BIOMETRICS 50, 88–97
March 1994

Estimating Population Size via Sample Coverage for Closed Capture–Recapture Models

Shen-Ming Lee and Anne Chao*
Institute of Statistics, National Tsing Hua University, Hsin-chu 30043, Taiwan

SUMMARY

A nonparametric estimation technique is proposed which uses the concept of sample coverage in order to estimate the size of a closed population for capture–recapture models where time, behavior, or heterogeneity may affect the capture probabilities. The technique also provides a unified approach to catch-effort models that allows for heterogeneity among removal probabilities. Real data examples are given for illustration. A simulation study investigates the behavior of the proposed procedure.

1. Introduction

We focus on the problem of estimating population size for the sequence of models proposed by Pollock (unpublished Ph.D. thesis, Cornell University, 1974; 1976, 1981) and Otis et al. (1978) for capture–recapture data in closed populations. Three basic models discussed by Pollock and Otis et al. are: (a) Model M_t, which allows capture probabilities to vary by time; (b) Model M_b, which allows behavioral responses to capture; and (c) Model M_h, which allows heterogeneous animal capture probabilities. Various combinations of these three types of unequal capture probabilities (i.e., models M_{tb}, M_{th}, M_{bh}, and M_{tbh}) and the model M_0, in which no variation exists, are also considered.

Only a few parameters exist for models M_0, M_t, and M_b. The commonly used estimators are the maximum likelihood estimators (MLE); see Darroch (1958) for models M_0 and M_t, Moran (1951) or Zippin (1956, 1958) for model M_b. The jackknife estimator for model M_h, proposed by Burnham and Overton (1978, 1979), was found to be a satisfactory estimator in Otis et al. (1978) and White et al. (1982). Previous estimators for model M_{bh} include the generalized removal estimator (Otis et al., 1978) and jackknife estimator proposed by Pollock and Otto (1983). Available estimation procedures for population size exist under models M_0, M_t, M_b, M_h, and M_{bh} (see Otis et al., 1978, p. 52). No appropriate estimations methods, however, exist for models M_{tb}, M_{th}, and M_{tbh}.

An estimation procedure for model M_{th} via the sample coverage approach was recently proposed by Chao, Lee, and Jeng (1992). Using exactly the same idea, we introduce in this paper a nonparametric approach to estimate population size for all eight models. The additional assumption needed here is that the relative time effects for models M_{tbh} and M_{tb} are known constants. For example, this assumption is satisfied when the time effects are proportional to a known available covariate, which could be the amount of effort expended in obtaining the sample or an environmental variable (e.g., temperature or humidity).

The model M_{tbh} (M_{tb}), with known relative time effects being regarded as relative catch-effort, is equivalent to the variable catch-effort model with heterogeneous (homogeneous) removal probabilities. The analysis of model M_{bh} (M_b) is the same as that of the constant catch-effort method with heterogeneous (homogeneous) removal probabilities. As stated by Pollock (1991, p. 231), "Currently, there is no catch per unit effort model that allows for heterogeneity. This appears to be an obvious deficiency because there is a heterogeneity model for the equal effort case (M_{bh})." This deficiency can then be removed by the proposed M_{tbh} with known relative time effects. The previous methods for the variable catch-effort without heterogeneity include three regression-type estimates

---

* To whom requests for reprints should be addressed.

Key words: Behavior response; Capture–recapture sampling; Catch-effort sampling; Heterogeneity; Population size; Sample coverage; Time variation.

proposed by Leslie and Davis (1939), De Lury (1947), and Ricker (1958). See Seber (1982, Chap. 7) for a review.

The sample coverage is defined in a classical species problem as the total probabilities of the observed species. The idea of sample coverage being applied to estimate the number of classes under a parametric model was first suggested by Esty (1985). This concept is generalized in this paper to capture–recapture studies by defining the sample coverage of a capture–recapture experiment as the proportion of the total individual effects on the first-capture probabilities of the captured animals. The expected sample coverage is next shown to be easily estimated for heterogeneous capture probabilities. The resulting estimator is subsequently used for estimating population size in a general nonparametric way.

Cormack (1966) and Carothers (1973, 1979) found that the coefficient of variation (CV) of the capture probabilities plays an important role on the effect of heterogeneity under various models. In this paper the relation between population size and the CV (via this sample coverage approach) is derived for closed capture–recapture models.

In Section 2, we list the notation. The mathematical formula for sample coverage and its relation to population size estimation are presented in Section 3. The estimator of population size via sample coverage as well as its variance estimator are obtained for each model. Models with heterogeneity are the main focus here, i.e., models M_{h}, M_{th}, M_{bh}, and M_{tbh}. Other models are treated as special cases of the above four models. Real data sets are given for illustration in Section 4. Results of a simulation are reported in Section 5 to show the general performance of the proposed procedure.

