimation

The Jolly-Seber model is very powerful, allowing estimations of populations, survival and recruitment. I identify two limitations of the method as applied to this study. First, information from three trapping sessions is required for one estimate of population, and four trapping sessions for one estimate of survival and recruitment. Thus many data are wasted, e.g. in 1993, when warm weather brought on an unexpectedly early harvest and allowed only three trapping sessions, hence only one estimate of population and none of survival.

Second, the estimated values of m, often fell below 10 and z_i rarely achieved 10 (Tables 1,3). Seber suggests (Dettmann 1995) that the Jolly-Seber model is inappropriate when m, or z, is less than 10. Values of m_i and z_i may be increased by increases in the recapture rate per trapping session, or by an increased number of trapping sessions. In this study, trapping rates were low except during an unpredictable, brief period of less than two months before harvest. Increasing the frequency of trapping sessions would increase the disturbance to birds and the probability of birds learning to avoid nets, so violating an assumption of the Jolly-Seber model. Hence it may well be that use of the Jolly-Seber model is inappropriate to a study of this scale.

The Peterson model assumes a closed population, which could not be assumed to be the case in this study. The imperative to make the sample periods as brief as possible (lest changes occur to the population during sampling) conflicted with the imperative to maximize recaptures so that calculations could ensue. This is a clear limitation of use of the Peterson model in a study such as this. On occasions when the capture rate was very low, e.g. 15/3/91, nets were left up for two full days in order to gain useful statistics, and the assumption of an unchanged population was almost certainly violated. If, as is likely, the population rose in this period, due to an influx of unmarked birds, the population would be overestimated.

Both models of population estimation assume that marking does not influence the probability of capture of a bird. I noticed late in the study (in the last year) that of the small number of birds caught above the pockets of nets, nearly all were banded birds caught by their bands. This artificial increase in the recapture rate would lead to an underestimate of the population. This problem of differing probabilities of capture does not affect the validity of estimations of survival using the Jolly-Seber model or the Seber model, as by both methods the capture rates of cohorts of marked birds are being compared, not marked versus unmarked.

The Seber model for estimating survival rates has the virtue of economy, as an estimate can be made on the basis of two mark/release sessions and a retrap session which ideally follows the second mark/release session immediately — in practice, on the same day as the second mark/release session.

All methods yield high standard errors. This is a necessary result of low recapture rates.

Three conflicting sets of population estimates and associated survival estimates provide a basis for judging which models were the more appropriate for this study: the population estimates for 25/4/89, 8/3/91 and 28/2/92 and estimates of survival between 16/4/89 and 25/4/89. In all cases the Jolly-Seber estimate was by far the higher, in fact surprisingly high. On none of the conflicting dates did the number of birds in the vineyard seem inordinately high. In fact, the capture per unit effort on 25/4/89 was fairly low (Table 1). Hence I suspect that the Jolly-Seber estimate is well out on these occasions. Moreover. the very high survival estimate 16-25/4/89 is unlikely at a time when intensive shooting (claimed to have been successful by the vineyard manager — pers. comm.) was going on. For this reason I base subsequent discussion of survival between trapping sessions on results obtained by use of the Seber model, which are more consistent with observations in the field.

Population changes

Whilst standard errors are high (Table 1), the fact that estimated populations rose during four of the five seasons supports the generalization that populations rise during the grape ripening season. This rise is only partly explained by the influx of Tasmanian birds, particularly in 1992, when no Tasmanian birds had arrived before the last banding session. Moreover, yellow-gaped juveniles were not captured during the ripening periods, indicating that the population rises were

not due to births in the vineyard. Thus the population increases were due largely to the movement into the vineyard of local Silvereyes.

There was much variation in estimated populations between years (Table 1). Whilst it is impossible to identify all of the variables limiting population sizes, it is possible to suggest some. For example, 1992 and 1993 were years when Silvereye numbers were low. 1992 was the best year for flowering of local Grey Box Eucalyptus microcarpus since 1942 or 1965 (differing estimates by local honey producers). This is consistent with Rooke's (1984) findings in Western Australia that the heavy flowering of Marri E. calophylla also correlates with low Silvereye numbers in vineyards. In 1993, downy mildew was prevalent in the vineyard, and the quantity of grapes was well down.

Survival

Survival rates between trapping sessions were generally well below 1.0 (Table 2) whether shooting took place in the vineyard (1989) or not. The low survival in non-shooting years, especially 1990 and 1993, combined with the estimates of populations in all years suggests that shooting is an ineffective control measure, but this idea needs to be tested in controlled experiments. This low survival in non-shooting years may have resulted from the birds either dying or leaving the vineyard on account of physiological stress (Rooke et al. 1986), perhaps due to declining insect numbers in the vineyard. As the populations rose despite low rates of survival, there must have been a large movement into the vineyard during the ripening period, and a high turnover in the populations.

Annual survival rates and estimated life expectancies were very low. This is consistent with Rooke's (1984) observation that over 91% of Silvereyes he sampled at one vineyard were first year birds, as mortality (cf. Zosterops l.

chlorocephala on Heron Island, Kikkawa 1980), and dispersal may be higher in first year birds than adults.

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