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Estimation of the size of a closed population when capture probabilities vary among animals

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SUMMARY

A model which allows capture probabilities to vary by individuals is introduced for multiple recapture studies on closed populations. The set of individual capture probabilities is modelled as a random sample from an arbitrary probability distribution over the unit interval. We show that the capture frequencies are a sufficient statistic. A nonparametric estimator of population size is developed based on the generalized jackknife; this estimator is found to be a linear combination of the capture frequencies. Finally, tests of underlying assumptions are presented.

Some key words: Capture frequency; Capture–recapture; Generalized jackknife; Population size estimation; Variable capture probability.

1. INTRODUCTION

There is a large statistical literature on capture–recapture methods; see Seber (1973) for a comprehensive review. But most previous work is based on the assumption that capture probabilities are equal for all animals in the population being trapped. However, it has long been recognized that this assumption is often violated. Indeed, equal capture probability is only a convenient mathematical assumption with no empirical justification. Controlled studies of small mammals have shown heterogeneity of capture probabilities among individuals (Young, Neess & Emlen, 1952; Tanaka, 1956; Crowcroft & Jeffers, 1961; Huber, 1962; Bailey, 1969). In such studies where the true population size was known, the usual estimators, e.g. Peterson or Schnabel, were severely negatively biased by heterogeneity of capture probabilities (Edwards & Eberhardt, 1967; Carothers, 1973a). Computer simulation studies by the authors of the present paper in an unpublished report, and by Manly (1971), Gilbert (1973) and Carothers (1973b), have also shown that heterogeneity can cause substantial bias in the commonly used estimators.

In spite of the evidence that accurate population estimation will usually require models providing for some degree of unequal probabilities of capture, there has been only meagre consideration and rigorous development of such models and associated relevant tests; see, however, Cormack (1966), Holgate (1966), Eberhardt (1969), Carothers (1971) and K. H. Pollock in a Cornell University thesis. The purpose of this paper is to present a general model and a derived estimator for closed populations which allows for variability of capture probabilities among animals; detailed derivations are given by K. P. Burnham in an Oregon State University thesis.

2. A VARIABLE CAPTURE PROBABILITY MODEL

Let p_{ji} be the probability of capturing the jth individual on the ith trapping occasion, and define for $j = 1, \ldots, N$; $i = 1, \ldots, t$ the indicator random variables

$$x_{ji} = \begin{cases} 1 & \text{if the } j\text{th individual is captured on the } i\text{th trapping occasion,} \\ 0 & \text{otherwise.} \end{cases}$$

Our model is specified by the following assumptions.

Assumption 1. The population at risk of capture is closed and is of size N.

Assumption 2. We have $p_{ji} = p_j$, where $p_1, \ldots, p_N$ are a random sample from a probability distribution F.

Assumption 3. The random variables x_{ji} $(j = 1, \ldots, N;\ i = 1, \ldots, t)$ are mutually independent for given $(p_1, \ldots, p_N)$.

Given this model the only source of variation in the capture probabilities is heterogeneity among individuals. We do not claim this model would be applicable to all live-trapping studies. In particular, it requires constant effort on each trapping occasion; however, constant effort is usually achieved in grid trapping studies of small mammals. Also, trapping occasions will often be equal short periods of time, such as consecutive days, with t in the range 3 to 10. Thus, it will often be reasonable to assume closure.

The basic data are the trapping histories of each individual, expressible as the N by t matrix $((x_{ji}))$. The sample space is the set of all possible 2^{Nt} such matrices. The following statistics will be needed: the number of times individual j was captured is

$$y_j = \sum_{i=1}^{t} x_{ji};$$

the number of individuals captured exactly i times is f_i; for $i = 1, \ldots, t$ these are the capture frequencies, and f_0 is the number of individuals never captured. The number of individuals seen at least once during the trapping is

$$S = \sum_{i=1}^{t} f_i,$$

and the total number of captures on day i is

$$n_i = \sum_{j=1}^{N} x_{ji}.$$

Only S rows of the matrix $((x_{ji}))$ can be observed, but this allows calculations of the capture–recapture statistics because the f_0 unobserved rows are all zeros. The joint conditional distribution of the x_{ji} is

$$\mathrm{pr}(x \mid p) = \prod_{j=1}^{N} \prod_{i=1}^{t} p_j^{x_{ji}} (1-p_j)^{1-x_{ji}} = \prod_{j=1}^{N} p_j^{y_j} (1-p_j)^{t-y_j}.$$

