Choice of Sampling Effort in a Schnabel Census for Accurate Population Size Estimates

Su Na Chin[1,2*] and Dankmar Böhning[1]

[1*]Mathematical Sciences and Southampton Statistical Sciences Research Institute, University of Southampton, University Road, Southampton, SO17 1BJ, United Kingdom.

[2]Faculty of Science and Natural Resources, Universiti Malaysia Sabah, Jalan UMS, Kota Kinabalu, 88400, Sabah, Malaysia.

*Corresponding author(s). E-mail(s): chinsuna@ums.edu.my;

Contributing authors: D.A.Bohning@soton.ac.uk;

Abstract

Population size estimation has long been a key area of interest across various fields. The Schnabel census, a widely applied capture-recapture method, is commonly used for population estimation. However, the topic of sampling effort in Schnabel census studies remains insufficiently explored. This study aims to determine the required sampling effort in Schnabel census studies, considering different levels of capture success rates and population heterogeneity. To address this, the number of capture occasions, T, is adjusted to achieved different probabilities of missing observation, p_0, with the goal of maintaining a appropriate width of confidence interval. Specifically, maintaining $p_0 < 0.5$ could limit uncertainty to within 20% of the true population size for $N \geq 100$. Zero-truncated counting distribution was applied by fitting three models: binomial, beta-binomial, and binomial mixture. The findings reveal an exponential relationship between the desired success capture rate and the required number of capture occasions. Additionally, lower detectability requires more capture occasions to achieve the same level of capture success rate compared to higher detectability. This methodological approach provides robust and efficient estimation strategies, ensuring the sustainability and feasibility of population monitoring program.

Keywords: capture-recapture, uncertainty, zero-truncated, mixture model, EM algorithm, bootstrap

1 Introduction

Population size estimation has long been a subject of interest for many years across various fields (McCrea and Morgan, 2015). One widely used method for statistical population size estimation is the Schnabel census method (Schnabel, 1938). This method involves taking successive independent random samples from a closed population. Whenever an unmarked individual is captured, it is given a unique identifying mark before being released back into the population. The usual assumption is that the probability of capturing any particular individual is the same (Seber, 1982).

A fundamental aspect of the Schnabel census design is determining the appropriate sampling effort. Figuring out the number of occasions needed to achieve the desired level of accuracy is crucial, especially when resources such as labour, time, and funding are limited. Xi et al. (2008) examined the minimum capture proportion required to obtain reliable population size estimates under various capture–recapture models, including discrete-time frameworks applicable to the Schnabel census. Sample size and sampling effort directly affect the accuracy and precision of estimates. Burke et al. (1995) demonstrated this using 26 years of capture-recapture data on slider turtles, examining the effects of sample size and study duration on population size estimates. Similarly, Otis et al. (1978) explained that live-capture studies require both a sufficiently large number of distinct animals captured and a sufficient number of recaptures.

Decreasing sample size or sampling effort can lead to decreased precision in estimates. McKelvey and Pearson (2001) found that 98 percent of samples in small animal population studies were insufficient to estimate population density. Likewise, Howe et al. (2013) discovered that 15-25 traps were often inadequate for determining female black bear population density. In practice, a larger sample size is usually preferred to ensure a more accurate estimate, but this is not always possible due to logistical or financial constraints. Kordjazi et al. (2016) demonstrates that precision exhibits only marginal improvements with higher level of sampling effort. This implies that there exists an optimal point where sampling effort and precision can be balanced, allowing for the collection of high-quality data without excessive resource costs and efforts. Ultimately, it is a matter of finding a balance between the desired precision and the feasibility of the study (Conner et al., 2015).

This study investigates the necessary sampling effort in Schnabel census studies, accounting for varying capture success rates and population heterogeneity. Initially, the relationship between sampling effort, capture probability, and capture success rate is analysed using a simple binomial likelihood. The framework is then extended to more flexible models, including the beta-binomial and binomial mixture, to incorporate heterogeneity in detectability.

Table 1: Structure of capture histories from a Schnabel census. Each entry $X_{i,j}$ indicates whether individual i was detected ($X_{i,j} = 1$) or not ($X_{i,j} = 0$) during occasion j. The observed data include capture counts for individuals $i = 1, 2, \ldots, n$. The remaining individuals $i = n + 1, \ldots, N$, who were never detected, contribute unobserved zero histories and are not present in the recorded sample.

Individual	Occasion j				
i	1	2	$\ldots$	T	
1	$X_{1,1}$	$X_{1,2}$	$\ldots$	$X_{1,T}$	$X_{1\cdot}$
2	$X_{2,1}$	$X_{2,2}$	$\ldots$	$X_{2,T}$	$X_{2\cdot}$
3	$X_{3,1}$	$X_{3,2}$	$\ldots$	$X_{3,T}$	$X_{3\cdot}$
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
n	$X_{n,1}$	$X_{n,2}$	$\ldots$	$X_{n,T}$	$X_{n\cdot}$
$n+1$	$X_{n+1,1}$	$X_{n+1,2}$	$\ldots$	$X_{n+1,T}$	$X_{n+1\cdot}$
$n+2$	$X_{n+2,1}$	$X_{n+2,2}$	$\ldots$	$X_{n+2,T}$	$X_{n+2\cdot}$
$n+3$	$X_{n+3,1}$	$X_{n+3,2}$	$\ldots$	$X_{n+3,T}$	$X_{n+3\cdot}$
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
$N-1$	$X_{N-1,1}$	$X_{N-1,2}$	$\ldots$	$X_{N-1,T}$	$X_{N-1\cdot}$
N	$X_{N,1}$	$X_{N,2}$	$\ldots$	$X_{N,T}$	$X_{N\cdot}$

2 Schnabel Census

In a Schnabel census, individuals captured on each occasion are first examined for existing tags, then marked, and released. This tagging process is repeated during each capture event. The core of the Schnabel census involves a series of sequential, independent random samplings of a closed population. Any unmarked individual is tagged upon capture, except for the final sampling (Schnabel, 1938; McCrea and Morgan, 2015).

