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A New Method of Estimating Population Size, Survivorship, and Birth Rate from Capture-Recapture Data

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PART V

A NEW METHOD OF ESTIMATING POPULATION SIZE, SURVIVORSHIP, AND BIRTH RATE FROM CAPTURE- RECAPTURE DATA

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Abstract

A method of estimating sampling intensity (p_i) in capture-recapture studies is described and hence an estimate of population size (N_i) is available from

$$*N_i = n_i / p_i$$

where n_i is sample size. Simple formulae are also given for estimating survivorship ($s_{i \rightarrow i+1}$) and ingress ($b_{i \rightarrow i+1}$). The method is illustrated with data obtained from a capture-recapture study of the Six-spot Burnet moth (*Zygaena filipendulae* L.).

Working with wildfowl data, Lincoln (1930) developed a mark-release-recapture method for estimating the total population size. This method, the Lincoln Index, suffers from the great disadvantage that it requires rather restrictive assumptions to be made. Many methods have been developed from the basic Lincoln Index to allow a chain of estimates of population size and other parameters to be obtained from a series of samples (Southwood, 1966; Parr, Gaskell & George, 1968). The first of these were the methods of Fisher & Ford (1947) and Jackson (1948). In recent years methods based on more realistic assumptions have been derived, of which those of Seber (1965) and Jolly (1965) seem to have the most general application in situations where "births", immigrations, deaths, and emigrations occur.

Jolly's (1965) method is probably the least restrictive of any in general use at the present time but, in common with the others mentioned here, it assumes that mortality is independent of age.

*Denotes estimates.

This implies that the probability of an animal surviving through any period of time is not affected by its age at the start of the period. For many organisms it is clear that this assumption is unjustified and in these cases a more suitable method is required. The method described below *does not assume that mortality is independent of age*, and, in fact, requires the minimum of assumptions to be made.

1. Data Format

The data required is obtainable in the following manner. The capture-recapture experiment lasts from a time t_1 until a later time t_m . At each of the times $t_1, t_2, \dots, t_i, \dots, t_m$ a random sample of animals is taken from the population, where the time interval between samples need not be constant. All of the animals seen in the sample at time t_i ($i=1, 2, \dots, m-1$) are marked in such a way that if they are seen in any later sample then it will be recognised that they were previously captured at time t_i . A convenient way of doing this is to use a different colour of mark for each sample. This form of marking is usually referred to as date-specific. (An alternative marking method involves giving each animal an individual mark when it is first captured. The individual can then be identified whenever it is recaptured.)

Using this marking technique it is possible to arrange the data as illustrated in Table 1. An example is given in Section 3. This table will contain all of the information relevant to population estimation by the present method. The entries in rows j and k of Table 1 relate to two hypothetical animals. The j th animal was

TABLE 1
Suggested Data Format

animal	Sampling times								
	t_1	t_2	t_3	t_4	t_5	t_6	t_7	...	t_m
1	x	y	z	x					
2	x	z	z	y	y	x			
3		x	y	z	z	y	z		x
:									
j		x	y	z	z	y	x		
:									
k			x	z	z	x			
:									
n					x	y	z		x

x: first or last capture of an animal

y: animal captured

z: animal not captured whilst known to be alive (in practice this symbol can be omitted)

first captured at time t_2 and last captured at time t_7 . It was also captured at times t_3 and t_6 , but not captured at times t_4 and t_5 . The k th animal was captured at times t_3 and t_6 , but at no other time.

2. Derivation of Formulae

If we let:—

N_i = the total number of animals in the population at time t_i ,
 $s_{i \rightarrow i+1}$ = the proportion of the population alive at time t_i still alive at time t_{i+1} , and

$b_{i \rightarrow i+1}$ = the number of animals entering the population in the interval t_i to t_{i+1} , and alive at t_{i+1}

then the present method allows the estimation of N_i for $i=2, 3, \dots, m-1$, $s_{i \rightarrow i+1}$ for $i=1, 2, \dots, m-2$, and $b_{i \rightarrow i+1}$ for $i=2, 3, \dots, m-2$. In what follows it is convenient to write $s_{i \rightarrow i+1}$ as s_i and $b_{i \rightarrow i+1}$ as b_i . The terms "alive" and "entering" are to be interpreted in a wide sense. Animals emigrating from the population are considered to "die", whilst those entering (ingress) include births or emergences.

The important assumptions that we make are

- (a) that sampling is random, with all individuals in the population having an equal chance of capture, and
- (b) that marking has no affect on animals.

