# ROBUST ESTIMATION OF POPULATION SIZE IN CLOSED ANIMAL POPULATIONS FROM CAPTURE-RECAPTURE EXPERIMENTS

Kenneth H. Pollock and Mark C. Otto
Department of Statistics, Box 5457
North Carolina State University
Raleigh, North Carolina 27650, U.S.A.

## SUMMARY

This paper considers the problem of finding robust estimators of population size in closed K-sample capture-recapture experiments. Particular attention is paid to models where heterogeneity of capture probabilities is allowed. First a general estimation procedure is given which does not depend on assuming anything about the form of the distribution of capture probabilities. This is followed by a detailed discussion of the usefulness of the generalized jackknife technique to reduce bias. Numerical comparisons of the bias and variance of various estimators are given. Finally a general discussion is given with several recommendations on estimators to be used in practice.

---

Key words: Capture-recapture sampling; Population size estimation; Heterogeneity; Trap Response; Weighted distributions; Jackknife.

## 1. Introduction

In this paper we address the problem of finding robust estimators of N, the population size, in a K-sample capture-recapture experiment with closure assumed and where an animal's capture probability is constant over sampling times except as influenced by trap response. The animals are also assumed to behave independently with respect to capture. The specific models considered are:

$M_o$: no heterogeneity, no trap response,

$M_b$: no heterogeneity, trap response,

$M_h$: heterogeneity, no trap response,

$M_{bh}$: heterogeneity, trap response,

with particular attention being paid to the models which allow heterogeneity ($M_h$, $M_{bh}$). These models have been considered in the senior author's unpublished Ph.D. thesis and also in Pollock (1975, 1981). Otis et al. (1978) in an important monograph gave a detailed discussion for biologists.

These models are likely to be useful in applied problems except that often we may also have variability of capture probabilities over time which is very difficult to deal with statistically unless there is no heterogeneity and trap response. Sometimes it is also hard to guarantee closure of the population.

First we give a general estimation procedure for all the models. This is followed by robust estimators for the heterogeneity models ($M_h$, $M_{bh}$), some based on jackknife techniques to reduce bias. An extensive numerical comparison of the bias and variance of the estimators is given for a wide range of capture distributions. Finally there is a general discussion section which gives recommendations on which estimator to use in practice.

## 2. Notation

The following notation will be used in this paper.

**Parameters**

$N$ = the population size (assumed constant over the whole study).

$p_j$ = the probability of capture of the $j^{th}$ animal prior to its initial capture, $j = 1, \ldots, N$.

$c_j$ = the probability of capture of the $j^{th}$ animal after its initial capture, $j = 1, \ldots, N$.

Various restrictions will be placed on the $(p_j, c_j)$ depending on the model under consideration.

**Statistics**

$M_i$ = the number of tagged animals in the population at the time of the $i^{th}$ sample $(i = 1, \ldots, K)$.

$M_{K+1}$ = the number of distinct animals seen during the experiment.

$n_i$ = the number of animals captured in the $i^{th}$ sample.

$m_i$ = the number of tagged animals captured in the $i^{th}$ sample.

$u_i$ = $n_i - m_i$, the number of untagged animals captured in the $i^{th}$ sample.

$X_\omega$ = the number of animals in the population with capture history $\omega$, for example if $K = 3$, $X_{101}$ is the number of animals seen in the first and third but not the second sample.

$\{X_\omega\}$ = the vector of the numbers of animals with each possible capture history.

$f_i$ = the number of animals captured $i$ times in the $K$ samples.

$f_i^{(\ell)}$ = the members of $f_i$ with first capture in the $\ell^{th}$ sample $(\ell = 1, \ldots, K-i+1)$.

## 3. A General Estimation Procedure

In this section a general estimation procedure is developed which can be applied to all 4 models given in Section 1. Let us first consider the joint probability distribution of $\{X_\omega\}$, the collection of all possible capture histories, under the Model $M_{bh}$ which allows heterogeneity and trap response of the capture probabilities. We define

$p_j$ = the probability of capturing the $j^{th}$ individual in any sample ($i = 1, \ldots, K$) given it has not previously been captured ($j = 1, \ldots, N$).

$c_j$ = the probability of capturing the $j^{th}$ individual in any sample ($i = 1, \ldots, K$) given it has previously been captured ($j = 1, \ldots, N$).

The pairs of capture probabilities $(p_1,c_1), \ldots, (p_N,c_N)$ are assumed to be a random sample from the multivariate distribution $F(p,c)$ $p \in (0,1]$, $c \in (0, 1]$. Thus the joint distribution of $\{X_\omega\}$ for a given $F(p,c)$ can then be written as

$$L(N) = P\left[\{X_\omega\}\,|\,F(p,c)\right] = \frac{N!}{\prod_\omega X_\omega!\,(N - M_{K+1})!}\left[\prod_\omega P_\omega^{X_\omega}\right]\left[E(1-p)^K\right]^{N-M_{K+1}} \qquad (1)$$

which is a multinomial distribution with $P_\omega$ being the cell probability of the capture history $\omega$. For example

$$P_\omega = E(pc^{K-1}) = \int_0^1\int_0^1 pc^{K-1}\,dF(p,c)$$

for $\omega$, the capture history of being captured in all K samples. It is important to note that the basic multinomial form of (1) remains the same for all 4 models.

Let us suppose for a moment that F(p,c) is known exactly so that $E(1-p)^K$ is a known constant. In this case considering Maximum Likelihood (M.L.) Estimation of N using L(N)/L(N-1) = 1 for an approximate maximum we obtain

$$\frac{\hat{N}_T}{(\hat{N}_T - M_{K+1})} \; E(1-p)^K = 1$$

which can be rearranged to

$$\hat{N}_T = \frac{M_{K+1}}{1 - E(1-p)^K} \qquad (2)$$

Obviously in practical situations (2) is not really a M.L. estimator of N because the capture probabilities are unknown. A practical estimator would be

$$\hat{N} = \frac{M_{K+1}}{1 - \widehat{E(1-p)^K}} \qquad (3)$$

where we now need to focus on how to estimate $E(1-p)^K$ under the four different models.

## 3.1 No Heterogeneity (Models $M_o$ and $M_b$)

Under $M_o$ and $M_b$ there is no heterogeneity of capture probabilities over animals so that F(p,c) is degenerate to the constant probabilities of capture p, for first time caught, and c for recaptures. For these two models (3) becomes

$$\hat{N} = \frac{M_{K+1}}{1 - (1-\hat{p})^K} \qquad (4)$$

and observe that the equation does not involve c. For these two models the M.L. estimators of p (in terms of N) are

$$M_o: p = c \text{ giving } \hat{p} = \sum_{i=1}^{K} n_i / K\hat{N} \text{ based on all captures,}$$

and

$$M_b: p \neq c \text{ giving } \hat{p} = M_{K+1}/(K\hat{N} - \sum_{i=1}^{K} M_i) \text{ based only on first captures.}$$

Substitution in (4) gives a $K^{th}$ degree polynomial which has to be solved iteratively.

The properties of these estimators have been discussed in detail in the literature (see in particular Otis et al. (1978) and Seber (1973)). These models are not considered further as we intend to concentrate on the more difficult problems associated with estimation of N when heterogeneity is present ($M_h$ and $M_{bh}$).

## 3.2 Heterogeneity (Model $M_h$ and $M_{bh}$)

Under $M_h$ and $M_{bh}$ which have heterogeneity operating (3) depends on

$$E(1-p)^K = \int_0^1 (1-p)^K f(p)\,dp$$

where f(p) is the marginal probability density function of p, the probability of first capture which may vary over animals. Here we are interested in finding a method of estimating N which does not require a specific form (for example a Beta distribution) for f(p).

