

Estimation of Population Size Using Open Capture–Recapture Models

Trent L. McDONALD and Steven C. AMSTRUP

One of the most important needs for wildlife managers is an accurate estimate of population size. Yet, for many species, including most marine species and large mammals, accurate and precise estimation of numbers is one of the most difficult of all research challenges. Open-population capture–recapture models have proven useful in many situations to estimate survival probabilities but typically have not been used to estimate population size. We show that open-population models can be used to estimate population size by developing a Horvitz–Thompson-type estimate of population size and an estimator of its variance. Our population size estimate keys on the probability of capture at each trap occasion and therefore is quite general and can be made a function of external covariates measured during the study. Here we define the estimator and investigate its bias, variance, and variance estimator via computer simulation. Computer simulations make extensive use of real data taken from a study of polar bears (*Ursus maritimus*) in the Beaufort Sea. The population size estimator is shown to be useful because it was negligibly biased in all situations studied. The variance estimator is shown to be useful in all situations, but caution is warranted in cases of extreme capture heterogeneity.

Key Words: Jolly–Seber; Mark; Radio telemetry; Resight; Tag; Trap.

1. INTRODUCTION

Analysis methods for capture–recapture data can be divided into two types, those for closed populations and those for open populations (see Pollock, Nichols, Brownie, and Hines 1990). Open populations are common in application and size estimates have been obtained for them using the Jolly–Seber model (Jolly 1965; Seber 1965) or one of a number of restrictions or extensions to the Jolly–Seber model (Darroch 1959; Jolly 1965, 1982; Pollock 1975; Brownie and Robson 1983; Pollock et al. 1990). Lebreton, Burnham, Clobert, and Anderson (1992) discussed a modeling method for open populations that allows incorporation of external covariates (such as age, age class, year, weight, sex, weather, geographic

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location, etc.) into linear-logistic equations for probability of capture and probability of survival. Lebreton et al. (1992) focused on estimation of survival and did not mention estimation of population size. Huggins (1989, 1991) and Yip, Zhou, Lin, and Fang (1999) discuss estimation of a closed population's size using general models that allow inclusion of external covariates.

In this article, we propose a population size and variance estimator for open populations that make use of the type of models found in Lebreton et al. (1992) to model capture heterogeneity. Our size estimator is a Horvitz–Thompson-type estimator that sums inverse estimated capture probabilities across individuals seen at each trap occasion. The variance estimator developed here was derived using Taylor series approximations and can be thought of as an approximately unbiased estimator of the approximate variance of the size estimator. We assert that our estimator of size is useful and will enhance the utility of open population capture–recapture models by allowing size estimates, not just survival estimates, to be constructed from capture–recapture data.

There are two reasons why a general estimator of population size is needed: (1) the Jolly–Seber estimates do not take account of capture heterogeneity and therefore can be badly biased when heterogeneity is present (Gillbert 1973) and (2) an open-population size estimator has not been proposed when external covariates are incorporated into the capture (or survival) probability model.

We start by defining the size and variance estimator. We then describe a Monte Carlo computer simulation to assess properties of the estimator, its variance, and the estimator of its variance. Three different simulation scenarios are presented, ranging from zero capture heterogeneity to highly complex capture heterogeneity. It is our goal to show that the estimator is useful because it tracks true open-population size, has negligible bias, and has relatively small variance. We also show that the estimator of variance is useful because it is easy to compute and is negligibly biased in many cases; however, the estimator of variance can have substantial bias in some cases. The motivating problem for this work was a large-scale capture–recapture study of polar bears (*Ursus maritimus*) in the Beaufort Sea north of Alaska and Western Canada.

2. POPULATION SIZE ESTIMATOR

We assume that n capture histories are available and that each contain information from m capture occasions. Let p_{ij} ($i = 1, \dots, n, j = 1, \dots, m$) represent the probability of capture for the i th animal during the j th capture occasion. Let τ_{ij} ($i = 1, \dots, n, j = 1, \dots, (m-1)$) represent the probability of survival for the i th animal during the time period between the j th and $(j+1)$ th capture occasions. The open-population capture–recapture models employed here relate a differentiable function of the p_{ij} and τ_{ij} to a linear function of external covariates. Let x_{ijk} ($k = 1, \dots, s$) and z_{ijl} ($l = 1, \dots, t$) represent values of the k th and l th external covariate for the i th animal during the j th capture occasion. The capture probabilities, p_{ij} , will be modeled as a function of the x_{ijk} . The survival probabilities, τ_{ij} , will be modeled as a function of the z_{ijl} . Both the capture probability covariates and survival

covariates can be viewed as three-dimensional arrays where rows are individuals, columns are trap occasions, and pages are different covariates. The open-population models used here stipulate that

$$\log \left(\frac{p_{ij}}{1 - p_{ij}} \right) = \beta_1 x_{ij1} + \dots + \beta_s x_{ijs} \tag{2.1}$$

and

$$\log \left(\frac{\tau_{ij}}{1 - \tau_{ij}} \right) = \alpha_1 z_{ij1} + \dots + \alpha_t z_{ijt}. \tag{2.2}$$

Generally, an intercept is desired in the models. If this is the case, set $x_{ij1} = 1$ and $z_{ij1} = 1$ for all i and j so that β_1 and α_1 are the intercepts. Values for the other covariate might include age, sex, year, mean temperature, whether or not the animal was wearing a radio collar, amount of effort expended to capture animals, geographic region of capture, etc.

