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A REGRESSION METHOD FOR MARK-RECAPTURE ESTIMATION OF POPULATION SIZE WITH UNEQUAL CATCHABILITY¹

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Abstract. The assumption of equal catchability of marked and unmarked animals in mark-recapture sampling is examined. Violation of this assumption may come from two basic sources, heterogeneity or contagion, and both produce a bias in the estimate of population size. Two approaches to this problem are discussed. First, it is noted that bias can be avoided by statistically independent sampling procedures for marking and recapturing. Second, a new regression method is presented for multiple captures on a closed population, which combines mark-recapture with "simulated" removal and tests whether the assumption of equal catchability holds, regardless of the source of bias. Furthermore, if the ratio of catchabilities between unmarked and marked animals is constant over at least two successive samples, the method provides an estimate of population size even if the assumption of equal catchability does not hold. Two suggestions are made to supplement the regression method. First, non-capture sampling to obtain the ratio of unmarked to marked animals has several advantages over trapping. Second, a subclass of the marked animals may satisfy the constant ratio assumption even when all marked animals do not. A worked example is provided to illustrate the method.

Mark-recapture techniques have been widely used for estimating the size of animal populations, but such techniques are valid only under certain restrictive assumptions. The assumption that marked animals have the same probability of capture (henceforth called "catchability") as unmarked animals is of crucial importance in practice. The several tests which have been developed to determine whether particular deviations from this assumption are present (Leslie 1958; Cormack 1966; Seber 1965) are reviewed by Cormack (1968). Several methods based on frequency distributions of captures have in addition been developed for estimating population size under particular deviations from this assumption (Holgate 1966; Eberhardt 1969).

However, there is a need for a method of general and practical utility for ecological research, which tests whether the assumption holds and which provides an estimate for population size even if it does not hold. The regression method to be presented here combines two well-known methods for estimating population size: mark-recapture (Petersen 1896) and removal (De Lury 1947). The discussion to follow will emphasize simplicity rather than statistical rigor, at no expense to the correctness or the utility of the results.

Mark-recapture has two steps: marking and sampling. In a population of unknown size N , a known number, M , of the animals are captured and marked, leaving an unknown number U unmarked. In a subsequent sample of n animals,

m are observed to be marked and u unmarked. Therefore

$$N = M + U \quad (1)$$

and

$$n = m + u. \quad (2)$$

The basic assumption underlying the estimate is that the proportion of marked animals in the sample (m/n) is, on the average, representative of the proportion of marked animals in the population (M/N). Therefore, on the average,

$$\frac{m}{n} = \frac{M}{N}, \quad (3)$$

from which N may be estimated by

$$\hat{N}_p = n \frac{M}{m}. \quad (4)$$

Substituting (1) and (2) in (3), and rearranging, yields

$$\frac{m}{M} = \frac{u}{U}. \quad (5)$$

The proportion of the marked animals which are expected to be captured corresponds to the average of their catchabilities, and similarly for unmarked animals. Equation (5) therefore indicates the basic assumption of mark-recapture is equivalent to one that the average catchabilities of marked animals (estimated by m/M) and unmarked animals (estimated by u/U) are equal.

Following an argument similar to that of Junge (1963), it can be shown that this assumption of equal catchability is true only when there is no statistical correlation between an animal's catch-

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ability and whether it has been marked. A positive correlation results in marked animals being overrepresented in the sample and a consequent bias in \hat{N} toward an underestimate of N . A negative correlation causes a corresponding overestimate of N . Any methods such as those of Schnabel (1938) or Hayne (1949), which in effect average mark-recapture over several samples, similarly underestimate or overestimate N .

Correlation may arise because of: (1) heterogeneity: all animals do not have the same catchability, or (2) contagion: capture at one time affects future catchability. With heterogeneity, the more catchable animals tend to be captured and marked, resulting in marked animals being more catchable on the average than unmarked animals. Heterogeneity always leads to a positive correlation. With contagion, a behavioral response or some other effect of capture and marking alters catchability in the subsequent sample. Contagion may result in a positive or a negative correlation depending upon the response. Whether the correlation is due to heterogeneity or contagion or both, the result is a bias in the estimate of population size.

It should be pointed out that although heterogeneity or contagion may lead to correlation, they do not necessarily do so. If the heterogeneity or contagion present during marking are statistically independent of the heterogeneity or contagion present in the sampling, there will be no correlation between catchability in the sample and whether an animal has been marked. This may be achieved in practice by making the sampling procedure appropriately different from the marking procedure. For example Lidicker (1966) randomly shifted traps between trappings in order to avoid some mice having traps in a favored location for both marking and subsequent sampling. Kott (1965) captured mice in traps to mark them, but found that sampling with pit-falls resulted in higher estimates than sampling with traps. This was presumably because the pit-falls sampled independently of the proneness some mice developed for traps.