Let $f^W(p)$ be the probability density function of first capture probabilities of all animals captured. Then $f^W(p)$ is derived from $f(p)$ as a weighted distribution (see Patil and Rao (1978)) with weight $w(p) = 1-(1-p)^K$, the probability of capture at least once.

$$f^W(p) = \frac{w(p)f(p)}{\mu} = \frac{[1 - (1-p)^K]f(p)}{[1 - E(1-p)^K]} \tag{5}$$

Equation (2) can be rewritten as

$$\hat{N}_T = M_{K+1}[1 - E(1-p)^K]^{-1}$$

and we note that an unbiased estimator of $[1 - E(1-p)^K]^{-1}$ is

$$\sum_{j=1}^{M_{K+1}} [1 - (1-p_j)^K]^{-1}/M_{K+1}$$

using the properties of weighted distributions. Thus it follows that

$$\hat{N}_w = \sum_{j=1}^{M_{K+1}} \left[\frac{1}{1 - (1-p_j)^K}\right] \tag{6}$$

would be an unbiased estimator of N if the $p_j$'s were known exactly for all animals captured. Overton (1969) first derived this result using a different method based on a theorem of Horvitz and Thompson (1952).

To make use of (6) we now require point estimators of the $p_j$'s for all animals captured. The form of these estimators and the resulting estimators of N will depend on the specific model considered ($M_h$ or $M_{bh}$) and are considered in the next sections.

## 3.3 Robust Estimators Allowing for Heterogeneity

### 3.3.1 Model $M_h$

Under this model the number of times (i) a particular animal j is captured follows a binomial distribution $(K p_j)$ and hence $\hat{p}_j = i/K$ is the obvious estimator of $p_j$. Now (6) reduces to

$$\hat{N}_o = \sum_{j=1}^{M_{K+1}} \left[\frac{1}{1-(1-i/K)^K}\right] = \sum_{i=1}^{K} \left[\frac{f_i}{1-(1-i/K)^K}\right] \tag{7}$$

where $f_i$ is the number of animals captured i times. This estimator was first derived by Overton (1969). See also Zarnoch (1979).

Note that this estimator is of the form

$$\hat{N} = \sum_{i=1}^{K} a_{iK} f_i \ , \tag{8}$$

a linear combination of the capture frequencies with the constants $a_{iK}$ only depending on i and K. Other estimators of this type are $M_{K+1} = \sum_{i=1}^{K} f_i$, the total number of animals captured at least once and $\hat{N}_j$, the jackknife estimator of Burnham and Overton (1978). For all estimators of form (8) we have

$$E[\hat{N}] = N \sum_{i=1}^{K} a_{iK} \Pi_i \tag{9}$$

and

$$\text{var}\,[\hat{N}] = N \sum_{i=1}^{K} a_{iK}^2 \Pi_i - \{E[N]\}^2/N \ , \tag{10}$$

where $\Pi_i = E\left[\binom{K}{i} p^i (1-p)^{K-i}\right]$ with the expectation over the distribution f(p). Further discussion of the properties of these estimators will be given in Section 5.

### 3.3.2 Model $M_{bh}$

Under this model only the time to first capture can be used to estimate the $p_j$'s because the recaptures are influenced by trap response. The number of trapping occasions to first capture (i) follows a geometric distribution which for animal j is given by

$$P(i) = p_j(1-p_j)^{i-1} .$$

The M.L. estimator of $\hat{p}_j = 1/i$ so that (6) now takes the form

$$\hat{N}_P = \sum_{i=1}^{K} \left[\frac{u_i}{1-(1-1/i)^K}\right] \tag{11}$$

where $u_i$ is the number of unmarked animals captured in the $i^{th}$ sample. In the above argument we have ignored uncaptured animals because we do not need to estimate their capture probabilities for (6).

Note that this estimator is of the form

$$\hat{N} = \sum_{i=1}^{K} b_{iK}\, u_i \quad , \tag{12}$$

a linear combination of the number of animals "removed" (by marking) in each sample as is the estimator $M_{K+1} = \sum_{i=1}^{K} u_i$, the total number of animals captured at least once in the K samples. All estimators of the form (12) have

$$E[\hat{N}] = N \sum_{i=1}^{K} b_{iK}\, \Pi_i^* \tag{13}$$

and

$$\mathrm{var}[\hat{N}] = N \sum_{i=1}^{K} b_{iK}^{2} \Pi_i^{*} - \{E[N]\}^2/N \tag{14}$$

the analogues of (9) and (10) in Model $M_h$. We have $\Pi_i^* = E\left[p(1-p)^{i-1}\right]$ with the expectation over the distribution f(p). Further discussion of the properties of these estimators will be given in Section 5.

## 4. Jackknife Methods for Bias Reduction of Estimators

Application of the jackknife technique to bias reduction in capture-recapture models has considerable potential. It was first considered by Burnham in his unpublished Ph.D. thesis (Oregon State University, 1972) and later in Burnham and Overton (1978, 1979) and Otis et al. (1978). Under Model $M_h$ and using $M_{K+1}$, the number of distinct animals seen, as the biased initial estimator he developed a series of jackknife estimators and showed that they were effective at reducing bias for a range of capture probability distributions (f(p)) using simulation.

Here we give the definition and properties of the generalized jackknife statistic (Gray and Schucany (1972, p. 2)). Then we consider the jackknife technique for both models $M_h$ and $M_{bh}$ using $M_{K+1}$ as the initial (biased) estimators. This is followed by use of the jackknife with $\hat{N}_0$ (7) and $\hat{N}_p$ (11) as the initial (biased) estimators for Models $M_h$ and $M_{bh}$ respectively.

### 4.1 The Generalized Jackknife Statistic

Let us define the generalized jackknife estimator of population size

$$\hat{N}_J = (\hat{N}_1 - R\hat{N}_2)/(1-R) \tag{15}$$

of Gray and Schucany (1972, p. 2) where $\hat{N}_1$ and $\hat{N}_2$ are consistent estimators of N and R is any real number not equal to unity.

Now let us consider the properties of this estimator (15). The first property of consistency follows directly from $\hat{N}_1$ and $\hat{N}_2$ being consistent. The potential bias reduction properties of this estimator become clear from the following theorem (Gray and Schucany (1972, p. 2) Theorem 2.1). If

$$E[\hat{N}_\ell] = N + b_\ell\,(N, \underline{\Theta}, K) \qquad \ell = 1, 2$$

with $\underline{\Theta}$, a set of nuisance parameters which are functions of the $p_j$'s (capture probabilities) then a choice of

$$R = b_1(N, \underline{\Theta}, K) \;/\; b_2(N, \underline{\Theta}, K) \tag{16}$$

makes $\hat{N}_J$ an unbiased estimator of population size. Of course, typically the form (16) of R will not be known because it depends on the unknown N and the nuisance parameters $\underline{\Theta}$. However it may be possible to find approximations to R which are known and give approximately unbiased estimators of N. As well as bias reduction we need to consider the variance of (15)

$$\mathrm{var}(\hat{N}_J) = [\mathrm{var}(\hat{N}_1) + R^2\mathrm{var}(\hat{N}_2) - 2R\,\mathrm{Cov}(\hat{N}_1, \hat{N}_2)] \;/\; (1-R)^2 \tag{17}$$

Within the class of estimators for which R is positive[1] it is then clearly desirable to choose $N_1$ and $N_2$ to be highly positively correlated. Quenouille (1956) has given a general procedure for achieving this and also we give another method specific to the capture-recapture problem.

---

[1] Gray and Schucany (1972, p. 4) state "On the other hand it would appear that in the set of all $N_J$ one would prefer to have $R < 0$ and $\hat{N}_1$ and $\hat{N}_2$ negatively correlated." Unfortunately there is no general way of achieving this at the present time.

The Quenouille (1956) method adapted to the capture-recapture problem can be stated as follows. An initial (biased) estimator based on the whole study is computed and is regarded as $\hat{N}_1$. Choice of $\hat{N}_2$ is then the average of the K estimators which would result from using the information of only (K-1) of the sampling periods. That is drop out each one of the sampling periods in turn. Quenouille (1956) then shows that if the bias in $\hat{N}_1$ can be approximated as a power series in (1/K) then R = (K-1)/K will give a generalized jackknife estimator with bias of order $1/K^2$.

Another method which may sometimes be useful is to take an initial (biased) estimator based on the whole study as $\hat{N}_1$. $\hat{N}_2$ is then chosen to be the same estimator but based only on the first (K-1) sampling periods. Once again R = (K-1)/K could be used. The advantage of this method over the other is that it does not require the form of estimator to be "symmetric" over the sampling periods.