If the sample size at time t_i is n_i then this will consist of a certain proportion, p_i , of the total population, N_i . This proportion will be the *sampling intensity* at that time, and the relationship

$$p_i = n_i / N_i$$

will clearly hold. It follows that an estimate of N_i can be obtained, whenever an estimate of p_i is available, from

$$*N_i = n_i / *p_i \quad (1)$$

The proportion of the population alive at time t_i surviving until t_{i+1} is the survivorship over the period, that we denote by s_i , as above. Assuming that mortality is unaffected by marking, so that the survival of the animals in the samples is similar to that of other animals, it is expected that $s_i n_i$ of the n_i animals in the sample at time t_i will survive until t_{i+1} . Since the sampling intensity at time t_{i+1} is p_{i+1} it is also expected that a proportion p_{i+1} of those animals still alive will be captured again in the sample at time t_{i+1} .

We have then the approximate relationship

$$r_i = n_i s_i p_{i+1}$$

*Denotes estimates.

where r_i denotes the number of animals captured in the i th and $(i + 1)$ th samples. An estimate of s_i is therefore

$$*s_i = r_i / (n_i * p_{i+1}) \tag{2}$$

The number of *new entries* to the population in the interval t_i to t_{i+1} can also be easily estimated. If a survival rate of s_i applies over the interval then the population size at time t_{i+1} will be $N_i s_i$, *apart from new entries*. The difference between this size and the actual size, N_{i+1} , will be the new entries alive at t_{i+1} :

$$b_i = N_{i+1} - s_i N_i$$

suggesting the estimator

$$*b_i = *N_{i+1} - *s_i *N_i \tag{3}$$

Equations (1) to (3) show that the estimation of population parameters is a simple matter, providing that estimates of the sampling intensities are available. The other quantities involved, n_i and r_i are obtained from inspection of the data. Fortunately, an estimator of sampling intensity is available for time t_i ($i = 2, 3, \dots, m-1$), providing that the data gives a reasonable number of animals captured three or more times throughout the experiment. The derivation of the estimator follows from dividing the population at time t_i into various classes of animal, according to capture-recapture patterns. The classes are illustrated in Table 2. It will be seen that there are four classes involved, and that any particular animal alive at time t_i must be in one, and only one, of the classes. An animal captured at any time before t_i and also at least once after t_i will be in one of the upper two classes. The importance of these two classes is that any animal in either class is known to be

TABLE 2
Animals Alive at Time t_i

	at time t_i	
	captured	not captured
captured at least once before t_i and also at least once after t_i	A_{1i}	B_{1i}
not captured before t_i and/or not captured after t_i	A_{2i}	B_{2i}
totals	n_i	$N_i - n_i$

*Denotes estimates.

alive before and after t_i on the basis of its captures at other times. It is therefore observed that, of the $A_{1i} + B_{1i}$ animals known to be alive before and after t_i , a proportion $A_{1i} / (A_{1i} + B_{1i})$ were captured at t_i . This proportion gives an estimate of the sampling intensity (p_i) at time t_i , and hence a method of obtaining population estimates is fully defined. Together with equations (1) to (3) we now have

$$*p_i = A_{1i} / (A_{1i} + B_{1i}). \quad (4)$$

The quantities A_{1i} and B_{1i} are obtainable from the data in the form of Table 1. Examination of this table will show that

$$\begin{aligned} \sum_i y &= A_{1i} \\ \sum_i (y + z) &= A_{1i} + B_{1i} \\ \text{and} \quad \sum_i (x + y) &= A_{1i} + A_{2i} = n_i \end{aligned}$$

where $\sum_i y$ denotes the total number of y's in the column relating to time t_i , $\sum_i (y + z)$ the total number of y's and z's, in the column, and $\sum_i (x + y)$ the total number of x's and y's in the column.

In order that the estimate of sampling intensity is not subject to large sampling fluctuations it is necessary for A_{1i} to be moderately large. It is, in fact, desirable that this quantity should be larger than about 10. Unfortunately, a value of zero leads to an infinite estimate of population size, unless B_{1i} is also zero. In the latter case no estimate of sampling intensity is available.

3. Example

The use of the new method will be illustrated by a short mark-recapture study of the Six-spot Burnet moth (*Zygaena filipendulae* L.) made at Dale, S.W. Pembrokeshire, in July 1968. The colony intermingled with a much smaller colony of the Five-spot Burnet (*Z. trifolii* Esp.) and occupied the tip of the Dale Fort Peninsula. Sunny weather throughout the period of study ensured adequate mixing of the population between samples. One sample was taken on each of five days.

The insects were given *date-specific* marks of cellulose 'dope' applied to the underside of the hindwings, the sexes not being distinguished for the purpose of the study. The colours of marking were allocated as follows:

19	July	green	(g)
20	,,	white	(w)
21	,,	blue	(b)
22	,,	orange	(o).

*Denotes estimates.

