



Sampling effort and its allocation in the Lincoln–Petersen experiment: A hierarchical approach

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ABSTRACT

Capture-recapture methods are widely used for estimating population sizes in ecological and epidemiological studies, yet the optimal allocation of sampling effort often remains underexplored. This study explores sampling efforts in a hierarchical framework that subdivides each capture occasion in a Lincoln–Petersen experiment into multiple sub-occasions, allowing for flexible resource allocation. When detection probabilities are equal across occasions, an even split minimizes variance; when probabilities differ, maximizing the joint detection probability is essential. A pseudo-Bayesian approach is also proposed to address scenarios with unknown catchabilities. Detailed simulation studies validate the theoretical findings and demonstrate the framework's robustness. The resulting guidelines offer practical insights for designing more efficient capture-recapture experiments and improving population size estimates.

1. Introduction

Capture-recapture is a widely used method for estimating population size in ecology and epidemiology. Originally developed for fisheries and wildlife studies (Petersen, 1896; Dahl, 1918; Lincoln, 1930), it has been extensively applied to assess animal abundance (Hickey and Sollmann, 2018), survival odds (Reinke et al., 2020), mortality (Jiménez-Ruiz et al., 2023), and migratory patterns (Matechou and Argiento, 2023). Since 1949, capture-recapture has also been used in human health research to estimate true population sizes from incomplete case listings (Sekar and Deming, 1949). It serves as an alternative to traditional prevalence studies by identifying undetected cases across multiple data sources. Early applications included birth defect incidence (Wittes and Sidel, 1968) and hospital infection rates (Lewis and Hassanein, 1969), and its use has since expanded to areas such as drug use, infectious diseases, cancer, and dementia (Plettinckx et al., 2021; Rocchetti et al., 2020; Plouvier et al., 2019; Bailly et al., 2019). The method's efficiency, cost-effectiveness, and ability to integrate multiple data sources make it valuable for public health decision-making (Ramos et al., 2020; Böhning et al., 2020). Its importance is underscored by the growing body of literature dedicated to its theoretical and applied advancements (Böhning et al., 2018; Borchers et al., 2002; McCrea and Morgan, 2015).

The optimization of sampling effort in capture-recapture studies has been a long-standing challenge, especially when sample size is dependent on numerous factors, such as the animals' detectability, desired precision, and study scope (Schorr et al., 2014). Selecting the appropriate sampling intensity and duration is challenging because insufficient data can lead to biased estimates. Kordjazi et al. (2016). In conservation biology, inefficient designs risk underestimating populations of elusive or rare species which exhibit patchy distributions and low detectability, resulting in datasets dominated by non-detections (Thompson,

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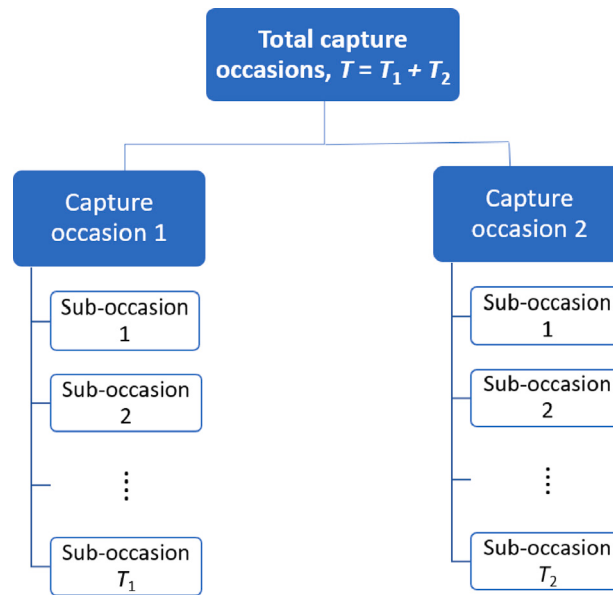


Fig. 1. A hierarchical structure for a Lincoln-Petersen experimental design.

2004). Similarly, in epidemiology, zero-inflated data from incomplete registries obscure true disease prevalence; for instance, undetected COVID-19 cases during the pandemic skewed infection fatality rates and hindered public health responses (Böhning et al., 2020).

It is often practical to employ multi-stage sampling strategies in a capture-recapture study. Each stage involves sampling within a specific time window, which can be continuous or discrete. For instance, a researcher may conduct repeated trapping sessions over several nights during the first capture occasion, followed by a pause before conducting additional nights of trapping during the subsequent capture occasion. For instance, two capture occasions in a Lincoln-Petersen experiment can be hierarchically levelled into a number of sub-occasions which totals a number T , as illustrated in Fig. 1. Traditional capture-recapture method treat capture occasions as single stages, ignoring the hierarchical potential to subdivide effort into sub-occasions that adaptively boost detectability. By framing sampling effort as a divisible resource, this hierarchical approach addresses the ‘too few recaptures’ issues in studies of rare or elusive populations.