Because this probability distribution is not useful for estimation of N we treat p as a random sample and average over it to obtain the compound distribution of $((x_{ji}))$:

$$\mathrm{pr}(x \mid F) = \prod_{j=1}^{N} \left\{ \int_0^1 p^{y_j} (1-p)^{t-y_j} dF(p) \right\}.$$

Further simplification is possible because the y_j take only the values $0, 1, \ldots, t$:

$$\mathrm{pr}\,(x|F) = \left\{\int_0^1 (1-p)^t\, dF(p)\right\}^{N-S} \prod_{i=1}^{t} \left\{\int_0^1 p^i(1-p)^{t-i}\, dF(p)\right\}^{f_i}$$

$$= \left\{\int_0^1 (1-p)^t\, dF(p)\right\}^{N} \prod_{i=1}^{t} \left[\left\{\int_0^1 p^i(1-p)^{t-i}\, dF(p)\right\} \Big/ \left\{\int_0^1 (1-p)^t\, dF(p)\right\}\right]^{f_i}.$$

Thus for this compound distribution of x_{ji}, the sufficient statistic is the set of capture frequencies. We emphasize that the sufficiency of the capture frequencies holds over the entire class of distributions F of capture possibilities. This justifies their use in a nonparametric approach to the problem of population size estimation.

The unconditional distribution of the capture frequencies is multinomial, specifically

$$\mathrm{pr}\,(f_0, \ldots, f_t|F) = \binom{N}{f_0 \cdots f_t} \prod_{i=0}^{t} \{\pi_i(F)\}^{f_i}, \tag{1}$$

where the cell probabilities are

$$\pi_i(F) = \int_0^1 \binom{t}{i} p^i(1-p)^{t-i}\, dF(p). \tag{2}$$

When the above model was first considered the intent was to let $F(p)$ be in the beta class of distributions and use a standard parametric approach such as maximum likelihood. This approach was fully developed by K. P. Burnham in his thesis, but found to be unsatisfactory. Attention was then turned to deriving an estimator of N without specifying any parametric form for $F(p)$. The approach taken was based on the generalized jackknife statistic.

3. The generalized jackknife

Gray & Schucany (1972) give a comprehensive introduction to the jackknife and its generalizations. Let $y_1, \ldots, y_n$ be a random sample from a distribution involving a parameter θ. Assume $\hat\theta_n = \hat\theta_n(y_1, \ldots, y_n)$ is an estimator of θ satisfying

$$E(\hat\theta_n) = \theta + a_1/n + a_2/n^2 + \ldots, \tag{3}$$

where $a_1, a_2 \ldots$ are constants.

Because $y_1, \ldots, y_n$ is a random sample, it may be assumed without loss of generality that $\hat\theta_n(y_1, \ldots, y_n)$ is a symmetric function of its arguments. Let $j_1, \ldots, j_i$ be a combination of i integers from the set $\{1, \ldots, n\}$. For any such combination define $\hat\theta_{n-i,j_1,\ldots,j_i}$ as the estimator based on the $n-i$ random variables remaining after $y_{j_1}, \ldots, y_{j_i}$ are dropped from the sample. By assumption the only available unbiased estimators of $E(\hat\theta_{n-i})$ are these $\hat\theta_{n-i,j_1,\ldots,j_i}$. Thus the minimum variance unbiased estimator of $E(\hat\theta_{n-i})$ is the U-statistic (Fraser, 1957, p. 142)

$$\hat\theta_{(n-i)} = \binom{n}{i}^{-1} \sum_{j_1<\ldots<j_i} \hat\theta_{n-i,j_1,\ldots,j_i}.$$

For notational convenience let $\hat\theta_{(n)} = \hat\theta_n$. The basis for the generalized jackknife method of bias reduction is the set of estimators $\hat\theta_{(n-i)}$.