The raw data from a Schnabel census consist of capture records for all observed individuals. The capture-recapture scenario is illustrated in Table 1. Here, $X_{i,j}$ represents the capture history of individual i during occasion j: $X_{i,j} = 1$ indicates that individual i was detected during occasion j, while $X_{i,j} = 0$ indicates that they were not. The indices $i = 1, 2, \ldots, N$ and $j = 1, 2, \ldots, T$ define the individuals and capture occasions, respectively. The sum $X_{i.} = \sum_{j=1}^{T} X_{i,j}$ represents the capture count for each individual i, where $X_{i.} = 0$ signifies that individual i was undetected across all T capture occasions.

The data consist of two parts: the observed counts $X_{1}., X_{2}., \ldots, X_{n}.$ for the sampled individuals, and $X_{n+1}., X_{n+2}., \ldots, X_{N}.$ for the unobserved individuals $n + 1, n + 2, \ldots, N$ that were not captured in the sample. This distinction allows us to differentiate between a full population of counts $X_{1}., X_{2}., \ldots, X_{N}.$ and a zero-truncated sample of counts $X_{1}., X_{2}., \ldots, X_{n}.$, assuming that $X_{n+1}., X_{n+2}., \ldots, X_{N}. = 0$. Capture-recapture methods aim to estimate the number of missed individuals, thereby providing an estimate of the total population size N.

2.1 Counting Distribution

From the capture-recapture histories, a count distribution is formed by creating a frequency table, such as Table 2, which summarizes how frequently each unit was identified. In this context, f_m indicates the number of individuals captured exactly m times during the study period, while $n = \sum_{m=1}^{T} f_m$ denotes the number of individuals captured at least once, where $m = 1, 2, \ldots, T$.

Table 2: Frequency Table for Capture Counts with T Capture Occasions/Sources

$\boldsymbol{m}$	0	1	2	$\ldots$	T
$\boldsymbol{f_m}$	f_0	f_1	f_2	$\ldots$	f_T

Individuals who were never captured result in a zero count, f_0, which is absent from the data and is known referred to as zero-truncated count data. Statistically, this requires dealing with zero-truncated count distributions. Let $p_x = P(X = x)$ represent an appropriate distribution model for the capture counts of each individual in the population. Here, $p_0 = P(X = 0)$ denotes the probability that an individual is not detected across all T capture occasions. This parameter can be interpreted as the proportion of the population that remains unobserved and is a key component in estimating the number of unseen individuals.

To estimate the number of missing observationf_0, the Horvitz-Thompson estimator is utilized:

$$\hat{N} = \frac{n}{1 - p_0}, \tag{1}$$

which further leads to

$$\hat{f}_0 = n \frac{p_0}{1 - p_0}. \tag{2}$$

It is important to note that

$$\mathrm{E}(\hat{N}) = \frac{1}{1 - p_0} \mathrm{E}(n) = \frac{1}{1 - p_0} N(1 - p_0) = N.$$

This holds under the assumption that p_0 is known. However, in most cases, p_x is unknown and need to be estimated. To achieve this, a distributional model is assumed, introducing parameters $\boldsymbol{\theta}$, such that $p_x = p_x(\boldsymbol{\theta})$.

2.2 Zero-truncated counting distribution

In a capture-recapture study, N and f_0 are unknown since they are unobserved in the sample. As individuals not detected in any capture occasion are excluded from the sample, we only observe a zero-truncated count of X. Inferences are thus based on a zero-truncated distribution, as shown in (3),

$$p_x{}^+ = \frac{p_x}{1 - p_0} \tag{3}$$

where $p_x(\boldsymbol{\theta}) = P(X = x|\boldsymbol{\theta})$ represents a model requiring the computation of the maximum likelihood estimator (MLE). Closed-form solutions for MLEs of zero-truncated count distributions are generally unavailable. However, these estimators can be derived using the expectation–maximization (EM) algorithm, as outlined in the works of Böhning et al. (2018) and Dempster et al. (1977).

EM Algorithm for Zero-Truncated Counting Distribution

First, initialize the parameters $\hat{\boldsymbol{\theta}}$ to some random values.

Step 1. In E-step, estimate f_0 with (2).

Step 2. In M-step, compute a new MLE $\hat{\boldsymbol{\theta}}$ using the full frequency table $\hat{f}_0, f_1, \ldots, f_m$.

Repeat E- and M-step with the newly generated estimates and continue the cycle until a convergence is achieved. This algorithm aims to compute $\hat{\boldsymbol{\theta}}$ that optimize the likelihood of truncated densities in (4).

$$\prod_{x=1}^{T} \left[\frac{p_x(\boldsymbol{\theta})}{1 - p_0} \right]^{f_x} \tag{4}$$

The procedure is illustrated in the next section.

