Penalized empirical likelihood estimation and EM algorithms for closed-population capture–recapture models

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Abstract
Capture–recapture experiments are widely used to estimate the abundance of a finite population. Based on capture–recapture data, the empirical likelihood (EL) method has been shown to outperform the conventional conditional likelihood (CL) method. However, the current literature on EL abundance estimation ignores behavioral effects, and the EL estimates may not be stable, especially when the capture probability is low. We make three contributions in this paper. First, we extend the EL method to capture–recapture models that account for behavioral effects. Second, to overcome the instability of the EL method, we propose a penalized EL (PEL) estimation method that penalizes large abundance values. We then investigate the asymptotics of the maximum PEL estimator and the PEL ratio statistic. Third, we develop standard expectation–maximization (EM) algorithms for PEL to improve its practical performance. The EM algorithm is also applicable to EL and CL with slight modifications. Our simulation and a real-world data analysis demonstrate that the PEL method successfully overcomes the instability of the EL method and the proposed EM algorithm produces more reliable results than existing optimization algorithms.

Keywords: Capture–recapture data analysis; Conditional likelihood; EM algorithm; Penalized empirical likelihood.

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1 Introduction

The abundance or size of a finite population is of great importance in many fields, such as fishery, ecology, demographics, and epidemiology (Böning et al., 2018). For example, fish abundances are fundamental for evaluating fishery resources and bird abundances are important indices for planning and assessing habitat conservation policies. This paper considers closed populations, in which there are no births, deaths, or migration, so that the population size is a constant over the time period of the study. The closed-population assumption is reasonable in most cases since the study period is usually short. Capture–recapture experiments are widely used to estimate the abundance of a closed population, as this is a cost-effective technique for collecting data. In such experiments, individuals from the population of interest are captured, marked, and then released. At a later time, after the captured individuals have mixed with other members of the population, another sample is taken.

Capture–recapture experiments can be discrete-time or continuous-time, according to whether the capture efforts are made for a finite number of discrete occasions or over a particular period of time. Regardless of whether a capture–recapture experiment is discrete-time or continuous-time, the probability or intensity of capture is often influenced by three factors: individual heterogeneity, time, and the behavioral response to capture (Otis et al., 1978). It is natural that different individuals have different capture probabilities since they have different covariates (individual heterogeneity), such as sex for the black bear population analyzed in Section 5. The time factor implies that an individual may have different capture probability on each capture occasion. In addition, individuals may make different behavioral responses to different types of capture equipment, leading to different capture probabilities. For example, black bears might develop a bait preference after being captured, and become so “happy” that they are more easily captured again. In contrast, cliff swallows are often caught by mist nets (Roche et al., 2013), so might tend subsequently to avoid nets and feel so “sad” that they are less easily recaptured. Throughout this paper, we restrict our attention to the discrete-time capture–recapture data and similar conclusions can be straightforwardly extended to the continuous-time capture–recapture data.
Any combination of the aforementioned three factors can be used to formulate a specific type of probability model (Otis et al., 1978); see Tables 1. Of all the possible models, the Huggins–Alho model is the most popular for discrete-time capture–recapture experiments. In these models, conditional likelihood (CL) (Huggins, 1991) and empirical likelihood (EL) (Liu et al., 2017) are the two most common ways to estimate abundance. The CL method has two steps. A maximum CL estimator is first obtained for the underlying nuisance model parameters, and then a Horvitz–Thompson type estimator and Wald-type confidence intervals are constructed for the abundance. However, if the estimated capture probabilities are small, the CL-based Horvitz–Thompson estimator for abundance is unstable and the corresponding Wald-type confidence intervals may have unconvincing widths or even infinite upper limits. The EL abundance estimation method, proposed by Liu et al. (2017) for discrete-time capture–recapture experiments, yields a more stable point estimator and a more accurate interval estimator than the CL method. It has been extended to continuous-time capture–recapture experiments (Liu et al., 2018) and to cases with missing covariates (Liu et al., 2021). Nevertheless, if the marginal capture probability is quite small, the EL method also becomes unstable and may produce poor estimates. These features are illustrated in our simulation results in Section 4 and the black bear data analysis in Section 5.

The EL literature on capture–recapture data takes the effects of time and individual heterogeneity into account but largely ignores the effects of different behavioral responses. Behavioral heterogeneity has attracted much attention in the CL literature. Huggins (1991) and Chao et al. (2000) considered that behavioral response could be enduring and proposed a CL estimation method. An enduring behavioral response means that the capture probabilities are different but remain constant before and after one individual is captured. Special cases include the “sad” and “happy” behavioral effects. As noted by Xi et al. (2009), the estimates may be quite unreliable if some major variables affecting the capture probability are not included in the model. Hence, it is necessary to develop EL methods for capture–recapture models that account for behavioral heterogeneity.

Besides the estimation methods themselves, there is an urgent need to improve the algorithms that implement the CL and EL methods. The R package VGAM developed by Yee...
et al. (2015) seems an appealing tool for implementing the CL method for discrete-time capture–recapture studies. Compared with the generalized linear model (GLM) classes, the vector GLM classes used there limit the applicability of **VGAM**. As the profile log EL function depends on a Lagrange multiplier, which is an implicit function, the EL method involves double optimizations. Its implementation is usually achieved via R built-in optimization functions (Liu et al., 2017, 2018, 2021), although the resulting solutions depend on the choice of initial values. The expectation–maximization (EM) algorithm (Dempster et al., 1977) is well known for its stable performance and several EM-like algorithms have been adapted to capture–recapture models (Wang, 2005; Xi et al., 2009; Farcomeni and Scacchiati, 2013; Farcomeni, 2016). Unfortunately, there is no guarantee for these algorithms that the iterations will converge to maximum likelihood estimators or that the likelihood will increase monotonically after each step, which are the most appealing properties of the standard EM algorithm.

The aforementioned imperfections of the existing EL approaches for capture–recapture data motivate our work, which has three main contributions. First, we extend the EL method of Liu et al. (2017) to general capture–recapture models, especially those accounting for behavioral heterogeneity.

Second, to overcome the instability of the EL method, we propose a penalized EL (PEL) approach based on the EL method that penalizes large abundance values. With an appropriately chosen data-adaptive penalty function, the maximum PEL estimator has a normal distribution and the PEL ratio statistic has a central chi-squared distribution asymptotically. The penalty term shrinks the maximum EL estimator toward Chao (1987, 1989)’s lower bound, making the maximum PEL estimator much more stable than the maximum EL estimator. Also, it quickly pushes the PEL ratio function to infinity for large abundance values. This allows the PEL method to overcome the possible flatness issue of the right tail of the EL ratio function, so that it produces better interval estimators with convincing upper limits, especially when the marginal capture probability is small. These desirable properties of the PEL method are confirmed by our simulation results.