If we assume $E(\hat\theta_n)$ satisfies (3), then the kth order jackknife estimator, given by K. P. Burnham in his thesis and by Sharot (1976), is

$$\hat\theta_{Jk} = \frac{1}{k!} \sum_{i=0}^{k} (-1)^i \binom{k}{i} (n-i)^k \hat\theta_{(n-i)}. \tag{4}$$

The bias of $\hat\theta_{Jk}$ is of the order n^{-k-1}.

4. A NONPARAMETRIC ESTIMATOR OF POPULATION SIZE

4·1. *Introductory comment*

In this section a procedure for estimating N will be developed wherein the distribution of capture probabilities, F, is neither specified nor estimated. The reason for considering such a nonparametric approach is to have a robust estimator of population size. There is no unique approach that can be taken to derive a nonparametric estimator if nothing is specified about F. Our approach has been to apply the generalized jackknife and use S as the naive estimator, which is equivalent to $\hat{\theta}_n$ in § 3.

4·2. *Application of the jackknife in the present problem*

Let the sample be represented as $X_1, \ldots, X_t$, where X_i is the vector of results for day i, that is $X_i = (x_{1i}, \ldots, x_{Si})'$. Let the initial estimator $\hat{N}_{J0}$ be S, the number of individuals known to be in the population; S is the nonparametric maximum likelihood estimator of N. Clearly S is biased and this bias decreases as t increases. We assume that

$$E(S) = N + a_1/t + a_2/t^2 + \ldots,$$

where $a_1, a_2, \ldots$ are constants. Making the identifications $t = n$ and $S = \hat{\theta}_n$, and letting X_i be analogous to an individual datum, we can apply (4) once the U-statistics $\hat{\theta}_{(t-j)}$ are known. The derivation of these statistics is tedious; we illustrate the approach for $j = 1$. Let z_{1i} be the number of individuals seen exactly once, that one time being on day i $(i = 1, \ldots, t)$. Then

$$\hat{\theta}_{(t-1),i} = S - z_{1i}, \quad \hat{\theta}_{(t-1)} = \frac{1}{t}\sum_{i=1}^{t} \hat{\theta}_{(t-1),i} = S - \frac{1}{t}\sum_{i=1}^{t} z_{1i} = S - \frac{1}{t} f_1.$$

If $k = 1$ in (4), it follows that

$$\hat{N}_{J1} = S + \frac{t-1}{t} f_1.$$

The general result is

$$\hat{\theta}_{(t-j)} = S - \binom{t}{j}^{-1} \sum_{r=1}^{j} \binom{t-r}{j-r} f_r. \tag{5}$$

Equation (5) may be substituted into (4) but no general simplification results. It is necessary to derive the formula for $\hat{N}_{Jk}$ by straightforward but lengthy algebra; for $k = 1$ to 5 this has been done and the results are given in Table 1. It is seen from (4) and (5) that $\hat{N}_{Jk} = \Sigma a_{ik} f_i$ is a linear combination of the capture frequencies which are the minimal sufficient statistic under the assumed model. It follows from elementary properties of the multinomial distribution (Rao, 1973, Chapter 5) that

$$E(\hat{N}_{Jk}) = N \sum_{i=1}^{t} a_{ik} \pi_i(F), \quad \operatorname{var}(\hat{N}_{Jk}) = \sum_{i=1}^{t} (a_{ik})^2 E(f_i) - \{E(\hat{N}_{Jk})\}^2/N. \tag{6}$$

4·3. *A proposed estimation procedure*

The pattern generally found in applying the jackknife to live-trapping data is exemplified by computing $\hat{N}_{Jk}$ and its estimated standard error using the data of Edwards & Eberhardt (1967) on a penned population of 135 wild cottontail rabbits ($t = 18$). Recorded capture frequencies were:

i	1	2	3	4	5	6	7	8	…	18
f_i	43	16	8	6	0	2	1	0	…	0.

Results are shown in Table 2. In this example the estimated mean squared error of $\hat{N}_{Jk}$ has a unique minimum, as a function of k, which occurs at $k = 2$.

