Ecology, 60(5), 1979, pp. 927–936
© 1979 by the Ecological Society of America

ROBUST ESTIMATION OF POPULATION SIZE WHEN CAPTURE PROBABILITIES VARY AMONG ANIMALS[1]

K. P. BURNHAM[2] AND W. S. OVERTON
Department of Statistics, Oregon State University, Corvallis, Oregon 97301 USA

Abstract. A model is given for multiple recapture studies on closed populations which allows capture probabilities to vary among individuals. The capture probability of each individual is assumed to be constant over time. Based on this model we give a nonparametric estimation procedure for population size. The estimator involves selecting one of a sequence of estimators which are each linear combinations of the capture frequencies. The individual estimators are derived from the generalized jackknife method. We also give a goodness of fit test for the model's assumption that individual capture probabilities do not change during the study. The robustness of this estimation procedure is investigated with a simulation study. By virtue of this study, and the theoretical nature of the estimator, it is judged to be robust to moderate variations in individual capture probabilities which may occur in commonly used short-term livetrapping studies.

Key words: capture-recapture; jackknife method; population size estimation; robust estimation; simulation; variable capture probabilities.

INTRODUCTION

Most of the literature on capture-recapture methods assumes that capture probabilities are equal for all animals in the population being trapped (see Seber 1973, for a comprehensive review). However, it has long been recognized that this assumption will often be violated. Controlled studies of small mammals have shown heterogeneity of capture probabilities among individuals (see e.g., Young et al. 1952, Tanaka 1956, Crowcroft and Jeffers 1961, Huber 1962, Edwards and Eberhardt 1967, Bailey 1969, Carothers 1973*a*). In studies where the true population size was known, the commonly used estimators were severely negatively biased by heterogeneity of capture probabilities (see e.g., Edwards and Eberhardt 1967, Carothers 1973*a*). Computer simulation studies have clearly shown that heterogeneity can cause substantial bias in the commonly used estimators (see e.g., Burnham and Overton 1969, Manly 1971, Gilbert 1973, Carothers 1973*b*, Otis et al. 1978). For a general discussion of the numerous factors that can affect capture probabilities see Smith et al. (1975), and Otis et al. (1978). In spite of this demonstrated need for models providing some degree of unequal probabilities of capture, there has been only meager consideration, or rigorous development of such models and associated relevant tests (Cormack 1966, Holgate 1966, Eberhardt 1969, Carothers 1971, Burnham 1972).

A comprehensive analysis of any capture-recapture study should test for a variety of sources of variability in capture probabilities and should consider the assumption of closure if a model assuming closure is being used. The population at risk of capture is said to be closed if no gains (immigration or birth) or losses (emigration or death) occur during trapping. Such a comprehensive analysis is now barely within the state-of-the-art for closed populations (see Otis et al. 1978) and has not yet been developed for open populations. The purpose of this paper is to present an estimator for closed populations which allows for variability of capture probabilities among animals, and to present evidence of its robustness. Detailed theory on the derivation of this estimator is given in Burnham (1972), and Burnham and Overton (1978).

THE JACKKNIFE ESTIMATOR

The model

Livetrapping studies on small mammals using a fixed grid of traps and trapping every day for a period of 3–10 d are common. In such studies it will often be more reasonable to adopt a model which assumes population closure, as opposed to the open models such as that of Jolly (1965) and Seber (1965). A general model for livetrapping studies conducted for t occasions (days) on a closed population of size N is based on assuming p_{ij} as the probability of capturing the j-th individual on the i-th day. This model is too general; some simplification is needed to obtain a model useful for making statistical inferences. Most previous work assumed either that the capture probabilities were all constant, or that they varied only by time. We assume capture probabilities are constant for any individual animal, but variable among individuals. In order to introduce a relationship among these capture probabilities we assume they are a random sample from some distribution on the unit interval. To summarize, our development rests on three mathematical assumptions:

[1] Manuscript received 12 April 1978; accepted 30 October 1978.

[2] Present address: United States Fish and Wildlife Service, 2526 Redwing Road, Fort Collins, Colorado 80526 USA.

TABLE 1. The jackknife estimators $\hat{N}_{Jk}$ of population size, for order k = 1 to 5, based on capture frequencies (f), number of distinct individuals encountered (S), and number of capture events (t).

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

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

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

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

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

1) Population closure.
2) $P_{ji} = p_i$ for all $i = 1, \ldots, t$ and $p_1, \ldots, p_N$ are a random sample from a probability distribution on the interval (0, 1).
3) Captures are independent events.

These mathematical assumptions require for their validity some constraints on the field sampling. One such constraint worth mentioning is equal sampling effort on each occasion, which itself implies the same number of traps used each time, preferably in a fixed grid.

The basic capture data can be expressed as a matrix of zeros and ones:

$$X_{ji} = \begin{cases} 1 \text{ if the j-th animal is caught on the i-th day,} \\ 0 \text{ otherwise.} \end{cases}$$

Numerous summary statistics can be computed from the basic capture data; in particular, let f_i represent the number of individuals captured exactly i times. For $i = 1, \ldots, t$ these are the capture frequencies, while f_0 is the number of individuals never captured. An additional statistic of interest is $S = \sum_{i=1}^{t} f_i$, the total number of distinct individuals seen during the study. Note that $N = S + f_0$.

Given the assumption that the set of N capture probabilities are a random sample, it follows that the capture frequencies have a multinomial distribution. This mathematical result, and others underpinning the developments presented here are given in Burnham and Overton (1978).

Applying the jackknife

The jackknife technique was originally devised by Quenouille (1956) as a bias reduction technique. Since then it has been extensively used, justified and developed as a statistical inference method. The basic idea of the jackknife is to reduce an estimator's bias by taking advantage of subsamples drawn from the entire sample. Let $y_1, \ldots, y_n$ denote a random sample of size n and let $\hat{\theta}_n$ estimate a parameter θ based on the entire sample. Let $E(\hat{\theta}_n)$ be the expected (average) value of $\hat{\theta}_n$; then the bias of $\hat{\theta}_n$ is $E(\hat{\theta}_n) - \theta$. Often this bias will be of the magnitude 1/n. Let any one datum, y_i, be dropped from the computation of $\hat{\theta}_n$; denote the resultant estimator as $\hat{\theta}_{n-1,-i}$. A new estimator computed as $n\hat{\theta}_n - (n-1)\hat{\theta}_{n-1,-i}$ will have a bias on the order of $1/(n)^2$. Greater efficiency is achieved if, instead of dropping one arbitrary datum, one computes the average of all n such estimators,

$$\hat{\theta}_{(n-1)} = \frac{1}{n}\sum_{i=1}^{n} \hat{\theta}_{n-1,-i}$$

and defines the jackknife estimator of θ as

$$\hat{\theta}_{J1} = n\hat{\theta}_n - (n-1)\hat{\theta}_{(n-1)}.$$

This is the first order jackknife.