2. Notation

t: Number of trapping samples
e_j: Known relative time effect of the jth trapping sample on capture probability
C: Sample coverage
C_k: Sample coverage of the first k samples, $k = 1, 2, \ldots, t$; $C_t = C$

Parameters:

N: Population size
p_{ij}: Capture probability of the ith animal in the jth trapping sample
p_i: Effect of the ith individual animal on the first-capture probability
$\mathbf{p}$ $= (p_1, p_2, \ldots, p_N)$; $p_1, p_2, \ldots, p_N$ have mean $\bar{p} = \Sigma_i\, p_i/N$ and coefficient of variation (CV) $\gamma = [\Sigma_i\, (p_i - \bar{p})^2/N]^{1/2}/\bar{p}$.
α_j: Unknown time effect of the jth sample on capture probability
b_i: Effect of the ith individual on recapture probability if behavior response exists

Statistics:

n_j: Number of animals captured in the jth sample
f_k: Number of animals captured exactly k times in t samples
u_j: Number of unmarked animals captured in the jth sample
D: Number of distinct animals captured in t samples
D_k: Number of distinct animals captured in the first k samples, $D_t = D$ [D_k is equal to M_{k+1} in the usual notation of Seber (1982) or Otis et al. (1978).]

3. Models and Estimators

The models and the assumptions considered here can be described as follows:

(1) Model M_{tbh}: $p_{ij} = p_i e_j$ for any first capture and $p_{ij} = b_i e_j^*$ for any recapture [It is equivalent to a variable catch-effort model with removal probability $p_{ij} = p_i$ for relative efforts $e_1, \ldots, e_t$.]
(2) Model M_{tb}: Same as M_{tbh} with $p_i = p$ and $b_i = b$ for all i
(3) Model M_{th}: $p_{ij} = p_i\alpha_j$
(4) Model M_{bh}: $p_{ij} = p_i$ for any first capture and $p_{ij} = b_i$ for any recapture
(5) Model M_{t}: $p_{ij} = p\alpha_j$
(6) Model M_{b}: $p_{ij} = p$ for any first capture and $p_{ij} = b$ for any recapture
(7) Model M_{h}: $p_{ij} = p_i$
(8) Model M_0: $p_{ij} = p$

All the effects occurring in multifactor models are in a "relative" sense. For example, p_i and e_j are defined only up to a multiplicative constant in model M_{tbh}. The mean $\bar{p} = \Sigma\, p_i/N$ is not uniquely defined, but the CV $= \gamma = [\Sigma\, (p_i - \bar{p})^2/N]^{1/2}/\bar{p}$ and the sample coverage defined in (3.1) are.

However, only identifiable functions (e.g., $\bar{p}e_j$ or $\bar{p}\alpha_j$) appear in the derivations that follow. All proposed estimators for multifactor models are invariant to the choice of scale of the p_i's and e_j's.

Only p_i's are involved in the definition of the sample coverage. For models without heterogeneity, $p_i \equiv p$, and p is kept in the model for convenience so that the sample coverage can be generally defined for all models. For example, p is actually not necessary in M_t.

The capture history consists of an $N \times t$ matrix $X = (X_{ij})$, where $X_{ij} = I$ [the ith animal is caught in the jth sample]. Animals are assumed to act independently.

The sample coverage, C, is defined as the proportion of the total individual effects that are associated with the captured animals. That is,

$$C = \sum_{i=1}^{N} p_i I[\text{the } i\text{th animal is captured}] \Big/ \sum_{i=1}^{N} p_i. \tag{3.1}$$

If all p_i's are equal (i.e., models M_0, M_t, M_b, M_{tb} for which $p_i \equiv p$), then $C = D/N$, the proportion of distinct animals observed. A natural estimator of N under a model without heterogeneity is then

$$\hat{N}_0 = D/\hat{C}, \tag{3.2}$$

where $\hat{C}$ is an estimator of C. We now find the discrepancy between $\mathrm{E}(D)/\mathrm{E}(C)$ and N when p_i's are different. For model M_{tbh},

$$\mathrm{E}(D) = N - \sum_{i=1}^{N} \prod_{j=1}^{t} (1 - p_i e_j) \tag{3.3}$$

and

$$\mathrm{E}(C) = 1 - \sum_{i=1}^{N} p_i \prod_{j=1}^{t} (1 - p_i e_j) \Big/ \sum_{i=1}^{N} p_i. \tag{3.4}$$

Both $\mathrm{E}(D)$ and $\mathrm{E}(C)$ are independent of behavioral effects. This leads to the following proposition. Refer to Chao et al. (1992) for a proof.