Estimates for the parameters β_i and α_i are obtained by the method of maximum likelihood. Given a set of observed capture histories, I_{ij} , where $I_{ij} = 1$ if the i th animal was seen at the j th occasion and $I_{ij} = 0$ otherwise, the open-population log-likelihood function is

$$\ln(L) = \sum_{i=1}^n \left(\left[\sum_{j=F_i}^{L_i-1} \ln(\tau_{ij}) \right] + \left[\sum_{j=F_i+1}^{L_i} I_{ij} \ln(p_{ij}) + (1 - I_{ij}) \ln(1 - p_{ij}) \right] + \chi_{iL_i} \right),$$

where F_i is the first occasion that animal i was captured, L_i is the last occasion that animal i was captured, and $\chi_{ij} = 1 - \tau_{ij}(1 - (1 - p_{i,j+1})\chi_{i,j+1})$, ($\chi_{i,m} = 1$) (Lebreton et al. 1992). Individuals that were captured but never released back into the population (e.g., loss on capture) can be accounted for by setting $\chi_{iL_i} = 1$ for those individuals. There exist a number of computer packages that maximize $\ln(L)$ to arrive at estimates for the coefficients β_i and α_j . These packages include MARK (<http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>), SURGE (<http://nhsbig.inhs.uiuc.edu/wes/populations.html>), and S-Plus routines written by the first author (<http://www.west-inc.com>). Likelihood-based variance estimates, $\text{var}(\hat{\beta}_i)$ and $\text{var}(\hat{\alpha}_j)$, are also computed by each computer package from either the second derivative of the likelihood surface or the Hessian of the maximization. Using the $\hat{\beta}_i$, estimated capture probabilities and variances can be computed for each occasion except the first. We label the estimated capture probability and standard error for the i th animal at occasion j as \hat{p}_{ij} and $\hat{\pi}_{\hat{p}_{ij}}$, respectively. Survival probabilities can also be estimated, but they are not the focus of this article. We assume that the capture probability model is correct so that $E[\hat{p}_{ij}] = p_{ij}$ and $E[\hat{\pi}_{\hat{p}_{ij}}] = \pi_{\hat{p}_{ij}}$.

Let the true number of animals alive at trap occasion j be denoted N_j . Assuming capture is statistically independent across animals (i.e., across subscript i), $E[I_{ij}] = p_{ij}$ and $\text{var}(I_{ij}) = p_{ij}(1 - p_{ij})$. Our estimator of population size at the j th capture occasion, denoted \hat{N}_j ($j = 2, \dots, m$), is

$$\hat{N}_j = \sum_{i=1}^n \frac{I_{ij}}{\hat{p}_{ij}}.$$

Conceptually, \hat{N}_j inverts and sums capture probabilities for individuals that were actually seen at occasion j . An alternate way to write \hat{N}_j is $\sum_{i=1}^{n_j} 1/\hat{p}_{ij}$, where n_j is the number of individuals seen at occasion j and the \hat{p}_{ij} are the capture probabilities for those n_j individuals. Leaving the I_{ij} 's in the formula for \hat{N}_j excludes individuals that were not seen at occasion j and makes the mathematical manipulations in the Appendix convenient. In the Appendix, we note that

$$E[\hat{N}_j] \approx N_j + \sum_{i=1}^{N_j} \frac{1}{\hat{p}_{ij}^2} \left(\pi_{\hat{p}_{ij}}^2 - \text{cov}(I_{ij}, \hat{p}_{ij}) \right),$$

so that $E[\hat{N}_j] \approx N_j$ provided $\text{cov}(I_{ij}, \hat{p}_{ij}) \approx \pi_{\hat{p}_{ij}}^2$ for all i . This equation implies that \hat{N}_j is positively biased when $\text{cov}(I_{ij}, \hat{p}_{ij}) < \pi_{\hat{p}_{ij}}^2$ (the usual case) and suggests a bias correction for \hat{N}_j . In our simulations, we have found very little bias in \hat{N}_j , particularly when capture probabilities are large ($>10\%$), and study of the performance of a bias correction is left as a topic for further research.

In the Appendix, we derive an estimator for the approximate variance of \hat{N}_j , i.e.,

$$\widehat{\text{var}}(\hat{N}_j) = \sum_{i=1}^n \left[\frac{I_{ij}(1 - \hat{p}_{ij})}{\hat{p}_{ij}^2} + \frac{I_{ij}\hat{\pi}_{\hat{p}_{ij}}^2}{\hat{p}_{ij}^3} + \frac{I_{ij}(1 - \hat{p}_{ij})\hat{\pi}_{\hat{p}_{ij}}^2}{\hat{p}_{ij}^4} \right].$$

In the remaining sections, we investigate both \hat{N}_j and $\widehat{\text{var}}(\hat{N}_j)$ via computer simulation.

3. SIMULATION METHODS

The Monte Carlo simulations investigating bias and variance of \hat{N}_j and $\widehat{\text{var}}(\hat{N}_j)$ were carried out in three steps: First, an open population of animals was constructed such that survival probabilities and size at each trap occasion were known; second, sampling of the constructed population at each trap occasion was simulated; and third, \hat{N}_j and $\widehat{\text{var}}(\hat{N}_j)$ were computed using results from a set of fitted capture–recapture models. Each step in the simulation is described in detail below.