Third, we develop a series of standard EM algorithms for the PEL method for various
capture–recapture models. These algorithms retain the nice increasing property of the PEL after each iteration. They are also applicable to the CL and EL methods with slight modifications. An appealing property of these EM algorithms is that one key optimization can easily be implemented with standard generalized linear regression programs. Our numerical studies show that the EM algorithms proposed are more flexible and produce more reliable results than the existing optimization algorithms.

The rest of this article is organized as follows. In Section 2, we extend the EL method to general capture–recapture models, introduce the proposed PEL method, and establish its asymptotic properties. In Section 3, we develop the standard EM algorithms and investigate their finite-sample properties. Our simulation results and an analysis of a real-world data set are provided in Sections 4 and 5, respectively. Section 6 concludes. For clarity, the technical proofs are in the online supplementary material.

2 PEL inference

Let $N$ be the size of the population of interest and $K$ the number of capture attempts made to collect data. For a generic individual in the population, we let $X$ denote its covariate with cumulative distribution function $F(x)$. Let $(D_{(1)}, \ldots, D_{(K)})^\top \in \{0, 1\}^K$ be its capture history, where $D_{(k)} = 1$ if the individual is captured on the $k$th occasion and 0 otherwise. Given $X = x$ and the first $(k - 1)$ capture statuses, the conditional probability of the individual being captured on the $k$th capture occasion is often characterized by a linear logistic model:

$$P(D_{(k)} = 1 \mid X = x, D_{(1)} = d_{(1)}, \ldots, D_{(k-1)} = d_{(k-1)}) = \frac{\exp(\beta^\top z_k)}{1 + \exp(\beta^\top z_k)} =: g(z_k; \beta)$$ (1)

for $k = 1, \ldots, K$, where $z_k$ is a summarized quantity of the vector $(x^\top, d_{(1)}, \ldots, d_{(k-1)})^\top$ and $\beta$ is an unknown vector-valued parameter. Here, we assume that $d_{(0)} = 0$, as no capture occurs before the first capture occasion. This model is the well-known Huggins–Alho model (Huggins 1989; Alho 1990). With different choices of $z_k$ and $\beta$, model (1) covers all the eight possible types of capture–recapture models (Otis et al. 1978) that account for time ($t$), individual heterogeneity ($h$), and/or behavioral response ($b$). See Table 1. The last
Table 1: Capture probability models.

| Model  | $\beta$                                      | $z_k$ | $z_{k0}$ |
|--------|---------------------------------------------|-------|----------|
| $M_0$  | $\beta(c)$                                  | 1     | 1        |
| $M_t$  | $\beta(t)$                                  | $e_k$ | $e_k$    |
| $M_b$  | $(\beta(c), \beta(b))^\top$                | $(1, f_k)^\top$ | $(1, 0)^\top$ |
| $M_{tb}$ | $(\beta(t)^\top, \beta(b))^\top$      | $(e_k^\top, f_k)^\top$ | $(e_k^\top, 0)^\top$ |
| $M_h$  | $(\beta(c), \beta(h)^\top)^\top$          | $(1, x^\top)^\top$ | $(1, x^\top, 0)^\top$ |
| $M_{ht}$ | $(\beta(h)^\top, \beta(t)^\top)^\top$  | $(x^\top, e_k^\top)^\top$ | $(x^\top, e_k^\top, 0)^\top$ |
| $M_{hb}$ | $(\beta(c), \beta(h)^\top, \beta(b))^\top$ | $(1, x^\top, f_k)^\top$ | $(1, x^\top, 0)^\top$ |
| $M_{htb}$ | $(\beta(h)^\top, \beta(t)^\top, \beta(b))^\top$ | $(x^\top, e_k^\top, f_k)^\top$ | $(x^\top, e_k^\top, 0)^\top$ |

$e_k$ is the $K$-order vector whose $k$th component is 1 whereas all the other components are 0.

$f_k = 1$ if $\sum_{j=0}^{k-1} d(j) > 0$ and 0 otherwise.

Since the effects of capture occasion and behavioral response are both discrete, models $M_0$, $M_t$, $M_b$, and $M_{tb}$ are completely parametric (Otis et al., 1978; Chao, 2001), and EL is degenerate or inapplicable for these models. Hereafter, we focus on $M_h$, $M_{ht}$, $M_{hb}$, and $M_{htb}$, for which individual heterogeneity is vital.

2.1 EL for general capture–recapture models

We begin by extending Liu et al.'s (2017)'s EL method to general capture–recapture models. Let $\{(X_i^\top, D_{i1}, \ldots, D_{iK}) : i = 1, \ldots, N\}$ be $N$ independent and identically distributed (i.i.d.) copies of $(X^\top, D_{(1)}, \ldots, D_{(K)})$, which is regarded as an ideal infinite population. Without loss of generality, we suppose that the first $n$ individuals are captured at least once and that the observations are recorded as $\{(x_i, d_{i1}, \ldots, d_{iK}) : i = 1, 2, \ldots, n\}$. We define $z_{ik}$ and $z_{ik0}$ in a similar way to $d_{ik}$.

Let $D = \sum_{k=1}^{K} D_{(k)}$ denote the number of times that a generic individual is captured. Then, $\alpha = \pr(D = 0)$ is the probability of an individual never being captured at all. Based
on the observations, the full likelihood is
\[
\text{pr}(n) \times \prod_{i=1}^{n} \text{pr}(X = x_i \mid D > 0) \times \prod_{i=1}^{n} \text{pr}(D_{(i)} = d_{i1}, \ldots, D_{(K)} = d_{ik} \mid X = x_i, D > 0). \quad (2)
\]

Since \( n \) has a binomial distribution \( \text{Bi}(N, 1 - \alpha) \), then \( \text{pr}(n) = \binom{N}{n} \alpha^{n-n}(1 - \alpha)^n \). It follows from \( X \sim F(x) \) that the second term in \( (2) \) is
\[
\prod_{i=1}^{n} \text{pr}(X = x_i \mid D > 0) \text{pr}(D > 0 \mid X = x_i) = \prod_{i=1}^{n} \frac{dF(x_i)\{1 - \phi(x_i; \beta)\}}{1 - \alpha},
\]
where \( \phi(x; \beta) = \text{pr}(D = 0 \mid X = x) = \prod_{k=1}^{K} \{1 - g(z_{ik}; \beta)\} \) is the probability of an individual never being captured given its covariate \( x \). For model \( (1) \), the third term in \( (2) \) is
\[
L_e(\beta) := \prod_{i=1}^{n} \prod_{k=1}^{K} \frac{\text{pr}(d_{ik} \mid d_{i1}, \ldots, d_{ik-1}, x_i)}{\text{pr}(D > 0 \mid X = x_i)} = \prod_{i=1}^{n} \prod_{k=1}^{K} \frac{\{g(z_{ik}; \beta)\}^{d_{ik}} \{1 - g(z_{ik}; \beta)\}^{1-d_{ik}}}{1 - \phi(x_i; \beta)}.
\]
In summary, the full likelihood \( (2) \) is
\[
\binom{N}{n} \alpha^{n-n} \times \prod_{i=1}^{n} dF(x_i) \times \prod_{i=1}^{n} \prod_{k=1}^{K} \{g(z_{ik}; \beta)\}^{d_{ik}} \{1 - g(z_{ik}; \beta)\}^{1-d_{ik}}.
\]