2.3 Likelihood based on binomial distribution

Assuming equal catchability, $X \sim \text{Binomial}(T, \theta)$, where $\theta \in (0, 1)$ is the capture probability for each individual in any random capture occasion.

$$p_x = P(X = x) = \binom{T}{x} \theta^x (1 - \theta)^{T-x} \tag{5}$$

The likelihood function is defined as

$$L(\theta) = \prod_{x=0}^{T} \left[\binom{T}{x} \theta^x (1 - \theta)^{T-x} \right]^{f_x} \tag{6}$$

Therefore, the log-likelihood for equation (6) is

$$l(\theta) = \sum_{x=0}^{T} f_x \ln \binom{T}{x} + \sum_{x=0}^{T} x f_x \ln \theta + NT \ln(1 - \theta) - \sum_{x=0}^{T} x f_x \ln(1 - \theta) \tag{7}$$

To obtain the MLE of parameter θ, the derivative of equation (7) is equated to 0, and the estimate of θ can be obtained by

$$\hat{\theta} = \frac{1}{(n + f_0)T} \sum_{x=0}^{T} x f_x \tag{8}$$

Based on the distribution in (5), we can obtain p_0,

$$P(X = 0) = p_0 = (1 - \theta)^T,$$

hence

$$\hat{f}_0 = n \frac{(1 - \hat{\theta})^T}{1 - (1 - \hat{\theta})^T}. \tag{9}$$

These lead to the set-up of the EM algorithm for estimating parameters of a zero-truncated binomial distribution. In the E-Step, with a given θ, we calculate the expected value of f_0 as described in (9). In the M-Step, using $\hat{f}_0$, we determine the MLE for the expected, complete likelihood of θ based on equation (8). The EM algorithm alternates between the E-Step and M-Step until it converges.

3 The Idea of Sampling Effort

To study on the sampling effort required in a Schnabel census, let n denote the number of observed units out of an unknown N,where n follows a binomial distribution: $n \sim \text{Bin}(N, 1 - p_0)$. The probability mass function and variance are given by

$$P(X = n) = \binom{N}{n} p_0^{N-n} (1 - p_0)^n,$$

and

$$\text{Var}(n) = N p_0 (1 - p_0).$$

Using the estimator in (1), $\text{Var}(\hat{N})$ is derived as

$$\text{Var}(\hat{N}) = \frac{1}{(1 - p_0)^2} \text{Var}(n) = N \frac{p_0}{1 - p_0} \tag{10}$$

From (10), the variance of estimated population size is equal to the product of actual N and the odds of missing observation. Hence, the uncertainty in $\hat{N}$ can be controlled by adjusting the width of the $(1 - \alpha)\%$ confidence interval for N:

$$\hat{N} \pm z_{\alpha/2} \sqrt{N \frac{p_0}{1 - p_0}}.$$

Suppose N is known to be 100, and let p_0=0.5, then $\text{Var}(\hat{N}) = N$. The 95% confidence interval for N would be $\hat{N} \pm 1.96\sqrt{N} \approx (80, 120)$, which seems reasonable.

Generalizing, assume the researcher is willing to accommodate variations in population size within $\kappa \times 100\%$ above/below the true N at $(1-\alpha\%)$ confidence level. The margin of the confidence interval will be equal to

$$z_{\alpha/2}\sqrt{N\frac{p_0}{1-p_0}} = \kappa N.$$

Hence,

$$p_0 = \frac{\left(\kappa/z_{\alpha/2}\right)^2 N}{1+\left(\kappa/z_{\alpha/2}\right)^2 N}.$$

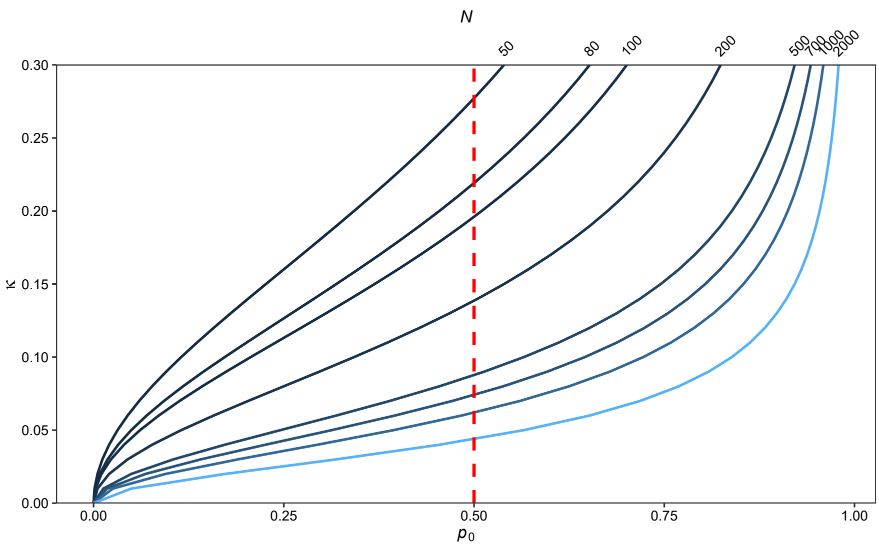


Fig. 1: Relationship between population size N, relative margin of error κ, and the proportion of undetected individuals p_0 at a 95% confidence level. The red dashed line indicates the reference point where $p_0 = 0.5$.