### 4.2 Jackknifing on the Number of Distinct Animals Seen ($M_{K+1}$)

#### 4.2.1 Model $M_h$

Burnham (unpublished thesis, Burnham and Overton (1978, 1979), Otis et al. (1978)) suggested using the jackknife approach with $M_{K+1}$ as the initial estimator and using the Quenouille (1956) approach which was described in Section 4.1. He gave a series of estimators for eliminating bias up to order $(1/K)^5$. The estimators all have the form (8) $(\hat{N} = \sum_{i=1}^{K} a_{iK} f_i)$. He also proposed an objective technique for choosing which one to use on a particular data set. Using simulation he showed that this approach is reasonably effective for a wide range of capture probability distributions.

4.2.2 Model $M_{bh}$

Here we find it necessary to use the other method described in Section 4.1. $\hat{N}_1$ is chosen to be $M_{K+1}$ and $\hat{N}_2$ to be $M_K$ (i.e., based on the first K-1 samples) with R = (K-1)/K. If we note that

$$\hat{N}_1 = M_{K+1} = \sum_{i=1}^{K} u_i \quad \text{and} \quad \hat{N}_2 = M_K = \sum_{i=1}^{K-1} u_i$$

We obtain using (15)

$$\hat{N}_{Jb} = \sum_{i=1}^{K-1} u_i + Ku_K \tag{18}$$

Notice that this estimator is of the form (12) $(N = \sum_{i=1}^{K} b_{iK} u_i)$ so that expectation and variance can be calculated using (13) and (14).

4.2.3 Approximation of R

Here let us consider the form of R which results from use of Theorem 2.1 of Gray and Schucany (1972) which was discussed in Section 4.1.

$$E(M_{K+1}) = N - N\,E(1-p)^K \quad \text{and} \quad E(M_K) = N - N\,E(1-p)^{K-1}$$

Using the theorem we find for $\hat{N}_J$ unbiased that $R = E(1-p)^K/E(1-p)^{K-1}$ which depends on the nuisance parameters and is thus unknown.

Let us now consider the form of R in more detail with the hope we may be able to find a useful approximation which only depends on K. First suppose that f(p) is uniform on (0, U) for which case

$$R = K[1-(1-u)^{K+1}] \; / \; (K+1)\,[1-(1-u)^K]$$

where $0 < U \le 1$. If U = 1 we have R = K/(K+1) whereas when U < 1 we have

$R < K/(K+1)$ but unless U is close to 0 $R \simeq K/(K+1)$ so that a jackknife estimator using $R = K/(K+1)$ should be highly effective at reducing bias. It is interesting to note that Burnham's jackknife procedure, $\hat{N}_{J1}$ uses $R = (K-1)/K$ which will be "close to" $R = K/(K+1)$ for reasonable size K and he showed it to be most effective when f(p) was uniform.

Next consider f(p) to be Beta $(\alpha,\beta)$ (Johnson and Kotz (1970, p. 37)). In this case we have $R = (\beta+K-1)/(\alpha+\beta+K-1)$ which only reduces to $K/(K+1)$ when $\alpha = \beta = 1$, the uniform distribution on (0, 1). If $\alpha = 1$, then f(p) is a reverse J shaped distribution for $\beta > 1$ and it has been suggested this may be a "typical" distribution in practice. For reasonable size K and $\beta$ not too large the jackknife with $R = K/(K+1)$ should do well with some underestimation. If $\alpha > 1$, then f(p) is a unimodal distribution if $\beta > 1$. In this case we find the jackknife using $R = K/(K+1)$ overshoots and gives a positive bias. These results are confirmed by Burnham's simulation results.

The message from this brief analysis is that Burnham's jackknife and the modification with $R = K/(K+1)$ will work reasonably well for reverse J shaped distributions ($\alpha = 1$, $\beta > 1$) or the uniform distribution. It will underestimate for severe heterogeneity ($\alpha < 1$, $\beta > 1$) because too many animals are essentially uncatchable and overestimate for small heterogeneity ($\alpha > 1$, $\beta > 1$).

### 4.3 Jackknifing on $\hat{N}_0$ under Model $M_h$

Here we use the Quenouille (1956) approach described in Section 4.1 with $\hat{N}_0$ of equation (7) as the basic estimator. We find

$$\hat{N}_{J0} = f_1 \left[ Ka_{1K} - \frac{(K-1)^2}{K} a_{1K-1} \right]$$

$$+ \sum_{i=2}^{K} f_i \left[ Ka_{iK} - \frac{K-1}{K}(ia_{i-1K-1} + (K-1)a_{iK-1}) \right] \qquad (19)$$

where $a_{iK} = \left[ 1 - (1-i/K)^K \right]^{-1}$ .

## 4.4 Jackknifing on $\hat{N}_p$ under Model $M_{bh}$

Here we use as the initial estimator $(\hat{N}_1)$ the estimator (11)

$$\hat{N}_1 = \hat{N}_{p1} = \sum_{i=1}^{K} \left[ \frac{u_i}{1-(1-1/i)^K} \right] = \sum_{i=1}^{K} b_{iK} u_i$$

and for $\hat{N}_2$ we are the same form of estimate but for the first (K-1) samples and $R = (K-1)/K$ to give the generalized jackknife statistic

$$\hat{N}_{JP} = \sum_{i=1}^{K-1} \left[ K(b_{iK} - b_{iK-1}) + b_{iK-1} \right] u_i + Kb_{iK} u_K \ . \qquad (20)$$

# 5. Comparison of Estimators

## 5.1 Model $M_h$

To begin with we compare the expectations and standard errors of 4 competing estimators of N for seven different trials originally used by Otis et al (1978) when assessing their jackknife estimators $(\hat{N}_h)$ for Model $M_h$. The description of the trials which have varying degrees of heterogeneity is given in Table 1.

(Table 1 to appear here)

The estimators are:

(i) $\hat{N}_h$ - This is Burnham's jackknife estimator which is recommended for this model. The results presented for this model are taken from Table N.4.6 of Otis et al (1978) and are based on at least 100 simulation runs.

(ii) $M_{K+1}$ - The number of distinct animals seen.

(iii) $\hat{N}_o$ - Overton's estimator which is given in Equation (7).

(iv) $\hat{N}_{Jo}$ - The Jackknife version of Overton's estimator which is given in equation (19).

It should be emphasized that the results presented in Table 2 are exact and based on Equations (9) and (10) except for $\hat{N}_h$, for which results based on simulation are presented.

(Table 2 to appear here)

Next we carry out a systematic comparison of the same estimators as above with the exception that we have used the first order jackknife estimator of Burnham ($\hat{N}_J$) rather than the estimator given in Otis et al (1978) ($\hat{N}_h$). We use a population of 400 animals divided into 4 potentially different subpopulations of 100 animals each. Five levels of heterogeneity from nonexistent to extreme are considered together with a range of sampling occasions (K = 5, 10, 15, 20) and average capture probabilities (E(p) = 0.05, 0.10, 0.15, 0.20). The exact expectations and standard errors of the estimators are presented in Tables 3a - 3d.

(Tables 3a - 3d to appear here)

The results presented here support the use of Burnham's jackknife estimator as recommended by Otis et al (1978). There is a tendency for the estimator to be positively biased for situations where the heterogeneity is moderate. Use of $\hat{N}_h$, which involves up to a 5 order jackknife in a complex procedure, reduces this positive bias from that of $\hat{N}_J$, the first order jackknife, but it can still be substantial.

The Overton estimator, $\hat{N}_o$, has a much smaller standard error than the jackknife estimator but it is severely negatively biased when substantial heterogeneity is present unless the average capture probability is high or the number of samples is large. It can also have a positive bias for moderate heterogeneity. Future research on modification of the coefficients in $\hat{N}_o$ could be productive.

The jackknife version of the Overton estimator, $\hat{N}_{Jo}$, has a higher standard error than any other estimator. Also it can have a large positive bias unless there is extreme heterogeneity. Use of a higher order jackknife might improve this estimator's performance.

## 5.2 Model $M_{bh}$

To begin with we compare the expectations and standard errors of 5 competing estimators of N for seven different trials originally used by Otis et al (1978) when assessing their generalized removal estimate ($\hat{N}_{bh}$) for Model $M_{bh}$. The description of the trials which have varying degrees of heterogeneity is given in Table 4.