In EL (Owen, 1988, 1990), we model the distribution of \( X \) by a multinomial distribution with support being the observations, i.e. \( F(x) = \sum_{i=1}^{n} p_i I(x_i \leq x) \), so that \( dF(x_i) = p_i \). Since \( F(x) \) is a distribution function, the feasible \( p_i \)'s should satisfy
\[
p_i \geq 0, \quad i = 1, \ldots, n, \quad \sum_{i=1}^{n} p_i = 1, \quad \sum_{i=1}^{n} \{\phi(x_i; \beta) - \alpha\} p_i = 0, \quad (3)
\]
where the last equation follows from \( \phi(x; \beta) = \text{pr}(D = 0 \mid X = x) \) and \( \alpha = \text{pr}(D = 0) \). Substituting \( p_i = dF(x_i) \) into the full likelihood and taking logarithms give the log EL:
\[
\tilde{\ell}_e(N, \beta, \alpha, \{p_i\}) = \log \binom{N}{n} + (N - n) \log(\alpha) + \sum_{i=1}^{n} \log(p_i)
+ \sum_{i=1}^{n} \sum_{k=1}^{K} [d_{ik} \log\{g(z_{ik}; \beta)\} + (1 - d_{ik}) \log\{1 - g(z_{ik}; \beta)\}]. \quad (4)
\]
Profiling out the \( p_i \)'s with the Lagrange multiplier method, we have the profile log EL:
\[
\ell_e(N, \beta, \alpha) = \log \binom{N}{n} + (N - n) \log(\alpha) - \sum_{i=1}^{n} \log[1 + \xi\{\phi(x_i; \beta) - \alpha\}]
+ \sum_{i=1}^{n} \sum_{k=1}^{K} [d_{ik} \log\{g(z_{ik}; \beta)\} + (1 - d_{ik}) \log\{1 - g(z_{ik}; \beta)\}].
\]
where \( \xi = \xi(\beta, \alpha) \) satisfies \( \sum_{i=1}^{n} \frac{\phi(x_i; \beta) - \alpha}{1 + \xi(\phi(x_i; \beta) - \alpha)} = 0 \).

Like Liu et al. (2017), we define the maximum EL estimator of \((N, \beta, \alpha)\) as \((\hat{N}_e, \hat{\beta}_e, \hat{\alpha}_e) = \arg \max \ell_e(N, \beta, \alpha)\). As an alternative, the Horvitz–Thompson type estimator of \(N\) proposed by Huggins (1991) is \(\hat{N}_c = \sum_{i=1}^{n} \{1 - \phi(x_i; \hat{\beta}_c)\}^{-1} \), where \(\hat{\beta}_c = \arg \max \beta L_c(\beta)\) is the maximum CL estimator of \(\beta\).

### 2.2 Penalized empirical likelihood

When the capture probability \((1 - \alpha)\) is small, the EL estimator \(\hat{N}_e\) can be unstable and the corresponding interval estimates can be extremely wide or even have infinite upper limits. A possible reason is that the EL ratio function of \(N\) increases too slowly or is even flat as \(N\) increases. Thus, we propose to penalize large values of \(N\) in the (profile) log EL function by adding a penalty. We define the penalized (profile) log EL function as:

\[
\tilde{\ell}_p(N, \beta, \alpha, \{p_i\}) = \tilde{\ell}_e(N, \beta, \alpha, \{p_i\}) + C f(N),
\]

where \(f(N)\) is a non-increasing penalty function and \(C > 0\) is a tuning parameter trading off the EL function and the penalty term. When \(C = 0\), the PEL method reduces to Liu et al. (2017)’s EL method. Given \(f(N)\) and \(C\), the proposed maximum PEL estimator is \((\hat{N}_p, \hat{\beta}_p, \hat{\alpha}_p) = \arg \max \ell_p(N, \beta, \alpha)\) and the proposed PEL ratio functions are

\[
R_p(N, \beta, \alpha) = 2\{\ell_p(\hat{N}_p, \hat{\beta}_p, \hat{\alpha}_p) - \ell_p(N, \beta, \alpha)\},
\]

\[
R'_p(N) = \inf_{(\beta, \alpha)} R_p(N, \beta, \alpha).
\]

The penalty \(f(N)\) plays an important role in the PEL method. To look for a reasonable function \(f(N)\), we recall Chao (1987, 1989)’s nonparametric estimator for \(N\), \(\tilde{N}_c = n + m_1^2/(2m_2)\), where \(m_1\) and \(m_2\) are the numbers of individuals captured once and twice, respectively. Although negatively biased, this estimator is rather stable and is widely used as a lower bound of \(N\). A desirable penalty \(f(N)\) should shrink large \(\hat{N}_e\) toward Chao’s lower bound \(\tilde{N}_c\) and make the log EL decrease quickly as \(N\) increases. Moreover, \(f(N)\) should put less or no penalty on small \(\hat{N}_e\) because the estimator itself is already stable. These expectations motivated us to consider a quadratic penalty function, \(f(N) = -(N - \tilde{N}_c)^2 I(N > \tilde{N}_c)\). With an appropriate choice of \(C\), Theorem 1 shows that the maximum PEL estimator is asymptotically unbiased and asymptotically normal.
Theorem 1 Let \((N_0, \beta_0, \alpha_0)\) with \(\alpha_0 \in (0, 1)\) be the true value of \((N, \beta, \alpha)\). Suppose that the matrix \(W\) defined in Equation (1) of the supplementary material is positive definite. When \(f(N) = -(N - \tilde{N}_c)^2I(N > \tilde{N}_c)\) and \(C = O_p(N_0^{-2})\), as \(N_0 \to \infty\), then: (a) \(\sqrt{N_0}\{\log(\tilde{N}_p/N_0)\}, (\tilde{\beta}_p - \beta_0)^\top, \tilde{\alpha}_p - \alpha_0\} \to \mathcal{N}(0, W^{-1})\), where \(\to\) stands for convergence in distribution. (b) \(R_p(N_0, \beta_0, \alpha_0) \to \chi^2_{2s+4}\) and \(R'_p(N_0) \to \chi^2_1\), where \(s\) is the dimension of \(\beta\) and \(\chi^2_{df}\) is the chi-squared distribution with \(df\) degrees of freedom.