Figure 1 depicts the relationship between p_0 and κ for various N when $1-\alpha$=0.95. The graph demonstrates that keeping p_0 below 0.5 limits the uncertainty of the estimate to within 20% above or below the true N for $N \geq 100$. Thus, p_0 is an effective tool for controlling uncertainty. Replacing $p_0 = (1-\theta)^T$ in (10) gives

$$\operatorname{var}(\hat{N}) = N\frac{(1-\theta)^T}{1-(1-\theta)^T}. \tag{11}$$

Reducing the population size, N to lower the variance in (11), is not possible as we have no information on the value of N. However, adjusting T to a large value can cause

$(1-\theta)^T \to 0$ for a positive $\theta \in (0,1)$, thereby reducing prediction variance. Since

$$p_0 = (1-\theta)^T, \tag{12}$$

solving T for (12) yields

$$T = \frac{\ln(p_0)}{\ln(1-\theta)} \tag{13}$$

Hence, T depends on p_0 and θ. Researchers can leverage this property to choose the appropriate T by specifying the desired capture success rate, i.e., $1-p_0$. For instance, when p_0=0.5, the required T to achieved the desired capture success rate for various θ is as shown in Table 3. The relationship between T, p_0, and θ is presented in (13) and illustrated in Figure 2.

Table 3: Required sampling occasions T for different capture probability θ to achieve a 50% of capture success rate ($1-p_0 = 0.50$).

θ	0.1	0.2	0.3	0.4	0.5
T	7	3	2	1	1

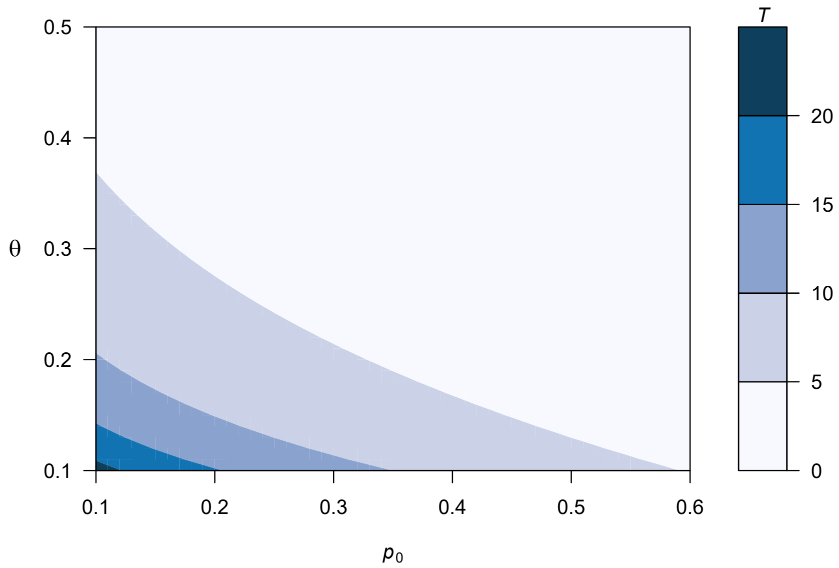


Fig. 2: Contour plot of the required number of capture occasions T in relation to the proportion of undetected individual p_0 and the capture probability θ.

4 Allowing Heterogeneity: Mixture Models

The previous section employed a simple binomial model to analyse capture counts. This model assumes that the observations are independent and the parameters are homogeneous. This section extends the framework to more flexible models using the beta-binomial distribution and the binomial mixture distribution.

4.1 Beta-binomial distribution

Assume capture counts $X \sim \text{BetaBinomial}(T, \alpha, \beta)$, where the capture probability varies among individuals and follows a $\text{Beta}(\alpha, \beta)$ distribution. The probability mass function is given by

$$p_x = P(X = x) = \binom{T}{x} \frac{B(\alpha + x, T + \beta - x)}{B(\alpha, \beta)}$$

Based on this model, the probability of zero captures is

$$p_0 = \frac{B(\alpha, T + \beta)}{B(\alpha, \beta)}, \tag{14}$$

leading to the estimate

$$\hat{f}_0 = \frac{n\ B(\alpha, T + \beta)}{B(\alpha, \beta) - B(\alpha, T + \beta)}. \tag{15}$$

The complete data likelihood is given by

$$L = \left[\frac{B(\alpha, T + \beta)}{B(\alpha, \beta)}\right]^{f_0} \times \prod_{x=1}^{T} \left[\binom{T}{x} \frac{B(\alpha + x, n + \beta - x)}{B(\alpha, \beta)}\right]^{f_x}. \tag{16}$$

To maximize the likelihood in (16), a quasi-Newton method with L-BFGS-B algorithm is run using `R` function `optim`. This sets up the EM algorithm to find the MLE for the zero-truncated beta-binomial distribution. In the E-step, given α and β, the expected value of f_0 is estimated as in (15). In M-step, given $\hat{f}_0$, the MLE of the expected, complete likelihood for α and β are found by maximising the log-likelihood in (16). The EM algorithm cycles between the E- and M-step until convergence.

4.1.1 Sampling effort with beta-binomial model

If the capture counts X follows a $\text{BetaBinomial}(T, \alpha, \beta)$ distribution, the optimal sampling effort, T, can be determined using the relationship in (14) based on the desired capture success rate, $1 - {p_0}^*$. No closed-form solution exists for T in (14). However, it can be solved using numerical methods such as Newton-Raphson. Starting with an initial guess T_0, iteratively apply

$$T_{n+1} = T_n - \frac{h(T_n)}{h'(T_n)},$$

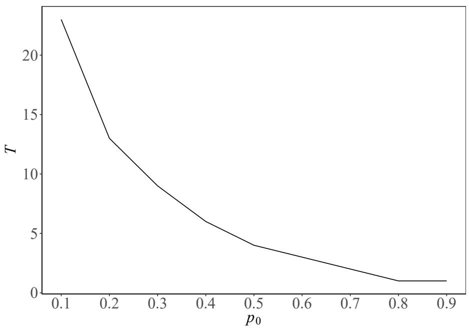
where

$$h(T) = \frac{B(\alpha, T+\beta)}{B(\alpha,\beta)} - {p_0}^*,$$

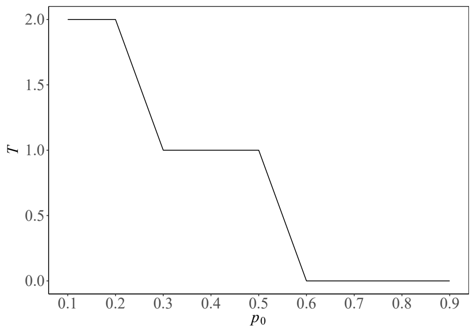
and

$$h'(T) = \frac{B(\alpha, T+\beta)}{B(\alpha,\beta)} \left[\psi(T+\beta) - \psi(\alpha+T+\beta)\right].$$

