

中國統計學報
第 43 卷 第 2 期
九十四年六月
89-96 頁

DISCRETE-TIME VS. CONTINUOUS-TIME
CAPTURE-RECAPTURE MODELS
---IN HONOR OF PROFESSOR T. Y. HWANG'S RETIREMENT

Shu-Ping Lin¹ and Anne Chao²

¹Department of Industrial Management, Chung Hua University and

²Institute of Statistics, National Tsing Hua University

敬獻黃提源教授榮退

三十年水木清華育沃土

八千里反核環保闢新路

ABSTRACT

We consider a framework for linking two types of capture-recapture models (discrete-time and continuous-time models). Under our framework, the inference procedures for population size under the two types of models and the relative asymptotic efficiency are examined. It has been conjectured or intuitively thought that that the population size estimation under a continuous-time model is more efficient than that under a corresponding discrete-time model, but this conjecture/thought has not been theoretically justified in the literature. Our linking framework enables us to provide a theoretical justification for the MLE of population size when time or behavior response affect the capture probabilities. When both time and behavioral response exist, although a theoretical proof is currently not feasible, all numerical results also support the validity of the conjecture.

Key words and phrases: Behavioral response, counting process, ecological models, maximum likelihood, time variation.

AMS 2000 subject classifications: Primary 62P10; secondary 62G05.

1. Introduction

The capture-recapture experiments are the most common sampling method used by biologists and ecologists to estimate the size of a closed population. Here the closure means that there is no birth, death or migration so that the population size is a constant over trapping times. The capture-recapture models have also been applied to many other disciplines including medical science, epidemiology, census undercount problem and software reliability. Seber (1982, 1986, 1992) and Schwarz and Seber (1999) provided comprehensive reviews of models for estimating animal abundance in general and on closed models in particular. Short review articles include Pollock (1991, 2000) and Chao (1998, 2001).

Depending on how the experiments are designed and conducted, we classify capture-recapture models as two types: discrete-time and continuous-time models. In a discrete-time model, the target population is sampled over a certain number of occasions using traps or nets. For each trapping occasion, any animal captured can be counted only once. A unique tag or mark is attached to a first-capture, whereas for a recapture its tag number is recorded. Marking or tagging is used to distinguish individuals caught in the samples, and thus the recapture information (overlap information) can be used to estimate the number of missing animals in the experiment. We also assume that animals do not lose their marks and all marks are recorded correctly. The complete capture history for each animal is conveniently expressed as a sequence of 0's and 1's, where 0 denotes absence and 1 denotes presence. For example, in a six-occasion capture-recapture experiment, a history (1 0 1 0 0 1) means that the animal was caught in the first, third and sixth occasions, but not in the others. The maximum count for each animal is the number of trapping occasions.

For a continuous-time model, only one animal is caught at each trapping occasion. In addition to the tagging process we also record the exact capture times for each animal. Thus any capture and recapture of an animal are regarded as a "trapping occasion" and the exact time for each occasion is recorded. Earlier works include an example of capturing butterflies (Craig, 1953) and mathematical treatment by Darroch (1958), although these authors did not refer to their methods as "continuous-time

models". As an example, an individual's capture history (4.5, 6.1, 8.0, 13.6, 33) means that the animal was caught in time units of 4.5, 6.1, 8.0, 13.6, and 33. The continuous-time models have been applied to studies of sperm whales, grizzly bears, insects and butterflies; see Wilson and Anderson (1995). The model has also found application in software reliability theory; see Nayak (1988). In the latter cases involving a debugging process, each bug is regarded as an individual and the detection times for each bug can be considered as "capture times".

Since more efforts are required to record each capture time and a continuous-time model usually contains more information than that of a corresponding discrete-time model, estimators based on continuous-time models should be preferable, in some senses, to those based on their corresponding discrete-time models. For example, it has been conjectured or intuitively thought that the population size estimation under a continuous-time model is more efficient than that under a corresponding discrete-time model. Wilson and Anderson (1995) compared the two types of models by simulations. Yip and Wang (2002) also used simulation to show that the above conjecture is valid under a related covariate model. However, to our knowledge, there has been no theoretical justification even under the commonly used time-variation or behavioral response models.