Initially, the jackknife was only concerned with eliminating biases of the order 1/n. More recent work has generalized the jackknife to eliminate higher-order bias terms by computing estimators after dropping 2, 3, etc., data values and defining corresponding average values of $\hat{\theta}_{(n-j)}$, $j = 2, 3, \ldots$. For a comprehensive introduction to the generalized jackknife see Gray and Schucany (1972) and Miller (1964); for an example of jackknifing applied to an ecological problem see Zahl (1977).

The general usefulness and success of the jackknife led us to try it in the current problem. For application of the jackknife to this capture-recapture problem the appropriate units of sampling effort are days; i.e., sample size n is equated to the number of days, t, of trapping. The initial, biased estimator is taken as S, the total number of distinct animals caught. Translated to the current application, the fundamental assumption of the jackknife is that the bias of S can be formulated as a series in 1/t:

$$E(S) - N = \frac{c_1}{t} + \frac{c_2}{t^2} + \cdots,$$

for some (unknown) constants $c_1, c_2, \ldots$.

Actual derivation of the resultant estimators of population size N in this application is tedious (Burnham and Overton 1978) and requires several steps including determining the statistics $\hat{\theta}_{(n-j)}$. However, the results are simple, closed-form formulae. For example, the first order jackknife estimator is

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

(recall that f_1 is the number of animals caught exactly once and S is the minimum number of animals known to be in the population). Formulae for the first five generalized jackknife estimators of N are given in Table 1.

The estimators of Table 1 are all linear functions of the capture frequencies. Because $S = \Sigma f_i$, it follows that

$$\hat{N}_{Jk} = \sum_{i=1}^{t} a_{ik} f_i.$$

for some known constants a_{ik}. For convenience the formulae of Table 1 are expressed as

$$\hat{N}_{Jk} = S + \sum_{i=1}^{k} \alpha_{ik} f_i$$

(note that $\alpha_{ik} = 0$ for $i > k$). For some purposes the constants a_{ik} are needed; they are obtained as $a_{ik} = \alpha_{ik} + 1$. For example

$$\hat{N}_{J1} = \left(\frac{t-1}{t} + 1\right) f_1 + \sum_{i=2}^{t} 1 \cdot f_i.$$

In discussing the properties of $\hat{N}_{Jk}$ the roles of t (sampling effort) and k (jackknife order) need to be distinguished. For any fixed value of t, the higher order jackknives (k increasing) lead to greater bias reduction, but at the cost of increased sampling variance. Conversely, for any fixed value of k as t increases $\hat{N}_{Jk}$ is (asymptotically) a consistent estimator of N and its sampling variance will decrease as sampling effort increases.

The pattern generally found in applying the jackknife to livetrapping data is exemplified by computing $\hat{N}_{Jk}$ and its estimated standard error for the data of Edwards and Eberhardt (1967). They conducted an 18-d livetrapping study on a penned population of 135 wild cottontail rabbits. Recorded capture frequencies f_1 to f_7 were 43, 16, 8, 6, 0, 2, 1. Capture frequencies f_8 to f_{18} were all zero. Results of applying $\hat{N}_{Jk}$ to these data are shown in Table 2. In this example the mean square error (variance plus bias-squared) of the sequence $\hat{N}_{Jk}$ has a unique minimum at k = 2 (This fact is known here only because the true value of N is known). Theoretical studies in Burnham (1972) support the conjecture that there will generally be a minimum mean square error at a small value of k; that is, there is a "best" $\hat{N}_{Jk}$. Hence it is meaningful to seek a procedure to select this best estimate.

A selection procedure.—By examining the theoretical mean square error of $\hat{N}_{Jk}$ over a variety of distributions of capture probabilities for $5 \leq t \leq 30$, we found the minimum was usually achieved at k = 1, 2 or 3. The exact $\hat{N}_{Jk}$ which achieved the minimum mean square 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 the $\hat{N}_{Jk}$ to be used for any given study. An objective procedure is presented below whereby the data can be used to select $\hat{N}_{Jk}$.

TABLE 2. Application of the jackknife estimator $\hat{N}_{Jk}$ of several orders (k) to the data of Edwards and Eberhardt (1967).

k	$\hat{N}_{Jk}$	$\hat{se}(\hat{N}_{Jk})$
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

First, we test the null hypothesis that there is no difference between the expected values of $\hat{N}_{J1}$ and $\hat{N}_{J2}$, i.e., test $H_{01}: E(\hat{N}_{J2} - \hat{N}_{J1}) = 0$ versus the alternative $H_{a1}: E(\hat{N}_{J2} - \hat{N}_{J1}) \neq 0$. If H_{01} is not rejected this is interpreted as evidence that the decrease in the 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 smaller variance of $\hat{N}_{J1}$ compared to $\hat{N}_{J2}$, it is therefore concluded that there is no reason to use $\hat{N}_{J2}$; rather $\hat{N}_{J1}$ should be taken as the estimator of N.

The rejection of H_{01} is interpreted as evidence of significant reduction in absolute bias relative even to the increased variance of $\hat{N}_{J2}$. The estimator of $\hat{N}_{J2}$ 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, 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 as follows: test the null hypotheses $H_{0k}: E(\hat{N}_{J,k+1} - N_{Jk}) = 0$ versus $H_{ak}: E(\hat{N}_{J,k+1} - \hat{N}_{Jk}) \neq 0$ sequentially for $k \leq 4$, and choose $\hat{N}_J = \hat{N}_{Jk}$ such that H_{0k} is the first null hypothesis not rejected. The actual test of H_{0k} is conditional on S, and is based on the fact that $\hat{N}_{J,k+1} - \hat{N}_{Jk} = \sum_{i=1}^{t} b_i f_i$ for the constants $b_i = a_{i,k+1} - a_{ik}$. Given the null hypothesis H_{0k}, the test statistic

$$T_k = \frac{\hat{N}_{J,k+1} - \hat{N}_{Jk}}{[(\hat{var}(\hat{N}_{J,k+1} - \hat{N}_{Jk} | S)]^{1/2}}$$

has approximately a standard normal distribution and

$$\hat{var}(\hat{N}_{J,k+1} - \hat{N}_{Jk} | S) = \frac{S}{S-1}\left[\sum_{i=1}^{t} (b_i)^2 f_i - \frac{(\hat{N}_{J,k+1} - \hat{N}_{Jk})^2}{S}\right].$$

TABLE 3. Results of applying the sequential selection tests to Edwards and Eberhardt's (1967) data. See text for further explanation.

Null hypothesis	T_k	P_k
H_{01}	4.053	<0.0001
H_{02}	2.071	0.0383
H_{03}	1.071	0.2842
H_{04}	0.417	0.6766

Because this test is conditional upon S, it does not depend upon the unknown value of N.