Early work by Robson and Regier (1964) established basic sample size thresholds, such as requiring $n_1 n_2 > 4N$, to reduce bias in Lincoln-Petersen estimates. Seber (1982) and Krebs (2014) suggest that the product of the sample size of both capture occasions in a Lincoln-Petersen experiment must exceed the population size and there must be at least seven recaptures of tagged individuals, while Greenwood and Robinson (2006) mentioned that when the number of tagged individuals in the second sample is greater than 50, the confidence level calculated with Lincoln-Petersen estimates was found to be reasonably accurate. Otis et al. (1978) explains that a live-capture study requires both a sufficiently large number of distinct animals captured and a sufficient number of recaptures. Gaskell and George (1972) emphasize that a number of recaptures less than 10 results in a poor estimator of N . 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. Ultimately, it is a matter of finding a balance between the desired precision and the feasibility of the study (Conner et al., 2015). 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.

A key limitation in the previous studies is the assumption that sampling effort is evenly distributed across capture occasions, regardless of changes in detectability. They did not explore how effort could be strategically shifted between sub-occasions to maximize detection efficiency. This issue is particularly relevant for rare or spatially scattered populations, where zero-inflated data and logistical fieldwork constraints make efficient sampling strategies essential. Current methods fail to provide a systematic way to optimize effort allocation in hierarchical designs, leaving a gap in the field.

This study addresses these gaps in three key ways: (1) introducing a hierarchical framework for sub-occasion allocation that generalizes the Lincoln-Petersen model; (2) deriving optimal effort allocation rules under both known and unknown catchabilities; and (3) providing field-ready guidelines validated through simulations.

2. Sampling effort in Lincoln-Petersen estimator

The Lincoln-Petersen method, developed by F.C. Lincoln and C.J.G. Petersen, is the fundamental capture-recapture technique that consists of a single catch-and-mark occasion, followed by one recapture occasion. Their method has been widely utilized to

Table 1

Observed frequency from a Lincoln–Petersen experiment.

		Occasion 2		
		1	0	
Occasion 1	1	m	$n_1 - m$	n_1
	0	$n_2 - m$	x	
		n_2		N

Table 2

Joint distribution of identifying a subject in a Lincoln–Petersen experiment.

		Occasion 2	
		1	0
Occasion 1	1	$p_1 p_2$	$(1 - p_1) p_2$
	0	$p_1(1 - p_2)$	$(1 - p_1)(1 - p_2)$

estimate population sizes in animal and human populations, with the latter case often referred to as the dual-list method. While the Lincoln–Petersen method is straightforward, it is crucial to note that its results heavily rely on several underlying assumptions associated with the data (Gerritse et al., 2015). The assumptions of the Lincoln–Petersen method include:

1. The population is closed, assuming no immigration, births, or deaths occurring within the population during the sampling period.
2. All individuals are equally catchable on any sub-occasions, but we assume that capture probability can change between capture occasions: it is θ_1 on occasion 1, and θ_2 on occasion 2.
3. Detection of individuals are independent events.

Violation of assumptions may affect the accuracy of the estimate. To address this issue, researchers have developed various variants of the Lincoln–Petersen model that accommodate the violation of these assumptions (Gaskell and George, 1972; Skalski and Robson, 1982; Wolter, 1990; Seber et al., 2000). However, in this study, we consider a model in which all assumptions are met.

Let N denote the total population size, n_1 the number of individuals captured and tagged during the first occasion, n_2 the number captured during the second occasion, and m the number recaptured on both occasions. Table 1 summarizes the observed frequencies in a typical Lincoln–Petersen experiment, while Table 2 outlines the joint detection probabilities, assuming the occasions are independent. p_i denotes the probability of detecting a subject at occasion i ($i = 1, 2$).

The frequency of the missing subjects, x , is unknown. Hence, the population size $N = n_1 + n_2 - m + x$ remains unknown and becomes the target of the inference. The well-known Lincoln–Petersen estimator (Chao and Huggins, 2005) in (1) can be used to estimate the population size.

$$\hat{N} = \frac{n_1 n_2}{m} \quad (1)$$

An estimator of $\text{var}(\hat{N})$ is given in (2). The development of this formula is shown in Appendix A.

$$\widehat{\text{var}}(\hat{N}) = \hat{N} \frac{n_1 - m}{m} \frac{n_2 - m}{m} \quad (2)$$

It is clear that the Lincoln–Petersen estimator becomes more reliable as m increases relative to n_1 or n_2 or both. As $E(m) = N p_1 p_2$, it is apparent that on average, m will not increase if p_1 and p_2 remain unaltered. Moreover, increasing the target population size, N , by itself is not practicable. However, certain studies are designed in such a way that sampling is repeated within a single occasion. For example, live trapping is conducted over multiple nights.

Consider a scenario in which T_1 replications of repeated identification are done on the capture occasion 1, and T_2 replications are done on the capture occasion 2. As a result, the probability of not detecting a subject on the capture occasion 1 is $1 - p_1 = (1 - \theta_1)^{T_1}$, where θ_1 is the individual detection probability for the T_1 sub-occasions in capture occasion 1. Similarly, the probability of not detecting a subject on the capture occasion 2 is $1 - p_2 = (1 - \theta_2)^{T_2}$. In order to maximize the frequency of joint identification, m , the interest of study is to maximize $p_1 p_2$, by keeping the total sampling effort $T = T_1 + T_2$ fixed. Note that

$$p_1 p_2 = [1 - (1 - \theta_1)^{T_1}] [1 - (1 - \theta_2)^{T_2}] = (1 - q_1^{T_1}) (1 - q_2^{T_2}),$$

where $q_i = (1 - \theta_i)$ for $i = 1, 2$. To address this problem, we introduce

$$f(t; q_1, q_2) = (1 - q_1^t) (1 - q_2^{T-t}), \quad (3)$$

for $t = 0, 1, 2, \dots, T$. In order to maximize the sampling effort, we need to find $\hat{t}$ that maximize $f(t; q_1, q_2)$ in $t = 0, 1, 2, \dots, T$. In the following sections, we explore different scenarios to determine the optimal allocation of sampling efforts between the two capture occasions.