In this paper, we provide a basic framework for linking discrete-time and continuous-time capture-recapture models when time and/or behavior response affect capture probabilities. Under our framework, the inference procedures for population size under the two types of models are compared and the relative efficiency for population size estimators under the two types of models can be readily examined. In Section 2, we introduce necessary notation. The basic framework for linking continuous-time models to discrete-time models is provided in Section 3.1. Then three models incorporating time-variation and/or behavioral response are respectively discussed in Sections 3.2-3.4. Concluding remarks and some discussion are given in Section 4.

2. Notation

- N The population size;
 ϕ A proportional constant relating recapture probability (or intensity) to initial-capture probability (or intensity).

Discrete-Time Models

- t The number of trapping occasions or trapping samples;
 P_j The capture probability of any animal on the j th trapping occasion;
 X_{ij} = 1 if the i th animal is caught on the j th occasion, = 0 otherwise;
 n_k The number of animals captured on the k th occasion;
 u_k The number of unmarked animals captured on the k th occasion;
 m_k The number of marked animals captured on the k th occasion, $m_1 = 0$;
 M_k The number of distinct animals captured just before the k th occasion, $M_1 = 0$;
 M_{t+1} The number of distinct animals captured in the experiment.

Continuous-Time Models

- τ Stopping time;
 $N_i(u)$ Number of times that the i th animal has been caught by time u , $0 \leq u \leq \tau$;
 t_{i1} The first capture time of the i th animal;
 F_u The σ -field generated by the capture process up to time u ;
 $\lambda_i(u)$ The capture intensity function of the i th animal;
 $\lambda(u)$ Any arbitrary function defined on $[0, \tau]$;
 $\Lambda(u)$ The cumulative intensity function, $\Lambda(u) = \int_0^u \lambda(x)dx$;
 M_u Number of distinct animals that have been marked by time u ;
 N_u Number of captures by time u , $N_u = \sum_{i=1}^N N_i(u)$;
 K_u Number of re-captures by time u , $K_u = N_u - M_u$.

3. Models and Comparisons

3.1 Models and linking framework

Assume the population size is N and our focus is on the inference of this parameter. To link the continuous-time and discrete-time models, we start with a continuous time scale and then divide the time interval into a fixed number of occasions. Assume that in a continuous-time setup, the experiment terminates at time τ . Let $N_i(u)$ denote the number of times that the i th animal has been captured in $[0, u]$. Each $\{N_i(u); n \geq 0\}$ is a continuous-time counting process with jumps of size 1 and no two processes can jump simultaneously. Let F_u be the capture history generated by $\{N_1(v), N_2(v), \dots, N_N(v); 0 \leq v \leq u\}$. The capture intensity for the i th animal, $\lambda_i(u)$, is defined as

$$Pr(dN_i(u) = 1 \mid F_{u-}) = \lambda_i(u)du, \quad 0 < u < \tau.$$

Let $\lambda(u)$ be any arbitrary function defined on $[0, \tau]$. In this paper, we consider the following three models :

Model(tb) : time-variation and behavior model

$$\lambda_j(u) \equiv \begin{cases} \lambda(u) & \text{for first capture} \\ \phi\lambda(u) & \text{for recapture} \end{cases}, j = 1, 2, \dots, N.$$

Model(b): behavior model

$$\lambda_j(u) \equiv \begin{cases} \lambda & \text{for first capture} \\ \phi\lambda & \text{for recapture} \end{cases}, j = 1, 2, \dots, N.$$

Model(t): time-variation model

$$\lambda_1(u) = \lambda_2(u) = \dots = \lambda_N(u) \equiv \lambda(u).$$

Let $N_u = \sum_{i=1}^N N_i(u)$ be the total number of captures by time u , and M_u be the number of animals that are marked by time u and $K_u = N_u - M_u$. Thus M_τ denotes the number of distinct animals caught in the experiment, and N_τ denotes the total number of captures.