A sample was also taken on 24 July but, as this was the last sample, no marking was required. During the five days of the experiment 141 different insects were seen. The recapture data were recorded in the following fashion, using the colour abbreviations indicated above:

19 July: 57 captured, marked and released.

20 July: 52 captured; 25*g*, 27 unmarked.

21 July: 52 captured; 8*g*, 9*w*, 11*gw*, 24 unmarked.

22 July: 31 captured; 2*g*, 3*w*, 4*b*, 5*gb*, 1*wb*, 2*gwb*, 14 unmarked.

24 July: 54 captured; 1*g*, 2*w*, 7*b*, 5*o*, 4*gw*, 2*gb*, 2*go*, 4*wb*, 1*wo*, 1*bo*, 5*gbo*, 1*gwbo*, 19 unmarked.

Using this information Table 3 was constructed, in the format of Table 1.

The computation of estimates is illustrated by the following three examples. The estimate of the population size on 21 July, which we denote by $*N_{21}$, was obtained by substituting the relevant data of Table 3 into equation (1):

$$\begin{aligned} *N_i &= n_i / *p_i = n_i (A_{ii} + B_{ii}) / A_{ii} \\ \therefore *N_{21} &= 52(14 + 12) / 14 = 96.6 \end{aligned}$$

The estimate of the survivorship over the period 20-21 July, which we denote by $*s_{20 \rightarrow 21}$ (or $*s_{20}$), was obtained from equation (2):

$$\begin{aligned} *s_{i \rightarrow i+1} &= r_i / (n_i *p_{i+1}) \\ \therefore *s_{20 \rightarrow 21} &= 20(14 + 12) / (52 \times 14) = 0.7143 \end{aligned}$$

Having calculated the population size estimates for 20 and 21 July, as indicated above, the estimated number of new insects joining the population in the period 20-21 July, which we denote by $*b_{20 \rightarrow 21}$ (or $*b_{20}$), was obtained from equation (3):

$$\begin{aligned} *b_{i \rightarrow i+1} &= *N_{i+1} - *s_i *N_i \\ \therefore *b_{20 \rightarrow 21} &= 96.6 - (0.7143 \times 90.1) = 32.24 \end{aligned}$$

The full series of estimates obtained from the data are given in Table 4.

TABLE 4
Zygaena filipendulae—population estimates

	Date-July				
	19	20	21	22	24
Population size ($*N_i$)	—	90.1	96.6	93.0	—
Survivorship ($*s_{i \rightarrow i+1}$)	0.7601	0.7143	0.6923	—	—
New entries ($*b_{i \rightarrow i+1}$)	—	32.24	26.12	—	—

*Denotes estimates.

fore using a method requiring it, is not fully understood. It would probably not be important providing that the total period covered by any capture-recapture experiment is small compared with the average life span of the animals in question. However, the present method can certainly be recommended whenever mortality is thought to be strongly influenced by age. If mortality is independent of age then Jolly's (1965) method uses the data more efficiently than does the present method, and his method is then superior because of this. (In practice the two methods appear to give rather similar estimates.)

One other advantage of the present method is its simplicity, with regard to the principles involved as well as the computations required for estimates. This has an important result: "curious" estimates can often be explained quite easily in terms of peculiarities of the data.

The assumption that marking does not affect mortality is not strictly required in order to obtain valid estimates of population size. Since sampling intensity is estimated from a group of animals known to be alive before and after a certain time, the only effect of changing the mortality rate is to change the *size* of this group, but not the *proportion captured* at a time when all of the animals in the group are alive. To this extent the estimates of population size are independent of the mortality rate. The estimates of survivorship and new entries could be seriously affected if marking alters the mortality rate.

The method can be used in the form of a triple catch. To do this only three samples need be taken, and this allows the estimation of the population size at the time of the second sample, together with the survivorship from the time of the first to the time of the second sample.

We have assumed so far that both losses and gains occur in the population of interest. If it can be assumed that only one, or none, of these occurs then the method can be changed slightly in order to take this into account. The important modification occurs in the dividing of the population into various classes (Table 2) in order to estimate sampling intensity. As an example we consider the case when only losses occur. In this case any animal seen *after* t_i was certainly alive when the sample at time t_i was taken. An estimate of sampling intensity at time t_i ($i=1, 2, \dots, m-1$) is therefore given by the proportion of the animals seen at any time after t_i that were in the sample at time t_i . Population estimates then follow from equations (1) and (2).

No attempt has been made to give standard errors for the estimators of this paper. Work is continuing in this direction. It is likely that there is a slight bias in the estimates, and this question is also under investigation.

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