(Table 4 to appear here)

The estimators are:

(i) $\hat{N}_{bh}$ - This is the generalized removal estimator which is recommended by Otis et al (1978) and the results given are taken from their Table N.6.b. and are based on at least 100 simulation runs.

(ii) $M_{K+1}$ - This is the number of distinct animals seen.

(iii) $\hat{N}_p$ - This is a new "distribution free" estimator derived here and given in Equation (11).

(iv) $\hat{N}_{Jb}$ - The Jackknife version of $M_{K+1}$ which is given in Equation (18).

(v) $\hat{N}_{Jp}$ - The Jackknife version of $\hat{N}_p$ which is given in Equation (20).

It should be emphasized that the results presented in Table 5 are exact and based on Equations (13) and (14) except for $\hat{N}_{bh}$, for which results based on simulation are presented.

(Table 5 to appear here)

Next we carry out a systematic comparison of the same 5 estimators considered above. We use a population of 400 animals divided into 4 potentially different subpopulations of 100 animals each. Five levels of heterogeneity from nonexistent to extreme are considered together with a range of sampling occasions (K = 5, 10, 15, 20) and average capture probabilities (E(p) = 0.10, 0.15, 0.20). The expectations and standard errors of the estimators are presented in Tables 6a - 6c. Again the results for $\hat{N}_{bh}$ are based on simulation while the other results are exact.

(Tables 6a - 6c to appear here)

Consideration of these results shows very clearly that there is a large loss in precision for estimators under Model $M_{bh}$ compared to under Model $M_h$. This is to be expected as estimators under Model $M_{bh}$ only use information from first captures whereas under Model $M_h$ the estimators use all captures (first captures and recaptures).

A simple clear cut recommendation on which estimator to use is not feasible. The two superior estimators are the generalized removal estimator ($\hat{N}_{bh}$) recommended by Otis et al (1978) and the new jackknife estimator ($\hat{N}_{Jb}$). The two estimators behave quite differently as the average capture probabilities and the number of samples change. The generalized removal estimator typically has a negative bias which can be large if there is a lot of heterogeneity of the capture probabilities. The jackknife estimator has less negative bias than the generalized removal estimator under high heterogeneity. If there is small to moderate heterogeneity the jackknife estimator can have a positive bias. The jackknife estimator ($\hat{N}_{Jb}$) has the same expectation as Burnham's first order jackknife ($\hat{N}_J$) discussed in Section 5.1. In terms of standard error the generalized removal estimator is greatly influenced by the number of samples. For sample numbers of fifteen and twenty the standard errors are very low. This decline in standard error with sample number is not followed by the jackknife estimator. It has a standard error which usually rises for five to ten samples and then stays constant. The typical situation is that the generalized removal estimator has much worse precision than the jackknife for five samples and much better for twenty samples. Overall we tend to favor the jackknife estimator ($\hat{N}_{Jb}$) for practical use as there will often be less than ten samples and heterogeneity will often be pronounced.

Future research could look at using a higher order jackknife corresponding to Burnham's $\hat{N}_h$ which was discussed in Section 5.1.

The new estimator ($\hat{N}_p$) usually has the smallest standard error of all the estimators but it has a severe negative bias which renders it impractical. Future research on modification of the coefficients in $\hat{N}_p$ could be productive. The jackknife version of $\hat{N}_p$ ($\hat{N}_{Jp}$) tends to have a high positive bias for moderate heterogeneity. Its standard error is usually the highest of all the estimators.

## 6. Discussion

This paper has presented a range of new estimators for the heterogeneity model (Model $M_h$) and the heterogeneity and trap response model (Model $M_{bh}$). The most important results are under Model $M_{bh}$. We feel that the new jackknife estimator ($\hat{N}_{Jb}$) should be seriously considered for use with this model rather than the generalized removal estimator given by Otis et al (1978). However, we emphasize that the results are not completely clear cut.

The jackknife estimator ($\hat{N}_h$) is clearly the best of those presented for Model $M_h$. However, it can have some positive bias for moderate heterogeneity. We recommend its continued use.

The estimators $\hat{N}_o$ and $\hat{N}_p$ both have too much negative bias to be used in practice. However, in both cases it may be possible to find better estimates of the capture probabilities ($\hat{p}_j$'s) and provide further new estimators of importance.

One other point should be made. No estimator can account for extreme heterogeneity where animals have capture probabilities very close to zero. An animal with a capture probability of 0.01 is essentially "invisible" to the sampling method and if the population has a lot of these animals all methods will have a severe negative bias!

# REFERENCES


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

Burnham, K. P. and Overton, W. S. (1979). Robust estimation of population size when capture probabilities vary among animals. Ecology 60, 927-936.

Gray, H. L. and Schucany, W. R. (1972). The Generalized Jackknife Statistic. Marcel Dekker: New York.

Horvitz, D. G. and Thompson, D. J. (1952). A Generalization of Sampling without replacement from a finite universe. Journal of the American Statistical Association 47, 663-685.

Johnson, N. L. and Kotz, S. (1970). Distributions in Statistics. Continuous Univariate Distributions-2. John Wiley and Sons: New York.

Otis, D. L., Burnham, K. P., White, G. C., and Anderson, D. R. (1978). Statistical inference for capture data from closed populations. Wildlife Monographs 62, 135 pp.

Overton, W. S. (1969). Estimating the numbers of animals in wildlife populations. In Wildlife Management Techniques, Ed. R. H. Giles, pp. 403-456, The Wildlife Society, Washington, D. C.

Patil, G. P. and Rao, C. R. (1978). Weighted distributions and size biased sampling with application to wildlife populations and human families. Biometrics 34, 179-189.

Pollock, K. H. (1975). Building models of capture-recapture experiments. The Statistician 25, 253-260.

Pollock, K. H. (1981). Capture-recapture models: a review of current methods, assumptions and experimental design. In Estimating Numbers of Terrestrial Birds, C. J. Ralph and J. M. Scott, (eds.), 426-435. Studies in Avian Biology No. 6.

Quenouille, M. H. (1956). Notes on bias reduction. Biometrika 43, 353-360.

Seber, G. A. F. (1973). The Estimation of Animal Abundance and Related Parameters. Griffin: London.

Zarnoch, S. J. (1979). Simulation of effects of learned trap response on three estimators of population size. Journal of Wildlife Management 43, 474-483.

## ACKNOWLEDGEMENTS

I wish to thank K. P. Burnham, D. R. Anderson and D. L. Otis who made helpful comments on an earlier draft of this manuscript.

TABLE 1

DESCRIPTION OF TRIALS USED FOR MODEL $M_h$

| Trial | N | $p_i$, i=1,2,...,N |
|---|---|---|
| 1 | 400 | $p_i$=0.05,i=1,200; $p_i$=0.15,i=201,300; $p_i$=0.50,i=301,400 |
| 2 | 400 | $p_i$=0.01,i=1,100; $p_i$=0.05,i=101,200; $p_i$=0.10,i=201,300; $p_i$=0.20,i=301,400 |
| 3 | 400 | $p_i$=0.10,i=1,100; $p_i$=0.20,i=101,200; $p_i$=0.25,i-201,300; $p_i$=0.30,i=301,400 |
| 4 | 400 | $p_i$=0.01,i=1,50; $p_i$=0.15,i=51,200; $p_i$=0.25,i=201,300; $p_i$=0.30,i=301,400 |
| 5 | 400 | $p_i$=0.20,i=1,100; $p_i$=0.30,i=101,200; $p_i$=0.40,i=201,300; $p_i$=0.50,i=301,400 |
| 6 | 200 | $p_i$=0.05,i=1,50; $p_i$=0.15,i=51,150; $p_i$=0.25,i=151,200 |
| 7 | 200 | $p_i$=0.15,i=1,50; $p_i$=0.20,i=51,100; $p_i$=0.25,i=101,150; $p_i$=0.30,i=151,200 |

TABLE 2

MODEL $M_h$ - COMPARISONS WITH TABLE N.4.b

| Trial | K | N | $E(\hat{N}_h)$ | $\sigma(\hat{N}_h)$[1] | $E(M_{K+1})$ | $\sigma(M_{K+1})$ | $E(\hat{N}_o)$ | $\sigma(\hat{N}_o)$ | $E(\hat{N}_{Jo})$ | $\sigma(\hat{N}_{Jo})$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 5 | 400 | 331.06 | 23.99 | 197.75 | 10.00 | 248.81 | 12.97 | 337.73 | 22.33 |
| 2 | 5 | 400 | 298.06 | 24.52 | 135.71 | 9.47 | 186.52 | 13.19 | 294.33 | 23.42 |
| 3 | 5 | 400 | 461.22 | 32.64 | 267.65 | 9.41 | 347.89 | 12.72 | 485.86 | 24.38 |
| 4 | 5 | 400 | 417.08 | 30.91 | 245.36 | 9.74 | 318.82 | 13.08 | 445.00 | 24.27 |
| 5 | 5 | 400 | 443.95 | 19.71 | 339.52 | 7.16 | 407.93 | 9.45 | 482.89 | 20.89 |
| 6 | 10 | 200 | 207.34 | 16.14 | 147.56 | 6.22 | 185.91 | 8.32 | 232.45 | 17.14 |
| 7 | 7 | 200 | 226.78 | 19.82 | 162.69 | 5.51 | 203.17 | 7.44 | 251.22 | 16.52 |

[1] These results for $\hat{N}_h$ are based on simulation while the other results are exact.