We first divide the interval $[0, \tau]$ into t equally-spaced discrete time interval I_1, I_2, \dots, I_t , where $I_k = [s_{k-1}, s_k]$ and $s_k = \frac{k\tau}{t}$ for $k = 0, 1, \dots, t$. If each interval is regarded as a trapping occasion and repeated animals within each interval are ignored, then we have a corresponding t -occasion discrete-time model. The capture matrix $\{X_{ij}\}$ for the discrete-time model becomes $X_{ij} = I([N_i(s_j) - N_i(s_{j-1})] \geq 1)$. Denote n_k , u_k and m_k respectively by the number of animals, number of unmarked and number of marked in the interval $I_k = [s_{k-1}, s_k]$, $k = 1, 2, \dots, t$. Let M_k be the number of distinct animals captured (i.e., marked) just before the k th occasion in the discrete-time model. Note here we use the same notation M to refer to the number of distinct animals marked for both types of models. No confusion would arise because in a discrete-time, the notation is used only for the positive integer sub-index $1, 2, \dots, t + 1$, that is, M_1, M_2, \dots, M_{t+1} whereas in a continuous-time model, the sub-index can be any time between 0 and τ and in most cases the index refers to the time points $s_1, s_2, \dots, s_t = \tau$. Obviously, we have $M_k = M_{s_{k-1}}$ and $M_{t+1} = M_{s_t} = M_\tau$. Because repeated captures for any individual in an interval can only be counted once, we have $N_{s_k} - N_{s_{k-1}} \geq n_k$ and $N_\tau \geq \sum_{k=1}^t n_k$.

3.2 Time-variation model(t)

This model assumes that $\lambda_1(u) = \lambda_2(u) = \dots = \lambda_N(u) \equiv \lambda(u)$. For notational convenience, we define the cumulative intensity as $\Lambda(u) = \int_0^u \lambda(x)dx$. An approximate MLE \hat{N}_C (where the sub-index stands for a continuous-time model) derived by Becker and Heyde (1990) is the solution of the following equation

$$1 - \frac{M_\tau}{N} = e^{-\frac{N_\tau}{N}}. \quad (3.1a)$$

Another type of MLE by using a finite difference method (Dahiya, 1981) is the solution satisfying

$$1 - \frac{M_\tau}{N} = \left(1 - \frac{1}{N}\right)^{N_\tau}; \quad (3.1b)$$

see also Craig (1953). Both types of MLEs have the same asymptotic variance formula under the condition $N \rightarrow \infty$ and fixed intensity function

$$AVar(\hat{N}_C) = N[e^{\Lambda(\tau)} - 1 - \Lambda(\tau)]^{-1}. \quad (3.2)$$

Note in the time-variation model, the exact capture times are not used at all in obtaining the MLE; only the total number of capture and total number of distinct captures are needed.

Breaking the whole time interval into t occasions as in Section 3.1, we have a corresponding discrete-time model with capture probability P_j on the j th occasion (i.e., in the interval I_j), where

$$P_j = 1 - \exp \left[- \int_{s_{j-1}}^{s_j} \lambda(x) dx \right] = 1 - e^{-[\Lambda(s_j) - \Lambda(s_{j-1})]}.$$

Under this classic discrete-time model, the MLE \hat{N}_D of N satisfies the equation (Otis et al., 1978) where the sub-index stands for a discrete-time model

$$1 - \frac{M_{t+1}}{N} = \prod_{j=1}^t \left(1 - \frac{n_j}{N} \right). \tag{3.3}$$

The asymptotic variance is given by

$$\begin{aligned} AVar(\hat{N}_D) &= N \left[\prod_{j=1}^t \frac{1}{1 - P_j} + t - 1 - \sum_{j=1}^t \frac{1}{1 - P_j} \right]^{-1} \\ &= N \left[e^{\Lambda(\tau)} + t - 1 - \sum_{j=1}^t e^{\Lambda(s_j) - \Lambda(s_{j-1})} \right]^{-1}. \end{aligned} \tag{3.4}$$

To compare the two estimators in (3.1) and (3.3), letting $t \rightarrow \infty$ such that $n_j = 1$ or 0 for all $j = 1, 2, \dots, t$ (i.e., the duration of any occasion is very short such that either no capture or only one capture on each occasion), we have $\prod_{j=1}^t \left(1 - \frac{n_j}{N} \right) = \left(1 - \frac{1}{N} \right)^{N\tau} \rightarrow e^{-\frac{N\tau}{N}}$ with probability 1 as N is large. Hence the two MLEs are asymptotically equivalent as $t \rightarrow \infty$.