To construct an open population of animals, true survival probabilities and true numbers of recruits were determined for the intervals between every capture occasion. True survivals were computed using Equation (2.2) given a set of covariates, $\{z_{ijl} : l = 1, \dots, t\}$, and values for the coefficients $\alpha_1, \dots, \alpha_t$. In our simulations, we set $z_{ij1} = 1$ for all i and j so that α_1 was the intercept. Given true survivals (i.e., τ_{ij}) for every animal during every interval, a Bernoulli random variable with probability τ_{ij} was generated for every animal alive at the time. If the outcome of the Bernoulli trial was one (success), animal i was defined to have survived from time j to time $(j + 1)$; otherwise (failure), animal i was defined to have died during the interval of time from occasion j to $(j + 1)$. To facilitate simulation of population growth or decline, recruits that represented either births or immigrants were added to the system at the beginning of each time interval (i.e., immediately after each trap occasion). Births and immigrants were not differentiated because interest was in total population size at each trap occasion. The end result was a list of random survival histories, s_{ij} , equaling one if animal i was alive and available for capture at capture occasion j and

zero if animal i had died sometime prior to trap occasion j . The true population size at occasion j was $N_j = \sum_i s_{ij}$.

Once a set of survival histories was determined, true capture probabilities were computed for every animal alive at each occasion using Equation (2.1) given a set of covariates $\{x_{ijk} : k = 1, \dots, s\}$ and values for the coefficients β_1, \dots, β_s . We set $x_{ij1} = 1$ so that β_1 was the intercept of our capture model. If a simulated animal died sometime before trap occasion j , the true probability of capture at occasion j for this animal was set to zero. Given the true probability of capture for animal i at occasion j (i.e., p_{ij}), a Bernoulli random variable with probability p_{ij} was generated. If the outcome of the Bernoulli random variable was one (success), animal i was defined to have been captured at occasion j ; otherwise (failure), animal i was not captured at occasion j . All captured animals were released alive back into the system (i.e., no deaths upon capture were simulated). The end result was a list of random capture histories, I_{ij} , equaling one if animal i was captured at occasion j and equaling zero otherwise.

Given a set of generated capture histories, a predefined set of capture–recapture models was fit to the random capture histories. From each fitted model, \hat{N}_j and $\widehat{\text{var}}(\hat{N}_j)$ were computed for $j = 2, \dots, m$ and stored. In addition, the Akaike information criterion (AIC) and quasi Akaike information criterion (QAIC) (Anderson, Burnham, and White 1994; Burnham and Anderson 1998) of each fitted model were computed and the minimum AIC and QAIC model was noted. Once all quantities were stored, a new set of capture histories were generated using the same survival histories. The predefined set of models were then refitted, and estimation of \hat{N}_j and $\widehat{\text{var}}(\hat{N}_j)$ was repeated. The process of generating capture histories, fitting models, and estimating \hat{N}_j and $\widehat{\text{var}}(\hat{N}_j)$ constituted one secondary iteration of the simulation. Five secondary iterations were performed for each randomly generated set of survival histories. The process of generating survival histories and then performing five secondary iterations constituted a primary iteration. In all, 250 primary iterations were performed. To make summary statistics clear, we add subscripts to \hat{N}_j and N_j to denote iterations. Let N_{j_a} be the true population size at time j during primary iteration a (constant across secondary iterations); let $\hat{N}_{j_{ab}}$ be the estimate of N_{j_a} from primary iteration a , secondary iteration b ; and let $\widehat{\text{var}}(\hat{N}_j)_{ab}$ be the estimated variance of $\hat{N}_{j_{ab}}$ from primary iteration a , secondary iteration b .

Bias in \hat{N}_j ($j = 2, \dots, m$) computed from any individual model or from the minimum AIC or QAIC model was estimated as

$$\begin{aligned} \text{bias}(\hat{N}_j) &= \sum_{a=1}^{250} \left[\sum_{b=1}^5 (\hat{N}_{j_{ab}} - N_{j_a}) / 5 \right] / 250 \\ &= \sum_{a=1}^{250} \sum_{b=1}^5 \frac{\hat{N}_{j_{ab}}}{1,250} - \sum_{a=1}^{250} \frac{N_{j_a}}{250} = E[\hat{N}_j] - \bar{N}_j. \end{aligned} \quad (3.1)$$

The true variance of \hat{N}_j during primary iteration a was estimated as

$$\text{var}(\hat{N}_j)_a = \sum_{b=1}^5 \left(\hat{N}_{j_{ab}} - \bar{N}_{j_a} \right)^2 / 4,$$

where $\bar{N}_{ja} = \sum_{b=1}^5 \hat{N}_{jab} / 5$. Bias in $\widehat{\text{var}}(\hat{N}_j)$ was estimated as

$$\begin{aligned} \text{bias}(\widehat{\text{var}}(\hat{N}_j)) &= \sum_{a=1}^{250} \left[\sum_{b=1}^5 (\widehat{\text{var}}(\hat{N}_j)_{ab} - \text{var}(\hat{N}_j)_a) / 5 \right] / 250 \\ &= \sum_{a=1}^{250} \sum_{b=1}^5 \frac{\widehat{\text{var}}(\hat{N}_j)_{ab}}{1,250} - \sum_{a=1}^{250} \frac{\text{var}(\hat{N}_j)_a}{250} \\ &= E[\widehat{\text{var}}(\hat{N}_j)] - \overline{\text{var}(\hat{N}_j)}. \end{aligned} \quad (3.2)$$