When it is not certain that the procedures for marking and sampling are independent, a method is needed to test for bias and correct for any bias present. A major difficulty in correcting for bias is that one seldom knows the exact nature of the heterogeneity or contagion which is operating in the particular population being sampled. A useful method must be approximately compatible with many different potential sources of bias. An approximate right estimate of population size is better than a precise wrong one.

The regression method presented below is based upon the simple assumption that the average catchabilities of unmarked and marked animals are in a constant ratio b to one another in successive samples. This assumption is compatible with many sources of bias, particularly when applied to a selected subclass of the marked animals, as is discussed after the description of the regression method.

A number of statistical approaches other than regression could have been used, and some such as maximum-likelihood might be more precise. The regression method was selected because (1) it is computationally simple, (2) it lends itself to graphical interpretation, and (3) it requires a minimum of assumptions about the statistical nature of the sampling process. No attention need be given to the source of bias; and errors, which may originate from complex and unknown causes, are simply evaluated in terms of the deviations of points about a best-fit regression line.

Morris (1955) has qualitatively anticipated one feature of the regression method—that a progressive increase or decrease in successive mark-recapture estimates on a closed population is an indicator that the equal-catchability assumption does not hold. Tanaka (1967) has anticipated the method in combining mark-recapture with removal, by using information from the capture of marked animals to compute a "corrected catch" for the removal method.

The sampling scheme is the following. A closed population (having no births, deaths, immigration, or emigration) of size N is sampled at times $0, 1, \dots, T$. Each sample is observed to contain m_t marked animals and u_t unmarked animals. (m_0 equals zero.) At each sample unmarked animals are marked and all animals returned to the population. The total number of marked animals in the population at sample t is known to be

$$M_t = \sum_{i=0}^{t-1} u_i, \quad (6)$$

and the remainder of the population

$$U_t = N - M_t \quad (7)$$

is unmarked.

Catchability may vary from sample to sample, but let us assume the average catchability of unmarked animals (estimated by u_t/U_t) is in a constant and unknown ratio b to the average catchability of marked animals (estimated by m_t/M_t). That is,

$$\frac{u_t/U_t}{m_t/M_t} = b \quad (8)$$

for all t . The estimate of the unmarked population at sample t , under the assumption of equal catch-

ability (that is, b equals 1), may be obtained from (8) as

$$\hat{U}_t = u_t \frac{M_t}{m_t}. \tag{9}$$

From (8) and (9),

$$\hat{U}_t = bU_t. \tag{10}$$

Thus \hat{U}_t , the estimate of the unmarked population under the assumption of equal catchability, consistently overestimates or underestimates the actual unmarked population by a constant proportion b .

In order to illustrate how removal can exploit this error of constant proportion, suppose the unmarked population is estimated on two occasions.

$$\hat{U}_1 = bU_1 \tag{11}$$

and

$$\hat{U}_2 = bU_2. \tag{12}$$

Subtracting (12) from (11),

$$\hat{U}_1 - \hat{U}_2 = b(U_1 - U_2). \tag{13}$$

That is, the difference between estimates of the unmarked population at two different samples, under the assumption of equal catchability, is also an overestimate or underestimate of the actual difference by the constant proportion b . If the actual difference in the unmarked population is known, by removing a known number of animals from it, then b may be estimated by rearranging (13) to

$$b = \frac{\hat{U}_1 - \hat{U}_2}{U_1 - U_2}. \tag{14}$$

If the population is closed, the number of animals marked anew at each sample represents a known difference in the unmarked population. The total numbers of marked animals M_t at successive samples therefore provide a succession of known differences in the unmarked population (a "simulated" removal) which may be exploited to obtain a composite estimate of b over all samples. This is accomplished by substituting (7) in (10), which gives

$$\hat{U}_t = bN - bM_t. \tag{15}$$

Note that equation (15) has a form suitable for linear regression analysis with M_t as the independent variable and \hat{U}_t as the dependent variable. The ratio b is the negative of the slope; and N may be obtained by extrapolating the line to $\hat{U}_t = 0$ (i.e., $M = N$ when $\hat{U} = 0$).