We measure the efficiency by the ratio of asymptotic standard errors of the two estimators and define for any fixed the number of trapping occasion t ,

$$eff(\hat{N}_C, \hat{N}_D) = \left[\frac{AVar(\hat{N}_D)}{AVar(\hat{N}_C)} \right]^{1/2} = \left[\frac{\exp(\Lambda(\tau)) - 1 - \Lambda(\tau)}{\exp(\Lambda(\tau)) + t - 1 - \sum_{j=1}^t \exp[\Lambda(s_j) - \Lambda(s_{j-1})]} \right]^{1/2}. \tag{3.5}$$

Since

$$\sum_{j=1}^t \{ \exp[\Lambda(s_j) - \Lambda(s_{j-1})] - 1 \} \geq \sum_{j=1}^t [\Lambda(s_j) - \Lambda(s_{j-1})] = \Lambda(\tau),$$

we have the efficiency is always greater than or equal to one. Thus we have demonstrated that the MLE associated with a continuous-time model is more efficient than that associated with a discrete-time model. If we further assume that the intensity function is bounded by a constant, then we have $\lim_{t \rightarrow \infty} \text{eff}(\hat{N}_C, \hat{N}_D) = 1$.

In order to examine the behavior of the asymptotic efficiency given in Equation (3.5) as a function of the number of trapping occasions, we plot in Figure 1 the efficiency as a function of t for three different intensity functions: $\lambda(u) = (0.4 + u)^{-1}$, $\lambda(u) = 1 + \sin(2\pi u)$ and $\lambda(u) = \sqrt{u}$. The percentages of the number of distinct animals caught in the experiment for these three intensities are respectively 71.4%, 63.2% and 48.6%. As expected, all efficiency plots are decreasing and approach to 1 as the number of trapping samples is increased. It is noted that the case with intermediate percentage has the greatest loss among the three cases. However, in all cases the efficiency loss is slight if the number of trapping samples is greater than 10.

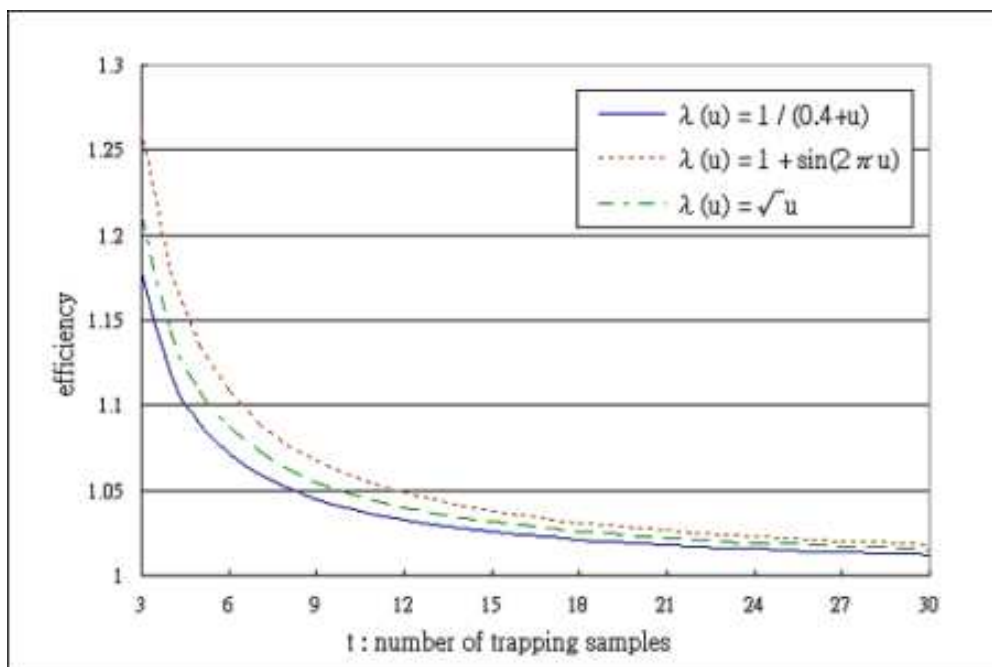


Figure 1. Plots of efficiency under Model(t) for three time-variation functions $\lambda(u) = (0.4 + u)^{-1}$ (solid line), $\lambda(u) = 1 + \sin(2\pi u)$ (dotted line) and $\lambda(u) = \sqrt{u}$ (dashed line), stopping time $\tau = 1$.