Average bias in \hat{N}_j across trap occasions was computed as $\text{avgbias}(\hat{N}_j) = \sum_{j=2}^m \text{bias}(\hat{N}_j) / (m - 1)$ and similarly for $\text{avgbias}(\widehat{\text{var}}(\hat{N}_j))$. Bias values computed during the simulation should be viewed as estimates of the true underlying bias in \hat{N}_j or $\widehat{\text{var}}(\hat{N}_j)$. An approximate 95% confidence interval for true bias was computed as ± 2 times the standard error of bias estimates across all 1,250 iterations of the simulations. The half-width of this 95% confidence interval will be called the resolution of our simulations.

The true underlying models for p_{ij} and τ_{ij} , as well as the models chosen to fit during each iteration, were motivated by a study of polar bears in the Beaufort Sea (Amstrup, McDonald, and Stirling 2001). Estimation of polar bear population size in the Beaufort Sea has been one of the most intractable population estimation problems in all biology. If \hat{N}_j performs well in this difficult situation, we are justified in recommending \hat{N}_j for other less difficult situations. To document performance of \hat{N}_j in a specific situation, more simulations could be performed. Our goal for these simulations was to construct realistically difficult situations by incorporating real data and all its natural characteristics. Consequently, simulation model structure, covariate values (x_{ijk} and z_{ijl}), and coefficient values (β_i and α_i) were taken from initial Beaufort Sea polar bear results.

Simulations were run under three general scenarios: (A) a relatively simple system with constant expected population size, constant probability of capture, and constant probability of survival; (B) a moderately complex system with increasing expected size, moderate capture probability heterogeneity, and age-dependent survival that increased throughout the simulated study; and (C) a highly complex system with increasing expected size, high capture probability heterogeneity, and age-dependent survival that increased throughout the simulated study. Due to the fact that population sizes were stochastic, true population size could have increased or decreased during any one iteration under any of the three simulation schemes. Methods for scenario A are presented first, followed by methods for scenarios B and C.

Simulation scenario A involved generating a population with constant expected size, constant probability of capture, and constant probability of survival. Survival was fixed at 93% ($\alpha_1 = 2.5867$) for all individuals and time periods. This value for survival is reasonable for adult polar bears in the Beaufort Sea (Amstrup et al. 2001). Initial population size was set to 300 individuals. With $\tau_{ij} = 0.93$ for all i and j , the expected number of deaths between trap occasions was $(1 - 0.93)(300) = 21$; consequently, 21 recruits were added to the population immediately after each trap occasion to maintain a constant expected population size. The number of trap occasions was set to 32, the number of years in the

Beaufort Sea polar bear study. Probability of capture was constant across individuals and trap occasions and was set to values that were reasonable for the Beaufort Sea polar bear study. Probability of capture was fixed at 10 and 15% ($\beta_1 = -2.1972$ and -1.7346 , respectively; Equation (2.1)).

Four models were fit during scenario A. These models were (1) constant probabilities of capture and survival; (2) a linear trend in probability of capture and a constant probability of survival; (3) a constant probability of capture and a linear trend in probability of survival; and (4) linear trends in both the probabilities of capture and survival. For the constant models, only the intercept term was fit. For the linear-trend models, an intercept was included and x_{ij2} or z_{ij2} were set to j for all i . In other words, $x_{i12} = 1, x_{i22} = 2, \dots, x_{im2} = m$ for all i and similarly for the z 's.

The moderately complex simulation, scenario B, involved generating a population with increasing expected size, moderate capture heterogeneity, and increasing survival across capture occasions. Survival was dependent on a sigmoidal function of year and age class. The sigmoidal function of year, labeled *sigmoid.year*, generated survival rates that increased slowly during initial years of the simulated study, increased rapidly during the middle part of the study, and increased slowly during the later years of the simulated study. Age class split the population into two age classes and produced survivals that were 14% higher for approximately one third of the population during initial years of the simulated study. The difference in survival between age classes decreased to 3% during later years of the simulated study. This model for survival was reasonable for the Beaufort Sea polar bear population. The age class variable was labeled *age.class*. Adequate recruits were added to the population to offset mortality and produce an average annual growth rate of approximately 1.3%. Heterogeneity was introduced in capture rates by simulating placement of radio collars on approximately one third of the population. Simulated radio collars functioned for a maximum of 5 years. During years when an individual was wearing a functioning radio collar, its probability of capture was 99%. Capture probability for individuals without functioning radios was 10%.

Models fit during scenario B were (1) a linear trend in probability of capture and a constant probability of survival; (2) a constant probability of capture and a linear trend in probability of survival; (3) linear trends in both probability of capture and probability of survival; and (4) a constant probability of capture with a covariate delineating whether or not an individual was wearing a radio collar and a sigmoidal trend in survival through time with differences allowed between two age classes. The last of these models (4) was the correct model in that it was used to generate true survival and capture histories.