Table 1. *The jackknife estimators $\hat{N}_{Jk}$ of population size, for $k = 1, \ldots, 5$*

$$\hat{N}_{J1} = S + \left(\frac{t-1}{t}\right) f_1$$

$$\hat{N}_{J2} = S + \left(\frac{2t-3}{t}\right) f_1 - \left\{\frac{(t-2)^2}{t(t-1)}\right\} f_2$$

$$\hat{N}_{J3} = S + \left(\frac{3t-6}{t}\right) f_1 - \left\{\frac{3t^2-15t+19}{t(t-1)}\right\} f_2 + \left\{\frac{(t-3)^3}{t(t-1)(t-2)}\right\} f_3$$

$$\hat{N}_{J4} = S + \left(\frac{4t-10}{t}\right) f_1 - \left\{\frac{6t^2-36t+55}{t(t-1)}\right\} f_2 + \left\{\frac{4t^3-42t^2+148t-175}{t(t-1)(t-2)}\right\} f_3 - \left\{\frac{(t-4)^4}{t(t-1)(t-2)(t-3)}\right\} f_4$$

$$\hat{N}_{J5} = S + \left(\frac{5t-15}{t}\right) f_1 - \left\{\frac{10t^2-70t+125}{t(t-1)}\right\} f_2 + \left\{\frac{10t^3-120t^2+485t-660}{t(t-1)(t-2)}\right\} f_3 - \left\{\frac{(t-4)^5-(t-5)^5}{t(t-1)(t-2)(t-3)}\right\} f_4 + \left\{\frac{(t-5)^5}{t(t-1)(t-2)(t-3)(t-4)}\right\} f_5$$

Table 2. *Application of $\hat{N}_{Jk}$ to data of Edwards & Eberhardt* (1967)

k	$\hat{N}_{Jk}$	Est. st. error
0	76	—
1	116·6	8·9
2	141·5	14·9
3	158·6	21·9
4	170·3	31·1
5	176·5	43·5

Examining the theoretical mean squared error of $\hat{N}_{Jk}$ over a variety of distributions $F(p)$ for $5 \leqslant t \leqslant 30$, we found the unique minimum was usually achieved at $k = 1$, 2 or 3. The exact $\hat{N}_{Jk}$ which achieved the minimum mean squared error varied considerably according to the distribution of capture probabilities and the value of t. Accordingly, no rule can be formulated independent of the data to specify a value of k such that $\hat{N}_{Jk}$ should be used for any given study. An objective procedure is needed whereby the data can be used to indicate which $\hat{N}_{Jk}$ should be used for that study. The following procedure is proposed.

Test the hypothesis that there is no difference between the expected values of $\hat{N}_{J1}$ and $\hat{N}_{J2}$, that is test

$$H_{01}: E(\hat{N}_{J2} - \hat{N}_{J1}) = 0 \quad \text{versus} \quad H_{a1}: E(\hat{N}_{J2} - \hat{N}_{J1}) \neq 0.$$

If H_{01} is not rejected this is interpreted as evidence that the decrease in absolute bias achieved by using $\hat{N}_{J2}$, rather than $\hat{N}_{J1}$, is small relative to the variance of $\hat{N}_{J2}$. Given the generally smaller variance of $\hat{N}_{J1}$, it is concluded that there is no reason to use $\hat{N}_{J2}$; instead $\hat{N}_{J1}$ should be taken as the estimator of N.

If H_{01} is rejected this is interpreted as evidence of significant bias reduction relative even to the increased variance of $\hat{N}_{J2}$. The estimator $\hat{N}_{J2}$ should be preferred to $\hat{N}_{J1}$. But further bias reduction may be possible. Before accepting $\hat{N}_{J2}$ as the estimator to be used with the study at hand, test $\hat{N}_{J2}$ versus $\hat{N}_{J3}$. If this test results in rejection the process continues in the obvious manner. The estimator, $\hat{N}_J$, chosen by this process will be called the jackknife estimator.

The general procedure for choosing $\hat{N}_J$ is to test sequentially the hypotheses

$$H_{0t}: E(\hat{N}_{J,t+1} - \hat{N}_{Jt}) = 0 \quad \text{versus} \quad H_{at}: E(\hat{N}_{J,t+1} - \hat{N}_{Jt}) \neq 0$$

for $i \leqslant 4$, and choose $\hat{N}_J = \hat{N}_{Ji}$ such that H_{0i} is the first null hypothesis not rejected.