Large absolute values of T_k indicate rejection of H_{0k}. In particular let P_k be the probability of a value of $|T_k|$ larger than the observed value (i.e., P_k is the achieved two-sided significance level of the test). Values of P_k can be determined from any table of the standard normal distribution. A conventional criterion for rejecting H_{0k} is that P_k be smaller than 0.05.

An estimator of the sampling variance of $\hat{N}_J = \hat{N}_{Jk}$ is

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

and $\hat{\text{se}}(\hat{N}_J) = (\hat{\text{var}}[\hat{N}_J])^{1/2}$. Assuming a small absolute relative bias, $|N - E(\hat{N}_J)|/\text{se}(\hat{N}_J)$, it follows that $(\hat{N}_J - N)/\hat{\text{se}}(\hat{N}_J)$ is approximately a standard normal variate. This allows approximate confidence intervals to be constructed for N. For example $\hat{N} \pm 1.96\hat{\text{se}}(\hat{N}_J)$ is the approximate 95% confidence interval on N.

Table 3 shows the results of applying the selection procedure to the data of Edwards and Eberhardt (1967). Both H_{01} and H_{02} are rejected at the 5% level, but H_{03} is not rejected. This suggests $\hat{N}_{J3}$ (=158.6 ± 21.9) as the estimate to use for these data; recall that N = 135.

A simulation study

To get an idea of the properties of $\hat{N}_J$, this estimation procedure has been applied to some simulated livetrapping data from Burnham and Overton (1969). Table 4 gives the results of this study. There may be some loss of generality because N was always 100 in these studies.

These simulated data were generated as follows. For a given distribution of capture probabilities, a random sample $p_1, \ldots, p_{100}$ was drawn to represent the population. Livetrapping was then simulated for 30 occasions. Twenty independent replications were done for each distribution (a different set of capture probabilities was used each time). Three types of distributions were used: beta, symbolized as $B(\alpha,\beta)$; uniform on $(0, \theta)$, symbolized as $U(0, \theta)$; and the constant distribution $C(\theta)$ which assigns the capture probability θ to all individuals. This last class of distributions corresponds to the model wherein all individuals have constant and equal capture probabilities. From these three classes, 32 different distributions of capture probabilities were used, with average capture probability, E(p), ranging from 0.24 to 0.04. This gives a total of 640 independent studies simulated. Each study was examined on occasions (days) 5, 10, 15, 20, 25 and 30, making a total of 3840 different, though not independent, simulated livetrapping studies. For this simulation evaluation the selection procedure tests were all conducted at the 5% level.

The entries in Table 4 are mostly averages. For each distribution of capture probabilities and each value of t, the 20 values of $\hat{N}_J = \hat{N}_{Jk}$ were averaged as were the 20 values of k. These averages are identified simply as "k" and "$\hat{N}_J$." The estimated standard error of $\hat{N}_J$ was computed for each study, and then averaged to obtain $\hat{\text{se}}(\hat{N}_J)$ given under that column heading. For each study the approximate 95% confidence interval was computed and it was recorded whether or not the interval covered N. The column headed "Coverage" gives the total times, out of 20 possible, that the interval covered N = 100.

The last three columns of Table 4 came from the original study of Burnham and Overton (1969). They are included here to aid in interpreting the properties of $\hat{N}_J$. The column headed by S gives the average number of distinct individuals seen. The Schnabel estimator (Schnabel 1938), $\hat{N}_{SH}$, is widely used to estimate population size; it is based on the assumption of equal capture probabilities during each trapping period. The average of $\hat{N}_{SH}$ over the 20 replications of each case is given in Table 4. The average estimated standard error of $\hat{N}_{SH}$ is also given.

The simulation study showed two unexpected situations that can arise when applying the selection procedure: (1) sometimes all H_{0k} are rejected, and (2) under certain circumstances the chosen $\hat{N}_J$ can be less than S. Both of these cases were examined in detail, and a decision was made as to an appropriate value of $\hat{N}_J$.

For t = 5, $\hat{N}_{J4} = \hat{N}_{J5}$, which results in H_{04} never being rejected. However, for the 3020 studies where t > 5, there was a total of 111 cases (3.7%) where all H_{0k}, k = 1, 2, 3, 4 were rejected at the 5% level. For the 800 studies where t > 5 and E(p) was 0.04 or 0.06, there were 69 such occurrences (8.6%), while for E(p) ≥ 0.09 and t > 5 there were only 42 such occurrences out of 2400 cases (1.8%). Based on an examination of these 111 cases when all four null hypotheses were rejected at the 5% level it was concluded that neither $\hat{N}_{J4}$ nor $\hat{N}_{J5}$ should be taken as $\hat{N}_J$. Rather a choice should be made from $\hat{N}_{J1}$, $\hat{N}_{J2}$ or $\hat{N}_{J3}$. By examining all information available it was usually not difficult to make a reasonable choice.

We emphasize that failure of the selection procedure was rare, especially for models with average capture probability >0.10. As stressed by Otis et al. (1978), to get reliable results from capture studies one should

TABLE 4. Simulation evaluation of the jackknife estimator ($\hat{N}_J$) and a comparison to the Schnabel estimator ($\hat{N}_{SH}$) under selected beta, uniform and constant distributions of capture probabilities. t = number of capture events; k, $\hat{N}_J$, S, and $\hat{N}_{SH}$ are averages for 20 replications. N = 100 in all cases.