TABLE 3a

MODEL $M_h$ - COMPARISON OF ESTIMATORS WITH E(p) = 0.05

| $p_1^*$ | $p_2$ | $p_3$ | $p_4$ | K | $E(M_{K+1})$ | $\sigma(M_{K+1})$ | $E(\hat{N}_o)$ | $\sigma(\hat{N}_o)$ | $E(\hat{N}_J)$ | $\sigma(\hat{N}_J)$ | $E(\hat{N}_{Jo})$ | $\sigma(\hat{N}_{Jo})$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.05 | 0.05 | 0.05 | 0.05 | 5 | 90.5 | 8.4 | 130.9 | 12.2 | 155.6 | 14.6 | 229.3 | 22.1 |
| | | | | 10 | 160.5 | 9.8 | 231.7 | 14.3 | 273.9 | 17.4 | 389.1 | 27.1 |
| | | | | 15 | 214.7 | 10.0 | 302.9 | 14.4 | 351.2 | 17.5 | 474.9 | 28.2 |
| | | | | 20 | 256.6 | 9.6 | 352.4 | 13.7 | 400.0 | 16.7 | 513.5 | 28.0 |
| 0.04 | 0.04 | 0.06 | 0.06 | 5 | 90.1 | 8.4 | 130.3 | 12.1 | 154.8 | 14.5 | 227.8 | 22.1 |
| | | | | 10 | 159.3 | 9.8 | 229.5 | 14.3 | 271.1 | 17.3 | 384.0 | 27.0 |
| | | | | 15 | 212.5 | 10.0 | 299.2 | 14.4 | 346.4 | 17.5 | 467.0 | 28.1 |
| | | | | 20 | 253.6 | 9.6 | 374.4 | 13.7 | 393.9 | 16.7 | 504.5 | 27.9 |
| 0.03 | 0.04 | 0.06 | 0.07 | 5 | 89.6 | 8.3 | 129.3 | 12.1 | 153.5 | 14.5 | 225.4 | 22.0 |
| | | | | 10 | 157.5 | 9.8 | 226.3 | 14.2 | 266.7 | 17.2 | 376.3 | 26.8 |
| | | | | 15 | 209.3 | 10.0 | 293.5 | 14.3 | 339.1 | 17.4 | 455.0 | 27.9 |
| | | | | 20 | 249.0 | 9.7 | 339.9 | 13.7 | 384.6 | 16.7 | 490.6 | 27.7 |
| 0.02 | 0.03 | 0.07 | 0.08 | 5 | 88.3 | 8.3 | 126.8 | 12.0 | 150.1 | 14.3 | 219.1 | 21.7 |
| | | | | 10 | 152.7 | 9.7 | 217.6 | 14.0 | 255.0 | 16.9 | 355.5 | 26.3 |
| | | | | 15 | 200.5 | 10.0 | 278.2 | 14.2 | 319.4 | 17.2 | 422.3 | 27.3 |
| | | | | 20 | 236.6 | 9.8 | 319.2 | 13.7 | 359.1 | 16.6 | 451.9 | 27.1 |
| 0.01 | 0.02 | 0.08 | 0.09 | 5 | 86.2 | 8.2 | 123.0 | 11.8 | 145.0 | 14.1 | 209.7 | 21.3 |
| | | | | 10 | 145.5 | 9.6 | 204.4 | 13.7 | 237.4 | 16.5 | 324.0 | 25.4 |
| | | | | 15 | 187.2 | 10.0 | 254.9 | 13.0 | 289.0 | 16.6 | 371.3 | 26.1 |
| | | | | 20 | 217.4 | 10.0 | 287.0 | 13.6 | 318.7 | 16.2 | 388.9 | 25.7 |

* There are 4 subpopulations each with 100 animals and potentially different capture probabilities.

TABLE 3b

MODEL $M_h$ - COMPARISON OF ESTIMATORS WITH E(p) = 0.10

| $p_1$* | $p_2$ | $p_3$ | $p_4$ | K | $E(M_{K+1})$ | $\sigma(M_{K+1})$ | $E(\hat{N}_o)$ | $\sigma(\hat{N}_o)$ | $E(\hat{N}_J)$ | $\sigma(\hat{N}_J)$ | $E(\hat{N}_{Jo})$ | $\sigma(\hat{N}_{Jo})$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.10 | 0.10 | 0.10 | 0.10 | 5 | 163.8 | 9.8 | 230.3 | 14.0 | 268.8 | 16.6 | 379.9 | 25.4 |
| | | | | 10 | 260.5 | 9.5 | 353.5 | 13.4 | 400.0 | 16.3 | 513.9 | 27.0 |
| | | | | 15 | 317.6 | 8.1 | 409.5 | 11.2 | 445.8 | 14.0 | 516.8 | 25.6 |
| | | | | 20 | 351.4 | 6.5 | 431.1 | 9.1 | 454.0 | 11.8 | 480.1 | 23.3 |
| 0.08 | 0.08 | 0.12 | 0.12 | 5 | 162.6 | 9.8 | 228.2 | 13.9 | 266.1 | 16.6 | 375.0 | 25.3 |
| | | | | 10 | 257.4 | 9.6 | 348.4 | 13.4 | 393.8 | 16.3 | 504.6 | 26.9 |
| | | | | 15 | 313.3 | 8.2 | 403.3 | 11.4 | 439.2 | 14.2 | 509.9 | 25.6 |
| | | | | 20 | 346.7 | 6.8 | 425.6 | 9.4 | 449.3 | 12.0 | 479.0 | 23.4 |
| 0.06 | 0.08 | 0.12 | 0.14 | 5 | 160.9 | 9.8 | 225.1 | 13.9 | 262.0 | 16.5 | 367.8 | 25.2 |
| | | | | 10 | 252.7 | 9.6 | 340.7 | 13.5 | 384.3 | 16.3 | 490.2 | 26.7 |
| | | | | 15 | 306.7 | 8.4 | 393.7 | 11.6 | 428.7 | 14.3 | 498.3 | 25.4 |
| | | | | 20 | 339.5 | 7.2 | 416.6 | 9.8 | 441.1 | 12.4 | 475.1 | 23.4 |
| 0.04 | 0.06 | 0.14 | 0.16 | 5 | 156.2 | 9.8 | 216.7 | 13.7 | 251.0 | 16.3 | 348.4 | 24.7 |
| | | | | 10 | 240.0 | 9.8 | 319.7 | 13.5 | 358.3 | 16.2 | 450.4 | 26.1 |
| | | | | 15 | 288.5 | 9.0 | 366.7 | 12.1 | 398.7 | 14.6 | 462.8 | 24.9 |
| | | | | 20 | 318.8 | 8.0 | 390.0 | 10.7 | 415.2 | 13.1 | 456.9 | 23.3 |
| 0.02 | 0.04 | 0.16 | 0.18 | 5 | 149.2 | 9.7 | 204.2 | 13.4 | 234.6 | 15.8 | 319.1 | 23.9 |
| | | | | 10 | 220.6 | 9.9 | 287.2 | 13.4 | 317.7 | 15.8 | 386.6 | 24.8 |
| | | | | 15 | 259.5 | 9.5 | 322.4 | 12.5 | 347.4 | 14.7 | 395.4 | 23.6 |
| | | | | 20 | 284.1 | 9.1 | 341.8 | 11.6 | 363.9 | 13.7 | 403.6 | 22.4 |

* There are 4 subpopulations each with 100 animals and potentially different capture probabilities.