Table 3Summary statistics for snowshoe hare data, with $T = 6$ partitioned into two capture occasions.

T_1	T_2	n_1	n_2	m	$\hat{N}$	$\text{var}(\hat{N})$
1	5	16	65	13	80	73.85
2	4	40	59	31	76.1	19.96
3	3	49	57	38	73.5	10.64
4	2	58	44	34	75.1	15.6
5	1	64	32	28	73.1	13.43

3. Optimizing sampling effort with fixed catchabilities

3.1. Scenario 1: Equal catchabilities $q_1 = q_2$

When the detection probabilities on both occasions are equal (i.e., $q_1 = q_2 = q$) the optimization problem in (3) simplifies,

$$f(t; q) = 1 - q^t - q^{T-t} + q^T, \quad (4)$$

leading to Theorem 1. The proof of Theorem 1 is provided in Appendix B.

Theorem 1. The function $f(t; q) = (1 - q^t)(1 - q^{T-t})$ is maximized at $\hat{t} = (T - 1)/2$ or $\hat{t} = (T - 1)/2 + 1$ if T is odd. If T is even, the function is maximized at $\hat{t} = T/2$.

Outcome from Theorem 1 can be utilized to identify the optimal t that maximizes (4). If T is even, an equal number of $T/2$ sub-occasions are allocated to each capture occasion. On the other hand, if T is odd, $(T - 1)/2 + 1$ sub-occasions are assigned to one occasion, while the remaining sub-occasions are allocated to the other occasion. Notably, it is interesting to observe that the optimal value is independent of both q and θ .

3.1.1. Example

The snowshoe hare data discussed in this section were initially collected by Burnham and Cushwa which was first presented by Otis et al. (1978). Six trapping occasions resulted in 145 captures of 68 distinct hares. For the six occasions, there were 16, 28, 20, 26, 23, and 32 captures. Given that the capturing period lasted only a few days, it was reasonable to assume that the population was closed.

For illustration, the total number of sub-occasions, $T = 6$, is partitioned into various combinations of T_1 and T_2 . N and $\text{Var}(\hat{N})$ are estimated using Eqs. (1) and (2). The results in Table 3 demonstrate that an equal split ($T_1 = T_2 = 3$) minimizes the variance of the population size estimate. This findings is consistent with our result in Section 3.1

3.2. Scenario 2: Proportional catchabilities $q_1 = kq_2$

In the scenario where $q_1 \neq q_2$, Theorem 1 is no longer applicable. Instead, the goal of optimizing the sampling effort is to determine the value of t^* that maximizes the function $f(t; q_1, q_2)$ in (3) for $t = 0, 1, 2, 3, \dots, T$. Let us consider a scenario where the catchabilities are proportional, with $q_1 = kq_2$, where k is a constant. In this case, the goal is to find the value of t^* that maximizes the function

$$\begin{aligned} f(t; q, k) &= (1 - (kq)^t)(1 - q^{T-t}) \\ &= 1 - (kq)^t - q^{T-t} + k^t q^T. \end{aligned} \quad (5)$$

To maximize $f(t; q, k)$ in (5), we need to minimize the term

$$h(t; q, k) = (kq)^t + q^{T-t} - k^t q^T. \quad (6)$$

Optimizing the function in (6) does not admit a closed-form solution for t . Nonetheless, we can obtain solutions using numerical method. In this paper, the Newton–Raphson method was employed, and it exhibited no convergence issues. We recommend initializing the value as $T/2$, since this choice can potentially reduce the number of iterations required for convergence. Fig. 2 provides a visualization of how the optimal t value changes with different values of k and q when $T = 20$. In the case when $k = 1$, which corresponds to $q_1 = q_2$ as discussed earlier, the optimal allocation of T is to distribute it equally between the two capture occasions. However, the graph demonstrates that as k increases beyond 1, indicating a higher q_1 compared to q_2 (thus indicating lower detectability in capture occasion 1), it is more beneficial to allocate a greater sampling effort to the first capture occasion rather than the second one. This allocation strategy aims to enhance the precision of the parameter estimates.