The test of H_{0i} is based on the fact that

$$\hat{N}_{J,i+1} - \hat{N}_{Ji} = \sum_{i=1}^{t} a_i f_i$$

is a linear combination of the capture frequencies, and the conditional distribution of these frequencies given S is free of N. It follows that the minimum variance unbiased estimator of the conditional variance is

$$\text{est var}\,(\hat{N}_{J,i+1} - \hat{N}_{Ji} \mid S) = \frac{S}{S-1}\left\{\sum_{i=1}^{t} a_i^2 f_i - (\hat{N}_{J,i+1} - \hat{N}_{Ji})^2/S\right\}.$$

Given H_{0i} the test statistic,

$$T_i = \frac{\hat{N}_{J,i+1} - \hat{N}_{Ji}}{\{\text{est var}\,(\hat{N}_{J,i+1} - \hat{N}_{Ji} \mid S)\}^{\frac{1}{2}}}$$

has approximately a standard normal distribution.

The procedure of testing these hypotheses should be viewed as a very useful guide to the choice of $\hat{N}_J$. Obviously, there is no unique significance level such that if $H_{0,i-1}$ is rejected at this level, and H_{0i} is not rejected, then $\hat{N}_J = \hat{N}_{Ji}$ is clearly indicated. It is anticipated that the achieved significance levels, P_i, will be increasing. If P_{i-1} is small, such as smaller than 0·05, while P_i is much larger than 0·05 it is reasonable to take $\hat{N}_J = \hat{N}_{Ji}$. One possible procedure of course is to carry out all the tests at the 5% level.

Results of this selection procedure applied to the data of Edwards & Eberhardt (1967) are given in Table 3. This suggests $\hat{N}_{J3} = 158{\cdot}6 \pm 21{\cdot}9$ as the estimate to use for these data.

Table 3. *The selection procedure applied to data of Edwards & Eberhardt* (1967)

Null hypothesis	T_i	P_i
H_{01}	4·053	< 0·0001
H_{02}	2·071	0·0383
H_{03}	1·071	0·2842
H_{04}	0·417	0·6766

Given that $\hat{N}_J = \hat{N}_{Jk}$ has been chosen, an estimator of its sampling variance, from (6), is

$$\text{est var}\,(\hat{N}_J) = \sum_{i=1}^{t} a_{ik}^2 f_i - \hat{N}_J. \tag{7}$$

If we assume a small relative bias, this allows approximate confidence intervals for N to be constructed, via a normal approximation.

This estimation procedure has been investigated by simulation and application to real data; results are available from the authors. Consequently we suggest the following modification to the selection procedure; this interpolated estimator smooths the otherwise discrete nature of choosing exactly one of the $\hat{N}_{Jk}$.

Find the first index m such that the significance level $P_m > 0{\cdot}05$. If $m = 1$, take $\hat{N}_{J1}$ as the estimator. If $m > 1$, then compute an interpolated estimator between $m-1$ and m, as $\hat{N}_J = c\hat{N}_{Jm} + (1-c)\,\hat{N}_{J,m-1}$, where

$$c = (0{\cdot}05 - P_{m-1})/(1 - P_m).$$

This interpolated estimator is still a linear combination of the frequencies with coefficients

$$b_i = ca_{im} + (1-c)\,a_{i,m-1};$$

the jackknife coefficients a_{im} come from Table 1. Hence (7) is applicable with the a_{ik} replaced by b_i.

When this estimate is found for Edwards & Eberhardt's (1967) data we have $m = 3$, $c = 0{\cdot}0476$, and the interpolated jackknife coefficients are

i	1	2	3	4	...	18
b_i	2·873	0·0907	1·033	1·000	...	1·000.

The resultant estimate is $\hat{N}_J = 142$ with an estimated standard error of 15·2.

5. A test of the model

A composite test of the assumed model can be made by testing the null hypothesis of no time variation in capture probabilities: $p_{ji} = p_j$ $(j = 1, \ldots, S;\ i = 1, \ldots, t)$. Let the individuals which have been captured at least once be indexed $1, \ldots, S$. Define the conditional random variables $X_{j|k} = (x_{j1}, \ldots, x_{jt})'$ given that $y_j = \Sigma x_{ji} = k$. Under the above null hypothesis the distribution of $x_{j|k}$ is

$$\operatorname{pr}(x_{j1}, \ldots, x_{jt} \mid y_j = k) = \binom{t}{k}^{-1} \quad (k = 0, 1, \ldots, t). \tag{8}$$

The conditional random variables $X_{j|k}$ are independent by assumption.