Proposition. For model M_{tbh}, we have

$$\frac{\mathrm{E}(D)}{\mathrm{E}(C)} = N - \frac{N \sum_{j=1}^{t} (\bar{p}e_j) \prod_{s \neq j} (1 - \bar{p}e_s)}{\mathrm{E}(C)} \gamma^2 + R_1, \tag{3.5}$$

where R_1 is a term involving only the third and fourth central moments of the p_i's. Replacing e_j's by α_j's in (3.5), we have the same conclusion for model M_{th}. For models M_h and M_{bh}, (3.5) reduces to

$$\frac{\mathrm{E}(D)}{\mathrm{E}(C)} = N - \frac{Nt\bar{p}(1 - \bar{p})^{t-1}}{\mathrm{E}(C)} \gamma^2 + R_2. \tag{3.6}$$

Our proposed estimators will be derived mainly from the results (3.5) and (3.6) by ignoring the remainder term. Some numerical discussions regarding the remainder term for various models can be found in Lee (unpublished Ph.D. thesis, National Tsing Hua University, 1990) and Chao et al. (1992).

3.1 *Model* M_{tbh}

The only relevant statistics for estimating N in model M_{tbh} are the first-capture data $(u_1, u_2, \ldots, u_t)$. The following procedure is suggested: Define C_k as the sample coverage of the first k samples, $k \leq t - 1$. Considering only these k samples, (3.5) becomes

$$N \approx \frac{\mathrm{E}(D_k)}{\mathrm{E}(C_k)} + \frac{N \sum_{j=1}^{k} (\bar{p}e_j) \prod_{s \neq j}^{k} (1 - \bar{p}e_s)}{\mathrm{E}(C_k)} \gamma^2. \tag{3.7}$$

We therefore need to find estimators for γ^2, $\mathrm{E}(C_k)$, and $N \Sigma (\bar{p}e_j) \Pi_{s \neq j} (1 - \bar{p}e_s)$. Under model M_{tbh},

$$\mathrm{E}(u_k) = \sum_{i=1}^{N} p_i e_k \prod_{j=1}^{k-1} (1 - p_i e_j) \tag{3.8}$$

$$\approx N\bar{p}e_k \prod_{j=1}^{k-1} (1 - \bar{p}e_j). \tag{3.9}$$

Using (3.9), we can show with some algebra that

$$N \sum_{j=1}^{k} (\bar{p}e_j) \prod_{s \neq j}^{k} (1 - \bar{p}e_s) \approx (\mathrm{E}u_{k+1}/e_{k+1}) \sum_{j=1}^{k} (e_{j+1}\mathrm{E}u_j/\mathrm{E}u_{j+1}). \tag{3.10}$$

Thus a natural estimator for the right-hand side of (3.10) is

$$A_k = (u_{k+1}/e_{k+1}) \sum_{j=1}^{k} (e_{j+1}u_j/u_{j+1}). \tag{3.11}$$

Combining (3.7), (3.10), and (3.11), we have the following estimator based on the sample coverage of the first k samples:

$$\hat{N}(k) = \frac{D_k}{\hat{C}_k} + \frac{A_k}{\hat{C}_k} \hat{\gamma}_k^2, \tag{3.12}$$

where $\hat{C}_k$ and $\hat{\gamma}_k^2$ are estimators of $\mathrm{E}(C_k)$ and γ^2 to be obtained below. First, it follows from (3.4) and (3.8) that $\mathrm{E}(C_k)$ can be written as

$$\mathrm{E}(C_k) = 1 - \sum_{i=1}^{N} p_i \prod_{j=1}^{k} (1 - p_i e_j) \Big/ \sum_i p_i = 1 - \frac{\mathrm{E}(u_{k+1})/e_{k+1}}{\mathrm{E}(u_1)/e_1}.$$

Hence, if $u_{k+1}/e_{k+1} < u_1/e_1$, an estimator for $\mathrm{E}(C_k)$ is

$$\hat{C}_k = 1 - \frac{u_{k+1}/e_{k+1}}{u_1/e_1}, \quad k = 1, 2, \ldots, t-1. \tag{3.13}$$

Second, it follows from (3.8) that

$$\gamma^2 = N[\mathrm{E}u_1 - \mathrm{E}u_2(e_1/e_2)]/(\mathrm{E}u_1)^2 - 1;$$

the following CV estimator is then obtained based on the first k samples:

$$\hat{\gamma}_k^2 = \max\{\hat{N}_0(k)[u_1 - u_2(e_1/e_2)]/u_1^2 - 1, 0\}, \tag{3.14}$$

where $\hat{N}_0(k) = D_k/\hat{C}_k$. The estimator $\hat{N}(k)$ for all $k = 1, 2, \ldots, t-1$ is independent of the scale of relative effects e_j's.

If $(p_1, p_2, \ldots, p_N)$ are fixed parameters, then $(u_1, u_2, \ldots, u_t)$ is not multinomially distributed, as noted by Cormack (1989, p. 404). Although an approximate variance can be derived (Lee, unpublished Ph.D. thesis, cited previously), it seems difficult to obtain a useful variance estimator. We thus assume that $(p_1, p_2, \ldots, p_N)$ is a random sample from an unknown distribution $F(p)$. The joint unconditional distribution of $(u_1, u_2, \ldots, u_t)$ then becomes multinomial. Since $\hat{N}(k)$ is a function of $(u_1, u_2, \ldots, u_{k+1})$, a variance estimator can be obtained by using a delta method. The adequacy of the unconditional variance estimators will be shown in the simulation section.