TABLE 3c

MODEL $M_h$ - COMPARISON OF ESTIMATORS WITH E(p) = 0.15

| $p_1$ * | $p_2$ | $p_3$ | $p_4$ | K | $E(M_{K+1})$ | $\sigma(M_{K+1})$ | $E(\hat{N}_o)$ | $\sigma(\hat{N}_o)$ | $E(\hat{N}_J)$ | $\sigma(\hat{N}_J)$ | $E(\hat{N}_{Jo})$ | $\sigma(\hat{N}_{Jo})$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.15 | 0.15 | 0.15 | 0.15 | 5 | 222.5 | 9.9 | 303.6 | 13.9 | 347.8 | 16.5 | 469.9 | 25.7 |
| | | | | 10 | 321.3 | 8.0 | 410.5 | 11.0 | 446.3 | 13.6 | 517.7 | 24.9 |
| | | | | 15 | 365.1 | 5.6 | 434.8 | 7.9 | 451.4 | 10.4 | 458.2 | 21.3 |
| | | | | 20 | 384.5 | 3.9 | 432.7 | 5.6 | 436.5 | 7.8 | 408.3 | 17.1 |
| 0.12 | 0.12 | 0.18 | 0.18 | 5 | 220.3 | 9.9 | 299.8 | 13.8 | 343.0 | 16.4 | 461.8 | 25.6 |
| | | | | 10 | 316.8 | 8.1 | 404.2 | 11.1 | 439.5 | 13.8 | 510.3 | 24.8 |
| | | | | 15 | 360.4 | 6.0 | 430.0 | 8.2 | 447.8 | 10.7 | 460.2 | 21.5 |
| | | | | 20 | 380.7 | 4.3 | 430.6 | 6.1 | 436.7 | 8.3 | 416.5 | 17.6 |
| 0.09 | 0.12 | 0.18 | 0.21 | 5 | 217.0 | 10.0 | 294.1 | 13.8 | 335.7 | 16.4 | 449.6 | 25.4 |
| | | | | 10 | 310.0 | 8.4 | 394.3 | 11.4 | 428.6 | 14.0 | 498.1 | 24.7 |
| | | | | 15 | 353.0 | 6.4 | 421.8 | 8.7 | 441.2 | 11.2 | 460.6 | 21.7 |
| | | | | 20 | 374.3 | 4.9 | 426.1 | 6.8 | 435.3 | 9.0 | 426.5 | 18.3 |
| 0.06 | 0.09 | 0.21 | 0.24 | 5 | 208.1 | 10.0 | 278.9 | 13.7 | 316.3 | 16.2 | 416.9 | 24.9 |
| | | | | 10 | 291.3 | 8.9 | 366.7 | 11.9 | 397.8 | 14.3 | 461.1 | 24.2 |
| | | | | 15 | 331.6 | 7.5 | 396.5 | 9.9 | 418.6 | 12.2 | 452.1 | 21.9 |
| | | | | 20 | 354.5 | 6.3 | 409.0 | 8.4 | 425.2 | 10.5 | 442.9 | 19.7 |
| 0.03 | 0.06 | 0.24 | 0.27 | 5 | 194.7 | 10.0 | 255.8 | 13.5 | 286.7 | 15.7 | 367.0 | 23.9 |
| | | | | 10 | 261.7 | 9.5 | 321.6 | 12.3 | 345.7 | 14.4 | 392.3 | 22.9 |
| | | | | 15 | 294.6 | 8.8 | 348.0 | 11.1 | 369.2 | 13.1 | 408.0 | 21.4 |
| | | | | 20 | 316.0 | 8.1 | 366.0 | 10.3 | 386.9 | 12.3 | 427.6 | 20.5 |

* There are 4 subpopulations each with 100 animals and potentially different capture probabilities.

TABLE 3d

MODEL $M_h$ - COMPARISON OF ESTIMATORS WITH E(p) = 0.20

| $p_1$* | $p_2$ | $p_3$ | $p_4$ | K | $E(M_{K+1})$ | $\sigma(M_{K+1})$ | $E(\hat{N}_o)$ | $\sigma(\hat{N}_o)$ | $E(\hat{N}_J)$ | $\sigma(\hat{N}_J)$ | $E(\hat{N}_{Jo})$ | $\sigma(\hat{N}_{Jo})$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.20 | 0.20 | 0.20 | 0.20 | 5 | 268.9 | 9.4 | 355.9 | 12.9 | 400.0 | 15.4 | 515.0 | 24.9 |
| | | | | 10 | 357.0 | 6.2 | 431.6 | 8.5 | 453.7 | 11.1 | 478.6 | 22.0 |
| | | | | 15 | 385.9 | 3.7 | 431.7 | 5.4 | 435.2 | 7.5 | 406.5 | 16.5 |
| | | | | 20 | 395.4 | 2.1 | 420.4 | 3.5 | 417.3 | 5.0 | 378.4 | 11.4 |
| 0.16 | 0.16 | 0.24 | 0.24 | 5 | 265.6 | 9.4 | 350.5 | 12.9 | 393.4 | 15.4 | 504.8 | 24.9 |
| | | | | 10 | 352.2 | 6.5 | 425.9 | 8.9 | 448.7 | 11.3 | 477.4 | 22.1 |
| | | | | 15 | 382.1 | 4.1 | 429.7 | 5.9 | 435.5 | 8.0 | 415.1 | 17.1 |
| | | | | 20 | 393.1 | 2.6 | 421.3 | 4.0 | 420.2 | 5.6 | 387.3 | 12.5 |
| 0.12 | 0.16 | 0.24 | 0.28 | 5 | 260.7 | 9.5 | 342.5 | 13.0 | 383.5 | 15.4 | 489.3 | 24.7 |
| | | | | 10 | 344.5 | 6.9 | 416.5 | 9.3 | 440.0 | 11.7 | 473.3 | 22.1 |
| | | | | 15 | 375.6 | 4.8 | 425.3 | 6.6 | 434.3 | 8.7 | 425.7 | 17.9 |
| | | | | 20 | 388.6 | 3.3 | 421.2 | 4.8 | 423.3 | 6.6 | 400.6 | 14.0 |
| 0.08 | 0.12 | 0.28 | 0.32 | 5 | 247.4 | 9.7 | 320.7 | 13.0 | 356.6 | 15.3 | 447.2 | 24.2 |
| | | | | 10 | 322.9 | 7.9 | 388.9 | 10.3 | 413.1 | 12.6 | 454.1 | 22.1 |
| | | | | 15 | 355.6 | 6.3 | 408.4 | 8.2 | 424.5 | 10.4 | 443.1 | 19.3 |
| | | | | 20 | 373.2 | 5.0 | 415.3 | 6.7 | 425.9 | 8.7 | 431.2 | 17.0 |
| 0.04 | 0.08 | 0.32 | 0.36 | 5 | 227.3 | 9.9 | 287.4 | 12.9 | 315.3 | 15.0 | 381.7 | 23.0 |
| | | | | 10 | 286.8 | 9.0 | 339.5 | 11.3 | 360.5 | 13.3 | 399.6 | 21.2 |
| | | | | 15 | 316.7 | 8.1 | 365.3 | 10.2 | 386.2 | 12.2 | 428.0 | 20.2 |
| | | | | 20 | 336.9 | 7.3 | 383.7 | 9.2 | 403.6 | 11.2 | 443.8 | 19.4 |

* There are 4 subpopulations each with 100 animals and potentially different capture probabilities.