When \(z_k\) is equal to \((1, x^\top)\), \(W\) reduces to the matrix \(W_s\) defined in Corollary 1 of Liu et al. (2017). Like the EL estimators of Liu et al. (2017), theoretically, the PEL estimators are equivalent to the CL estimators asymptotically, and hence, they have the same limiting distributions.

Proposition 1 Under the conditions in Theorem 1, as \(N_0 \to \infty\), then: (a) \(\tilde{\beta}_p - \beta = O_p(N_0^{-1})\) and \(\tilde{N}_p - \tilde{N}_c = O_p(1)\). (b) \(\sqrt{N_0}(\tilde{\beta}_p - \beta_0) \to \mathcal{N}(0, -V_{22}^{-1})\) and \(\sqrt{N_0}(\tilde{\alpha}_p - \alpha_0) \to \mathcal{N}(0, -V_{22}^{-1})\). (c) \(N_0^{-1/2}(\tilde{N}_p - N_0) \to \mathcal{N}(0, \sigma^2)\) and \(N_0^{-1/2}(\tilde{N}_c - N_0) \to \mathcal{N}(0, \sigma^2)\), where \(\sigma^2 = \varphi - 1 - V_{32}V_{22}^{-1}V_{23}\) and where \(\varphi\) and the \(V_{ij}\)’s are defined in Section 1.1 of the supplementary material.

In practice, the performance of the PEL method depends on the tuning parameter \(C\), which may itself depend on the true value of \(N\). Like Wang and Lindsay (2005), we recommend a data-adaptive value, \(C = 2m^2/(nm^2)\), which clearly satisfies the requirement \(C = O_p(N_0^{-2})\) in Theorem 1. From a Bayesian perspective, adding the penalty \(Cf(N)\) to the log EL is equivalent to assuming a prior distribution:

\[
q(N) = \frac{1}{2(\tilde{N}_c - n)}I(n \leq N \leq \tilde{N}_c) + \frac{1}{\sqrt{2\pi} \tilde{\sigma}_c} \exp\left\{ -\frac{(N - \tilde{N}_c)^2}{2\tilde{\sigma}_c^2} \right\}I(N > \tilde{N}_c),
\]

with \(\tilde{\sigma}_c^2 = n(\tilde{N}_c - n)^2\), for \(N\). When \(N > \tilde{N}_c\), the prior \(q(N)\) is a normal distribution with mean \(\tilde{N}_c\) and variance \(\tilde{\sigma}_c^2\). Otherwise, it reduces to a non-informative uniform distribution. The EL estimator \(\tilde{N}_c\) is hardly less than \(\tilde{N}_c\). Therefore, the normal part of the prior takes effect in most cases. The variance \(\tilde{\sigma}_c^2\) increases and \(C\) decreases as \((\tilde{N}_c - n)\) increases. This is reasonable since a larger gap between \(\tilde{N}_c\) and \(n\) implies that more individuals are not sampled and there is more uncertainty in the data.
3 EM algorithms

The main numerical task in the proposed PEL approach to abundance estimation is to maximize the penalized log EL function $\tilde{\ell}_p(N, \beta, \alpha, \{p_i\})$ or the penalized profile log EL $\ell_p(N, \beta, \alpha)$. In the implementation of the EL method, Liu et al. (2017) proposed using optimization functions. However, the calculated results may depend on the choice of initial values and be unreliable. Considering that the EM algorithm (Dempster et al., 1977) is well known for its stability, we develop EM algorithms for the PEL method to improve the numerical performance of the EL abundance estimation method.

3.1 Preparation

As we assumed in Section 2.1, only the first $n$ individuals are observed. Given the population size $N$, we use $x^*_j$'s to denote the covariates of the other $N - n$ individuals. The $x^*_j$'s are independent of each other and are also independent of $x_i$ ($i = 1, \ldots, n$). They have a common distribution $F_X$ and serve as missing data in the subsequent EM algorithm. We regard $O^* \cup O$ as complete data, where $O^* = \{x^*_j : j = n + 1, \ldots, N\}$ and

$$O = \{(x_i, d_{i1}, \ldots, d_{iK}) : 1 \leq i \leq n\} \cup \{(d_{i1}, \ldots, d_{iK}) : d_{ik} = 0, 1 \leq k \leq K, n+1 \leq i \leq N\}.$$

Let $\boldsymbol{\theta} = (\beta^\top, \alpha)^\top$ and $\boldsymbol{\psi} = (\theta^\top, p_1, \ldots, p_n)^\top$. In this case, the complete-data likelihood is

$$\prod_{i=1}^{n} \{ \prod_{k=1}^{K} \text{pr}(d_{ik} | x_i, d_{i1}, \ldots, d_{i-1}) \} \text{pr}(X_i = x_i) \times \prod_{j=n+1}^{N} \{ \phi(x^*_j; \beta) \text{pr}(X_j = x^*_j) \},$$

and the corresponding log likelihood of $\boldsymbol{\psi}$ is

$$\ell(\psi) = \sum_{i=1}^{n} \sum_{k=1}^{K} [d_{ik} \log \{g(z_{ik}; \beta)\} + (1 - d_{ik}) \log \{1 - g(z_{ik}; \beta)\}] + \sum_{i=1}^{n} \log(p_i)$$

$$+ \sum_{i=1}^{n} \sum_{j=n+1}^{N} [I(X_j = x_i) \log \{\phi(x_i; \beta) p_i\}],$$

where the last term is obtained from the definition of the $p_i$'s and since the $X_j$'s take values from $\{x_1, \ldots, x_n\}$. 10
As in [Dempster et al. (1977)], the standard EM algorithm consists of a sequence of iterations. Each iteration involves two steps: an E-step and an M-step. Suppose that \( r \) iterations \((r = 0, 1, \ldots)\) have been finished. In the \((r+1)\)th iteration, we need to calculate the expectation of the above log likelihood \( \ell(\psi) \) conditioned on the observed data \( \mathbf{O} \) and given \( \psi = \psi^{(r)} \). For \( j = n + 1, \ldots, N \), it follows from \( \mathbf{X}_j \sim F_{\mathbf{X}} \) that

\[
\mathbb{E} \{ \mathbf{I}(\mathbf{X}_j = \mathbf{x}_i) \mid \mathbf{O}, \psi = \psi^{(r)} \} = \Pr(\mathbf{X}_j = \mathbf{x}_i \mid D_{j1} = \cdots = D_{jk} = 0) = \frac{\phi(\mathbf{x}_i; \beta^{(r)})p_i^{(r)}}{\alpha^{(r)}},
\]

where \( \alpha^{(r)} = \sum_{k=1}^{\infty} \phi(\mathbf{x}_i; \beta^{(r)})p_i^{(r)} \). Thus, the conditional expectation of \( \ell(\psi) \) can be written as \( Q(\psi \mid \psi^{(r)}) = \ell_1(\beta) + \ell_2(p_1, \ldots, p_n) \), where

\[
\ell_1(\beta) = \sum_{i=1}^{n} \sum_{k=1}^{K} d_{ik} \log \{ g(z_{ik}; \beta) \} + (1 - d_{ik}) \log \{ 1 - g(z_{ik}; \beta) \} + w_i^{(r)} \log \{ 1 - g(z_{ik0}; \beta) \},
\]

\[
\ell_2(p_1, \ldots, p_n) = \sum_{i=1}^{n} (w_i^{(r)} + 1) \log(p_i), \quad w_i^{(r)} = (N - n)\phi(\mathbf{x}_i; \beta^{(r)})p_i^{(r)}/\alpha^{(r)}.
\]

This completes the E-step of the EM algorithm for the \((r+1)\)th iteration.