t	k	$\hat{N}_J$	$\hat{se}(\hat{N}_J)$	Coverage	S	$\hat{N}_{SH}$	$\hat{se}(\hat{N}_{SH})$
Distribution = B(0.3158, 1.0) E(p) = 0.24							
5	1.7	65.7	6.7	1	48.1	48.3	5.4
10	1.4	72.6	6.3	3	57.0	53.2	4.7
15	1.4	77.7	6.3	4	62.2	56.7	4.4
20	1.4	80.5	6.4	5	65.1	59.1	4.4
25	1.7	86.1	7.6	6	67.9	61.0	4.3
30	1.2	80.2	5.2	3	69.1	62.5	4.3
Distribution = B(1.0, 3.1667) E(p) = 0.24							
5	1.6	83.8	7.6	9	59.3	65.8	6.6
10	1.1	91.6	6.1	14	74.1	72.4	5.2
15	1.1	95.3	5.6	17	80.8	76.9	4.5
20	1.2	99.7	5.9	19	85.3	79.2	3.7
25	1.2	101.9	5.9	15	87.7	81.2	3.4
30	1.0	99.2	4.5	17	89.7	82.9	3.1
Distribution = B(6.0, 19.0) E(p) = 0.24							
5	2.2	115.0	11.2	14	71.8	92.8	10.8
10	1.1	110.6	6.7	15	89.7	93.9	4.2
15	1.2	109.3	5.7	19	95.9	95.6	2.7
20	1.0	103.8	3.5	20	98.1	96.6	2.0
25	1.0	102.6	2.8	20	99.1	97.3	1.6
30	1.0	101.3	1.9	18	99.5	97.7	1.3
Distribution = U(0, 0.48) E(p) = 0.24							
5	1.8	99.5	9.4	18	67.0	80.4	9.6
10	1.1	98.5	6.2	19	81.3	82.3	5.1
15	1.0	99.2	5.0	18	87.2	84.8	4.0
20	1.0	99.8	4.5	20	90.3	86.6	3.3
25	1.0	99.3	4.0	20	92.1	87.9	2.8
30	1.0	99.3	3.6	18	93.2	89.0	2.5
Distribution = C(0.24) E(p) = 0.24							
5	2.2	122.4	12.0	14	75.5	102.0	7.2
10	1.1	111.0	6.4	9	93.5	100.4	3.2
15	1.0	106.9	4.3	14	98.2	100.2	2.2
20	1.0	102.7	2.5	20	99.7	100.3	1.6
25	1.0	100.9	1.4	20	99.9	100.2	1.2
30	1.0	100.2	0.6	19	99.9	100.1	1.1
Distribution = B(0.25, 1.0) E(p) = 0.2							
5	1.5	56.7	5.7	0	43.3	43.1	5.6
10	1.5	67.0	6.3	1	51.9	48.0	5.4
15	1.3	69.0	5.7	1	55.8	50.9	5.4
20	1.3	72.0	5.6	2	59.3	53.3	5.4
25	1.3	75.1	6.0	2	61.5	55.1	5.4
30	1.6	80.2	7.2	5	63.4	56.6	5.3
Distribution = B(1.0, 4.0) E(p) = 0.2							
5	2.1	87.6	8.7	12	55.5	66.8	7.0
10	1.5	97.0	8.3	16	72.1	72.5	4.8
15	1.4	101.7	7.8	18	79.8	79.5	4.1
20	1.0	98.8	5.6	20	84.2	79.2	3.6
25	1.1	100.5	5.4	20	87.3	81.3	3.3
30	1.0	99.4	4.7	19	89.1	83.0	3.0
Distribution = B(4.0, 16.0) E(p) = 0.2							
5	2.6	110.7	12.2	16	64.8	89.6	11.4
10	1.1	105.9	7.1	19	83.1	89.4	5.0
15	1.0	105.9	5.8	18	91.4	91.6	3.5
20	1.0	104.9	4.6	17	94.9	93.1	3.0
25	1.0	103.2	3.7	18	96.8	94.3	2.6
30	1.0	102.1	2.8	18	98.0	99.0	2.2
Distribution = U(0, 0.4) E(p) = 0.2							
5	2.3	96.6	10.6	17	58.6	77.5	8.4
10	1.1	97.1	6.7	18	76.4	80.7	5.7
15	1.1	97.9	5.8	16	83.2	82.9	4.5
20	1.0	96.9	4.7	15	86.6	84.4	4.0
25	1.0	97.5	4.3	15	89.1	85.7	3.8
30	1.1	98.5	4.3	15	90.4	86.7	3.7
Distribution = C(0.2) E(p) = 0.2							
5	2.4	116.8	12.5	17	67.7	100.1	11.0
10	1.1	113.7	7.6	11	88.9	99.0	4.2
15	1.1	105.8	5.1	18	95.8	99.1	2.6
20	1.0	103.6	3.2	19	98.6	99.4	1.7
25	1.0	101.6	2.1	20	99.4	99.5	1.3
30	1.0	100.9	1.3	19	99.9	99.6	1.1
Distribution = B(0.1905, 1.0) E(p) = 0.16							
5	2.1	51.4	6.6	0	35.1	35.9	3.5
10	1.7	58.9	7.0	2	42.3	39.8	2.6
15	1.2	57.0	5.1	0	46.0	42.2	2.6
20	1.4	61.3	5.6	2	48.5	44.0	2.7
25	1.3	63.8	5.7	2	51.2	45.7	2.8
30	1.7	69.2	7.1	4	52.9	47.0	2.9
Distribution = B(1.0, 5.25) E(p) = 0.16							
5	2.4	79.2	10.2	10	46.5	63.2	9.6
10	1.4	89.2	8.1	9	64.0	67.5	4.5
15	1.6	101.0	9.2	16	73.4	71.8	3.5
20	1.1	98.5	7.6	18	79.2	75.0	2.9
25	1.0	97.7	5.6	17	83.0	77.4	2.9
30	1.1	99.1	5.5	18	85.7	79.3	2.9
Distribution = B(4.0, 21.0) E(p) = 0.16							
5	3.4	110.0	14.1	19	55.4	87.0	13.2
10	1.3	108.8	8.7	18	77.9	90.0	5.8
15	1.1	110.3	7.2	15	87.7	91.6	4.4
20	1.0	107.6	5.6	16	92.6	92.9	3.6
25	1.0	106.1	4.8	19	95.3	93.9	3.1
30	1.0	104.7	4.2	19	96.8	94.7	2.6
Distribution = U(0, 0.32) E(p) = 0.16							
5	3.0	97.8	12.3	17	53.5	77.4	10.5
10	1.2	98.6	7.9	18	72.1	80.0	4.9
15	1.2	101.1	6.9	19	80.6	82.3	3.6
20	1.0	98.3	5.4	19	84.6	83.8	3.0
25	1.0	98.5	4.9	18	87.4	85.0	2.9
30	1.0	98.8	4.6	18	89.2	86.0	2.8
Distribution = C(0.16) E(p) = 0.16							
5	3.3	118.2	14.6	16	58.9	100.7	10.0
10	1.2	114.6	8.5	15	83.2	99.9	4.8
15	1.1	112.5	6.6	9	93.2	100.3	2.9
20	1.0	107.7	4.8	19	96.8	100.0	2.0
25	1.0	105.0	3.6	18	99.0	100.1	1.5
30	1.0	102.6	2.5	18	99.4	100.0	1.3
Distribution = B(0.1364, 1.0) E(p) = 0.12							
5	1.8	36.5	5.3	0	25.5	26.3	5.3
10	1.4	44.2	5.5	1	32.2	30.2	5.4
15	1.2	46.0	4.7	0	36.1	32.6	5.7
20	1.2	49.3	4.9	1	39.0	34.5	6.1
25	1.6	50.4	5.0	1	40.3	35.9	6.3
30	1.2	51.7	5.0	1	41.5	37.0	6.3

TABLE 4. Continued.