3.3 Behavioral model(b)

In this model, we assume the following intensity

$$\lambda_j(u) \equiv \begin{cases} \lambda & \text{for first capture} \\ \phi\lambda & \text{for recapture} \end{cases}, j = 1, 2, \dots, N.$$

The inference procedures for this continuous-time model are provided in Hwang, Chao, Yip (2002). The MLE of (ϕ, λ, N) is the solution of the following system of equations

$$\begin{aligned} \lambda &= \frac{M_\tau}{(N - M_\tau)\tau + \sum_{i=1}^{M_\tau} t_{i1}}, \\ \phi\lambda &= \frac{N_\tau - M_\tau}{\sum_{i=1}^{M_\tau} (\tau - t_{i1})}, \\ 1 - \frac{M_\tau}{N} &= \exp[-M_\tau / (N - M_\tau + \frac{\sum_{i=1}^{M_\tau} t_{i1}}{\tau})], \end{aligned} \tag{3.6}$$

where t_{i1} denotes the first-capture time for animal i . Here only the first capture times are needed. All capture times for recaptures are not involved. When $N \rightarrow \infty$, the asymptotic variance of the MLE of N for fixed ϕ and λ is given by

$$AVar(\hat{N}_C) = \frac{Ne^{-\lambda\tau}(1 - e^{-\lambda\tau})}{(1 - e^{-\lambda\tau})^2 - e^{-\lambda\tau}(\lambda\tau)^2}. \tag{3.7}$$

Under our framework described in Section 3.1, the capture probability for a first capture in any interval of the t intervals, $I_1 = [0, \frac{\tau}{t}]$, $I_2 = [\frac{\tau}{t}, \frac{2\tau}{t}]$, ..., $I_t = [\frac{(t-1)\tau}{t}, \tau]$, is $p = 1 - e^{-\lambda\tau/t}$ and the probability for any recapture is $b = 1 - e^{-\phi\lambda\tau/t}$ for any re-capture. It follows from Otis et al. (1978, p. 107) that for such a discrete-time behavioral model, the MLE \hat{N}_D is the solution of the following equation:

$$\begin{aligned} p &= M_{t+1} / \left[t(N - M_{t+1}) + \sum_{i=1}^t iu_i \right], \\ b &= \sum_{i=1}^t m_i / \sum_{i=1}^t M_i, \\ 1 - \frac{M_{t+1}}{N} &= \left(1 - \frac{M_{t+1}/t}{(N - M_{t+1}) + \sum_{i=1}^t iu_i/t} \right)^t. \end{aligned} \tag{3.8}$$

with the asymptotic variance

$$AVar(\hat{N}_D) = \frac{N(1-p)^t[1 - (1-p)^t]}{[1 - (1-p)^t]^2 - t^2p^2(1-p)^{t-1}}.$$

Substituting $p = 1 - e^{-\lambda\tau/t}$ into the above equation, we have

$$AVar(\hat{N}_D) = \frac{Ne^{-\lambda\tau}(1 - e^{-\lambda\tau})}{(1 - e^{-\lambda\tau})^2 - t^2(1 - e^{-\lambda\tau/t})^2e^{-\lambda\tau(t-1)/t}}. \quad (3.9)$$

To compare (3.6) and (3.8), we let $t \rightarrow \infty$ such that $u_j = 1$ or 0 for $j = 1, 2, \dots, t$ (i.e., the duration of any occasion is very short such there is at most one first-capture on each occasion). Note that for a first-capture on the interval I_i , its first-capture time is i , and the normalized (to 1) first-capture time is i/t . Thus, $\sum_{i=1}^t iu_i/t$ in (3.8) denotes the average capture time, which corresponds to $\sum_{i=1}^{M_\tau} t_{i1}/\tau$ in (3.6). Thus it is readily seen that the two estimators are asymptotically equivalent if t is large enough.

Based on (3.7) and (3.9), we similarly define the efficiency in the following for any fixed the number of trapping occasion t ,

$$eff(\hat{N}_C, \hat{N}_D) = \left[\frac{AVar(\hat{N}_D)}{AVar(\hat{N}_C)} \right]^{1/2} = \left[\frac{(1 - e^{-\lambda\tau})^2 - e^{-\lambda\tau}(\lambda\tau)^2}{(1 - e^{-\lambda\tau})^2 - t^2(1 - e^{-\lambda\tau/t})^2e^{-\lambda\tau(t-1)/t}} \right]^{1/2}. \quad (3.10)$$

Since it can be readily shown that $t^2(1 - e^{-\lambda\tau/t})^2e^{\lambda\tau/t} = t^2(e^{\lambda\tau/t} - 2 + e^{-\lambda\tau/t}) \geq (\lambda\tau)^2$, we have the above efficiency is always greater than or equal to one. As in Model(b), we also have $\lim_{t \rightarrow \infty} eff(\hat{N}_C, \hat{N}_D) = 1$. Figure 2 plots the behavior of the efficiency functions for two stopping times. The efficiency loss is less for a larger stopping time for which more animals are caught. Note the efficiency in (3.10) is independent of the parameter ϕ because the estimators are only function of first-captures.