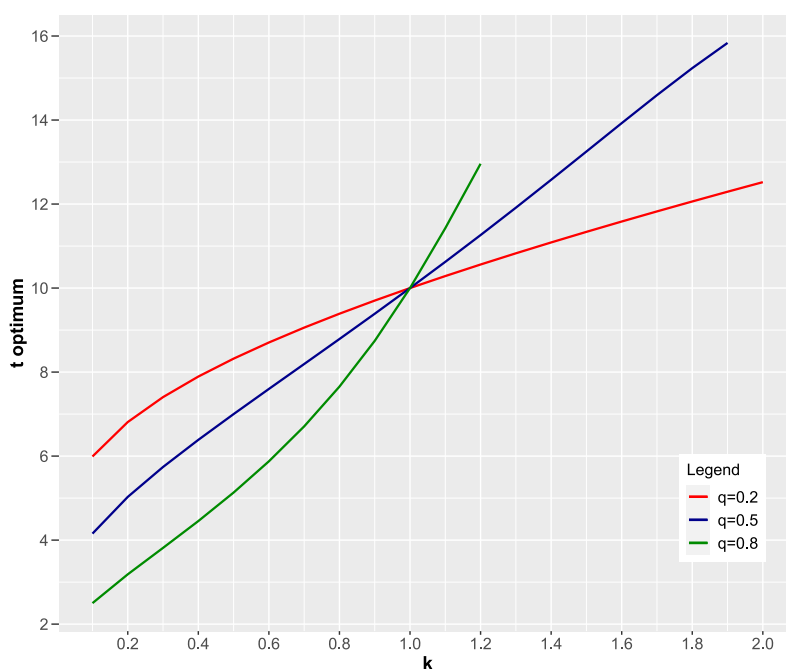


Fig. 2. Optimal t based on k and q values for $T = 20$, with constrain $kq \in (0, 1)$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Description of trials components.

N	T	(θ_1, θ_2)
1000	20	(0.40, 0.20)
400	11	(0.40, 0.04)
200	9	(0.20, 0.30)
100	6	(0.20, 0.20)

3.2.1. Simulation

To validate the theoretical findings and evaluate the performance of the proposed hierarchical allocation framework, a simulation study was conducted under controlled conditions. The design was structured to reflect realistic ecological and epidemiological contexts, with parameter choices guided by three key objectives: population size variation, sampling effort constraints, and detectability scenarios. Population sizes ($N = 1000, 400, 200, 100$) were selected to represent a spectrum from large populations to small populations, assessing robustness across scales. Sampling effort constraints were incorporated by selecting total sub-occasions ($T = 20, 11, 9, 6$), reflecting varying field study durations. Four capture probability scenarios were explored: $(\theta_1, \theta_2) = (0.4, 0.2)$, $(0.4, 0.04)$, $(0.2, 0.3)$, $(0.2, 0.2)$. These scenarios represent different ecological conditions. The first case $(\theta_1 = 0.4, \theta_2 = 0.2)$ mimics species with high detectability in one occasion and moderate detectability in another. The second case $(\theta_1 = 0.4, \theta_2 = 0.04)$ represents extreme difference in detectability, while the last case $(\theta_1 = \theta_2 = 0.2)$ represents balanced moderate detectability case. Table 4 provides an overview of the various parameter values utilized in the simulation study.

For each parameter combination, 10,000 replicate datasets ($B = 10,000$) were generated using Bernoulli trials. Detection at each sub-occasion (j) within a capture occasion (i) followed $X_{ijk} \sim \text{Bernoulli}(\theta_i)$ for $k = 1, \dots, N$. The Lincoln–Petersen estimator ($\hat{N}$) and its variance were computed for all possible allocations ($t \in \{1, \dots, T\}$), with the optimal allocation (t^*) identified as the value that minimized $\text{var}(\hat{N})$. Table 5 presents a subset of the simulation results for when $N = 100$, $T = 20$, $\theta_1 = 0.4$, $\theta_2 = 0.2$. It illustrates that the variance of the estimates changes with t , with t^* being 7. This allocation (7 sub-occasions to capture occasion 1, and 13 to capture occasion 2), yields the most precise estimate.

Table 6 summarizes the results from all 64 combinations, comparing the optimal t values from the simulation with those from Newton–Raphson optimization. The findings confirm that t^* remains stable across various population sizes N , although it shifts with changes in T or capture probabilities θ . Both methods are in close agreement, with discrepancies less than 1, indicating a robust validation of the simulation results. Our findings recommend a T value greater than 10 to prevent large variances, optimizing design efficiency.

Table 5

Simulation results of Lincoln–Petersen estimation procedure applied on data generated with $B = 10\,000$ replicates for $N = 1000$, $T = 20$, $\theta_1 = 0.4$, $\theta_2 = 0.2$.

t	$\text{mean}(\hat{N})$	$\text{var}(\hat{N})$	$p_1 \times p_2$
1	999.9959	1.6376	0.3996
2	999.9926	1.0238	0.6388
3	1000.0090	0.8053	0.7816
4	999.9832	0.7403	0.8660
5	1000.0000	0.7077	0.9145
6	999.9998	0.6898	0.9400
7	1000.0080	0.6834	0.9495
8	999.9903	0.7220	0.9452
9	999.9960	0.7031	0.9261
10	1000.0020	0.7274	0.8872
11	1000.0060	0.7197	0.8616
12	999.9956	0.7965	0.8290
13	1000.0020	0.8211	0.7878
14	1000.0040	0.8967	0.7360
15	999.9932	0.9525	0.6710
16	999.9953	1.0809	0.5895
17	1000.0150	1.3725	0.4874
18	999.9927	1.7833	0.3596
19	1000.0060	3.2584	0.1998

Table 6

Newton–Raphson optimization and simulated results concerning the optimal t .