Now, the M-step of the EM algorithm is undertaken by choosing \( \psi = \psi^{(r+1)} \), which maximizes \( Q(\psi \mid \psi^{(r)}) \) with respect to \( \psi \) under the constraint \( \{ \alpha \} \). Since \( Q(\psi \mid \psi^{(r)}) \) does not involve \( \alpha \), we propose to update \( \alpha^{(r)} \) as \( \alpha^{(r+1)} = \sum_{i=1}^{n} \phi(\mathbf{x}_i; \beta^{(r+1)})p_i^{(r+1)} \). Here, the \( p_i^{(r+1)} \)'s are obtained by maximizing \( \ell_2(p_1, \ldots, p_n) \) such that \( p_i \geq 0 \) for \( i = 1, \ldots, n \) and \( \sum_{i=1}^{n} p_i = 1 \). The maximizer is \( p_i^{(r+1)} = (w_i^{(r)} + 1)/N, \ i = 1, \ldots, n \). Then, \( \beta^{(r+1)} \) is obtained by maximizing \( \ell_1(\beta) \), which can be solved by the standard Newton–Raphson method or by fitting a binomial regression model.

### 3.2 Algorithm

Based on the preceding analysis, we propose using the following EM algorithm to maximize the penalized log EL function \( \tilde{\ell}_p(N, \beta, \alpha, \{p_i\}) \) for a given \( N \).

**Step 0.** Set \( \beta^{(0)} = 0, \ p_i^{(0)} = 1/n \) for \( i = 1, \ldots, n \), \( \alpha^{(0)} = \sum_{i=1}^{n} \phi(\mathbf{x}_i; \beta^{(0)})p_i^{(0)} \), and the iteration number \( r = 0 \).

**Step 1.** Calculate \( w_i^{(r)} = (N - n)\phi(\mathbf{x}_i; \beta^{(r)})p_i^{(r)}/\alpha^{(r)} \). Update \( \beta^{(r)} \) to \( \beta^{(r+1)} \) by fitting a binomial regression model with a logistic link function to the observations \( \{(y_{ik}, z_{ik}^\top) : \).
\( i = 1, \ldots, n; k = 1, \ldots, K \) and \( \{(0, z_{ik0}) : i = 1, \ldots, n; k = 1, \ldots, K\} \) with weights 1’s and \( w_i^{(r)} \)'s, respectively.

**Step 2.** Update \( p_i^{(r)} \) to \( p_i^{(r+1)} = (w_i^{(r)} + 1)/N \) for \( i = 1, \ldots, n \), and calculate \( \alpha^{(r+1)} = \sum_{i=1}^{n} \phi(x_i; \beta^{(r+1)})p_i^{(r+1)} \).

**Step 3.** Set \( r = r + 1 \) and repeat steps 1 and 2 until the increment of the penalized log EL in Equation (4) after an iteration is no greater than a tolerance, say, \( 10^{-5} \).

**Remark 1** The parameter \( N \) is fixed in the above algorithm. To calculate the maximum PEL estimator \((\hat{N}_p, \hat{\beta}_p, \hat{\alpha}_p)\), we have two alternative methods. One is to directly maximize the profile function \( \max_{\{\beta, \alpha, \{p_i\}\}} \tilde{L}_p(N, \beta, \alpha, \{p_i\}) \) with respect to \( N \). The other is to use \( w_i^{(r)} = (N^{(r)} - n)\phi(x_i; \beta^{(r)})p_i^{(r)}/\alpha^{(r)} \) and \( p_i^{(r+1)} = (w_i^{(r)} + 1)/N^{(r)} \) in steps 1 and 2, respectively, and add the following maximization step after step 2:

**Step 2’.** Update \( N^{(r)} \) to \( N^{(r+1)} \), the maximizer of \( \log \left( \binom{N}{n} \right) + (N - n)\log(\alpha^{(r+1)}) + Cf(N) \).

The unpenalized EL estimator \((\hat{N}_e, \hat{\beta}_e, \hat{\alpha}_e)\) can be calculated with the same algorithm after setting \( C = 0 \).

We have integrated the above EM algorithm into the \( \mathbb{R} \) package \texttt{Abun}, where steps 1 and 2’ are, respectively, implemented via \( \mathbb{R} \) functions \texttt{glm} and \texttt{optimize}. The use of standard GLM classes makes the EM algorithm very reliable and flexible. Besides this advantage, the proposed EM algorithm inherits many appealing properties of the classical EM algorithm.

**Theorem 2** With discrete-time capture-recapture models, the EM algorithm proposed for the PEL method has following properties: (a) When \( N \) is fixed, the penalized log EL is nondecreasing after each EM iteration. (b) When \( N \) is unknown, the penalized log EL is nondecreasing after each EM iteration. (c) When \( N \) is unknown, the sequence of EM iterations \((N^{(r)}, \beta^{(r)}, \alpha^{(r)})\) converges to a local maximum PEL estimator \((\hat{N}_p, \hat{\beta}_p, \hat{\alpha}_p)\).

**Remark 2** The proposed EM algorithm is applicable to the CL method if \( N^{(r+1)} \) is set to \( n/(1 - \alpha^{(r+1)}) \) in step 2’ and the iteration stops when the log CL \( \log \{L_c(\beta)\} \) converges in step 3. A justification for setting \( N^{(r+1)} = n/(1 - \alpha^{(r+1)}) \) is that if we regard \( N \) as a random
variable, it is reasonable to assume that $N$ given $n$ follows a negative binomial distribution, which implies that $\mathbb{E}(N \mid n) = n/(1 - \alpha)$.

**Proposition 2** Considering Remark 2, the sequence of EM iterations $\{(N^{(r)}, \beta^{(r)}) : r = 1, 2, \ldots\}$ converges to a local maximum CL estimator $(\widehat{N}_c, \widehat{\beta}_c)$.

Although the proposed EM algorithm is designed for capture–recapture models with individual heterogeneity, if we set the coefficient of $x$ to 0 in step 2, then it is also applicable to models without individual heterogeneity, such as $M_0$, $M_t$, $M_b$, and $M_{tb}$.