TABLE 4

DESCRIPTION OF TRIALS USED FOR MODEL $M_{bh}$

| Trial | N | $p_i$, i=1,2,...,N |
|---|---|---|
| 1 | 400 | $p_i$=0.05,i=1,200; $p_i$=0.15,i=201,300; $p_i$=0.50,i=301,400 |
| 2 | 400 | $p_i$=0.01,i=1,50; $p_i$=0.15,i=51,200; $p_i$=0.25,i=201,300; $p_i$=0.30,i=301,400 |
| 3 | 400 | $p_i$=0.10,i=1,100; $p_i$=0.20,i=101,200; $p_i$=0.25,i=201,300; $p_i$=0.30,i=301,400 |
| 4 | 400 | $p_i$=0.20,i=1,100; $p_i$=0.30,i=101,200; $p_i$=0.40,i=201,300; $p_i$=0.50,i=301,400 |
| 5 | 200 | $p_i$=0.05,i=1,50; $p_i$=0.15,i=51,151; $p_i$=0.25,i=151,200 |
| 6 | 200 | $p_i$=0.15,i=1,50; $p_i$=0.20,i=51,100; $p_i$=0.25,i=101,150; $p_i$=0.30,i=151,200 |
| 7 | 100 | $p_i$=0.10,i=1,40; $p_i$=0.20,i=41,80; $p_i$=0.30,i=81,100 |

TABLE 5

MODEL $M_{bh}$ - COMPARISONS WITH TABLE N.6.b

| Trial | K | N | $E(\hat{N}_{bh})$ | $\sigma(\hat{N}_{bh})$[1] | $E(M_{K+1})$ | $\sigma(M_{K+1})$ | $E(\hat{N}_p)$ | $\sigma(\hat{N}_p)$ | $E(\hat{N}_{Jb})$ | $\sigma(\hat{N}_{Jb})$ | $E(\hat{N}_{Jp})$ | $\sigma(\hat{N}_{Jp})$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 5 | 400 | 246.59 | 38.04 | 197.75 | 10.00 | 220.97 | 11.39 | 274.15 | 21.64 | 301.28 | 31.20 |
| 2 | 5 | 400 | 340.83 | 57.57 | 245.36 | 9.74 | 278.43 | 11.34 | 354.71 | 24.23 | 394.39 | 35.96 |
| 3 | 5 | 400 | 366.43 | 41.87 | 267.65 | 9.41 | 303.76 | 11.01 | 387.11 | 24.69 | 430.48 | 37.07 |
| 4 | 5 | 400 | 383.00 | 21.30 | 339.52 | 7.16 | 373.12 | 8.31 | 434.34 | 20.90 | 460.26 | 32.26 |
| 5 | 10 | 200 | 175.51 | 16.26 | 147.56 | 6.22 | 164.72 | 7.20 | 201.46 | 23.18 | 217.06 | 35.89 |
| 6 | 7 | 200 | 193.72 | 13.90 | 162.69 | 5.51 | 181.37 | 6.45 | 219.33 | 19.37 | 235.78 | 30.09 |
| 7 | 5 | 100 | 94.14 | 43.26 | 59.91 | 4.90 | 68.48 | 5.75 | 89.28 | 12.51 | 100.43 | 18.60 |

[1] These results for $\hat{N}_{bh}$ are based on simulation while the other results are exact.

TABLE 6a

MODEL $M_{bh}$ - COMPARISON OF ESTIMATORS WITH E(p) = 0.10

| $p_1$ * | $p_2$ | $p_3$ | $p_4$ | K | $E(\hat{N}_{bh})^+$ | $\sigma(\hat{N}_{bh})^+$ | $E(M_{K+1})$ | $\sigma(M_{K+1})$ | $E(\hat{N}_p)$ | $\sigma(\hat{N}_p)$ | $E(\hat{N}_{Jb})$ | $\sigma(\hat{N}_{Jb})$ | $E(\hat{N}_{Jp})$ | $\sigma(\hat{N}_{Jp})$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.10 | 0.10 | 0.10 | 0.10 | 5 | 343.3 | 83.8 | 163.8 | 9.8 | 191.7 | 11.7 | 268.8 | 24.8 | 313.0 | 36.2 |
| | | | | 10 | 457.5 | 133.1 | 260.5 | 9.5 | 299.2 | 11.3 | 400.0 | 37.3 | 449.0 | 57.7 |
| | | | | 15 | 404.2 | 37.0 | 317.6 | 8.1 | 357.5 | 9.5 | 445.8 | 43.3 | 482.8 | 67.9 |
| | | | | 20 | 398.8 | 17.4 | 351.4 | 6.5 | 388.3 | 7.7 | 454.0 | 44.6 | 476.2 | 70.4 |
| 0.08 | 0.08 | 0.12 | 0.12 | 5 | 323.9 | 76.8 | 162.6 | 9.8 | 190.2 | 11.7 | 266.1 | 24.6 | 309.5 | 36.0 |
| | | | | 10 | 413.5 | 95.6 | 257.4 | 9.6 | 295.3 | 11.3 | 393.8 | 37.0 | 441.5 | 57.2 |
| | | | | 15 | 404.1 | 45.9 | 313.3 | 8.2 | 352.4 | 9.7 | 439.2 | 42.9 | 475.7 | 67.4 |
| | | | | 20 | 393.8 | 20.8 | 346.7 | 6.8 | 383.1 | 8.0 | 449.3 | 44.7 | 472.0 | 70.4 |
| 0.06 | 0.08 | 0.12 | 0.14 | 5 | 311.6 | 70.8 | 160.9 | 9.8 | 188.0 | 11.7 | 262.0 | 24.4 | 304.2 | 35.6 |
| | | | | 10 | 430.7 | 134.4 | 252.7 | 9.6 | 289.4 | 11.4 | 384.3 | 36.5 | 430.0 | 56.2 |
| | | | | 15 | 391.6 | 36.8 | 306.7 | 8.4 | 344.5 | 9.9 | 428.7 | 42.4 | 464.1 | 66.4 |
| | | | | 20 | 381.8 | 15.0 | 339.5 | 7.2 | 374.8 | 8.4 | 441.1 | 44.6 | 464.4 | 70.2 |
| 0.04 | 0.06 | 0.14 | 0.16 | 5 | 269.2 | 51.4 | 156.2 | 9.8 | 181.9 | 11.6 | 251.0 | 23.8 | 290.2 | 34.6 |
| | | | | 10 | 346.1 | 46.3 | 240.0 | 9.8 | 273.6 | 11.5 | 358.3 | 34.9 | 398.6 | 53.6 |
| | | | | 15 | 354.9 | 31.0 | 288.5 | 9.0 | 322.7 | 10.4 | 398.7 | 40.7 | 430.5 | 63.4 |
| | | | | 20 | 352.3 | 13.8 | 318.8 | 8.0 | 351.1 | 9.2 | 415.2 | 43.7 | 438.8 | 68.6 |
| 0.02 | 0.04 | 0.16 | 0.18 | 5 | 259.7 | 56.9 | 149.2 | 9.7 | 172.8 | 11.4 | 234.6 | 22.9 | 269.1 | 33.1 |
| | | | | 10 | 299.5 | 41.4 | 220.6 | 9.9 | 249.3 | 11.5 | 317.6 | 32.2 | 349.0 | 49.0 |
| | | | | 15 | 298.2 | 20.3 | 259.5 | 9.5 | 287.6 | 10.9 | 347.4 | 36.9 | 371.4 | 57.1 |
| | | | | 20 | 306.7 | 11.0 | 284.1 | 9.1 | 310.4 | 10.2 | 363.9 | 40.4 | 383.6 | 62.8 |

* There are 4 subpopulations each with 100 animals and potentially different capture probabilities.

+ These estimates are based on 100 simulation runs while other results are exact.