t	k	$\hat{N}_J$	$\hat{se}(\hat{N}_J)$	Cover-age	S	$\hat{N}_{SH}$	$\hat{se}(\hat{N}_{SH})$
Distribution = B(1.0, 7.333) E(p) = 0.12							
5	2.7	74.4	10.5	8	39.3	59.0	9.7
10	1.5	84.9	8.8	5	57.0	64.0	6.6
15	1.3	90.9	7.8	10	66.7	67.9	6.2
20	1.0	90.0	6.1	12	72.8	70.6	6.2
25	1.2	97.6	6.9	18	77.7	73.4	5.2
30	1.1	98.1	6.1	19	81.2	75.7	4.8
Distribution = B(3.0, 22.0) E(p) = 0.12							
5	3.3	93.2	13.0	17	45.0	80.1	18.3
10	1.7	104.7	11.1	16	64.6	81.6	8.7
15	1.3	108.1	9.0	17	76.6	84.7	6.6
20	1.1	105.8	7.0	19	83.5	86.6	5.0
25	1.0	104.3	5.9	18	87.8	88.1	4.7
30	1.0	104.5	5.4	18	91.0	89.4	4.0
Distribution = U(0, 0.24) E(p) = 0.12							
5	3.5	92.2	13.2	15	43.9	79.2	16.2
10	1.7	101.0	10.5	18	64.2	80.9	10.0
15	1.2	101.0	8.0	18	74.6	81.8	6.2
20	1.3	105.3	7.5	18	81.2	83.5	4.3
25	1.2	103.2	6.6	18	84.8	84.7	3.8
30	1.1	101.2	5.5	18	87.4	85.7	3.3
Distribution = C(0.12) E(p) = 0.12							
5	3.8	110.6	14.9	17	48.6	111.8	33.4
10	1.8	119.7	11.4	12	73.3	101.6	13.5
15	1.2	114.9	8.3	12	85.8	99.8	7.1
20	1.0	109.2	6.0	13	91.7	99.2	5.6
25	1.0	107.3	5.2	15	95.7	99.5	4.5
30	1.0	105.9	4.1	19	97.9	99.6	3.6
Distribution = B(1.0, 10.111) E(p) = 0.09							
5	3.1	69.3	11.0	8	33.2	64.5	25.5
10	1.9	89.5	11.3	10	51.4	66.1	11.4
15	1.4	90.1	8.9	13	60.8	67.5	8.7
20	1.4	94.5	8.6	11	67.1	69.5	7.4
25	1.2	94.8	7.5	13	71.9	71.6	6.8
30	1.3	97.6	8.0	14	75.1	73.1	6.5
Distribution = B(9.0, 91.0) E(p) = 0.09							
5	3.8	88.3	13.3	17	37.2	110.5	48.5
10	2.3	112.0	14.6	16	58.6	92.7	12.4
15	1.4	111.3	10.3	17	73.2	93.4	8.8
20	1.2	112.4	8.4	15	82.4	94.3	7.0
25	1.0	112.6	7.2	10	88.8	95.5	5.3
30	1.0	112.0	6.7	12	92.4	96.1	4.4
Distribution = U(0, 0.18) E(p) = 0.09							
5	3.7	79.1	12.6	12	34.2	84.2	22.9
10	2.4	105.4	14.4	18	54.1	78.4	10.5
15	1.3	98.5	8.8	14	66.7	80.0	8.0
20	1.3	102.4	8.6	17	74.0	81.4	6.3
25	1.1	101.1	6.9	20	79.4	83.1	5.7
30	1.0	99.8	6.2	20	84.4	83.8	5.0
Distribution = C(0.09) E(p) = 0.09							
5	3.9	94.5	14.0	18	38.7	117.1	34.2
10	2.5	123.4	16.2	18	60.9	104.7	15.2
15	1.5	117.1	10.8	14	75.6	101.2	9.9
20	1.1	115.6	8.4	10	84.7	101.2	6.6
25	1.0	111.6	6.9	12	89.9	100.4	4.7
30	1.0	111.1	6.0	13	94.0	100.5	3.3
Distribution = B(1.0, 15.6667) E(p) = 0.06							
5	3.4	50.8	9.8	0	23.0	47.1	11.1
10	2.2	74.7	11.6	8	38.2	54.0	8.6
15	1.6	82.9	10.0	9	49.3	60.0	8.0
20	1.5	87.7	9.6	9	56.3	62.9	7.2
25	1.6	92.7	9.9	11	61.5	65.1	6.9
30	1.3	88.9	7.9	10	65.1	66.5	6.6
Distribution = B(3.0, 47.0) E(p) = 0.06							
5	3.6	61.0	10.9	3	24.5	85.0	52.6
10	2.6	92.6	14.4	18	41.8	81.2	20.7
15	1.9	98.6	12.2	20	54.1	79.9	9.6
20	1.8	108.5	12.4	17	63.5	82.6	8.4
25	1.4	104.7	9.7	18	70.1	83.5	7.4
30	1.2	106.3	10.5	17	75.5	84.8	6.0
Distribution = U(0, 0.12) E(p) = 0.06							
5	3.8	61.8	11.1	4	24.6	98.0	45.1
10	2.6	94.7	14.5	17	42.2	83.0	14.8
15	1.9	98.3	12.3	18	54.0	80.9	9.7
20	1.5	97.1	10.0	12	62.0	79.9	8.1
25	1.2	96.3	8.1	16	69.0	80.9	6.4
30	1.1	98.0	7.5	18	73.1	81.3	5.5
Distribution = C(0.06) E(p) = 0.06							
5	3.9	68.4	11.8	6	26.7	122.5	65.8
10	2.6	103.8	15.3	18	45.5	101.6	22.4
15	1.8	106.3	12.3	16	59.3	96.7	13.0
20	1.6	114.4	11.6	15	70.1	98.6	11.1
25	1.2	111.5	9.0	17	77.6	98.3	7.9
30	1.0	111.5	7.7	17	83.4	98.7	6.5
Distribution = B(1.0, 24.0) E(p) = 0.04							
5	3.2	40.2	8.4	0	17.5	44.3	21.0
10	2.4	65.7	11.5	6	29.4	58.3	27.8
15	2.1	79.2	12.1	10	39.0	59.1	13.5
20	2.2	90.5	13.3	13	45.8	60.9	11.4
25	1.8	89.2	11.4	14	51.6	62.8	10.3
30	1.6	91.1	10.5	11	56.5	64.2	8.7
Distribution = B(2.0, 48.0) E(p) = 0.04							
5	3.4	44.3	9.1	0	17.7	66.9	31.8
10	2.7	72.2	12.9	8	30.7	67.3	23.1
15	2.2	80.2	12.4	12	40.3	67.6	12.5
20	1.8	89.8	11.5	13	48.8	71.1	10.3
25	1.6	92.2	10.6	11	55.6	73.7	8.7
30	1.5	98.3	10.4	13	61.8	75.2	7.5
Distribution = U(0, 0.08) E(p) = 0.04							
5	3.4	43.1	8.9	0	17.5	72.3	46.0
10	2.3	68.6	11.6	8	30.2	76.5	21.9
15	2.4	89.4	14.0	17	41.4	77.6	14.8
20	2.1	98.2	13.8	15	49.7	78.3	11.1
25	1.6	96.1	11.6	13	56.3	77.7	8.3
30	1.5	97.8	10.4	17	62.5	79.0	5.9
Distribution = C(0.04) E(p) = 0.04							
5	3.5	48.2	9.6	0	18.5	104.3	41.2
10	2.6	82.7	13.8	13	33.3	102.5	34.0
15	2.5	107.6	16.1	20	45.8	101.8	18.1
20	2.2	116.8	15.4	17	55.9	102.0	14.1
25	1.8	115.2	13.5	17	63.6	98.6	12.4
30	1.7	118.9	13.1	14	70.2	98.0	10.2