### 4 Simulation study

In this section, we carry out simulations to investigate the finite-sample performance of the PEL methods and the proposed EM algorithms for discrete-time capture–recapture models. For point estimation of $N$, we study the maximum PEL estimator $\widehat{N}_p$, the maximum CL estimator $\widehat{N}_c$, and the EL estimator $\widehat{N}_e$. For interval estimation, we compare

1. the PEL ratio confidence interval $I_p = \{N : R_p'(N) \leq \chi^2_1(1 - a)\}$,
2. the EL ratio confidence interval $I_e = \{N : R_e'(N) \leq \chi^2_1(1 - a)\}$, and
3. the Wald-type confidence interval $I_c = \{N : (\widehat{N}_c - N)^2/(\widehat{N}_c \widehat{\sigma}_c^2) \leq \chi^2_1(1 - a)\}$,

where $\chi^2_1(1 - a)$ is the $(1 - a)$th quantile of $\chi^2_1$ and $\widehat{\sigma}_c^2$ is a consistent estimate of $\sigma^2$. Theorem 1 together with Proposition 1 guarantees that these confidence intervals all have a coverage probability of $(1 - a)$ asymptotically.

We consider four interesting questions:

1. **Question 1.** Is the EM algorithm more reliable than the standard optimization algorithm?
2. **Question 2.** How does individual behavior effect the maximum EL estimator $\widehat{N}_e$?
3. **Question 3.** Is the maximum PEL estimator $\widehat{N}_p$ more stable than its competitors?
Question 4. Is the PEL ratio confidence interval $I_p$ superior to its competitors?

To answer these questions, we generate data for the following three scenarios:

(A) Let $\mathbf{X} = (X_1, X_2)^\top$, where $X_1 \sim N(0, 1)$ and $X_2 \sim \text{Bi}(1, 0.5)$. We consider model $M_h$ with $
abla = (0.1, -2.5, -0.15)^\top$.

(B) The settings are the same as (A) except that we use model $M_{hb}$ with $
abla_0 = (0.1, -2.5, -0.15, 0.8)^\top$.

(C) The settings are the same as (B) except that $
abla_0 = (0.1, -2.5, -0.15, -0.8)^\top$.

In each scenario, we set the population size to $N_0 = 200$ or $400$ and the number of capture occasions to $K = 2$ or $6$, where the capture probability is about $63\%$ or $79\%$. All our simulation results were calculated for $5000$ samples.

Answer to question 1. We calculate the three point estimators of $N$ with both the proposed EM algorithm and the optimization algorithm of [Liu et al. (2017)](#). Figure 1 displays the scatter plots of the EM-based versus optimization-based point estimates when data were generated for Scenario A with $N_0 = 200$ and $K = 2$. For all three estimators, $\hat{N}_c$, $\hat{N}_e$, and $\hat{N}_p$, the optimization algorithm tends to produce larger estimates than the EM algorithm does, especially when the EM-based estimates are close to or greater than $N_0 = 200$. To some extent, this implies that the optimization algorithm is less robust than the EM algorithm. Moreover, there are quite a few cases where the log likelihoods based on the optimization algorithm are less than those based on the EM algorithm by $0.01$ or more. This indicates that in these cases, the optimization algorithm might not find the maximum likelihood estimates even when the estimates themselves are not large. It also suggests that the proposed EM algorithm is more reliable than the optimization algorithm. In the following, unless stated otherwise, all estimates are calculated by the EM algorithm.

Answer to question 2. To investigate the impact of individual behavior, we consider the EL estimator $\hat{N}_e$ for the $M_h$ and $M_{hb}$ models. Figure 2 displays the box plots of $\hat{N}_e$ when data were generated for scenarios B and C with $N_0 = 200$ and $K = 6$. Since model
Figure 1: Scatter plots of the EM-based versus optimization-based estimates. The solid blue dots show where the EM-based log likelihoods are greater than the optimization-based log likelihoods by 0.01 or more.

Figure 2: Box plots of $\hat{N}_e$ for models $M_h$ and $M_{hb}$ for scenarios B (left) and C (right). $M_{hb}$ is satisfied in both scenarios B and C; we expect that the EL estimator for $M_h$ may perform less well, whereas for $M_{hb}$, it should do better. From Figure 2, we see that the $M_{hb}$-based $\hat{N}_e$ is nearly unbiased, as expected. However, the $M_h$-based $\hat{N}_e$, which ignores the behavior effect, produces obvious underestimates for scenario B and obvious overestimates for scenario C. We also see that $\hat{N}_e$ has increasingly stable performance as the capture probability increases (63% in scenario B and 79% in scenario C). Similar simulations were conducted for the PEL estimator $\hat{N}_p$, and the behavior response had the same influence on $\hat{N}_p$. 
| $K$ | $N_0$ | $\hat{N}_v$ | $\hat{N}_c$ | $\hat{N}_e$ | $\hat{N}_p$ | $\mathcal{I}_v$ | $\mathcal{I}_c$ | $\mathcal{I}_e$ | $\mathcal{I}_p$ |
|-----|------|--------|--------|--------|--------|--------|--------|--------|--------|
| 2   | 200  | 366    | 271    | 273    | 50     | 87.52  | 87.72  | 92.66  | 93.22  |
|     | 400  | 191    | 167    | 156    | 88     | 90.18  | 90.26  | 93.74  | 93.92  |
| 6   | 200  | 32     | 30     | 27     | 24     | 87.14  | 87.44  | 90.94  | 90.76  |
|     | 400  | 44     | 41     | 38     | 36     | 88.62  | 88.66  | 91.24  | 91.26  |
|     |      |        |        |        |        |        |        |        |        |
| 2   | 200  | 70302  | 10271  | 726    | 44     | 87.92  | 88.00  | 92.70  | 92.92  |
|     | 400  | 626    | 381    | 394    | 86     | 89.64  | 89.54  | 93.58  | 94.24  |
| 6   | 200  | 38     | 36     | 32     | 24     | 87.44  | 87.68  | 91.72  | 90.22  |
|     | 400  | 49     | 46     | 43     | 37     | 89.52  | 89.38  | 91.80  | 91.70  |
|     |      |        |        |        |        |        |        |        |        |
| 2   | 200  | 563    | 383    | 386    | 72     | 87.12  | 87.12  | 92.88  | 93.84  |
|     | 400  | 215    | 192    | 176    | 120    | 89.28  | 89.26  | 93.36  | 93.64  |
| 6   | 200  | 32     | 31     | 28     | 26     | 87.12  | 87.50  | 91.58  | 91.56  |
|     | 400  | 44     | 41     | 39     | 38     | 89.48  | 89.48  | 92.16  | 92.12  |

**Answer to question 3.** We use the root mean square error (RMSE) to evaluate the stability of a point estimator for the population size $N$. Table 2 presents the true value $N_0$ and the RMSEs of the PEL estimator $\hat{N}_p$ and its competitors: the CL estimator $\hat{N}_c$ and the EL estimator $\hat{N}_e$. We also include the RMSE of the CL estimator $\hat{N}_v$ calculated by the R package `VGAM`.