The highly complex simulation, scenario C, involved generating a population with increasing expected size, high capture heterogeneity, and increasing survival across capture occasions. The true underlying model for survival was the same as that used for scenario B (i.e., survival was a function of sigmoidal year and age class). Average population size increased by an annual growth rate of approximately 1.3% but was higher during the initial years of the simulated study than in scenario B.

Marked heterogeneity was introduced in capture rates by incorporating two time-vary-

Table 1. Capture–Recapture Models Fit During Simulation Scenario C, Where Capture Heterogeneity Was High. Terms in the models are described in the text.

<i>Model number</i>	<i>Correct model?</i>	<i>Capture model</i>	<i>Survival model</i>
1	No	(Intercept)	(Intercept)
2	No	(Intercept) + year	(Intercept)
3	No	(Intercept)	(Intercept) + year
4	No	(Intercept) + radio	(Intercept)
5	No	(Intercept) + radio	(Intercept) + sigmoid.year + age.class
6	No	(Intercept) + radio + year + effort	(Intercept) + sigmoid.year + age.class
7	No	(Intercept) + radio + year + group.size	(Intercept) + sigmoid.year + age.class
8	No	(Intercept) + radio + effort + group.size	(Intercept) + sigmoid.year + age.class
9	No	(Intercept) + year + effort + group.size	(Intercept) + sigmoid.year + age.class
10	Yes	(Intercept) + radio + year + effort + group.size	(Intercept) + sigmoid.year + age.class

ing covariates, one individual-varying covariate, and one individual \times time-varying covariate into the model for capture probability. The two time-dependent covariates were a linear year effect and number of aerial survey hours flown during the Beaufort Sea polar bear study. The linear year effect will be labeled year. The number of hours flown during the real study will be called effort. Mean effort was 125 hours with standard error 103. The individual-dependent covariate in the model for capture probability was equal to one if the average number of bears seen with a captured animal was greater than one but less than or equal to two and was zero otherwise. This last covariate simulated the presence of cubs during capture of a female and was labeled group.size. Thirty-seven percent of bears in the real study had group.size = 1. The final covariate in the model for capture probabilities varied across both individuals and trap occasions and delineated whether or not an individual was wearing a radio collar. This covariate was labeled radio and is the same covariate used in scenario B. Overall, capture probabilities varied from approximately 7.5 to 20% for individuals without radio collars. Capture probability for individuals with radio collars was 99%.

The 10 models listed in Table 1 were fit during each iteration of scenario C.

4. SIMULATION RESULTS

Table 2 contains $\text{avgbias}(\hat{N}_j)$, estimated coefficient of variation for \hat{N}_j , and $\text{avgbias}(\widehat{\text{var}}(\hat{N}_j))$ for all simulations. An approximate 95% confidence interval for the bias numbers reported in Table 2 had half-width less than ± 7 individuals. All confidence intervals on average bias estimates contained zero and indicated that average bias in \hat{N}_j was less than the resolution of our simulation; however, occasionally bias at a single trap occasion was greater than seven, confirming a small positive bias in \hat{N}_j .

Figure 1a contains a plot of average population size (\bar{N}_j in Equation (3.1)) and average \hat{N}_j ($E[\hat{N}_j]$ in Equation (3.1)) estimated from the minimum AIC model under scenario A with $p = 15\%$. Results from scenario A with $p_{ij} = 10\%$ are not graphed but were similar

Table 2. Estimated Average Bias of the Proposed Population Size Estimator ($\text{avgbias}(\hat{N}_j)$), the Coefficient of Variation for \hat{N}_j , and Average Bias of the Variance Estimator ($\text{avgbias}(\widehat{\text{var}}(\hat{N}_j))$) for the Simulations Run During This Study. An approximate 95% confidence interval for bias numbers was ± 7 individuals.

Simulation scenario	Description	Average Bias of \hat{N}_j	Coefficient of variation for \hat{N}_j	Average bias of $\widehat{\text{var}}(\hat{N}_j)$
A	Low heterogeneity, $p_{ij} = 10\%$	2.04 (0.68%)	18.2%	-4.0%
A	Low heterogeneity, $p_{ij} = 15\%$	0.38 (0.13%)	13.8%	-0.2%
B	Moderate heterogeneity	4.59 (2.55%)	23.3%	0.8%
C	High heterogeneity	4.34 (1.67%)	18.6%	-19.6%

to results from scenario A with $p_{ij} = 15\%$ except that bias was larger when $p_{ij} = 10\%$. With $p_{ij} = 10\%$, estimated bias in \hat{N}_j was as high as eight individuals, or 2.6%, during early trap occasions but fell to less than six individuals, or $<2\%$, in absolute value after the fourth capture occasion. Overall, estimated average bias in \hat{N}_j was 2.04 individuals (0.67%) for $p_{ij} = 10\%$ and 0.38 (0.1%) for $p_{ij} = 15\%$.

Figure 1b contains a plot of average population size and average \hat{N}_j from the minimum AIC model for scenario B, where heterogeneity was present in capture probabilities. Estimated bias in \hat{N}_j varied from -2.5 individuals (-1.5%) to 10.7 individuals (6.2%), with average bias equal to 4.59 individuals, or 2.55% (Table 2).