have $E(p) \geq 0.10$. Failure to achieve this will seriously compromise the usefulness of the study.

In 96.3% of the cases the objective procedure arrived at a decision for k. However, in 119 of these cases $\hat{N}_J$ was $\leq S$. All of these cases were examined and almost without exception this only occurs when $S \geq 90$ (that is, 90% of the population had been seen). When $\hat{N}_J \leq S$, it was always the case that $\hat{N}_{J2} \leq S \leq \hat{N}_{J1}$, so that it was sufficient to take $\hat{N}_J = \hat{N}_{J1}$, which always provided a good estimate in these cases. We

concluded that this situation of the selection procedure choosing $\hat{N}_J < S$ does not constitute a problem because it seems only to occur with very good data wherein either S or $\hat{N}_{J1}$ is a good estimator.

By examining Table 4 it is seen that $\hat{N}_J$ is quite robust. For those distributions examined it only performs poorly for the B(α, 1) type. But for these distributions of capture probabilities no estimators examined (Burnham and Overton 1969) were found to have good properties. It is also seen that the standard error of $\hat{N}_J$ is of similar magnitude to that of $\hat{N}_{SH}$.

The order of the jackknife chosen by this procedure is seen to vary. The chief factors appear to be the number of trapping occasions and the average capture probability. At t = 5, k may easily be 2, 3, or 4. But at t = 10, k is probably 1, 2 or 3.

The coverage of N by the approximate 95% confidence intervals varied, and was not always good. Table 4 indicates that the nominal confidence level will not be achieved if the absolute value of the bias of $\hat{N}_J$ is as large or larger than the standard error of $\hat{N}_J$. Often this is not the case and then the true coverage of N appears to be 70% or more. In general, ignoring the B(α, 1) distributions, the confidence interval coverage appears to be 50% or better in this simulation study.

Most estimators do well under particular circumstances. For example, $\hat{N}_{SH}$ performs well if capture probabilities are constant over individuals. However, when capture probabilities vary it is apparent from Table 4 that $\hat{N}_{SH}$ has a consistently negative bias which may be quite large. The jackknife estimator is often biased but this bias may be either positive or negative; often $\hat{N}_J$ tends not to have a large absolute bias. In fact, when the results in Table 4 for $\hat{N}_J$ and $\hat{N}_{SH}$ are averaged over all distributions (28 of them) except the B(α, 1) type the results given in Table 5 show $\hat{N}_J$ to perform quite well.

An improved selection procedure

The stopping rule for selection of an estimator as given above was used for the simulation study and for application to some real data, including Carothers' (1973*a*) study on a real population (of taxicabs) with known N. As a result of these studies we suggest the following as an improved estimation procedure. (It was not possible to re-do the simulation study using this new procedure.)

Compute the test statistics T_i and their two-sided significance levels P_i. Find the first index k such that $P_k > 0.05$. If k = 1, take $\hat{N}_{J1}$ as the estimator of N. If k > 1, then compute an interpolated estimator between $\hat{N}_{J,k-1}$ and $\hat{N}_{Jk}$, as $\hat{N}_J = c\hat{N}_{Jk} + (1 - c)\hat{N}_{J,k-1}$, where $c = (0.05 - P_{k-1})/(P_k - P_{k-1})$. This interpolated estimator is still a linear combination of the capture frequencies, say $\hat{N}_J = \Sigma\, d_i f_i$, with coefficients $d_i = ca_{ik} + (1 - c)a_{i,k-1}$. The standard error of $\hat{N}_J$ is estimated by

TABLE 5. Average values of $\hat{N}_J$ and $\hat{N}_{SH}$ from all distributions of Table 4, except the B(α,1) type.

t	Average $\hat{N}_J$	Average $\hat{N}_{SH}$
5	84.2	84.4
10	97.6	82.9
15	99.7	83.9
20	102.2	85.2
25	101.6	86.5
30	101.7	88.4

$$\hat{se}(\hat{N}_J) = \left(\sum_{i=1}^{t} (d_i)^2 f_i - \hat{N}_J\right)^{1/2}.$$

This interpolated estimator smooths the otherwise discrete nature of choosing exactly one of the $\hat{N}_{Jk}$ and seems to be an improvement over the non-interpolated procedure.

When applied to Edwards and Eberhardt's (1967) data we have k = 3, c = 0.0476, and the interpolated jackknife coefficients are $d_1 = 2.873$, $d_2 = 0.0907$, $d_3 = 1.033$ while d_4 through d_{18} are all 1. The resultant estimate is $\hat{N}_J = 142$ (true N = 135) with an estimated standard error of 15.2.

Testing for time variation in capture probabilities

Three mathematical assumptions are basic to this model for capture-recapture studies: 1) closure, 2) independence of captures over individuals and occasions (which we can consider for convenience as days, and 3) individual capture probabilities are constant during trapping. Given the independence assumption we present some tests for variation in individual capture probabilities. First, we give a general test of the null hypothesis $H_0: p_{ji} = p_j$, j = 1, . . . , S; i.e., all captured individuals have constant capture probabilities over time but capture probabilities may vary among animals. Then a more specific test is suggested which is sensitive to behavioral variation, including failure of closure.

A general test.—Let the individuals which have been captured at least once be indexed from 1 through S. Define z_{ki} as the number of individuals captured on day i that were captured exactly k total times. The z_{ki} can be expressed analytically as a function of the basic data x_{ji}; doing so shows z_{ki} is a sum over f_k independent random variables. To compute any given z_{ki}, first determine the subset of animals caught exactly k times, then count how many of them were caught on day i. We note that

$$n_i = \sum_{k=1}^{t} z_{ki} = \text{total captures on day i.}$$

A test statistic for the null hypothesis of no time variation in capture probabilities is

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

(see Burnham 1972, Burnham and Overton 1978). Under H_0, this statistic is approximately a central chi-square variable with $t - 1$ degrees of freedom. Consequently, H_0 is rejected for large values of χ; in this case one is concluding that the capture probabilities of some animals changed during the study.