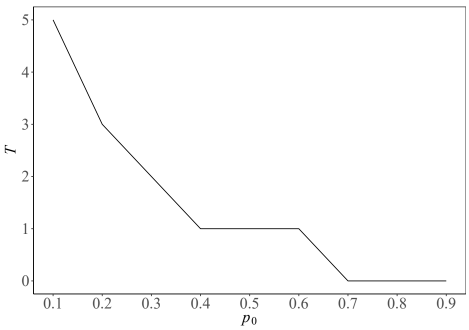
Here, $\psi(\cdot)$ denotes a digamma function. Figure 3 displays the required sampling effort for various combination of Beta(α,β).



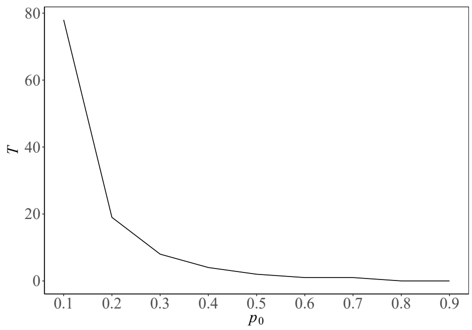
(a) $\theta \sim$ beta(5,10)



(b) $\theta \sim$ beta(10,5)



(c) $\theta \sim$ beta(2,2)



(d) $\theta \sim$ beta(0.5,1)

Fig. 3: Required sampling effort T for different combination of beta(α,β).

4.2 Binomial mixture distribution

Assume the capture counts, X, follows a binomial mixture distribution with k components of binomial distribution

$$p_x = P(X = x) = \sum_{j=1}^{k} w_j \,\text{Bino}(x|T, \theta_j),$$

where

$$\text{Bino}(x|T, \theta_j) = \binom{T}{x} \theta_j^x (1-\theta_j)^{T-x}, \quad j = 1, 2, \dots, k.$$

The mixing distribution, Θ, assigns non-negative weights w_j to θ_j, with $\sum_{j=1}^{k} w_j = 1$. The probability of non-detection is given by

$$p_0 = \sum_{j=1}^{k} w_j (1-\theta_j)^T, \tag{17}$$

leading to the estimate

$$\hat{f}_0 = n \left[\frac{\sum_{j=1}^{k} w_j \, (1-\theta_j)^T}{1 - \sum_{j=1}^{k} w_j \, (1-\theta_j)^T} \right]. \tag{18}$$

By fitting a zero-truncated binomial mixture distribution to the capture data, a nested EM algorithms, adopted from Böhning et al. (2005), was employed to estimate the parameters, $\Theta = \{w_1, w_2, \dots, w_k, \theta_1, \theta_2, \dots, \theta_k\}$. In E-Step, given Θ, the expected value of f_0 is estimated as in (18). In M-step, the full frequency table $\hat{f}_0, f_1, f_2, \dots, f_m$ is utilised to calculate a new set of MLE, Θ'. The non-parametric maximum likelihood estimator (NPMLE) of Θ can be calculated using the EM algorithm framework for mixtures of distribution (McLachlan et al., 2019). Define

$$e_{ij} = \frac{w_j \, \text{Bino}(i|T, \theta_j)}{\sum_{j=1}^{k} w_j \, \text{Bino}(i|T, \theta_j)},$$

this nested EM algorithm uses the expressions (19) and (20) to update $\boldsymbol{w}$ and $\boldsymbol{\theta}$, and are only executed exactly one step and go back to E-step (Böhning et al., 2005). The EM algorithm cycles between the E- and M-step until convergence.

$$w_j = \frac{\sum_{i=0}^{m} f_i \, e_{ij}}{\sum_{i=0}^{m} f_i} \tag{19}$$

$$\theta_j = \frac{\sum_{i=0}^{m} i \, f_i \, e_{ij}}{\sum_{i=0}^{m} T \, f_i \, e_{ij}} \tag{20}$$

4.2.1 Sampling effort with binomial mixture model

If the capture count follows a binomial mixture distribution, the sampling effort, T, can be determined using the relationship in (17). By setting the desired capture success rate, $1 - p_0{}^*$, the required number of capture occasions can be determined by finding the root T, which provides no closed-form solution. However, it can be solved using numerical methods such as Newton-Raphson. Starting with an initial guess T_0, iteratively apply the formula:

$$T_{n+1} = T_n - \frac{h(T_n)}{h'(T_n)},$$

where

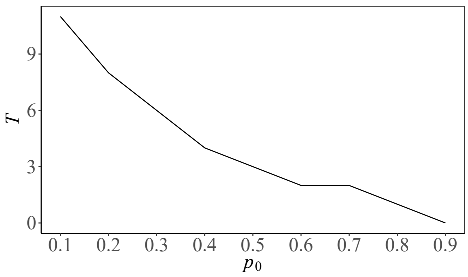
$$h(T) = \sum_{j=1}^{k} w_j (1 - \theta_j)^T - {p_0}^*,$$

and

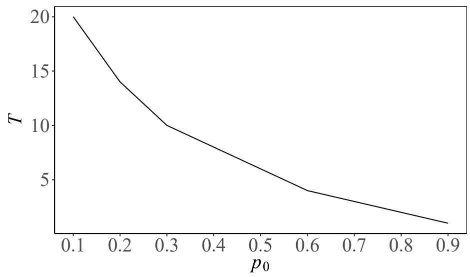
$$h'(T) = \sum_{j=1}^{k} \ln(1 - \theta_j) w_j (1 - \theta_j)^T.$$