In all scenarios, the PEL estimator $\hat{N}_p$ always has the smallest RMSEs, indicating that it has the most stable performance of these four estimators. In particular, when $K = 2$ and $N_0 = 200$, the RMSEs of $\hat{N}_c$, $\hat{N}_v$, and $\hat{N}_e$ are even greater than $N_0$ itself, which is undesirable. In contrast, the PEL estimator has significantly smaller RMSEs,
80% or more lower, which is very surprising. When $K = 6$, all four estimators are very stable although the PEL estimator still performs best. In summary, we have an affirmative answer to question 3, namely the maximum PEL estimator $\hat{N}_p$ is, indeed, more stable than its competitors.

**Answer to question 4.** Parallel to the four point estimators, we compare the finite-sample performances of four interval estimators ($I_c$, $I_e$, $I_p$, and $I_v$) where $I_v$ is the Wald-type confidence interval calculated by the R package `VGAM`. We report the coverage probabilities of the four interval estimators at the 95% confidence level in Table 2. The PEL interval $I_p$ always has the same coverage probabilities as the EL interval $I_e$, and both have much better coverage accuracy than the two CL intervals $I_c$ and $I_v$. The increase in coverage for the PEL and EL intervals is at least 2% and can be as high as 6%. For example, when $K = 2$ and $N_0 = 200$ for scenario C, the increases in coverage are 6.72% and 5.76%, respectively.

We also calculate the average widths of the four interval estimators. Figure 3 displays the box plots of the logarithm of these average widths for scenarios A–C with $N_0 = 200$ and $K = 2$. Compared with the EL interval $I_e$, the PEL interval $I_p$ has much narrower average widths although they have almost the same coverage probabilities. The CL intervals $I_c$ and $I_e$ also have narrower average widths than the EL interval $I_e$. However, they have much lower coverage probabilities than the latter. In addition, the width of the PEL interval $I_p$ has the lowest dispersion of the four intervals.

In summary, the proposed EM algorithm produces more reliable results than the standard optimization algorithm. The PEL point estimator calculated with the proposed EM algorithm has much more stable performance than the other estimators. The corresponding PEL intervals are much narrower than the EL intervals with nearly no loss of coverage probabilities and with the most stable widths.
Figure 3: Box plots of the logarithm of the widths of the confidence intervals.

5 Real-world data analysis

In this section, we analyze a real-world data set, named black bear data, to demonstrate the advantages of the proposed PEL estimation method and the proposed EM algorithm.

To estimate the abundance of black bears at the military installation Fort Drum in northern New York, USA, data on black bears were collected over 8 weeks during June and July 2006 (Gardner et al., 2010; Royle et al., 2013). Although the survey was conducted using 38 baited traps, we integrate the capture histories of 47 individuals and treat this data set as discrete-time capture-recapture data. Besides the encounter histories, the covariate sex is also available for the bears caught. We analyze the data with the CL, EL, and PEL estimation methods for the capture probability models $M_{hb}$ and $M_{htb}$. Table 3 tabulates the estimates of the abundance of black bears. The PEL and EL methods were implemented by the proposed EM algorithm (R package Abun) and the CL method was implemented by the optimization algorithm (R package VGAM) or the proposed EM algorithm.

For model $M_{hb}$, the PEL and EL methods produce the same point estimates and lower bounds of interval estimates, and nearly identical standard errors. This is probably because the common point estimate 65 is close to Chao (1987)'s lower bound 63, and the penalty is hardly applied. Even so, the PEL interval has a much smaller upper limit and, hence, a much narrower width than the EL interval. With the CL method, the two algorithms produce almost the same point estimates, standard errors, and Wald confidence intervals.
Table 3: Estimates for black bear abundances.†

| Algorithm | Method | Model $M_{hb}$ | Model $M_{htb}$ |
|-----------|--------|---------------|-----------------|
|           |        | Est. SE CI    | Est. SE CI      |
| EM        | PEL    | 65 14.52 [50, 165] | 106 111.37 [51, 295] |
| EM        | EL     | 65 14.54 [50, 226] | 257 947.17 [52, –]‡ |
| EM        | CL     | 70 18.75 [34, 107] | 949 $1 \times 10^5$ $[-3 \times 10^4, 3 \times 10^4]$ |
| Optimization | CL    | 70 18.53 [34, 107] | $7 \times 10^8$ $7 \times 10^{10}$ $[-1 \times 10^{12}, 1 \times 10^{12}]$ |

† Est.: point estimate, SE: standard error, and CI: confidence interval at the 95% confidence level.
‡ –: A number greater than $10^9$.

The results are totally different for the most general $M_{htb}$ model. The most stable and reasonable results are those from the PEL method. The PEL abundance estimate is about 106 with a standard error of 111.37, whereas the PEL interval estimate is [51, 295]. The point estimate of 106 is close to the 114 of Gardner et al. (2010), which was also based on spatial information. In contrast, the EL method produces rather unstable results. The point estimate (257) and standard error (947.17) are both much larger, and the interval estimate has a nearly infinite upper limit. This comparison implies that the penalty in the PEL method is applied. The results for the CL method are too unstable to be acceptable, whether they are calculated by the proposed EM algorithm or the optimization algorithm.

To gain insights about the remarkable difference between the PEL and EL methods for model $M_{htb}$, we display the PEL and EL ratio functions of $N$ in Figure 4. It is clear that the EL ratio function is decreasing and becomes flat for large $N$, which explains the undesirable poor performance of the EL method. With the recommended penalty, the PEL ratio function increases quickly for $N > 150$. Therefore, the PEL method successfully overcomes the instability of the EL method and produces better and reliable point and interval estimates. For model selection diagnostics, we apply the PEL-based Akaike information criterion (AIC) to the goodness-of-fit of the probabilistic models. The AICs of models $M_{hb}$ and $M_{htb}$ are 829.33 and 828.73, respectively, suggesting that model $M_{htb}$ fits the data better than model $M_{hb}$.
6 Conclusion and discussion

When the capture probability is moderate or low, the general capture–recapture model \( M_{htb} \) may be weakly identified by the data and the likelihood function of abundance may be so flat that the estimation results may be unstable; see also Section 5. We compensate for the instability of model fitting by penalizing large maximum EL estimates of abundance and drawing them closer to Chao (1987)’s lower-bound estimate, which is known to be stable. The penalty has a similar effect to imposing an informative prior in a Bayesian setting, and the result is naturally a better fit with narrower confidence intervals as it makes use of more information. There is a close relation between our recommended penalty function and that in the penalized likelihood \( \ell_3 \) of Wang and Lindsay (2005). Both penalties are data-adaptive and the target parameters have a quadratic form. The difference is that Wang and Lindsay (2005)’s penalty is added to a CL of an odd parameter, namely \( \alpha/(1 - \alpha) \) in our notation, whereas our penalty is added to an EL of the abundance. We could use other penalty functions in the PEL method, such as \( f(N) = N \) or \(-\log(N)\). Our simulation experience shows that with these penalties, the resulting PEL estimators are somewhat

Figure 4: PEL (solid line) and EL (dashed line) ratio functions of \( N \) for the black bear data.
sensitive to the choice of tuning parameters. Also, the non-concavity of $-\log(N)$ would make calculating the PEL more challenging.