T	θ_1	θ_2	Optimal t				
			Newton–Raphson	$N = 1000$	$N = 400$	$N = 200$	$N = 100$
20	0.4	0.2	7.16	7	7	7	7
	0.4	0.04	4.82	5	5	5	5
	0.2	0.3	11.54	12	12	12	12
	0.2	0.2	10.00	10	10	10	10
11	0.4	0.2	4.29	4	4	4	4
	0.4	0.04	3.36	4	4	4	4
	0.2	0.3	6.13	7	6	6	6
	0.2	0.2	5.50	6	6	6	6
9	0.4	0.2	3.61	3	2	5	5
	0.4	0.04	2.95	3	2	5	5
	0.2	0.3	4.96	3	2	5	5
	0.2	0.2	4.50	3	2	5	5
6	0.4	0.2	2.54	2	2	2	2
	0.4	0.04	2.21	2	2	2	2
	0.2	0.3	3.23	3	4	4	4
	0.2	0.2	3.00	3	3	3	3

4. Optimizing sampling effort in the presence of unknown catchabilities

The methods described in Section 3 assume that the detection probabilities are known. In practice, when these probabilities are unknown, a pseudo-Bayesian approach can be used by introducing prior distributions for q_1 and q_2 . The first step is to find the expectation of $f(t; q_1, q_2)$ with respect to q_1 and q_2 , denoted as $g(t)$:

$$g(t) = E_{q_1 q_2} \left[f(t; q_1, q_2) \right]. \quad (7)$$

4.1. Scenario 1: Uniform priors for catchabilities

In the first scenario, where no prior information is available regarding the distribution of q_1 and q_2 , we make the assumption that both q_1 and q_2 follow a uniform distribution: $q_1 \sim U(0,1)$ and $q_2 \sim U(0,1)$. As a result, this leads to Eq. (8), and the optimal value of t is determined as $T/2$.

$$g(t) = \frac{Tt - t^2}{Tt - t^2 + T + 1} \quad (8)$$

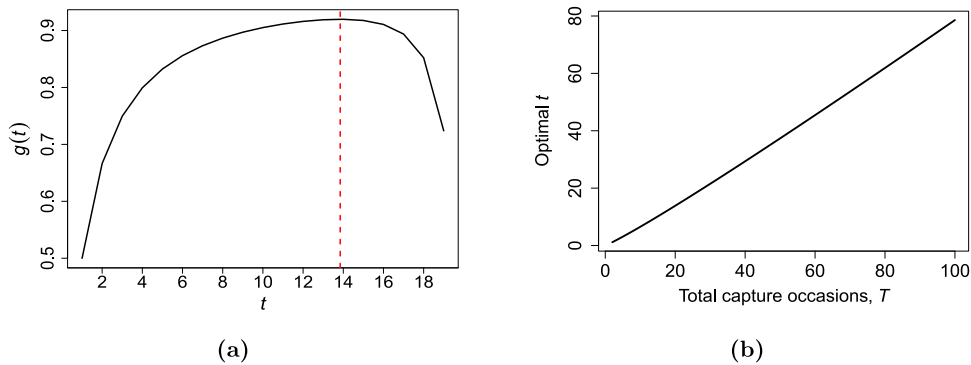


Fig. 3. Optimal t when $q_1 \sim U(0,1)$, while $q_2 < q_1$. (a) $g(t)$ function when $T = 20$, with the dashed line indicating the optimal t . (b) Relationship between optimal t and T .

4.2. Scenario 2: Higher Re-catchability $q_2 < q_1$

In the second scenario, we consider q_2 to be smaller than q_1 , where $q_1 \sim U(0,1)$ and $q_2 \sim U(0, q_1)$. The joint probability density function(pdf) and marginal function can be described by (9)–(11):

$$f(q_1, q_2) = \frac{1}{q_1}, \quad (9)$$

$$f(q_1) = 1, \quad (10)$$

$$f(q_2) = -\ln(q_2), \quad (11)$$

where $0 \leq q_2 \leq q_1 \leq 1$. To calculate the expectation of $f(t; q_1, q_2)$ in Eq. (3) with respect to q_1 and q_2 , we apply the Law of Total Expectation and obtain

$$g(t) = 1 - \frac{1}{t+1} - \frac{1}{(T-t+1)^2} + \frac{1}{(T-t+1)(T+1)}. \quad (12)$$

The optimization of function $g(t)$ in (12) has no closed form solution for t . However, we can find the solutions using the Newton–Raphson method. Fig. 3(a) illustrates an example of the graph of $g(t)$ when $q_1 \sim U(0,1)$, $q_2 < q_1$, and $T = 20$. Using the Newton–Raphson algorithm, the optimal t is determined to be $t^* = 13.848$. The relationship between T and t^* is depicted in Fig. 3(b) for the scenario where $q_2 < q_1$, demonstrating the optimal t^* values for various values of T ranging from 2 to 100.

4.3. Scenario 3: Lower re-catchability $q_1 < q_2$

Moving on to the third scenario, where q_1 is smaller than q_2 , we consider $q_2 \sim U(0,1)$ and $q_1 \sim U(0, q_2)$. The joint probability density function(pdf) and marginal function are given by (13)–(15):

$$f(q_1, q_2) = \frac{1}{q_2}, \quad (13)$$

$$f(q_1) = -\ln(q_1), \quad (14)$$

$$f(q_2) = 1, \quad (15)$$

where $0 \leq q_1 \leq q_2 \leq 1$. We reapply the Law of Total Expectation to calculate the expectation of $f(t; q_1, q_2)$ in (3) with respect to q_1 and q_2 , resulting in:

$$g(t) = 1 - \frac{1}{(t+1)^2} - \frac{1}{(T-t+1)} + \frac{1}{(T+1)(t+1)}. \quad (16)$$

Similar to the previous scenario, the optimization of $g(t)$ in Eq. (16) does not have a closed form solution for t . We can utilize the Newton–Raphson method to find the optimal t numerically. Fig. 4(a) presents an example of the graph of $g(t)$ when $q_2 \sim U(0,1)$, $q_1 < q_2$, and $T = 20$. Using the Newton–Raphson algorithm, the optimal t is determined to be $t^* = 6.152$. Fig. 4(b) illustrates the relationship between T and t for the scenario where $q_1 < q_2$, displaying the t^* values for various values of T ranging from 2 to 100.