This approach to testing the hypothesis that capture probabilities do not change is based on a number of assumptions. If no one assumption stands out as weaker or more doubtful than the others, then this test constitutes a general test of the conformity of the data to our model.

A specific test for behavior changes including failure of closure.—A more specific test is suggested below as a suitable test for closure. If animals are entering or leaving the population during trapping they will have zero capture probabilities during some initial or terminal part of the trapping period. We would then expect the period of time between first and last capture for such individuals to be less, on the average, than it would be under the closure assumption. The specific alternatives to H_0 to which the following test is sensitive include those like $p_{ji} = 0$ for $i = 1, \ldots, r$ or $p_{ji} = 0$ for $i = s + 1, \ldots, t$ for $r < s$, while $p_{ji} = p_j$ for $i = r + 1, \ldots, s$.

For all animals captured at least twice, but not more than $t - 1$ times, define W_j as the first day of capture and V_j as the last day of capture. Then $1 \leq W_j < V_j \leq t$ and defining $Q_j = V_j - W_j$, we have Q_j is in the range $y_j - 1$ to $t - 1$, where y_j is the number of times the j-th animal is captured. Conditional on $y_j = k$, the expected value of Q_j is

$$E(Q_j | y_j = k) = \frac{k - 1}{k + 1}(t + 1).$$

If there is a failure of closure, we expect

$$E(Q_j | y_j = k) < \frac{k - 1}{k + 1}(t + 1)$$

for some animals caught at least twice.

To test this hypothesis, first determine Q_j for all animals caught between 2 and $t - 1$ times inclusive. Group the Q_j according to capture frequencies, so there are f_k values of Q for those animals caught k times. Then the average value of Q from each frequency group is an estimate of $E(Q_j | y_j = k)$; let this average be represented by $\hat{E}(Q | k)$. An overall test statistic of H_0 which is sensitive to behavioral changes in capture probabilities is

$$z = \frac{\sum_{k=2}^{t-1} \hat{E}(Q|k) - \frac{k - 1}{k + 1}(t + 1)}{\left[\sum_{k=2}^{t-1} \frac{2(t - k)(k - 1)(t + 1)}{(k + 2)(t + 1)^2 f_k}\right]^{1/2}}.$$

This statistic, z, is approximately a standard normal random variable under the null hypothesis. The approximation should be excellent if the sum $f_2 + \cdots + f_{t-1}$ is larger than 20. The actual test procedure is one-sided; specifically, reject the null hypothesis at the 5% level of significance if $z < -1.645$ occurs.

Examples.—It would be too lengthy to give detailed examples of all steps of these tests including the basic input data (the z_{ki} or the Q_j values). We will give the results of some applications.

From Edwards and Eberhardt (1967) we can easily compute

$$\sum_{i=1}^{18} (n_i - \bar{n})^2 = 391.77,$$

$$\sum_{i=1}^{18} f_i\left(\frac{i}{t}\right)\left(1 - \frac{i}{t}\right) = 6.67,$$

and hence the omnibus chi square test statistic for time variation in capture probabilities is 55.5 with 17 df ($t = 18$). Thus, there is clear evidence of time variation in the capture probabilities of this study ($P < .001$). Given the true population size, it is not difficult to show there is also evidence of considerable heterogeneity (this latter point is difficult to show without utilizing the known N). Under these circumstances we do not know if the interpolated jackknife estimator ($\hat{N}_j = 142$) is a fluke, or if the procedure is not sensitive to the time variation. There is evidence that $\hat{N}_j$ is robust to time variation in capture probabilities provided that closure holds (Burnham 1972, Otis et al. 1978).

The overall "closure" test applied to Edwards and Eberhardt's data gave a test value of $z = -2.132$ ($P = .0165$). This demonstrates the test is not just sensitive to the closure assumption failing; rather it is sensitive to certain types of alternatives to $p_{ji} = p_j$. In particular, time trends in capture probabilities can cause rejection. In this example the average capture probabilities decreased in the second 9 d of trapping.

Application to estimating species numbers

The procedure presented here can also be used to estimate the number of species of a given taxonomic group in a community. There is a simple analogy between our capture-recapture model and the species estimation problem. Let N be the number of species in the community. There will be differing numbers of individuals of each species, and different species may have differing behaviors. For those reasons we would expect that different species do not have equal capture probabilities. Rather, a model to represent the captures of these species (making no distinction between individuals of the same species) should allow different capture probabilities for each species.

If sampling to estimate the number of species has a design with t identified units of equal effort, the formulae and procedures previously discussed are appli-

cable. In so doing the basic data are the frequencies of encounter with the species. That is, in this application one interprets f_i as the number of species encountered exactly i times in the various samples. Note that an encounter occurs on the i-th sample if one or more individuals of that species is captured (i.e., the number of individuals seen for each species is not relevant for estimating numbers of species).

Most existing attempts to estimate species numbers are based on modeling the statistical distribution of these frequency data (see e.g., Engen 1974). Hence, such methods are parametric, relying on a particular parametric model. In many such models there is no concept of the number of trapping occasions. This arises because often the number of capture attempts (e.g., sweeps with an insect collection net) is both large and may not even be recorded. Our model can fit this situation by taking the limiting values of the coefficients a_{ik} and α_{ik} as t becomes infinite. Such a limit exists; in fact it is

$$\hat{N}_{Jk} = S + \sum_{i=1}^{k} (-1)^{i+1}\binom{k}{i} f_i,$$

where $\binom{k}{i}$ is the binomial coefficient, $(k!)/([k-i]!i!)$. The formula for the a_{ik} when t becomes infinite is

$$a_{ik} = \begin{cases} (-1)^{i+1}\binom{k}{i} + 1, & i = 1, \ldots, k \\ 1 & i > k. \end{cases}$$

As an example we use a set of data on insects from Mehninick (1964) (also see Engen 1974 who analyzed these data), where S = 124. The first five frequencies, in order, are 50, 20, 11, 6, 5. Using formulae for $\hat{N}_{Jk}$, $\hat{se}(\hat{N}_{Jk})$ and the selection procedure with the above formula for a_{ik} we computed the jackknife estimator of N for these data. Basic results are given in Table 6. Without computing the interpolated version of $\hat{N}_J$ we would take k = 2, hence $\hat{N}_J$ = 204 (±17.3). Using the interpolated selection procedure we have c = 0.665, hence $\hat{N}_J$ = (0.665)(204) + (0.335)(174) = 194. The corresponding coefficients b_i are d_1 = 2.665, d_2 = 0.335 and the rest of the d_i are all 1. Using these d_i, the standard error of $\hat{N}_J$ is estimated to be 14.7. An approximate 95% confidence interval on the number of insects in this sampled community is 194 ± (1.96)(14.7) or 165 to 223.