Now define the conditional random variable z_{ki} as the number of individuals captured on day i that were captured a total of exactly k times; it is a sum of f_k independent random variables. Finally $n_i = z_{1i} + \ldots + z_{ti}$ is the total captured on day i.

Given the above null hypothesis of no time variation in capture probabilities, then

$$E(n_i \mid f_1, \ldots, f_t) = \sum_{k=1}^{t} \frac{k}{t} f_k = \bar{n} = \frac{1}{t}\sum_{i=1}^{t} n_i, \quad \operatorname{var}(n_i \mid f_1, \ldots, f_t) = \sum_{k=1}^{t} f_k \left(\frac{k}{t}\right)\left(1 - \frac{k}{t}\right)$$

and a test statistic is

$$\left\{\sum_{i=1}^{t} (n_i - \bar{n})^2 (t-1)\right\} \Big/ \left\{\sum_{k=1}^{t} f_k \left(\frac{k}{t}\right)\left(1 - \frac{k}{t}\right) t\right\}.$$

This statistic is approximately a central chi-squared variable with $t-1$ degrees of freedom under the null hypothesis. This test is conditional on the capture frequencies. We note that the above test is related to Leslie's test (Carothers, 1971) with the role of individuals and sampling periods interchanged. Also, Carothers's (1971) modification of Leslie's test is appropriate for use here when S is small, say less than 30.

Individual goodness-of-fit tests based only on f_k are also possible if f_k is large enough to justify the chi-squared approximation. Then for $k = 1, \ldots, t-1$, a test of the null hypothesis that $p_{ji} = p_j$, for all j such that $y_j = k$, is given by

$$\sum_{i=1}^{t} \frac{(z_{ki} - kt^{-1} f_k)^2}{kt^{-1} f_k} \left(\frac{t-1}{t-k}\right)$$

which has approximately the distribution $\chi^2(t-1)$. K. P. Burnham proves these results in his thesis.

From Edwards & Eberhardt (1967), the 18 values of n_i are 9, 8, 9, 14, 8, 5, 18, 11, 4, 3, 16, 5, 2, 7, 9, 0, 4, 10. Thus $\Sigma(n_i - \bar{n})^2 = 391{\cdot}77$, $\Sigma f_i\, it^{-1}(1 - it^{-1}) = 6{\cdot}67$, and hence the overall chi-squared test statistic for time variation in capture probabilities is 55·5 with 17 degrees of freedom. There is clear evidence of time variation in the capture probabilities of this study.

From knowledge of the true $N = 135$ it is not difficult to show there is also evidence of considerable heterogeneity. From this one example we cannot conclude that the jackknife estimator is not sensitive to the time variation in capture probabilities. However, there is evidence that $\hat{N}_J$ has some robustness to such time variation, i.e. model failure, given that closure holds; see K. P. Burnham's thesis, and Otis *et al.* (1978).

6. Discussion

We have given a model for capture–recapture studies on closed populations which incorporates heterogeneity of capture probabilities. This model is especially oriented to the typical live-trapping study which uses a fixed grid of traps and daily trapping on several consecutive days. The derived jackknife estimator is nonparametric in the sense that no distribution $F(p)$ was assumed. The derivation of this estimator gives us reason to believe it will have some robustness to heterogeneity of capture probabilities. Tests of the assumption of no time variation in individual capture probabilities have also been given. We have not, however, presented any test for heterogeneity itself. This is deliberate; the scope of this paper has been limited to this one model and results derived thereunder. However, we believe any comprehensive analysis of live-trapping data should test for a variety of possible variations in capture probabilities, due to time, behaviour and heterogeneity, and combinations of these. The only comprehensive works along these lines we know of are K. H. Pollock's thesis and Otis *et al.* (1978). The latter reference builds on Pollock's theoretical work, is application-oriented and includes several examples of results presented here.

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