TABLE 6b

MODEL $M_{bh}$ - COMPARISON OF ESTIMATORS WITH E(p) = 0.15

| $p_1$* | $p_2$ | $p_3$ | $p_4$ | K | $E(\hat{N}_{bh})^+$ | $\sigma(\hat{N}_{bh})^+$ | $E(M_{K+1})$ | $\sigma(M_{K+1})$ | $E(\hat{N}_p)$ | $\sigma(\hat{N}_p)$ | $E(\hat{N}_{Jb})$ | $\sigma(\hat{N}_{Jb})$ | $E(\hat{N}_{Jp})$ | $\sigma(\hat{N}_{Jp})$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.15 | 0.15 | 0.15 | 0.15 | 5 | 401.8 | 85.8 | 222.5 | 9.9 | 255.7 | 11.8 | 347.8 | 25.9 | 398.0 | 38.5 |
| | | | | 10 | 406.9 | 37.4 | 321.3 | 8.0 | 360.9 | 9.4 | 446.3 | 34.6 | 483.1 | 54.2 |
| | | | | 15 | 396.3 | 11.7 | 365.1 | 5.6 | 399.2 | 6.7 | 451.4 | 35.2 | 465.9 | 55.6 |
| | | | | 20 | 397.9 | 5.7 | 384.5 | 3.9 | 411.2 | 4.8 | 436.5 | 31.6 | 435.6 | 50.1 |
| 0.12 | 0.12 | 0.18 | 0.18 | 5 | 409.9 | 103.2 | 220.3 | 9.9 | 254.6 | 11.8 | 343.0 | 25.7 | 392.0 | 38.2 |
| | | | | 10 | 396.3 | 31.6 | 316.8 | 8.1 | 355.6 | 9.5 | 439.5 | 34.4 | 475.6 | 53.7 |
| | | | | 15 | 391.9 | 12.8 | 360.4 | 6.0 | 394.1 | 7.1 | 447.9 | 35.5 | 463.6 | 56.0 |
| | | | | 20 | 394.2 | 5.7 | 380.7 | 4.3 | 407.7 | 5.2 | 436.7 | 32.8 | 438.3 | 52.0 |
| 0.09 | 0.12 | 0.18 | 0.21 | 5 | 361.9 | 65.2 | 217.0 | 10.0 | 250.4 | 11.8 | 335.7 | 25.4 | 382.9 | 37.7 |
| | | | | 10 | 379.4 | 29.9 | 310.0 | 8.4 | 347.4 | 9.8 | 428.6 | 34.0 | 463.6 | 53.0 |
| | | | | 15 | 383.6 | 13.7 | 353.0 | 6.4 | 386.0 | 7.5 | 441.2 | 35.7 | 458.5 | 56.3 |
| | | | | 20 | 388.0 | 5.9 | 374.3 | 4.9 | 401.4 | 5.8 | 435.3 | 34.4 | 440.3 | 54.3 |
| 0.06 | 0.09 | 0.21 | 0.24 | 5 | 343.6 | 79.3 | 208.1 | 10.0 | 239.0 | 11.7 | 316.3 | 24.6 | 358.4 | 36.2 |
| | | | | 10 | 346.4 | 26.4 | 291.3 | 8.9 | 325.0 | 10.3 | 397.8 | 32.7 | 428.9 | 50.5 |
| | | | | 15 | 361.0 | 13.1 | 331.6 | 7.5 | 362.0 | 8.6 | 418.6 | 35.9 | 438.3 | 56.2 |
| | | | | 20 | 368.8 | 8.1 | 354.5 | 6.3 | 381.1 | 7.3 | 425.2 | 37.2 | 437.7 | 58.6 |
| 0.03 | 0.06 | 0.24 | 0.27 | 5 | 265.5 | 27.5 | 194.7 | 10.0 | 221.8 | 11.6 | 286.7 | 23.3 | 321.2 | 33.9 |
| | | | | 10 | 295.8 | 17.5 | 261.7 | 9.5 | 289.0 | 10.8 | 345.7 | 29.8 | 368.8 | 45.5 |
| | | | | 15 | 314.9 | 12.1 | 294.6 | 8.8 | 319.4 | 9.8 | 369.2 | 33.9 | 387.4 | 52.4 |
| | | | | 20 | 326.5 | 9.5 | 316.0 | 8.1 | 339.0 | 9.0 | 386.9 | 37.8 | 404.3 | 59.1 |

* There are 4 subpopulations each with 100 animals and potentially different capture probabilities.

+ These estimates are based on 100 simulation runs while other results are exact.

TABLE 6c

MODEL $M_{bh}$ - COMPARISON OF ESTIMATORS WITH E(p) = 0.20

| $p_1$* | $p_2$ | $p_3$ | $p_4$ | K | $E(\hat{N}_{bh})^+$ | $\sigma(\hat{N}_{bh})^+$ | $E(M_{K+1})$ | $\sigma(M_{K+1})$ | $E(\hat{N}_p)$ | $\sigma(\hat{N}_p)$ | $E(\hat{N}_{Jb})$ | $\sigma(\hat{N}_{Jb})$ | $E(\hat{N}_{Jp})$ | $\sigma(\hat{N}_{Jp})$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.20 | 0.20 | 0.20 | 0.20 | 5 | 403.9 | 80.6 | 268.9 | 9.4 | 307.5 | 11.1 | 400.0 | 25.6 | 449.4 | 38.6 |
| | | | | 10 | 399.0 | 16.8 | 357.0 | 6.2 | 392.9 | 7.3 | 453.7 | 30.1 | 474.3 | 47.4 |
| | | | | 15 | 397.6 | 6.5 | 385.9 | 3.7 | 411.8 | 4.6 | 435.2 | 26.5 | 433.5 | 42.0 |
| | | | | 20 | 398.2 | 2.5 | 395.4 | 2.1 | 412.8 | 2.9 | 417.3 | 20.5 | 406.7 | 32.5 |
| 0.16 | 0.16 | 0.24 | 0.24 | 5 | 384.2 | 49.0 | 265.6 | 9.4 | 303.3 | 11.1 | 393.4 | 25.4 | 441.3 | 38.2 |
| | | | | 10 | 391.8 | 17.5 | 352.2 | 6.5 | 387.4 | 7.6 | 448.7 | 30.2 | 470.0 | 47.5 |
| | | | | 15 | 395.5 | 5.7 | 382.1 | 4.1 | 408.3 | 5.0 | 435.5 | 27.6 | 436.5 | 43.7 |
| | | | | 20 | 396.7 | 3.2 | 393.1 | 2.6 | 411.4 | 3.3 | 420.2 | 22.8 | 412.2 | 36.2 |
| 0.12 | 0.16 | 0.24 | 0.28 | 5 | 383.2 | 53.3 | 260.7 | 9.5 | 297.1 | 11.2 | 383.5 | 25.1 | 429.2 | 37.6 |
| | | | | 10 | 380.4 | 14.9 | 344.5 | 6.9 | 378.7 | 8.1 | 440.0 | 30.2 | 462.0 | 47.3 |
| | | | | 15 | 387.9 | 6.4 | 375.6 | 4.8 | 402.0 | 5.6 | 434.3 | 29.0 | 438.9 | 45.9 |
| | | | | 20 | 391.7 | 3.6 | 388.6 | 3.3 | 408.1 | 4.0 | 423.3 | 25.9 | 419.4 | 41.0 |
| 0.08 | 0.12 | 0.28 | 0.32 | 5 | 335.8 | 36.0 | 247.4 | 9.7 | 280.4 | 11.3 | 356.6 | 24.2 | 396.2 | 35.9 |
| | | | | 10 | 350.2 | 13.1 | 322.9 | 7.9 | 353.8 | 9.0 | 413.1 | 29.8 | 435.4 | 46.3 |
| | | | | 15 | 369.0 | 8.5 | 355.6 | 6.3 | 381.6 | 7.2 | 424.5 | 31.7 | 436.9 | 49.9 |
| | | | | 20 | 379.0 | 5.6 | 373.2 | 5.0 | 394.8 | 5.7 | 425.9 | 32.0 | 432.2 | 50.6 |
| 0.04 | 0.08 | 0.32 | 0.36 | 5 | 281.8 | 28.0 | 227.3 | 9.9 | 255.0 | 11.4 | 315.3 | 22.5 | 345.3 | 32.9 |
| | | | | 10 | 305.8 | 12.9 | 286.8 | 9.0 | 311.6 | 10.1 | 360.5 | 27.8 | 379.1 | 42.5 |
| | | | | 15 | 329.3 | 11.1 | 316.7 | 8.1 | 339.1 | 9.0 | 386.2 | 32.5 | 403.7 | 50.5 |
| | | | | 20 | 347.8 | 12.0 | 336.9 | 7.3 | 358.0 | 8.1 | 403.6 | 36.5 | 420.6 | 57.1 |

* There are 4 subpopulations each with 100 animals and potentially different capture probabilities.

+ These estimates are based on 100 simulation runs while other results are exact.