4.4. Addressing potential biases in estimation

In this section, we address the concern regarding the use of a uniform prior distribution on catchabilities and its potential impact on introducing heterogeneity on the events, which could lead to biases in the estimation process. To investigate this problem and

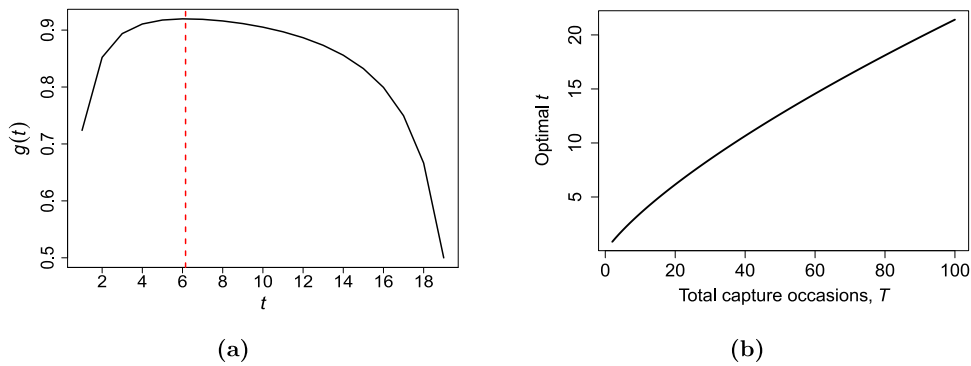


Fig. 4. Optimal t when $q_2 \sim U(0,1)$, while $q_1 < q_2$. (a) $g(t)$ function when $T = 20$, with the dashed line indicating the optimal t . (b) Relationship between optimal t and T .

Table 7

Estimation results for (a) Scenario 1 with uniform catchabilities ($q_1 \sim U(0,1)$ and $q_2 \sim U(0,1)$), (b) Scenario 2 with higher re-catchabilities ($q_1 \sim U(0,1)$ and $q_2 \sim U(0, q_1)$), and (c) Scenario 3 with lower re-catchabilities ($q_1 \sim U(0, q_2)$ and $q_2 \sim U(0,1)$) - $N=1000$, $T=20$. The percentages (%) represent the proportion of overestimation ($\hat{N} > N$), underestimation ($\hat{N} < N$), and accurate estimation ($\hat{N} = N$) based on $B = 10\,000$ draws.

t	(a) Scenario 1: $q_1 \sim U(0,1)$ and $q_2 \sim U(0,1)$				(b) Scenario 2: $q_1 \sim U(0,1)$ and $q_2 < q_1$				(c) Scenario 3: $q_2 \sim U(0,1)$ and $q_2 > q_1$			
	mean($\hat{N}$)	Over-estimate (%)	Under-estimate (%)	Accurate (%)	mean($\hat{N}$)	Over-estimate (%)	Under-estimate (%)	Accurate (%)	mean($\hat{N}$)	Over-estimate (%)	Under-estimate (%)	Accurate (%)
1	999.818	8.1	10.6	81.3	999.734	3.6	6.7	89.7	999.956	5.0	5.2	89.8
2	1000.278	10.1	10.4	79.6	1000.108	4.6	6.3	89.1	1000.095	6.2	5.4	88.4
3	999.839	12.1	10.4	77.5	999.983	5.2	6.0	88.9	999.982	8.4	5.2	86.4
4	999.828	13.9	10.7	75.5	999.858	5.9	6.0	88.1	1000.078	11.0	5.4	83.6
5	999.954	17.2	10.0	72.8	999.821	6.6	6.0	87.4	1000.099	13.3	5.5	81.2
6	1000.079	19.5	10.0	70.6	1000.051	7.7	5.8	86.6	999.836	15.3	5.4	79.3
7	1000.087	19.4	10.1	70.5	999.947	8.3	5.8	85.8	1000.088	15.0	5.4	79.6
8	999.858	18.4	10.8	70.9	1000.083	9.7	5.7	84.6	999.997	14.2	5.7	80.1
9	1000.275	18.1	10.2	71.7	1000.128	10.2	5.8	84.0	1000.082	12.6	5.5	82.0
10	999.887	17.0	10.1	72.9	999.937	11.3	6.0	82.8	1000.145	10.3	5.8	83.9
11	999.997	17.9	10.4	71.7	999.925	13.3	6.0	80.7	1000.142	10.1	5.6	84.3
12	999.976	18.7	10.7	70.6	999.956	15.2	5.7	79.0	1000.052	8.9	5.1	85.9
13	999.941	19.5	10.3	70.2	1000.020	16.1	5.9	78.0	999.948	8.0	5.4	86.7
14	999.938	19.0	10.0	71.0	999.964	15.4	5.8	78.8	1000.049	7.1	5.3	87.6
15	1000.071	16.8	10.8	72.4	999.866	14.1	5.7	80.2	999.919	6.6	5.3	88.2
16	999.953	14.8	10.1	75.1	1000.028	11.5	5.6	83.0	999.927	5.6	5.5	88.9
17	999.877	12.0	10.5	77.5	999.903	8.7	5.8	85.5	1000.079	5.0	5.5	89.5
18	999.646	9.9	10.7	79.5	999.889	6.6	6.1	87.3	999.995	4.4	5.6	90.0
19	999.977	7.7	10.9	81.5	1000.153	5.5	5.5	89.0	999.517	3.5	5.9	90.6