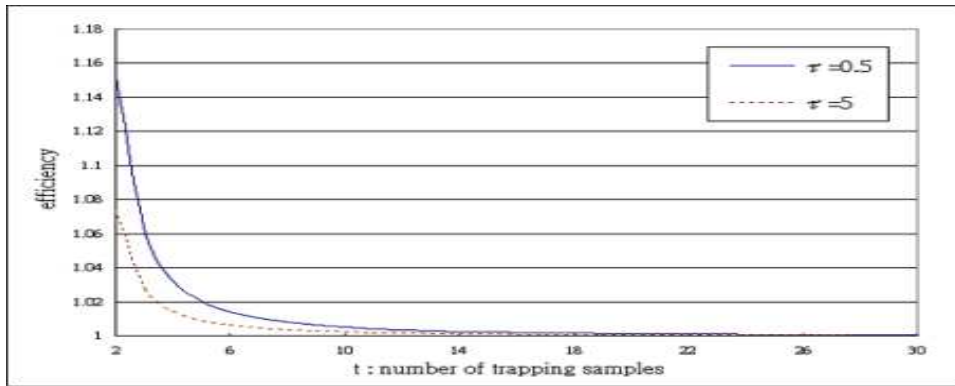


Figure 2. Plots of efficiency under Model(b) for $\lambda = 1$ and two stopping times $\tau = 5$ (dotted line) and $\tau = 0.5$ (solid line)

3.4 Time-variation and behavior model m(tb)

Under model, we assume

$$\lambda_j(u) \equiv \begin{cases} \lambda(u) & \text{for first capture} \\ \phi\lambda(u) & \text{for recapture} \end{cases}, j = 1, 2, \dots, N.$$

Hwang, Chao and Yip (2002) derived the likelihood function and showed that the MLE are solved from the following estimating equations:

$$\begin{aligned} d\Lambda_u &= (N - M_{u-} + \phi M_{u-})^{-1} dN_u, \\ \int_0^\tau \frac{1}{N - M_{u-}} dM_u - \int_0^\tau \frac{1}{N - M_{u-} + \phi M_{u-}} dN_u &= 0, \\ \frac{K_\tau}{\phi} - \int_0^\tau \frac{M_{u-}}{N - M_{u-} + \phi M_{u-}} dN_u &= 0. \end{aligned}$$

The asymptotic variance of the MLE of the population size is given by

$$AVar(\hat{N}_C) = \frac{N\phi[A(1-\phi) + \log B]}{[\Lambda(\tau) - (1-\phi)A - 2\Lambda(\tau)\phi - \phi(1 - e^{\Lambda(\tau)})] \log(B) + (1-\phi)[\Lambda^2(\tau)(1-\phi) - A\phi(1 - e^{\Lambda(\tau)}) - \Lambda(\tau)A]}, \quad (3.11)$$

where $A = 1 - \exp(-\Lambda(\tau))$, $B = \phi + (1 - \phi) \exp(-\Lambda(\tau))$.

When we divide the interval as t equally-spaced discrete occasion, the probability of capturing an unmarked animal on the j th occasion is $P_j = 1 - e^{-[\Lambda(s_j) - \Lambda(s_{j-1})]}$ and the probability for any recapture is $1 - e^{-\phi[\Lambda(s_j) - \Lambda(s_{j-1})]}$. The likelihood function for the resulting discrete-time experiment can be derived as follows:

$$L \propto \frac{N!}{(N - M_{t+1})!} \prod_{j=1}^t P_j^{u_j} (1 - P_j)^{N - M_j} \left[\prod_{j=2}^t [1 - (1 - P_j)^\phi]^{m_j} (1 - P_j)^{\phi(M_j - m_j)} \right].$$