Figure 1c contains a plot of results from scenario C, where capture heterogeneity was greatest. Estimated bias in \hat{N}_j varied from -11.5 individuals (-4.2%) to 27.5 individuals (9.8%). Average bias over all trap occasions was 4.34 individuals, or 1.67%.

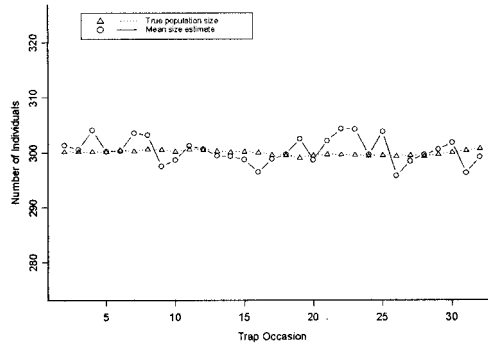
For the most part, the distributions of \hat{N}_j seen throughout the simulation study could be characterized as unimodal, symmetric, and approximately normal. Under marked heterogeneity, approximately 5% of the distributions of \hat{N}_j at specific capture times had heavy right-hand tails that are typical of Horvitz-Thompson estimators. In general, observed bias in the distribution of \hat{N}_j was caused by heavy right-hand tails, not a shift in the mode or median of the distribution.

True standard errors of \hat{N}_j ($[\text{var}(\hat{N}_j)]^{1/2}$, Equation (3.2)) and $E[\widehat{\text{var}}(\hat{N}_j)]^{1/2}$ (Equation (3.2)) are pictured in Figure 2. Overall, the true standard error of \hat{N}_j varied during the course of the simulated study and generally increased as \hat{N}_j increased. Average coefficients of variation for \hat{N}_j ($[\text{var}(\hat{N}_j)]^{1/2}/E[\hat{N}_j]$) were relatively low (for wildlife/ecology studies) and varied between 13.8 and 23.3% (Table 2). $\text{avgbias}(\widehat{\text{var}}(\hat{N}_j))$ ranged from -4.0 to 0.8% during scenarios A and B; however, average estimated bias increased to -19.6% during scenario C. In both situations with capture heterogeneity (i.e., B and C), $E[\widehat{\text{var}}(\hat{N}_j)]$ tracked the true average variance of \hat{N}_j because $E[\widehat{\text{var}}(\hat{N}_j)]$ generally increased when variance of \hat{N}_j increased and vice versa.

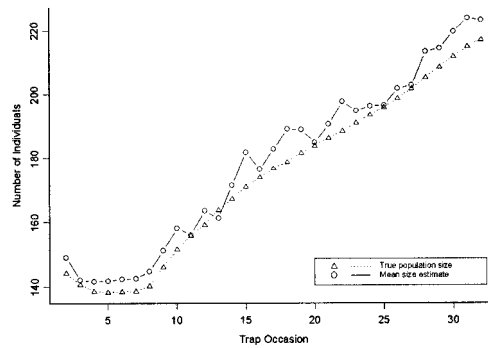
5. CONCLUSIONS

The Horvitz-Thompson-type estimator of population size, \hat{N}_j , provides a useful estimate of an open population's size. Figure 1 demonstrates that \hat{N}_j tracks true population

a. Homogeneous Capture Probabilities



b. Moderate Capture Probability Heterogeneity



c. High Capture Probability Heterogeneity

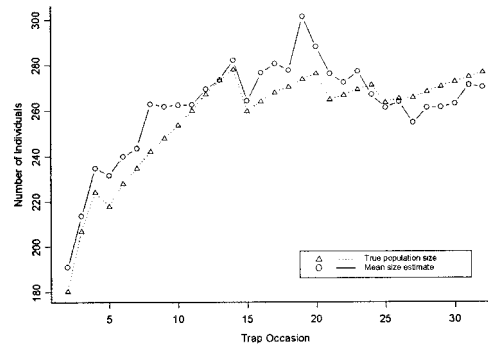
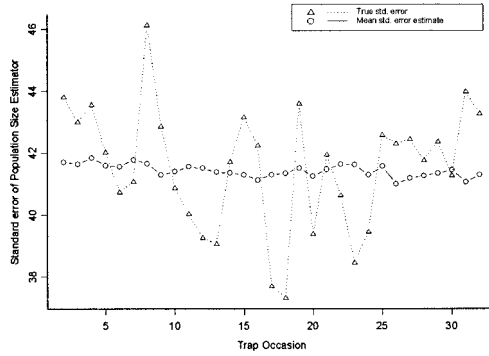
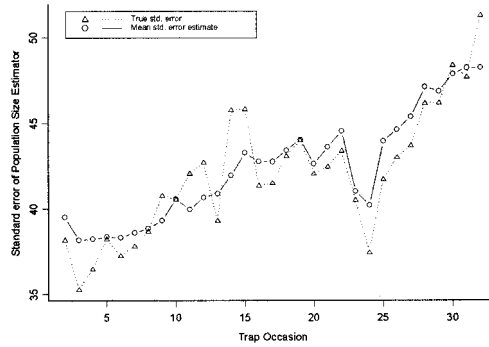


Figure 1. True Average Population Sizes (\bar{N}_j , Equation (3.1)) and Mean \hat{N}_j ($E\hat{N}_j$], Equation (3.1)) for Three Simulation Scenarios: (a) Constant Capture Probability Equal to 15%, (b) Moderate Capture Heterogeneity Wherein One Segment of the Population Was Sampled With 10% Probability, Another With 99% Probability, and (c) High Capture Heterogeneity That Was a Function of Four External Covariates.