For the choice of an appropriate k, we would suggest $k = t - 1$ if $u_t/e_t < u_1/e_1$ since all data are used in this case. If $u_t/e_t \geq u_1/e_1$ and t is large, we may choose a k such that $u_{k+1}/e_{k+1} < u_1/e_1$ $(k \leq t - 2)$ and discard the last $t - k - 1$ observations $u_{k+2}, \ldots, u_t$.

3.2 *Model* M_{bh}

Under the condition that $e_j = 1$ for all $j = 1, 2, \ldots, t$, (3.7) reduces to

$$\frac{\mathrm{E}(D_k)}{\mathrm{E}(C_k)} \approx N - \frac{Nk\bar{p}(1-\bar{p})^{k-1}}{\mathrm{E}(C_k)}\gamma^2. \tag{3.15}$$

For model M_{bh}, $\mathrm{E}(u_k) \approx N\bar{p}(1-\bar{p})^{k-1}$; we thus consider for $k = 1, 2, \ldots, t-1$,

$$\hat{N}(k) = \frac{D_k}{\hat{C}_k} + \frac{ku_k}{\hat{C}_k}\hat{\gamma}_k^2, \tag{3.16}$$

where, as special cases of (3.13) and (3.14) if $u_{k+1} < u_1$,

$$\hat{C}_k = 1 - u_{k+1}/u_1$$

and

$$\hat{\gamma}_k^2 = \max\{\hat{N}_0(k)(u_1 - u_2)/u_1^2 - 1, 0\}. \tag{3.17}$$

3.3 *Model* M_{th}

Based on (3.5), the following two estimators were proposed in Chao et al. (1992):

$$\hat{N} = \frac{D}{\hat{C}} + \frac{f_1}{\hat{C}}\hat{\gamma}^2, \tag{3.18}$$

$$\tilde{N} = \frac{D}{\tilde{C}} + \frac{f_1}{\tilde{C}}\tilde{\gamma}^2, \tag{3.19}$$

where $\hat{C}$ and $\tilde{C}$ are estimators of $\mathrm{E}(C)$ and the following forms are obtained:

$$\hat{C} = 1 - \frac{f_1}{\sum_{k=1}^{t} kf_k}, \tag{3.20}$$

$$\tilde{C} = 1 - \frac{f_1 - 2f_2/(t-1)}{\sum_{k=1}^{t} kf_k}. \tag{3.21}$$

The CV estimate $\hat{\gamma}^2$ is

$$\hat{\gamma}^2 = \max\left\{\hat{N}_0 \sum_k k(k-1)f_k \Bigg/ \left[2\sum\sum_{j<k} n_j n_k\right] - 1, 0\right\}, \tag{3.22}$$

where $\hat{N}_0 = D/\hat{C}$, and $\tilde{\gamma}^2$ is obtained by replacing $\hat{N}_0$ above by $\tilde{N}_0 = D/\tilde{C}$.

Variance estimators for $\hat{N}$ and $\tilde{N}$ are provided in Chao et al. (1992) assuming that $p_1, p_2, \ldots, p_N$ are a random sample from an unknown distribution $F(p)$ as previously obtained in model M_{tbh}.

3.4 *Model* M_h

All the procedures described for model M_{th} are valid for model M_h. However, under model M_h, a simpler estimator for the CV can be obtained:

$$\hat{\gamma}^2 = \max\left\{\frac{\hat{N}_0 t \sum k(k-1)f_k}{(t-1)\left(\sum kf_k\right)^2} - 1, 0\right\}, \tag{3.23}$$

and $\tilde{\gamma}^2$ is defined analogously.

3.5 *Other Special Models and a Unified Table*

Models M_t, M_b, and M_{tb} are treated here as special cases of previously discussed models:

(1) Model M_t: Model M_{th} with CV = 0
(2) Model M_b: Model M_{bh} with CV = 0
(3) Model M_{tb}: Model M_{tbh} with CV = 0

The proposed estimator in the above three models then has the form of $D/\hat{C}$ or $D_k/\hat{C}_k$. Also refer to (3.2). As for the sample coverage estimation, respectively refer to models M_{th}, M_{bh}, and M_{tbh}.

All the above results are summarized in Table 1.