We propose to implement the PEL method by the EM algorithm, which was proposed by [Liu et al. (2022)] under one-inflated capture–recapture models. The EM algorithm guarantees that the likelihood increases after each iteration and that the final estimator is equal to the maximum likelihood estimator. Alternatively, the PEL method can be implemented in a full Bayesian framework where the impact of the prior is transparent. To investigate the behavioral effect of individuals on captures, we consider an enduring (long-term) memory of the behavior in the capture–recapture model $M_{htb}$ which means that after an individual is captured, the individual has a long memory of its first-capture experience and the effect lasts in the remaining period of the experiment. In practice, ephemeral (short-term) behaviors are also frequently seen, which means that the capture probability may depend on whether or not it is caught on the most recent occasion [Yang and Chao, 2005; Bartolucci and Pennoni, 2007]. The proposed PEL method and EM algorithm are both applicable to such cases, as noted in Section 2 of the supplementary material.

There may not be enough information in conventional capture–recapture data to fit the demanding probability models reliably. Recently, biologists have focused on using sampling designs that do deliver better information. A prime example of this is the burgeoning field of spatial capture–recapture, where individual heterogeneity is attributed to an animal’s spatial location relative to the traps, and the spatial information in the data is used in the fitting of the model. It’s notable that the real-data analysis of black bears was actually taken from a spatial capture-recapture study, but we discarded the spatial information and used a sex covariate instead. It is of interest to extend the proposed methods to the complicated spatial capture–recapture data.

**SUPPLEMENTARY MATERIAL**

**Title:** The supplementary material for “Penalized empirical likelihood estimation and EM algorithms for closed-population capture–recapture models” contains proofs of all the theorems and propositions and extends the PEL method to more general capture–recapture models with ephemeral behavioral effect. (Abun_supp.pdf)
**R-package for Abun routine:** This package contains the code to perform the EL and PEL methods by the proposed EM algorithms. The package also contains the real-world data set analyzed in the article. (Abun_0.1-1.tar.gz)

**Black bear data set:** Data set used in the illustration of the PEL method and the EM algorithm in Section 5 (blackbear.txt)

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**References**

Alho, J. M. (1990). Logistic regression in capture–recapture models. *Biometrics* 46(3), 623–635.

Bartolucci, F. and F. Pennoni (2007). A class of latent Markov models for capture–recapture data allowing for time, heterogeneity, and behavior effects. *Biometrics* 63(2), 568–578.

Böhning, D., P. G. M. Heijden, and J. Bunge (2018). *Capture–recapture methods for the social and medical sciences*. CRC Press Boca Raton.

Chao, A. (1987). Estimating the population size for capture–recapture data with unequal catchability. *Biometrics* 43(4), 783–791.

Chao, A. (1989). Estimating population size for sparse data in capture–recapture experiments. *Biometrics* 45(2), 427–438.

Chao, A. (2001). An overview of closed capture–recapture models. *Journal of Agricultural, Biological, and Environmental Statistics* 6(2), 158–175.
Chao, A., W. Chu, and C.-H. Hsu (2000). Capture–recapture when time and behavioral response affect capture probabilities. *Biometrics* 56(2), 427–433.

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

Farcomeni, A. (2016). A general class of recapture models based on the conditional capture probabilities. *Biometrics* 72(1), 116–124.

Farcomeni, A. and D. Scacciatelli (2013). Heterogeneity and behavioral response in continuous time capture–recapture, with application to street cannabis use in Italy. *The Annals of Applied Statistics* 7(4), 2293–2314.

Gardner, B., J. A. Royle, M. T. Wegan, R. E. Rainbolt, and P. D. Curtis (2010). Estimating black bear density using DNA data from hair snares. *The Journal of Wildlife Management* 74(2), 318–325.

Huggins, R. (1989). On the statistical analysis of capture experiments. *Biometrika* 76(1), 133–140.

Huggins, R. (1991). Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47(2), 725–732.

Liu, Y., P. Li, Y. Liu, and R. Zhang (2022). Semiparametric empirical likelihood inference for abundance from one-inflated capture–recapture data. *Biometrical Journal*. Doi: 10.1002/bimj.202100231.

Liu, Y., P. Li, and J. Qin (2017). Maximum empirical likelihood estimation for abundance in a closed population from capture–recapture data. *Biometrika* 104(3), 527–543.

Liu, Y., Y. Liu, P. Li, and J. Qin (2018). Full likelihood inference for abundance from continuous time capture–recapture data. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 80(5), 995–1014.
Liu, Y., Y. Liu, P. Li, and L. Zhu (2021). Maximum likelihood abundance estimation from capture–recapture data when covariates are missing at random. *Biometrics* 77(3), 1050–1060.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62, 1–135.

Owen, A. B. (1988). Empirical likelihood ratio confidence intervals for a single functional. *Biometrika* 75(2), 237–249.

Owen, A. B. (1990). Empirical likelihood ratio confidence regions. *The Annals of Statistics* 18(1), 90–120.

Roche, E. A., C. R. Brown, M. B. Brown, and K. M. Lear (2013). Recapture heterogeneity in cliff swallows: increased exposure to mist nets leads to net avoidance. *PloS One* 8(3), e58092.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner (2013). *Spatial capture–recapture*. Academic Press.

Wang, J.-P. Z. and B. G. Lindsay (2005). A penalized nonparametric maximum likelihood approach to species richness estimation. *Journal of the American Statistical Association* 100(471), 942–959.

Wang, Y. (2005). A semiparametric regression model with missing covariates in continuous-time capture–recapture studies. *Australian & New Zealand Journal of Statistics* 47(3), 287–297.

Xi, L., R. Watson, J. P. Wang, and P. S. Yip (2009). Estimation in capture–recapture models when covariates are subject to measurement errors and missing data. *Canadian Journal of Statistics* 37(4), 645–658.

Yang, H.-C. and A. Chao (2005). Modeling animals’ behavioral response by Markov chain models for capture–recapture experiments. *Biometrics* 61(4), 1010–1017.
Yee, T. W., J. Stoklosa, and R. M. Huggins (2015). The VGAM package for capture-recapture data using the conditional likelihood. *Journal of Statistical Software* 65(5), 1–33.