evaluate the performance of the method, we conducted simulations for all three scenarios with a sample size of $N = 1000$ and a total number of sampling sub-occasions $T = 20$.

Table 7 present the results of the simulation, including the percentage of overestimation ($\hat{N} > N$), underestimation ($\hat{N} < N$), and accurate estimation ($\hat{N} = N$) based on $B = 10\,000$ draws. These results provide insights into the accuracy of the method in estimating the true population size, thereby addressing concerns related to potential underestimation or overestimation biases. The simulation results demonstrate that the proposed method achieves accurate estimations with a low rate of overestimation and underestimation. This finding indicates that the method performs well and provides reliable population size estimates, mitigating any doubts regarding potential biases in the estimation process.

5. Generalization in multiple-capture studies

This study examines the optimal allocation of sampling effort within the Lincoln–Petersen experiment, by minimizing the asymptotic variance of the population size estimator. This principle naturally extends to the Schnabel census, which can be viewed as the k -sample extension of the Lincoln–Petersen model. In this approach, sampling is organized into primary capture occasions, each subdivided into several sub-occasions, forming a hierarchical structure that facilitates the optimized allocation of sampling effort. The detection probability on each primary occasion is modelled as

$$p_j = 1 - (1 - \theta)^{S_j},$$

where θ represents the per-sub-occasion capture probability and S_j is the number of sub-occasions allocated to the j th primary occasion. The probability of not detecting an individual at occasion j is given by

$$q_j = (1 - \theta)^{S_j}.$$

The likelihood for this model is constructed as

$$L(N, p_j) \propto \frac{N!}{(N - n)!} \prod_{j=1}^k \left\{ p_j^{n_j} q_j^{N - n_j} \right\},$$

where n_j represents the number of individuals detected in the j th occasion, and n the total number of unique individuals detected throughout the experiment. Darroch (1958) demonstrated that the maximum likelihood estimate $\hat{N}$ for the population is the unique root, exceeding n , of the polynomial of degree $k - 1$ given by

$$\left(1 - \frac{n}{N}\right) = \prod_{j=1}^k \left(1 - \frac{n_j}{N}\right).$$

The asymptotic variance of the population estimate, according to Seber and Schofield (2023), is

$$\text{Var}(\hat{N}) \approx N \left[\frac{1}{\prod_{j=1}^k q_j} + k - 1 - \sum_{j=1}^k \frac{1}{q_j} \right]^{-1}. \quad (17)$$

To optimize the allocation strategy, it is crucial to note that the first term inside the rectangular brackets in (17) remains constant, regardless of how the sampling effort is allocated, as long as the total number of sub-occasions satisfies $S_1 + \dots + S_k = T$. Therefore, the variance minimization depends solely on the term $\sum_{j=1}^k q_j^{-1} = \sum_{j=1}^k (1 - \theta)^{-S_j}$. By recognizing that $(1 - \theta)^{-S_j}$ is a convex function of S_j , Jensen's inequality states that for any convex function, the function's value at the mean is less than or equal to the mean of the function's values. More formally, this relationship can be expressed as

$$\frac{1}{(1 - \theta)^{T/k}} \leq \frac{1}{k} \sum_{j=1}^k \frac{1}{(1 - \theta)^{S_j}}.$$

This inequality implies that an equal allocation of $S_j = T/k$ minimizes $\sum_{j=1}^k \frac{1}{(1 - \theta)^{S_j}}$, leading to a reduction in the variance of the population size estimate.

6. Discussion

This work has provided a guide to effective planning on allocating the sub-occasions hierarchically into two capture occasions in a Lincoln–Petersen experiment. The proposed method uses a hierarchical structure that enhances the capture probabilities within a single capture occasion, thereby improving estimation accuracy and reducing the likelihood of zero-captures. Detectability affects the precision of population size estimates and the required sample size. Instead of capturing and marking a large number of individuals, increasing the detectability of marked individuals through advanced technology and improved techniques can lead to more efficient population size estimation (Burnham, 1987; Papadatou et al., 2012; Schorr et al., 2014; Conner et al., 2015).

When individuals are equally catchable on both occasions, an optimal design is achieved by evenly splitting the sampling effort between the two occasions. This facilitates the optimal design of the sampling effort as $t = T/2$, without requiring knowledge of individual detection probability values, θ . This assumption holds particular relevance in situations where the sampling process is conducted within a short time span, such as in the example of snowshoe hares. Also, as suggested by Robson and Regier (1964) as well as Goetze and Rodriguez (2018), an equitable allocation of resources between both occasions is optimal for minimizing errors when funding is limited, making it cost-effective to exert the same sampling effort during each occasion.