Table 1
Estimators for various models
($k = t - 1$ if $u_t/e_t < u_1/e_1$)

Model	Estimator	A or A_k	$\hat{C}$, $\tilde{C}$, or $\hat{C}_k$	$\hat{\gamma}^2$, $\tilde{\gamma}^2$, or $\hat{\gamma}_k^2$
M_{tbh}	$\hat{N}(k) = \frac{D_k}{\hat{C}_k} + \frac{A_k}{\hat{C}_k}\hat{\gamma}_k^2$	A_k = eq. (3.11)	$\hat{C}_k = 1 - \frac{u_{k+1}/e_{k+1}}{u_1/e_1}$	$\hat{\gamma}_k^2$ = eq. (3.14)
M_{tb}	$\hat{N}_0(k) = D_k/\hat{C}_k$	—	(same as above)	—
M_{bh}	$\hat{N}(k) = \frac{D_k}{\hat{C}_k} + \frac{A_k}{\hat{C}_k}\hat{\gamma}_k^2$	$A_k = ku_k$	$\hat{C}_k = 1 - \frac{u_{k+1}}{u_1}$	$\hat{\gamma}_k^2$ = eq. (3.17)
M_b	$\hat{N}_0(k) = D_k/\hat{C}_k$	—	(same as above)	—
M_{th}	$\hat{N} = \frac{D}{\hat{C}} + \frac{A}{\hat{C}}\hat{\gamma}^2$	$A = f_1$	$\hat{C}$ = eq. (3.20)	$\hat{\gamma}^2$ = eq. (3.22)
	$\tilde{N} = \frac{D}{\tilde{C}} + \frac{A}{\tilde{C}}\tilde{\gamma}^2$	$A = f_1$	$\tilde{C}$ = eq. (3.21)	$\tilde{\gamma}^2$: replace $\hat{C}$ by $\tilde{C}$ in (3.22)
M_h	(same as M_{th})	$A = f_1$	(same as M_{th})	$\hat{\gamma}^2$ = eq. (3.23)
M_t and M_0	$\hat{N}_0 = D/\hat{C}$, $\tilde{N}_0 = D/\tilde{C}$	—	(same as M_{th})	—

4. Real Data Examples

4.1 *Meadow Vole Example (Model M_h)*

Capture–recapture data for meadow vole were analyzed in Pollock et al. (1990). From five consecutive trapping days, $f_1 = 29$, $f_2 = f_3 = 15$, $f_4 = 16$, and $f_5 = 27$. A total of 102 distinct voles were caught out of 303 captures. Pollock et al. applied a model selection procedure to these data and concluded that model M_h was adequate. The jackknife estimate was 139, with a standard error (s.e.) of 10.85.

We now apply our method to these data with model M_h assumed. The sample coverage estimates are $\hat{C} = 1 - f_1/\Sigma\, if_i = 90.43\%$ and $\tilde{C} = 92.9\%$; consequently $\hat{N}_0 = D/\hat{C} = 113$ and $\tilde{N}_0 = D/\tilde{C} = 110$. The estimates for CV based on (3.23) are $\hat{\gamma} = .555$ and $\tilde{\gamma} = .523$. In (3.18) and (3.19), the CV term for $\hat{N}_0$ is $29(.555)^2/.9043 = 10$ and for $\tilde{N}_0$ is $29(.523)^2/.929 = 9$. Thus the estimates under model M_h are $\hat{N} = 113 + 10 = 123$ with s.e. = 7.72 and $\tilde{N} = 110 + 9 = 119$ with s.e. = 7.03. Using a log-transformation, we obtain 95% confidence intervals for N based on $\hat{N}$ and $\tilde{N}$ of (112, 144) and (110, 139), respectively. The MLE under model M_0 is 103, implying that almost all animals were captured. However, our estimate is that approximately 20 animals were never caught in the experiments.

4.2 *Lobster Data (Model M_{tbh} with Relative Time Effects Known)*

This example consists of a 17-occasion catch-effort lobster data set originally given in De Lury (1947) and also discussed in Seber (1982, Chap. 7). For each occasion, the number of traps and the number of pounds of lobster caught were recorded. "Pounds" is identified here with numbers of individuals since lobster sizes remained fairly constant during the sampling period (De Lury, 1947). We remark that this measure casts doubt on the use of a multinomial assumption, as indicated by Pollock, Hines, and Nichols (1984). This variable catch-effort model clearly has the same probability structure as model M_{tbh} with the relative time effects being proportional to the number of traps.

Typical regression-type estimates for these data are the following: Leslie's regression estimate is 120.5 (in 1,000 pounds) with s.e. = 8.92; Ricker's estimate is 119.1 with s.e. = 6.72; De Lury's estimate is 115.2 with s.e. = 6.83. The problem with the regression approach is that it assumes all animals have the same probability of being caught for a fixed sample. Our simulation results (reported in next section) show that the regression-type estimates usually underestimate when a strong heterogeneity among animals is present.

From (3.12)–(3.14), $\hat{N}_0(16) = D_{16}/\hat{C}_{16} = 130$ and $\hat{\gamma}_{16} = .8$. The estimate $\hat{N}_0(16)$, without considering the heterogeneity, is close to the regression results. However, the estimate of CV shows evidence of heterogeneity. The proposed estimate based on the sample coverage of the first 16 samples, $\hat{N}(16)$, is 189.0 (s.e. 29.1), which is substantially higher than the regression estimates. If the last occasion is sequentially truncated, we have $\hat{N}(15) = 233.3$ (s.e. 41.2), $\hat{N}(14) = 182.9$ (s.e. 29.5), and $\hat{N}(13) = 200.6$ (s.e. 34.5).