Therefore, we can obtain that the MLE is the solution of the following equations:

$$\begin{aligned} \log\left(\frac{N}{N - M_{t+1}}\right) + \sum_{j=1}^t \log(1 - P_j) &= 0, \\ \sum_{j=2}^t \left(M_j - \frac{m_j}{1 - (1 - P_j)^\phi}\right) \log(1 - P_j) &= 0, \\ \frac{-u_1}{1 - P_1} + \frac{N - u_1}{P_1} &= 0, \\ \frac{-u_j}{P_j} + \frac{N - M_j + \phi(M_j - m_j)}{1 - P_j} + \frac{\phi m_j (1 - P_j)^{\phi-1}}{1 - (1 - P_j)^\phi} &= 0. \end{aligned}$$

Similar derivations to those in Chao, Chu and Hsu (2000) lead to the following asymptotic variance of population size as $N \rightarrow \infty$ and all other parameters are fixed:

$$AVar(\hat{N}_D) = \frac{N \sum_{j=2}^t \left(\frac{Q_j \log(1-P_j)}{P_j} \right)^2 A_j}{\phi^2 \sum_{j=2}^t A_j \sum_{j=2}^t \left(\frac{Q_j \log(1-P_j)}{P_j} \right)^2 A_j - \left[\sum_{j=2}^t \frac{\phi Q_j \log(1-P_j)}{P_j} A_j \right]^2}, \quad (3.12)$$

where $Q_j = \prod_{k=1}^j (1 - P_k)$ and

$$A_j = \frac{(1 - Q_{j-1})(1 - P_j)^{\phi-2} P_j^2}{Q_{j-1}[\phi^2(1 - Q_{j-1})(1 - P_j)^{\phi-1} P_j] + Q_{j-1}[1 - (1 - P_j)^\phi]}.$$

Since the MLEs under both continuous-time and discrete-time become analytically untractable, their asymptotic equivalence as $t \rightarrow \infty$ cannot be theoretically verified at present. However, simulation results have shown its validity under various scenarios. Based on (3.11) and (3.12), we can obtain the asymptotic efficiency when $N \rightarrow \infty$ as the other two models. Figures 3 and 4 respectively plots the trap-shy ($\phi = 0.75$) and trap-happy ($\phi = 1.5$) cases for three intensity functions.

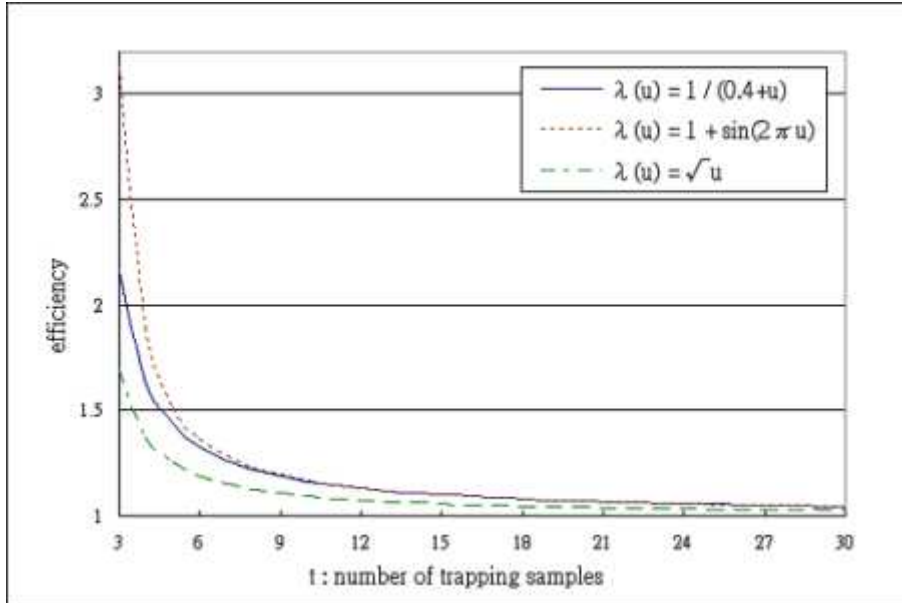


Figure 3. Plots of efficiency under Model(tb) for stopping time $\tau = 1$ and $\phi = 0.75$ $\lambda(u) = (0.4 + u)^{-1}$ (solid line), $\lambda(u) = 1 + \sin(2\pi u)$ (dotted line), $\lambda(u) = \sqrt{u}$ (dashed line)