The \hat{U}_t are not exactly distributed normally, independently, and with equal variance over all samples, as is assumed in regression analysis; but this is of small practical significance. The procedure, then, is to compute the M_t from equation (6) and the \hat{U}_t from equation (9). The appropriateness of the regression method, which de-

pends upon whether the catchability ratio b is in fact constant over all samples, may be evaluated graphically by the extent to which the points (M_t, \hat{U}_t) fall along a straight line.

If judged appropriate, equation (15) is then fitted to the M_t and \hat{U}_t by conventional linear regression analysis. The estimates of b and N (following Bennett and Franklin 1954, Section 6.22) are

$$\hat{b} = \frac{-\sum_{t=1}^T \hat{U}_t (M_t - \bar{M})}{\sum_{t=1}^T (M_t - \bar{M})^2} \tag{16}$$

$$\hat{N} = \bar{M} + \frac{\bar{\hat{U}}}{\hat{b}}. \tag{17}$$

(\bar{M} and $\bar{\hat{U}}$ are the averages of the M_t and \hat{U}_t respectively.)

The standard error of \hat{b} (following Bennett and Franklin 1954, Section 6.23) is

$$s_{\hat{b}} = \sqrt{\frac{\sum_{t=1}^T (\hat{U}_t - [\hat{b}\hat{N} - \hat{b}M_t])^2}{(T-2) \sum_{t=1}^T (M_t - \bar{M})^2}}. \tag{18}$$

A first-order approximation for the standard error of \hat{N} (following Bennett and Franklin 1954, Section 6.24) is

$$s_{\hat{N}} = \sqrt{\frac{\sum_{t=1}^T (\hat{U}_t - [\hat{b}\hat{N} - \hat{b}M_t])^2}{T(T-2)\hat{b}^2} + \frac{[s_{\hat{b}}\bar{\hat{U}}]^2}{\hat{b}^4}} \tag{19}$$

The confidence limits of \hat{b} may be obtained by multiplying $s_{\hat{b}}$ by the appropriate value from a t -table with $T-2$ degrees of freedom. To test for equal catchability of marked and unmarked animals (equivalent to $b = 1$), the hypothesis $H: b = 1$ is rejected if the confidence limits of \hat{b} do not overlap 1. The confidence limits of \hat{N} may be obtained by multiplying $s_{\hat{N}}$ by a value from a normal probability table. It must be remembered that confidence limits for \hat{N} based on equation (19) are only an approximation for both practical and statistical reasons. Finney (1964, p. 27-29) describes a statistical procedure which can be applied to obtain a more precise formula for $s_{\hat{N}}$, but this is unnecessary as practical errors normally predominate over statistical errors.

Now that the regression method has been presented, it should be pointed out that computing \hat{U}_t by equation (9) need not be restricted to u_t

and m_t based literally upon captures. That is, mark-recapture censusing is more generally mark-and-sample censusing. Any procedure for tabulating u_t and m_t will suffice as a sampling if it detects members of the population and interrogates them for a mark. For example, foot prints may be collected on smoked-cards, where a marked animal leaves a characteristic toe-clipped print. Alternatively, a remote sensing system which electronically detects members of the population crossing a network of cables can interrogate them for an electronic marker.

Small sample sizes can be a serious limitation when population size is small or catchability in traps is low. Noncapture sampling has the advantage that each individual in the population may be counted many times at each sampling, instead of just once as in trapping. This generates large sample sizes for the u_t and m_t and therefore a more precise estimate of the ratio u_t/m_t used to compute \hat{U}_t . Furthermore, noncapture sampling is more likely than trapping to be independent of marking; and if bias is present, it is more likely to conform to the assumption of constant ratio of catchabilities which underlies the regression method.

The use of marked animals also deserves some comment. The catchabilities of marked animals may differ from one another at any particular sample-time, depending upon the source of bias. The catchabilities of unmarked animals may similarly vary. The proportions of animals with different catchabilities may shift with successive samples, so that the average catchability of the marked, or of the unmarked, animals also shifts. This may happen in such a way that the catchabilities of marked and unmarked animals shift relative to one another with successive samples. The ratio b is not constant under such circumstances, and the points (\hat{U}_t, M_t) cannot be expected to fall along a straight line.

However, there may be a subclass of the marked animals, M_t' , whose average catchability relative to unmarked animals remains approximately constant through all samples. This subclass may itself include animals with capture histories different from one another, but different in ways that do not substantially affect catchability. If each sample is observed to contain m_t' marked animals of this subclass and u_t unmarked animals, the unmarked population may be estimated by

$$\hat{U}_t' = u_t \frac{M_t'}{m_t'} \tag{20}$$

U_t' may then be plotted against M_t (not M_t')

$$\hat{U}_t' = bN - bM_t \tag{21}$$

and equations (16), (17), (18), and (19) applied

with \hat{U}_t replaced by \hat{U}_t' . If the chosen subclass does not allow computation of all \hat{U}_t' ($t = 1, \dots, T$), the summations and averages of equations (16), (17), (18), and (19) are replaced by summations and averages of the M_t and \hat{U}_t' actually used, and T is replaced by T' , the number of M_t and \hat{U}_t' actually used.