Repeat this process until the change between successive values of T is minimal, indicating that an approximate root has been found.

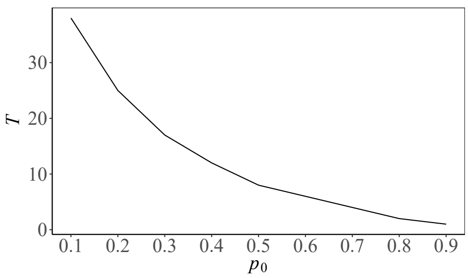
To illustrate the effect of population heterogeneity on required sampling effort, four representative scenarios are presented in Figure 4, each based on a two-component binomial mixture model. These scenarios reflect different structures of heterogeneity, defined by specific combinations of weights $\boldsymbol{w}$ and capture probabilities $\boldsymbol{\theta}$.



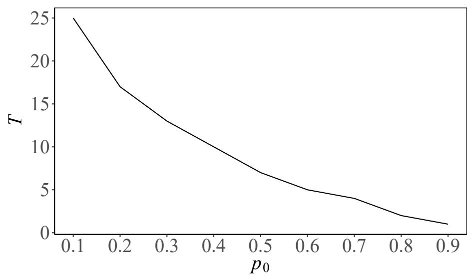
(a) w=(0.1,0.9) and θ=(0.1,0.2)



(b) w=(0.2,0.8) and θ=(0.2,0.1)



(c) w=(0.3,0.7) and θ=(0.2,0.05)



(d) w=(0.5,0.5) and θ=(0.1,0.08)

Fig. 4: Required sampling effort T, for different combination of w and θ.

Subfigure (a) represents a population in which 10% of individuals have low detectability ($\theta = 0.1$), while the remaining 90% are moderately detectable ($\theta = 0.2$). This pattern may arise in cases where a small subgroup, such as elusive juveniles or trap-averse individuals, is less likely to be captured than the majority. In subfigure (b), 20% of individuals exhibit moderate detectability ($\theta = 0.2$), while the remaining 80% are harder to capture ($\theta = 0.1$). This skewed structure may reflect differences due to sex, territoriality, or other behavioural traits.

Subfigure (c) illustrates a stronger degree of heterogeneity, where 30% of the population has moderate detectability ($\theta = 0.2$) and 70% are highly elusive ($\theta = 0.05$). This configuration aligns with populations exhibiting strong trap-avoidance behaviour among certain subgroups. Subfigure (d) shows a more balanced scenario, with equal proportions of individuals having slightly different detectabilities ($\theta = 0.1$ and $\theta = 0.08$), a pattern often observed in age-structured populations such as adults versus subadults.

Together, these scenarios demonstrate how varying levels and forms of heterogeneity influence the sampling effort required for reliable population estimation, as displayed in Figure 4.

5 Real Data Example

The study by Edwards and Eberhardt (1967), later republished by Chao (1987), involved an investigation on a restricted population of known size using live-trapping techniques. Within a 4-acre rabbit-proof enclosure, 135 wild cottontail rabbits were subject to live trapping over 18 consecutive nights. Among them, 76 were captured at least once. The recorded capture frequencies ($f_1 - f_7$) were as follows:

43,16,8,6,0,2,1

Four zero-truncated models were fitted on the data, namely the binomial (ZTB), beta-binomial (ZTBB), two-binomial mixture (ZTMB2), and three-binomial mixture (ZTMB3). Table 4 presents the estimated population size and the result of the model fitting to the data. It appears that while ZTBB and ZTMB2 model provide adequate fits to the data, the ZTB model fails to adequately fit the data. Meanwhile, chi-square goodness-of-fit test cannot be executed with ZTMB3 model as several cells ($f_5 - f_{18}$) were combined due to small expected values, resulting in 0 degrees of freedom for the test. The estimated N based on ZTMB2 and ZTMB3 are close to the actual size, $N = 153$. ZTB model provides underestimated size, while ZTBB provides estimated way too large when compared to the actual size. Binomial mixture models seems to fit the cottontail rabbits data well. Akaike's information criterion (AIC) and Bayesian information criteria (BIC) were used to determine the best fitted model. Overall, the two-binomial mixture model fits the data the best, according to the findings.

5.1 Sampling effort determination

To determine the required number of capture occasions, T, for the zero-truncated two-binomial mixture distribution, the Newton-Raphson method was employed as described in Section 4.2. The parameter estimates used in the calculation were $\hat{w}_1 =$

Table 4: Model fitting on cottontail rabbits data. Model fitted includes ZTB(Zero-truncated binomial), ZTBB(Zero-truncated Beta-Binomial), ZTMB2(Zero-truncated two-binomial), and ZTMB3(Zero-truncated three-binomial). The p-value is derived from a chi-square goodness-of-fit test.

distribution	$\hat{N}$	p**-value**	**log-likelihood**	**AIC**	**BIC**
ZTB	97	0.011	-105.109	212.218	214.549
ZTBB	300	0.569	-97.764	201.528	208.521
ZTMB2	150	0.411	-97.761	**201.521**	**208.514**
ZTMB3	148	-	-97.755	205.510	217.163

0.163, $\hat{w}_2 = 0.837$, $\hat{\theta}_1 = 0.170$, and $\hat{\theta}_2 = 0.030$. Table 5 presents the required values of T for achieving various levels of capture success rates, $1 - p_0$.