In scenarios where capture probabilities differ between capture occasions, having prior knowledge of these probabilities aids in the design of the sampling scheme. Therefore, conducting a pilot study is recommended before embarking on a large-scale capture-recapture investigation. A thoughtful and suitable design of the Lincoln–Petersen experiment in a capture-recapture study is crucial for obtaining reliable and valid results. It is essential to emphasize that all the relationships presented in this paper rely on the assumption that all practical conditions necessary for a valid use of the estimate are met. Robson and Regier (1964) highlight that using the Lincoln–Petersen estimate effectively involves more than just determining the sample size. It also requires a thorough comprehension of subjects' behaviours, instrument bias, and other relevant factors, as well as proficiency in obtaining appropriate samples.

The hierarchical framework presented shares structural similarities with Pollock (1982)'s robust design, which organizes sampling into primary periods (open population) and secondary occasions (closed within periods). However, a key difference lies in the population closure assumption: the hierarchical design assumes that the population remains closed throughout the study, whereas the robust design explicitly models demographic events such as births, deaths, and migration between primary periods. This closure assumption simplifies the model, enabling precise allocation of effort across sub-occasions without the need to account for demographic changes.

Future studies could expand this approach to open populations by incorporating aspects of the robust design framework. Specifically, the method could optimize sampling effort within each closed primary period of the robust design to enhance detectability. This hybrid approach would maintain adaptability to population changes while improving precision within each period. Such advancements would be especially beneficial for research on migratory species or in long-term monitoring programs.

7. Conclusion

In conclusion, this paper presents a hierarchical framework for sampling effort allocation within the Lincoln–Petersen experiment, emphasizing the importance of maximizing the joint detection probabilities across capture occasions. This framework offers clear guidelines for designing capture-recapture studies that achieve precise population estimates without unnecessary resource expenditure. The contributions of this work include extending traditional methodologies to account for variable capture probabilities and proposing a pseudo-Bayesian approach for scenarios where these probabilities are unknown.

Appendix A. Variance of Lincoln–Petersen estimator

Asymptotic variance of $\hat{N}$ can be derived using delta method (Sekar and Deming, 1949) given by:

$$\text{var}[f(x)] \simeq \left(\frac{\partial f}{\partial x} \right)^2 \text{var}(x). \quad (\text{A.1})$$

If n_1, n_2 are fixed, and N be the parameter, m follows a hypergeometric distribution with p.d.f. in the form of:

$$p(m) = \frac{\binom{n_1}{m} \binom{N-n_1}{n_2-m}}{\binom{N}{n_2}},$$

then the expected value and the variance of m are given respectively by:

$$E(m) = n_1 n_2 / N = N p_1 p_2,$$

and

$$\begin{aligned} \text{var}(m) &= n_2 \left(\frac{n_1}{N} \right) \left(\frac{N-n_1}{N} \right) \left(\frac{N-n_2}{N-1} \right) \\ &\simeq N p_1 (1-p_1) p_2 (1-p_2). \end{aligned} \quad (\text{A.2})$$

Based on (1), the variance of $\hat{N}$ is:

$$\text{var}(\hat{N}) = n_1^2 n_2^2 \text{var}\left(\frac{1}{m}\right),$$

which by the application of the delta method in (A.1), can be estimated as:

$$\widehat{\text{var}(\hat{N})} \simeq n_1^2 n_2^2 \left(\frac{-1}{m^2} \right)^2 \text{var}(m).$$

By substitute $\text{var}(m)$ from Eq. (A.2), we obtain

$$\begin{aligned} \widehat{\text{var}(\hat{N})} &\simeq n_1^2 n_2^2 \frac{1}{m^4} N p_1 p_2 (1-p_1)(1-p_2) \\ &\simeq n_1^2 n_2^2 \frac{m}{m^4} \left(\frac{n_2-m}{n_2} \right) \left(\frac{n_1-m}{n_1} \right) \\ &\simeq \frac{n_1 n_2 (n_1-m)(n_2-m)}{m^3} \\ &\simeq \hat{N} \frac{n_1-m}{m} \frac{n_2-m}{m}. \end{aligned} \quad (\text{A.3})$$

Appendix B. Proof of Theorem 1

To solve the optimization problem, our focus narrows down to minimizing the function $s(t) = q^t + q^{T-t}$ with respect to the variable t , where $q \in (0, 1)$. Take note that $s(t)$ is symmetric in t as $s(t) = s(T-t)$. Let $t = T > 1$, it can be shown that:

$$s(T) = 1 + q^T \geq s(T-1) = q + q^{T-1}.$$

This is correct as:

$$(1-q) \geq q^{T-1}(1-q).$$

Let $t = T-1$, it can be shown that:

$$s(T-1) = q + q^{T-1} \geq s(T-1) = q^2 + q^{T-2}.$$

This is correct as:

$$q(1-q) \geq q^{T-2}(1-q),$$

or

$$q \geq q^{T-2}.$$

In general, the argument can be continued as:

$$q' \geq q^{T-(t+1)},$$

so that

$$s(t) \geq s(t+1). \quad (\text{B.1})$$

as long as $t \leq T-t$. If $t = T-t$ which can only be the case if T is even, $s(t)$ becomes minimum for $\hat{t} = T/2$. If T is odd $s(t)$ becomes minimum for $\hat{t} = (T-1)/2$ or $\hat{t} = (T-1)/2 + 1$.

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