TABLE 6. Application of the jackknife to estimate total species of insects from Mehninick's (1964) data. See text for further explanation.

k	$\hat{N}_{Jk}$	$\hat{se}(\hat{N}_{Jk})$	T_k	P_k
1	174	10.0	3.51	0.0004
2	204	17.3	1.78	0.0750
3	225	27.2	0.93	0.3520
4	242	42.7	0.58	0.5620
5	259	68.1	—	—

DISCUSSION

We have presented a model for capture-recapture studies on closed populations which incorporates heterogeneity of capture probabilities. The jackknife estimator is shown to be robust when capture probabilities vary among individuals. In comparison, commonly used estimators are negatively biased in this situation. We applied $\hat{N}_J$ to the data reported by Carothers (1973*a*), wherein the true value of N was known. The results supported our conclusions above. (Because Carothers gives the capture frequencies the interested reader can also apply $\hat{N}_J$ to Carothers' data and compare the results to estimators he computes. Alternatively, the results of computing $\hat{N}_J$ for these data are available from the authors.) Finally, we showed that our model and estimator are appropriate for estimating species numbers.

Tests of the assumption of no time variation in individual capture probabilities have also been given, and they appear to perform satisfactorily. We have not, however, presented any test for heterogeneity itself. This is deliberate; the scope of the paper has been limited to this one model and results derived thereunder. However, we believe any comprehensive analysis of livetrapping data should test for a variety of possible variations in capture probabilities due to time, behavior and heterogeneity (and combinations of these). The only comprehensive works along these lines we know of are Pollock (1974) and Otis et al. (1978).

We also do not discuss study design features which can serve to eliminate the biasing effects of heterogeneity. A particularly useful device is to use quite different capture methods on each different occasion. Often this will allow one to safely assume marked and unmarked animals have the same average capture probability. But application of this idea is limited in that one cannot usually find five (or more) truly different capture methods. Where numerous recapture occasions are required to accumulate sufficient data, the investigator usually must rely on one method of livetrapping, and hence heterogeneity of capture probabilities may be unavoidable. The jackknife estimator presented here is especially appropriate for use in the typical small-mammal study which uses a fixed grid of livetraps, and daily trapping on five or more consecutive days. For such studies, the jackknife estimator will often be more reliable than estimators, such as the Schnabel, which assumes equal capture probabilities for all animals.

ACKNOWLEDGMENTS

The work reported in this paper was supported in part by the National Science Foundation Grant Number GB-20963 to the Coniferous Forest Biome, United States Analysis of Ecosystems, International Biological Program. Support for computer time for the simulation results reported here was

provided by the Oregon State University Computer Center. To both these sources of support we express our gratitude. Thanks are also extended to A. D. Carothers and W. R. Edwards for giving us access to their complete data. Finally, we appreciate the assistance of D. Radtke in preparing this paper.

Literature Cited

Bailey, J. A. 1969. Trap responses of wild cottontails. Journal of Wildlife Management **33**:48–58.

Burnham, K. P. 1972. Estimation of population size in multiple capture recapture studies when capture probabilities vary among animals. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Burnham, K. P., and W. S. Overton. 1969. A simulation study of livetrapping and estimation of population size. Technical Report No. 14. Department of Statistics, Oregon State University, Corvallis, Oregon, USA.

Burnham, K. P., and W. S. Overton. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. Biometrika **65**:625–633.

Carothers, A. D. 1971. An examination and extension of Leslie's test of equal catchability. Biometrics **27**:615–630.

———. 1973*a*. Capture recapture methods applied to a population with known parameters. Journal of Animal Ecology **42**:125–146.

———. 1973*b*. The effects of unequal catchability on Jolly-Seber estimates. Biometrics **29**:79–100.

Cormack, R. M. 1966. A test for equal catchability. Biometrics **22**:330–342.

Crowcroft, P., and J. N. R. Jeffers. 1961. Variability in the behavior of wild house mice (*Mus musculus* L.) towards live traps. Proceedings of the Zoological Society of London **137**:573–582.

Eberhardt, L. L. 1969. Population estimates from recapture frequencies. Journal of Wildlife Management **33**:28–39.

Edwards, W. R., and L. L. Eberhardt. 1967. Estimating cottontail abundance from live trapping data. Journal of Wildlife Management **31**:87–96.

Engen, S. 1974. On species frequency models. Biometrika **61**:263–270.

Gilbert, R. O. 1973. Approximations of the bias in the Jolly-Seber capture-recapture model. Biometrics **29**:501–526.

Gray, H. L., and W. R. Schucany. 1972. The generalized jackknife statistic. Marcel Dekker, Inc., New York, New York, USA.

Holgate, P. 1966. Contributions to the mathematics of animal trapping. Biometrics **22**:925–936.

Huber, J. J. 1962. Trap response of confined cottontail populations. Journal of Wildlife Management **26**:177–185.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. Biometrika **52**:225–247.

Manly, B. F. J. 1971. Estimates of a marking effect with capture recapture sampling. Journal of Applied Ecology **8**:181–9.

Mehninick, E. F. 1964. A comparison of some species individuals diversity indices applied to samples of field insects. Ecology **45**:859–861.

Miller, R. G., Jr. 1964. The jackknife—A review. Biometrika **61**:1–15.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62, The Wildlife Society, Washington, District of Columbia, USA.

Pollock, K. H. 1974. The assumption of equal catchability of animals in tag-recapture experiments. Dissertation. Cornell University, Ithaca, New York, USA.

Quenouille, M. H. 1956. Notes on bias in estimation. Biometrika **43**:353–360.

Schnabel, Z. E. 1938. The estimation of the total fish population of a lake. American Mathematical Monthly **45**.348–352.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika **52**:249–259.

———. 1973. Estimation of Animal Abundance and Related Parameters. Griffin, London, England.

Smith, M. H., R. H. Gardner, J. B. Gentry, D. W., and M. H. O'Farrell. 1975. Density estimations of small mammal populations. Pages 25–53 *in* F. B. Golley, K. Petrusewicz, and L. Ryszkowski, editors. Small mammals: their productivity and population dynamics. Cambridge University Press, London, England.

Tanaka, R. 1956. On differential response to live traps of marked and unmarked small mammals. Annotationes Zoologicae Japonenses **29**:44–51.

Young, H., J. Neess, and J. T. Emlen, Jr. 1952. Heterogeneity of trap response in a population of house mice. Journal of Wildlife Management **16**:169–180.

Zahl, S. 1977. Jackknifing an index of diversity. Ecology **58**:907–913.