5. Simulation Study

A simulation study was carried out to investigate the performance of the proposed estimators and to compare them with other estimators. The parameters of the trials are given in Table 2. The true population size (N) was fixed to be 400 and $t = 7$ was chosen. For the effects of individual animals on first-capture probabilities, equal numbers of animals were assigned to have four distinct individual effects. For the time effects (e_j's or α_j's), we considered (e_1–e_7) or (α_1–α_7) = (.9, .8, .4, .5, .4, .7, .8). Recapture probabilities are not specified in Table 2 since they are irrelevant in the analysis. We concentrate mainly on models with heterogeneity.

Table 2
Description of the trials
(In each trial, N = 400 and 100 animals, respectively, exist with individual effects of p_1, p_2, p_3, and p_4, $\bar{p}$ = mean, CV = coefficient of variation.)

Trial	p_1	p_2	p_3	p_4	$\bar{p}$	CV	Time effects
1	.25	.25	.25	.25	.25	0	(.9, .8, .4, .5, .4, .7, .8)
2	.15	.2	.3	.35	.25	.32	
3	.125	.15	.25	.475	.25	.55	
4	.1	.15	.2	.55	.25	.71	
5	.08	.11	.14	.67	.25	.97	
6	.06	.084	.096	.36	.15	.81	
7	.08	.112	.125	.48	.2	.81	
8	.1	.14	.16	.6	.25	.81	
9	.12	.168	.192	.72	.3	.81	
10	.14	.196	.224	.84	.35	.81	

The following previously published estimators were compared in the simulation study conducted here: the MLE under models M_0, M_t, and M_b; the interpolated jackknife for model M_h; the generalized removal and jackknife (Pollock and Otto, 1983, eq. (17)) for model M_{bh}; and regression estimators for model M_{tb} with known relative time effects.

For each trial of a fixed model, 500 data sets were generated. The proposed estimators and previously published estimators as well as their estimated standard errors were calculated for each set. These 500 estimates and their standard errors were averaged. Based on these 500 estimates, the sample standard deviation as well as the sample root mean squared error (RMSE) were also obtained. In Table 3, we present only the results for model M_{tbh} (including M_{tb}). All the other outputs for models M_h (including M_0), M_{bh} (including M_b), and M_{th} (including M_t) are given in Lee (unpublished thesis cited previously). In Table 3, we also list the averages of D_t (number of distinct captured animals), C_{t-1} (coverage), and $\hat{C}_{t-1}$ (coverage estimate) for each trial. The following discussion is based on broader simulation results that include the one reported here and those considered in Lee's thesis.

Table 3

Simulation results for comparing estimates for M_{tb} and M_{tbh}; 500 runs (those runs with $\hat{C}_{t-1} \le 0$ were discarded and not counted); $\hat{N}_0(t-1)$, $\tilde{N}(t-1)$: see Table 1; $\hat{N}_r$: Leslie's regression estimator.

Trial	Method	Estimate	Bias	Estimated s.e.	Sample s.d.	Sample RMSE
1 (M_{tb})	$\hat{N}_0(t-1)$	408	8	48.1	46.6	47.2
$D_t = 284$	$\hat{N}_r$	405	5	45.0	44.3	44.6
$C_{t-1} = .638$	$\tilde{N}(t-1)$	459	59	104.3	97.4	114.1
$\hat{C}_{t-1} = .634$						
2 (M_{tbh})	$\hat{N}_0(t-1)$	383	−17	41.7	40.6	44.0
$D_t = 275$	$\hat{N}_r$	378	−22	38.2	34.5	41.2
$C_{t-1} = .660$	$\tilde{N}(t-1)$	432	32	94.5	88.0	93.6
$\hat{C}_{t-1} = .654$						
3 (M_{tbh})	$\hat{N}_0(t-1)$	343	−57	32.3	34.8	66.7
$D_t = 260$	$\hat{N}_r$	336	−64	29.3	29.1	71.0
$C_{t-1} = .693$	$\tilde{N}(t-1)$	388	−12	78.1	71.4	72.5
$\hat{C}_{t-1} = .692$						
4 (M_{tbh})	$\hat{N}_0(t-1)$	315	−85	26.5	29.8	90.4
$D_t = 246$	$\hat{N}_r$	304	−96	24.0	25.3	98.9
$C_{t-1} = .717$	$\tilde{N}(t-1)$	361	−39	68.7	66.5	77.1
$\hat{C}_{t-1} = .717$						
5 (M_{tbh})	$\hat{N}_0(t-1)$	262	−138	17.6	21.7	139.5
$D_t = 218$	$\hat{N}_r$	248	−152	16.3	18.2	153.3
$C_{t-1} = .765$	$\tilde{N}(t-1)$	312	−88	55.0	57.1	105.1
$\hat{C}_{t-1} = .766$						
6 (M_{tbh})	$\hat{N}_0(t-1)$	287	−113	65.5	74.1	134.8
$D_t = 177$	$\hat{N}_r$	275	−125	50.6	50.7	135.1
$C_{t-1} = .577$	$\tilde{N}(t-1)$	386	−14	192.8	230.3	230.7
$\hat{C}_{t-1} = .567$						
7 (M_{tbh})	$\hat{N}_0(t-1)$	285	−115	33.8	39.1	121.2
$D_t = 209$	$\hat{N}_r$	276	−124	30.3	30.0	127.6
$C_{t-1} = .669$	$\tilde{N}(t-1)$	338	−62	88.3	102.8	119.9
$\hat{C}_{t-1} = .670$						
8 (M_{tbh})	$\hat{N}_0(t-1)$	296	−104	23.3	24.6	106.6
$D_t = 236$	$\hat{N}_r$	282	−118	21.3	21.4	119.7
$C_{t-1} = .732$	$\tilde{N}(t-1)$	350	−50	68.3	65.5	82.3
$\hat{C}_{t-1} = .729$						
9 (M_{tbh})	$\hat{N}_0(t-1)$	305	−95	17.6	19.1	96.3
$D_t = 258$	$\hat{N}_r$	289	−111	16.9	17.1	112.2
$C_{t-1} = .776$	$\tilde{N}(t-1)$	357	−43	53.0	52.8	68.0
$\hat{C}_{t-1} = .776$						
10 (M_{tbh})	$\hat{N}_0(t-1)$	315	−85	14.1	15.5	86.1
$D_t = 276$	$\hat{N}_r$	296	−104	15.7	14.0	104.7
$C_{t-1} = .808$	$\tilde{N}(t-1)$	374	−26	46.9	49.1	55.6
$\hat{C}_{t-1} = .811$						