Equation (21) is compatible with many kinds of heterogeneity and contagion, or combination of the two, provided equation (20) is based on the proper subclass of marked animals. Intuition and ingenuity may provide guesses as to which subclass is appropriate, but in the last analysis the proper subclass can only be determined graphically as that which results in a straight-line plot. It should be cautioned that the points (\hat{U}_t', M_t) might fall along a straight line by chance alone if enough different subclasses are tried. Furthermore, data selected to produce a straight line may cause equation (19) to underestimate the actual value of $s_{\hat{N}}$. These problems will be minimized when the values of u_t , M_t' , and m_t' are large enough to produce sufficiently precise estimates \hat{U}_t' .

Data on tide-pool snails *Polinices* (Hunter and Grant 1966) are now analyzed to illustrate the method (Table 1). The population was sampled

TABLE 1. Sampling data on *Polinices*^a

t	u_t	M_t	m_t	\hat{U}_t	\hat{N}_p	M_t'	m_t'	\hat{U}_t'
0.....	142	—	—	—	—	—	—	—
1.....	129	142	3	6080	6222	—	—	—
2.....	122	271	23	1437	1708	139	19	892
3.....	99	393	58	670	1063	248	35	701
4.....	94	492	67	690	1182	335	63	500
5.....	147	586	273	315	901	425	219	285

^a The u_t , m_t , M_t' and m_t' are based upon Table 1 of Hunter and Grant (1966). The M_t are computed from equation (6), the \hat{U}_t from (9), \hat{N}_p from (4), and \hat{U}_t' from (20).

on 6 consecutive days and was closed for all practical purposes over the sampling period. A plot of \hat{U}_t against M_t shows considerable scatter, so the entire class of marked snails is rejected as a suitable basis for estimates to be used in the regression method. However M_t' and m_t' based upon marked snails last captured at least 2 days before a particular sample, result in a straight-line plot (Fig. 1). With $T' = 4$, a t -value of $t(2, .05) = 4.3$ yields 95% confidence limits for \hat{b} of $1.93 \pm .53$. Since the confidence limits do not overlap 1, the hypothesis of equal catchability is rejected at the 95% level of confidence. Using a value of 1.96 from a normal probability table, the 95% confidence limits of \hat{N} are 743 ± 39 . Thus a

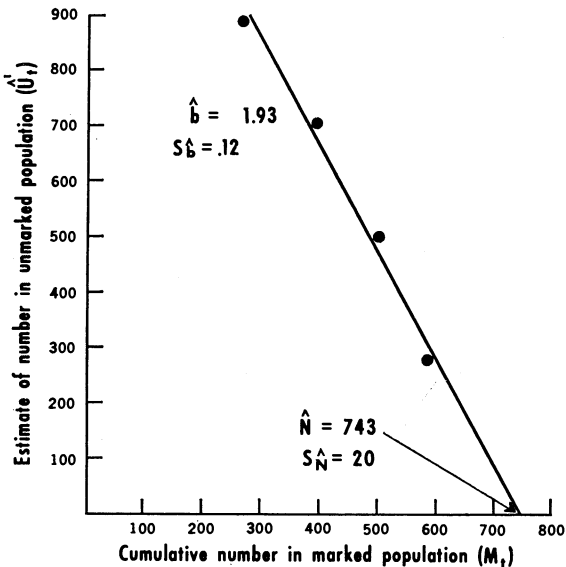


FIG. 1. Linear regression plot of equation (21) based upon a select subclass of marked snails. Estimates are based upon equations (16), (17), (18), and (19) using M_t and \hat{U}_t from Table 1.

value of b greater than 1 indicates the \hat{U}_t overestimate the U_t due to underrepresentation of marked snails in the samples.

The observation by Hunter and Grant that the snails burrow into the mud when released may explain the fact that marked snails were less catchable than unmarked ones. The observation that high tides stimulated burrowed snails to emerge, and that such tides sometimes preceded the next day's sample and sometimes did not, may explain the unsuitability of marked snails captured the day before a particular sample. However, it should be emphasized that applying the regression method requires no explanation of the cause of unequal catchability or of why a particular subclass of marked animals is appropriate.

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