a. Homogeneous Capture Probabilities



b. Moderate Capture Probability Heterogeneity



c. High Capture Probability Heterogeneity

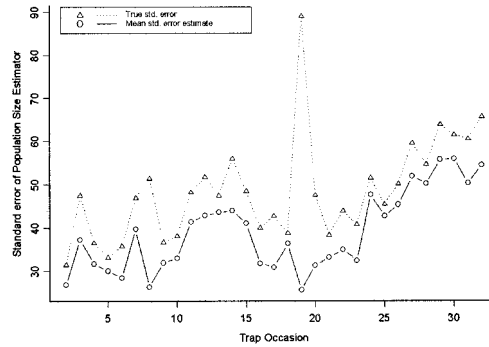


Figure 2. True Standard Error of \hat{N}_j ($-\widehat{\text{var}}(\hat{N}_j)$)^{1/2}, Equation (3.2)) and Average Standard Error Estimate ($E-\widehat{\text{var}}(\hat{N}_j)$)^{1/2}, Equation (3.2)) for Three Simulation Scenarios: (a) Constant Capture Probability Equal to 15%, (b) Moderate Capture Heterogeneity Wherein One Segment of the Population Was Sampled With 10% Probability, Another With 99% Probability, and (c) High Capture Heterogeneity That Was a Function of Four External Covariates.

size even when the open population experiences relatively large and rapid changes. \hat{N}_j performed well, with perhaps a slight positive bias, both when capture rates were constant and when capture rates were heterogeneous across individuals and occasions. Use of \hat{N}_j for open populations will increase the utility of capture–recapture data by allowing a reasonable estimate of population size to be computed alongside estimates of survival. Modeling of capture probability heterogeneity through external covariates effectively removes bias problems that have plagued other estimators.

The Taylor series estimate of the approximate variance of \hat{N}_j (i.e., $\widehat{\text{var}}(\hat{N}_j)$) is a reasonable estimate of the variance of \hat{N}_j in situations without too much capture heterogeneity. This study found that $\widehat{\text{var}}(\hat{N}_j)$ worked well in situations with no or moderate amounts of capture heterogeneity but performed worse, with bias near -20% , in situations with marked heterogeneity. Guidance regarding the amount of capture heterogeneity that the variance estimator will tolerate before significant bias occurs and/or a bias correction for $\widehat{\text{var}}(\hat{N}_j)$ remain topics for further research. Bootstrap variance estimators, wherein capture histories are randomly resampled with replacement, are alternative estimates in situations where high capture heterogeneity is a concern.

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APPENDIX

A1. EXPECTED VALUE OF \hat{N}_j

$$E[\hat{N}_j] = E\left[\sum_{i=1}^n \frac{I_{ij}}{\hat{p}_{ij}}\right] = E\left[\sum_{i=1}^{N_j} \frac{I_{ij}}{\hat{p}_{ij}}\right] = \sum_{i=1}^{N_j} E\left[\frac{I_{ij}}{\hat{p}_{ij}}\right].$$

In $E[\hat{N}_j]$, it is possible to sum from $i = 1$ to the unknown N_j because $I_{ij} = 0$ for all unseen and unsampled animals. Mood, Graybill, and Boes (1972, p. 181, eq. (14)) give the approximate expected value of a ratio of random variables. Using their formula,

$$\begin{aligned} \sum_{i=1}^{N_j} E\left[\frac{I_{ij}}{\hat{p}_{ij}}\right] &\approx \sum_{i=1}^{N_j} \left[\frac{E[I_{ij}]}{E[\hat{p}_{ij}]} - \frac{\text{cov}(I_{ij}, \hat{p}_{ij})}{E^2[\hat{p}_{ij}]} + \frac{E[I_{ij}]\text{var}(\hat{p}_{ij})}{E^3[\hat{p}_{ij}]} \right] \\ &= \sum_{i=1}^{N_j} \left[\frac{p_{ij}}{p_{ij}} - \frac{\text{cov}(I_{ij}, \hat{p}_{ij})}{p_{ij}^2} + \frac{p_{ij}\pi_{\hat{p}_{ij}}^2}{p_{ij}^3} \right] \\ &= N_j + \sum_{i=1}^{N_j} \frac{1}{p_{ij}^2} \left(\pi_{\hat{p}_{ij}}^2 - \text{cov}(I_{ij}, \hat{p}_{ij}) \right). \end{aligned}$$

A2. VARIANCE OF \hat{N}_j

Let \hat{p}_j be the vector of estimated capture probabilities at occasion j . An estimator for $\text{var}(\hat{N}_j)$ is derived from the well-known equation

$$\text{var}(\hat{N}_j) = \text{var}(E[\hat{N}_j \mid \hat{p}_j]) + E[\text{var}(\hat{N}_j \mid \hat{p}_j)]$$

(Mood et al. 1974, p. 159, theorem 7) and the Taylor series expansions for $E[1/x]$ and $\text{var}(1/x)$, i.e.,

$$\begin{aligned} E[1/x] &\approx \frac{1}{E[x]} + \frac{1}{2} \frac{\pi_x^2}{(E[x])^3} \\ \text{var}(1/x) &\approx \frac{\pi_x^2}{(E[x])^4}. \end{aligned}$$