(1) Models M_0 and M_h:

For model M_0 (trial 1), the MLE associated with M_0 works, as expected, better than the proposed $\hat{N}_0$ or $\tilde{N}_0$ in terms of bias and RMSE. As far as the s.e.'s are concerned, both $\hat{N}_0$ and $\tilde{N}_0$ generally have high efficiency relative to the MLE, which agrees with the finding of Darroch and Ratcliff (1980).

For model M_h with CV = .32 (trial 2), the MLE still has the smallest RMSE. When CV becomes large (say, CV $\ge$ .4), the MLE becomes negatively biased and the magnitude of the bias increases with CV. The interpolated jackknife tends to overestimate in most cases, as also found by Pollock and Otto (1983). Our proposed estimator $\hat{N}$ or $\tilde{N}$ usually has the smallest bias and the smallest RMSE. The general guideline for the choice between $\hat{N}$ or $\tilde{N}$ is still unclear to us.

(2) Models M_b and M_{bh}:

For model M_b and model M_{bh} with CV = .32, the MLE associated with model M_b performs best under both bias and RMSE criteria. Like the finding for model M_0, the estimator $\hat{N}_0(t-1)$ has relatively high efficiency compared to the MLE. The MLE, however, produces a large negative bias when CV increases.

For the other trials of model M_{bh}, the jackknife estimator proposed by Pollock and Otto (1983) produces the smallest RMSE for most of the trials. However, two drawbacks regarding the jackknife were noted. First, it usually overestimates the true population size severely if the number of captured animals is relatively large. Second, its variability sometimes increases with t, the number of samples. Our estimator $\hat{N}(t-1)$ is generally better than the generalized removal estimator but worse than the jackknife with respect to RMSE.

(3) Models M_t and M_{th}:

As before, the MLE associated with M_t is superior to any other estimate when CV is 0 and .32. When CV $\geq$ .4, our proposed $\hat{N}$ and $\tilde{N}$ incorporating the CV term provide an improvement on the MLE. Refer to Chao et al. (1992) for other trials and detailed comparisons.

(4) Models M_{tb} and M_{tbh} (Table 3):

Only Leslie's regression estimates are tabulated in Table 3 because De Lury's estimator in most cases severely underestimates the population size and Ricker's estimator is not independent of the choice of scale of the effort. Hence both were excluded in the comparisons.

For model M_{tb}, Leslie's regression estimate and the proposed $\hat{N}_0(t-1)$ (both are derived under the equal-catchability hypothesis) have the same magnitude of bias and RMSE. Both are biased downward under model M_{tbh}. The proposed estimator $\hat{N}(t-1)$ is always higher than the above two estimates. For CV $\geq$ .4 our estimator $\hat{N}(t-1)$ has the smallest bias. Trial 6 is an example which shows that even when CV is large, the reduction in bias cannot compensate for the increase in s.e., which then subsequently yields an increase in RMSE. Therefore, it is still not worth using an estimated CV if the data are too sparse.

In Table 3, the column headed "estimated s.e." provides the averages of estimated s.e.'s calculated under a multinomial assumption as described in Section 3.1. The performance of the approximate s.e. formulas can be shown as compared with the sample standard deviation of the estimator (column headed "sample s.d.").