The 25th and 75th percentiles for T were derived from bootstrap samples based on cottontail rabbit capture-recapture data. Starting with the true value $N = 135$, f_0 was calculated to be 59. Capture count probabilities $\hat{p}_i = f_i/N$ for $i = 0, 1, 2, \ldots, 7$ were then computed. Subsequently, 5000 bootstrap samples were generated by drawing capture counts from a multinomial distribution defined by $(\hat{N}, \hat{p_0}, \hat{p_1}, \hat{p_2}, \cdots, \hat{p_7})$. For each sample, f_0 was ignored, and the EM algorithm was applied to the observed frequencies $(f_1, f_2, \ldots, f_7)$ to estimate the parameters $(w_1, w_2, \theta_1, \theta_2)$. These estimates were used to compute the required sampling effort T. The resulting distribution of T values was analyzed, and the 25th and 75th percentiles were calculated to evaluate the variability in T.

Table 5: Required number of capture occasions T for different levels of capture success rate $1 - p_0$, along with the 25th to 75th percentile range derived from bootstrap estimates.

desired capture success rate, $1 - p_0$	required sampling effort, T	$25^{th} - 75^{th}$ percentile
0.4	12	8 - 17
0.5	17	11 - 24
0.6	24	15 - 34
0.7	34	21 - 47
0.8	47	29 - 69
0.9	70	42 - 98

For a relatively high p_0 value of 0.6, indicating a lower desired success rate of 40%, 12 capture occasions are sufficient. As the success rate requirement increases, the number of capture occasions also increases significantly. For a success rate of 50% ($p_0 = 0.5$), 17 capture occasions are required. This corresponds roughly to the value of T actually used in the study. Further increasing the success rate to 60% ($p_0 = 0.4$) requires 24 capture occasions. For a 70% success rate ($p_0 = 0.3$), the required number of capture occasions jumps to 34. When aiming for an 80% success rate ($p_0 = 0.2$), 47 capture occasions are needed. Finally, to achieve a 90% success rate ($p_0 = 0.1$), 70 capture occasions are required.

6 Discussion and Conclusion

This paper aims to determine the optimal sampling effort in Schnabel census capture-recapture studies. One major challenge in achieving this is that it requires the information of population size, which is typically the main parameter of interest in Schnabel census. This dependency creates an unresolved, non-ending loop. To address this issue, some prior knowledge about the population is essential. This information can be obtained from pilot studies, previous research, or educated guesses (Bröder et al., 2020).

The findings of this study shows that there is an exponential relationship between the desired success capture rate and the required number of capture occasions. For instance, in the case of cottontail rabbits discussed in Section 5, 12 capture occasions are required to achieve a capture success rate of 40%, while 47 capture occasions are needed to double the success capture rate to 80%. This relationship highlights the escalating efforts and resources needed to substantially improve the capture success rate, which then influences the uncertainty of estimates. This finding aligns with the results of Kordjazi et al. (2016).

In Table 4, the beta-binomial and two-binomial mixture models both provide strong fits to the data based on AIC and BIC criteria. However, previous studies have highlighted limitations of beta-binomial model for zero-truncated count data. Böhning (2015) points out that the beta-binomial model can exhibit erratic behaviour at boundary values, which may lead to significant overestimation of unobserved counts. This behaviour arises because the beta-binomial distribution assumes continuous heterogeneity but struggles to manage extreme parameter values effectively. In practical applications, this limitation could result in misleading estimates of population size, particularly when the true population heterogeneity deviates from the assumed beta distribution.

In addition to model selection considerations, the capture probability parameter, θ, plays a key role in driving the uncertainty of estimates and determining the necessary sampling effort (Burnham et al., 1987). As lower detectability requires more capture occasions to achieve the same level of capture success rate compared to higher detectability, Papadatou et al. (2012) suggest that enhancing detectability using modern analytic techniques can reduce sampling effort required and increase estimate precision.

One important feature in modelling the counting distribution in Schnabel census is the application of zero-truncated distribution. This distribution accounts for the fact that zero captures do not necessary imply the absences of individuals but maybe because they have been left out from the sampling (Böhning et al., 2005). Zero-truncated modelling normally offers no closed-form solution for the MLE of parameters, which is where EM algorithm come in. This algorithm iteratively estimating the latent data (i.e. the undetected individuals) and updating the MLE for the expected, complete likelihood for parameters. The combination of the zero-truncated distribution and the EM algorithm offers a robust framework for modelling the counting distribution in Schnabel census to estimate the parameter.

Both this study and Xi et al. (2008) highlight the significance of capture success rate (denoted as π in Xi et al. and as $1 - p_0$ in the current study) for obtaining reliable estimates. Xi et al. determine the minimum required π by specifying an upper bound on the asymptotic variance. Their method requires prior knowledge of the population size N, which is typically unknown.The present study establishes a similar variance relationship via (10) and Figure 1, demonstrating that high p_0 leads to unreliable estimates and should be avoided. Rather than identifying a minimum π retrospectively, this study treats p_0 as a design input and derives closed-form solution for the number of capture occasions T needed to achieve it. This enables prospective planning based on realistic detectability assumptions including heterogeneity.