Each term in $\text{var}(\hat{N}_j)$ will be derived separately. Assuming the distribution of \hat{p}_{ij} is approximately independent of whether or not an individual is captured,

$$E[\hat{N}_j | \hat{p}_j] = \sum_{i=1}^{N_j} \frac{E[I_{ij} | \hat{p}_{ij}]}{\hat{p}_{ij}} = \sum_{i=1}^{N_j} \frac{p_{ij}}{\hat{p}_{ij}}.$$

Assuming individuals are independent and that \hat{p}_{ij} is unbiased for p_{ij} ,

$$\text{var}(E[\hat{N}_j | \hat{p}_j]) = \sum_{i=1}^{N_j} p_{ij}^2 \text{var}(1/\hat{p}_{ij}) \approx \sum_{i=1}^{N_j} \left(\frac{\pi \hat{p}_{ij}}{p_{ij}} \right)^2.$$

For the second term of $\text{var}(\hat{N}_j)$,

$$\text{var}(\hat{N}_j | \hat{p}_j) = \sum_{i=1}^{N_j} \text{var}\left(\frac{I_{ij}}{\hat{p}_{ij}} | \hat{p}_{ij}\right) = \sum_{i=1}^{N_j} \left(\frac{1}{\hat{p}_{ij}}\right)^2 \text{var}(I_{ij} | \hat{p}_{ij}) = \sum_{i=1}^{N_j} \frac{p_{ij}(1-p_{ij})}{\hat{p}_{ij}^2}$$

and

$$\begin{aligned} E[\text{var}(\hat{N}_j | \hat{p}_j)] &= \sum_{i=1}^{N_j} p_{ij}(1-p_{ij}) E[(1/\hat{p}_{ij})^2] \\ &= \sum_{i=1}^{N_j} p_{ij}(1-p_{ij}) (\text{var}(1/\hat{p}_{ij}) + (E[1/\hat{p}_{ij}])^2) \\ &\approx \sum_{i=1}^{N_j} \left[\frac{(1-p_{ij})\pi^2 \hat{p}_{ij}}{p_{ij}^3} + \frac{(1-p_{ij})}{p_{ij}} \right], \end{aligned}$$

which uses only the first-order approximation for $E[1/\hat{p}_{ij}]$ and the well-known fact that $E[x^2] = \text{var}(x) + E^2[x]$. Combining the first and second terms,

$$\text{var}(\hat{N}_j) \approx \sum_{i=1}^{N_j} \left[\frac{(1-p_{ij})}{p_{ij}} + \frac{\pi^2 \hat{p}_{ij}}{p_{ij}^2} + \frac{(1-p_{ij})\pi^2 \hat{p}_{ij}}{p_{ij}^3} \right].$$

To derive an estimator for $\text{var}(\hat{N}_j)$, assume temporarily that p_{ij} and $\pi \hat{p}_{ij}$ are known. Let

$$v_{ij} = \frac{(1-p_{ij})}{p_{ij}} + \frac{\pi^2 \hat{p}_{ij}}{p_{ij}^2} + \frac{(1-p_{ij})\pi^2 \hat{p}_{ij}}{p_{ij}^3}$$

and consider the estimator $\widetilde{\text{var}}(\hat{N}_j) = \sum_{i=1}^n I_{ij} v_{ij} / p_{ij}$. Then

$$\begin{aligned} E[\widetilde{\text{var}}(\hat{N}_j)] &= E\left[\sum_{i=1}^n I_{ij} v_{ij} / p_{ij}\right] = E\left[\sum_{i=1}^{N_j} I_{ij} v_{ij} / p_{ij}\right] \\ &= \sum_{i=1}^{N_j} E[I_{ij}] v_{ij} / p_{ij} = \sum_{i=1}^{N_j} v_{ij} \\ &= \text{var}(\hat{N}_j). \end{aligned}$$

Thus, $\widetilde{\text{var}}(\hat{N}_j)$ is unbiased for $\text{var}(\hat{N}_j)$ if p_{ij} and $\pi_{\hat{p}_{ij}}$ are known. This justification for the unbiasedness of $\widetilde{\text{var}}(\hat{N}_j)$ is essentially a reproof of the Horvitz–Thompson theorem (Särndal, Swensson, and Wretman 1992, p. 42).

If p_{ij} and $\pi_{\hat{p}_{ij}}$ are not known, methods in Särndal et al. (1992) and others substitute \hat{p}_{ij} for p_{ij} and $\hat{\pi}_{\hat{p}_{ij}}$ for $\pi_{\hat{p}_{ij}}$ to arrive at an approximately unbiased estimator. An approximately unbiased estimator of the approximate variance of \hat{N}_j is

$$\widehat{\text{var}}(\hat{N}_j) = \sum_{i=1}^n \left[\frac{I_{ij}(1 - \hat{p}_{ij})}{\hat{p}_{ij}^2} + \frac{I_{ij}\hat{\pi}_{\hat{p}_{ij}}^2}{\hat{p}_{ij}^3} + \frac{I_{ij}(1 - \hat{p}_{ij})\hat{\pi}_{\hat{p}_{ij}}^2}{\hat{p}_{ij}^4} \right].$$