6. Conclusion

For the models without heterogeneity (M_0, M_t, M_b, M_{tb}), our proposed estimators $\hat{N}_0$ and $\tilde{N}_0$ (if no behavior response exists) or $\hat{N}_0(t-1)$ (if behavior response exists) performs less well than the usual MLE, but it generally has high relative efficiency. For those models with heterogeneity, traditional estimators without considering heterogeneity are still appropriate for CV < .4. For CV $\geq$ .4 and sufficient data to generate a stable estimator of the CV, our proposed estimator $\hat{N}$ and $\tilde{N}$ (if no behavior response exists) or $\hat{N}(t-1)$ (if behavior response exists) is recommended for models M_h, M_{th}, and M_{tbh}. For model M_{bh}, the jackknife proposed by Pollock and Otto (1983, eq. (17)) has the smallest RMSE in most trials.

Acknowledgements

The authors would like to thank an associate editor and two referees for carefully reading the manuscript, improving the exposition, and providing insightful suggestions. This work is based on part of the Ph.D. thesis of the first author under supervision of the second author. Research was supported by the National Science Council under Contracts NSC-79-0208-M007-18 and NSC-80-0208-M007-39.

Résumé

Une technique non-paramétrique d'estimation est proposée qui utilise le concept de couverture d'échantillon afin d'estimer l'effectif d'une population fermée à l'aide de modèles de capture–recapture dans lesquels les probabilités de capture peuvent être affectées par le comportement ou être hétérogènes. Cette technique fournit aussi une approche unifiée des modèles d'effort de capture qui permettent des probabilités de prélèvement hétérogènes. Des exemples de données réelles sont données pour illustration. Le comportement de la procédure proposée est étudié par simulation.

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.
Carothers, A. D. (1973). The effects of unequal catchability on Jolly–Seber estimates. *Biometrics* **29,** 79–100.
Carothers, A. D. (1979). Quantifying unequal catchability and its effect on survival estimates in an actual population. *Journal of Animal Ecology* **48,** 863–869.
Chao, A., Lee, S.-M., and Jeng, S.-L. (1992). Estimating population size for capture–recapture data when capture probabilities vary by time and individual animal. *Biometrics* **48,** 201–216.
Cormack, R. M. (1966). A test for equal catchability. *Biometrics* **22,** 330–342.
Cormack, R. M. (1989). Log-linear models for capture–recapture. *Biometrics* **45,** 395–413.
Darroch, J. N. (1958). The multiple recapture census. I: Estimation of a closed population. *Biometrika* **45,** 343–359.
Darroch, J. N. and Ratcliff, D. (1980). A note on capture–recapture estimation. *Biometrics* **36,** 149–153.
De Lury, D. B. (1947). On the estimation of biological populations. *Biometrics* **3,** 145–167.
Esty, W. W. (1985). Estimation of the number of classes in a population and the coverage of a sample. *Mathematical Scientist* **10,** 41–50.
Leslie, P. H. and Davis, D. H. S. (1939). An attempt to determine the absolute number of rats on a given area. *Journal of Animal Ecology* **8,** 94–113.
Moran, P. A. P. (1951). A mathematical theory of animal trapping. *Biometrika* **38,** 307–311.
Otis, D. L., Burnham, K. P., White, G. C., and Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62,** 1–135.
Pollock, K. H. (1976). Building models of capture–recapture experiments. *The Statistician* **25,** 253–260.
Pollock, K. H. (1981). Capture–recapture models: A review of current method, assumptions and experimental design. In *Estimating Number of Terrestrial Birds, Studies in Avian Biology* **6,** 426–435, C. J. Ralph and J. M. Scott (eds).
Pollock, K. H. (1991). Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: Past, present, and future. *Journal of the American Statistical Association* **86,** 225–238.
Pollock, K. H., Hines, J. E., and Nichols, J. D. (1984). The use of auxiliary variables in capture–recapture and removal experiments. *Biometrics* **40,** 329–340.
Pollock, K. H., Nichols, J. D., Brownie, C., and Hines, J. E. (1990). Statistical inference for capture–recapture experiments. *Wildlife Monographs* **107,** 1–97.
Pollock, K. H. and Otto, M. C. (1983). Robust estimation of population size in closed animal populations from capture–recapture experiments. *Biometrics* **39,** 1035–1049.
Ricker, W. E. (1958). Handbook of computations for biological statistics of fish populations. *Bulletin Fisheries Research Board of Canada* **119,** 1–300.
Seber, G. A. F. (1982). *The Estimation of Animal Abundance*, 2nd edition. London: Griffin.
White, G. C., Anderson, D. R., Burnham, K. P., and Otis, D. L. (1982). Capture–recapture and removal methods for sampling closed populations. Publication LA-8787-NERP. Los Alamos, New Mexico: Los Alamos National Laboratory.
Zippin, C. (1956). An evaluation of the removal method of estimating animal populations. *Biometrics* **12,** 163–189.
Zippin, C. (1958). The removal method of population estimation. *Journal of Wildlife Management* **22,** 82–90.

Received December 1990; *revised July* 1991, *and March and October* 1992; *accepted October* 1992.