The findings of this study offer practical guidance for ecologists and wildlife biologists seeking to determine the optimal sampling effort for population monitoring using the Schnabel census method. A recommended approach begins with a small-scale pilot capture-recapture study involving a limited number of visits. Based on the pilot data, practitioners can fit a range of candidate models, and perform model selection. Once the best-fitting model is identified, the desired capture success rate, $1 - p_0$, can be chosen based on the management goals. From there, the number of visits T necessary to achieve the desired level of accuracy can be estimated using the protocols outlined in this paper.

In conclusion, this paper provides valuable insight in understanding the relationship between capture success rate and sampling effort in Schnabel census studies. The guideline enables researchers to design experiments that achieve desired outcomes within practical constraints, which is essential in ensuring the sustainability and feasibility of population monitoring program.

Declaration

Funding

None declared.

Conflicts of interest/competing interests

The authors have no conflicts of interest or competing interests to declare that are relevant to the content of this article.

References

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., Pollock, K.H.: Design and Analysis Methods for Fish Survival Experiments Based on Release-recapture. American Fisheries Society Monograph, vol. 5. American Fisheries Society, Bethesda, Md

(1987)

Böhning, D., Dietz, E., Kuhnert, R., Schön, D.: Mixture models for capture-recapture count data. Statistical Methods and Applications **14**(1), 29–43 (2005) https://doi.org/10.1007/BF02511573

Burke, V.J., Greene, J.L., Gibbons, J.W.: The effect of sample size and study duration on metapopulation estimates for slider turtles *Trachemys scripta*. Herpetologica **51**(4), 451–456 (1995)

Bröder, L., Tatin, L., Hochkirch, A., Schuld, A., Pabst, L., Besnard, A.: Optimization of capture–recapture monitoring of elusive species illustrated with a threatened grasshopper. Conservation Biology **34**(3), 743–753 (2020) https://doi.org/10.1111/cobi.13449

Böhning, D., Heijden, P.G.M., Bunge, J.: Capture-Recapture Methods for the Social and Medical Sciences. Chapman and Hall/CRC, Boca Raton, FL (2018)

Böhning, D.: Power series mixtures and the ratio plot with applications to zero-truncated count distribution modelling. METRON **73**(2), 201–216 (2015) https://doi.org/10.1007/s40300-015-0071-6

Conner, M.M., Bennett, S.N., Saunders, W.C., Bouwes, N.: Comparison of tributary survival estimates of steelhead using Cormack–Jolly–Seber and Barker models: implications for sampling efforts and designs. Transactions of the American Fisheries Society **144**(1), 34–47 (2015) https://doi.org/10.1080/00028487.2014.963254

Chao, A.: Estimating the population size for capture-recapture data with unequal catchability. Biometrics **43**(4), 783 (1987) https://doi.org/10.2307/2531532

Dempster, A.P., Laird, N.M., Rubin, D.B.: Maximum likelihood from incomplete data via the EM algorithm. Journal of the Royal Statistical Society: Series B (Methodological) **39**(1), 1–22 (1977)

Edwards, W.R.., Eberhardt, L.: Estimating cottontail abundance from livetrapping data. The Journal of Wildlife Management **31**(1), 87–96 (1967)

Howe, E.J., Obbard, M.E., Kyle, C.J.: Combining data from 43 standardized surveys to estimate densities of female American black bears by spatially explicit capture-recapture. Population Ecology **55**(4), 595–607 (2013) https://doi.org/10.1007/s10144-013-0389-y

Kordjazi, Z., Frusher, S., Buxton, C., Gardner, C., Bird, T.: The influence of mark-recapture sampling effort on estimates of rock lobster survival. PLoS ONE **11**(3) (2016) https://doi.org/10.1371/journal.pone.0151683

McLachlan, G.J., Lee, S.X., Rathnayake, S.I.: Finite mixture models. Annual Review of Statistics and Its Application **6**(1), 355–378 (2019) https://doi.org/10.1146/annurev-statistics-031017-100325

McCrea, R.S., Morgan, B.J.T.: Analysis of Capture-Recapture Data. CRC Press, Boca Raton, FL (2015)

McKelvey, K.S., Pearson, D.E.: Population estimation with sparse data: the role of estimators versus indices revisited. Canadian Journal of Zoology **79**(10), 1754–1765 (2001) https://doi.org/10.1139/z01-139

Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R.: Statistical inference from capture data on closed animal populations. Wildlife Monographs **62**, 3–135 (1978)

Papadatou, E., Pradel, R., Schaub, M., Dolch, D., Geiger, H., Ibañez, C., Kerth, G., Popa-Lisseanu, A., Schorcht, W., Teubner, J., Gimenez, O.: Comparing survival among species with imperfect detection using multilevel analysis of mark-recapture data: a case study on bats. Ecography **35**(2), 153–161 (2012) https://doi.org/10.1111/j.1600-0587.2011.07084.x

Schnabel, Z.E.: The estimation of the total fish population of a lake. The American Mathematical Monthly **45**(6), 348–352 (1938) https://doi.org/10.1080/00029890.1938.11990818

Seber, G.A.F.: The Estimation of Animal Abundance and Related Parameters. Griffin Publishing Company, London (1982)

Xi, L., Watson, R., Yip, P.S.F.: The minimum capture proportion for reliable estimation in capture-recapture models. Biometrics **64**(1), 242–249 (2008) https://doi.org/10.1111/j.1541-0420.2007.00876.x