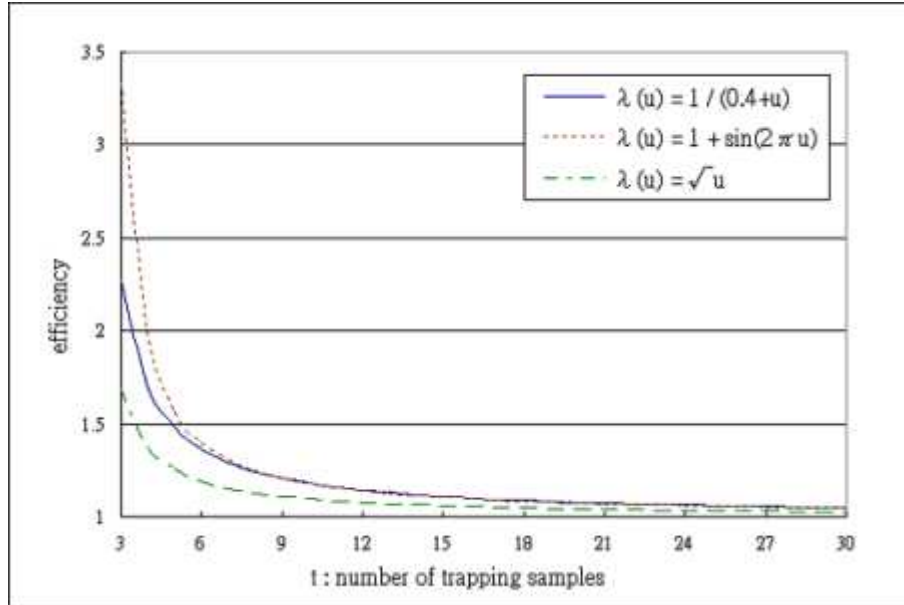


Figure 4. Plots of efficiency under Model(tb) for stopping time $\tau = 1$ and $\phi = 1.5$ $\lambda(u) = (0.4 + u)^{-1}$ (solid line), $\lambda(u) = 1 + \sin(2\pi u)$ (dotted line), $\lambda(u) = \sqrt{u}$ (dashed line)

Figures 3 and 4 numerically show that the MLE in continuous-time model is also more efficient than that in a corresponding discrete-time model for the three selected types of intensities and two values of ϕ . The efficiency is little affected by the value of ϕ . Consistent finding is also shown for other types of intensities and values of ϕ .

4. Concluding Remarks and Discussion

We have theoretically or numerically shown that for any finite number of occasions in a discrete-time capture-recapture model, its MLE of population size has larger asymptotic variance than that in a corresponding continuous-time model. When the number of occasions in a discrete-time capture-recapture model tends to infinity, its MLE of population size is asymptotically equivalent to that under a continuous-time model. Thus a continuous-time model is essentially equivalent to a discrete-time model with infinite number of trapping occasions. We have presented analytic formula for the relative efficiencies and those formulas would help biologists to assess the relative

merits of the two types of experiments and determine how many trapping occasions will be used to achieve a required efficiency.

For the three models considered in this paper, in addition to the MLE, there are other types of estimators available for estimating population size such as martingale estimating function approaches; see Yip (1991), Chao, Chu and Hsu (2000), and Chao (2001) for a review of various methods. Although in this paper we have only discussed the MLE, we expect similar results are also valid for other types of estimators.

In this paper, we only considered the models in which time and/or behavior response affect the capture probability and we did not discuss any models with individual heterogeneity in the capture probabilities. As indicated in the ecological literature, individual heterogeneity of capture probability may arise in many ways in practice. One commonly used parametric random-effect assumption for taking heterogeneity into account is that the individual effects are a random sample from a parametric distribution. Lin (2001) investigated an exponential model and similar conclusion can also be obtained; see Lin (2001) for details. The extension to other generalized distributions remains an issue of worthy of further study.

We remark that the conclusion about efficiency is under an essential condition that the population size tends to infinity and the parameters are fixed constants. This condition under the three models subsequently implies that the number of capture and the number of distinct animals caught in the experiment also tend to be large. Therefore, the conclusion may not be applicable to small population sizes. Under small sizes, simulation studies are needed to assess the relative merits of the two types of models. More research along this direction is anticipated.

Acknowledgement

做為黃提源教授的學生與同事,在許多方面(包括教學、研究、與對社會、對環境、對環保的關懷與付出)他都是我們的典型模範,我們雖達不到他的境界,然而衷心嚮往之。Part of the material is based on the PhD thesis of the first author under the supervision of the second author.

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